Physiological Ecology of Tropical Plants
Physiological Ecology of Tropical Plants

Second Edition
Cover photo showing the fringe of a rainforest on Sierrania Parú, Guayana Highlands, Venezuela; 1250 m a.s.l., 04°25’N, 65°32’W.
Recently, in many countries, particularly in the industrialized parts of the world, there has been an upsurge in public opinion concerned about the alarming rate of destruction of tropical ecosystems by man, and particularly the continuing elimination of tropical rainforest. The response to the public concern has led to a burgeoning of popular literature. More dispassionate scientific books are often devoted to special topics of tropical ecology, e.g. biotopes such as rainforests or savannas, ecologically defined groups of plants such as mangroves, epiphytes or succulent plants, and special taxa such as palms. The ecological approach of this scientific literature is predominantly floristic (and faunal) description and analysis of the diversity in associations, biotopes and ecosystems.

However, the development of modern experimental technology, which is increasingly well adapted to the use in field work in the tropics, is also allowing more and more detailed ecophysiological studies. Observations in the field lead to delineation of precise problems for studies in laboratories, growth chambers and phytotrons. The results of such work are built into hypotheses, whose ecological significance in turn is tested again in the field. This fruitful ecophysiological interplay between work in the field and in the laboratory leads to an increasing understanding of physiological, biochemical and molecular bases of ecological adaptations. Phenotypic physiological plasticity is important in mechanisms of ecological adaptations and may also be involved in mechanisms of generation and maintenance of floristic and faunal diversity in ecosystems.

I am therefore convinced that ecology must be studied at various levels of complexity and integration, namely the phytogeographical, ecosystem or biotope level, also called the synecological level, the whole organism level, also called the autecological level, and the cellular, organelle, membrane and molecular levels. These various levels may, in fact, not be so much distinguished by their respective degree of complexity. One may consider them as fractals. With each additional magnification, i.e. on each level, similar problems of complexity with integration of subsystems, feedback and non-linear behaviour will be encountered. Therefore, the distinction between levels does not appear to be basically conceptual and is more a matter of scaling. Studies with ecological relevance must not remain isolated within the in-
dividual levels. In addition to the interplay between work in the field and in the laboratory, there must be continuous feedback and feedforward within and between the levels of different scaling. Thus, although the aim is to progress towards levels at finer scales as far as possible, I think we must also refer to the levels at larger scales in order to put mechanisms of ecological adaptations into context.

Alexander von Humboldt was the first to recognize the relations between physiognomy of plants and the environment. In this vein, it seemed appropriate to begin the various chapters and sections of this book with descriptions of the physiognomy of biotopes and plants and to deduce the ecophysiological problems from them. This may also help to motivate readers, depending on their individual starting points, either to be carried on from the experienced environment to more abstract levels of understanding, or to consider the function of molecular, biochemical or physiological units in relation to the performance of plants in habitats.

It is the aim of this book to cover plants of all major tropical ecosystems. In the tropics we encounter biotopes with vast expanses. Thus, I felt that a brief record of current trends in large scale sensing and diagnosis would be useful (Chap. 2). The largest and most dominating tropical biomes are forests (Chap. 3) and savannas (Chap. 7). Ecophysiology of tropical plants is, in general, still a limited field, which is in its early stages of development, and in some areas knowledge is still poor. In limited areas, however, progress is already quite advanced. For example much work is available on epiphytes, which therefore have been given their own chapter (Chap. 4) although they are important parts of tropical forests. Mangroves are very specific tropical forests and also are treated in a separate chapter (Chap. 5). Salinas, inselbergs and páramos are very characteristic tropical environments and are covered each in a short chapter (Chaps. 6, 8 and 9). Although plants of dry and arid habitats are discussed in various chapters, genuine deserts are excluded. First, the major deserts lie outside the tropics. Second, very much ecophysiological work has already been performed on desert plants, and this would go much beyond the scope of this book.

Physiognomy is depicted with photographs, most of which were taken during my own excursions in the tropics. Ecophysiological work on tropical plants was compiled from the literature wherever available and I also refer to studies of my own group. Some original publications are cited when necessary, but when possible and appropriate preference was given to quoting summarizing and reviewing works, because it is the aim of this book to give a general overview rather than specific interpretations of specialized research contributions.

Abundant illustrations with drawings and tables are used to elucidate ecophysiological relations. It was, moreover intended to write a simple and readily flowing text, which is easy to read. In fact, it was aimed to make this book useful for a wide audience interested in the tropical environment. Thus, while writing I found that, for some readers, basic knowledge behind ideas, results and hypotheses presented would need at least brief repetition and explanation. In order to avoid interruption of the text, this was separated into boxes, which the reader may consult or overlook, depending on the individual level of understanding.
I am indebted to former students and postdoctoral fellows in my laboratory and friends and colleagues who work in various tropical countries and made it possible for me to become acquainted with tropical environments and to perform ecophysiological field research in the tropics. Most of this occurred in the Caribbean, in Venezuela and Brazil. Unavoidably, this led to a noticeable South American bias of the book. This may be of some disadvantage in the selection of the concrete physiognomic descriptions, but in the more abstract ecophysiological context it may be less important.

There is much goodwill in industrialized countries for an understanding of the tropics, but much more knowledge is needed. Many efforts are being made, and there is much research in the developing tropical countries, but more encouragement is needed. I hope this book, may make some contribution, if humble, towards both. I have written this book in English, which is not my mother tongue, but the scientific lingua franca to address people in the different parts of the world. In striving to build bridges, Alexander von Humboldt is chosen as a mentor for this book, and citations from his lucid descriptions of his journey to South America are used here and there as a guide.

I owe particular thanks to Professor Dr. Dr. h.c. mult. Hubert Ziegler for his encouragement in publishing this text, and also to him and Professor Dr. Erwin Beck for reading some of the chapters. With great empathy, Professor Dr. Howard Griffiths went through the painstaking work of correcting my English, and with a great deal of sensitivity, being an expert in tropical plant ecophysiology himself, he made invaluable contributions far beyond establishing linguistic discipline. I thank the students who attended my courses and lectures on tropical plant ecophysiology and served as guinea pigs for the development of this text. My own research in the tropics and exchange with colleagues in tropical countries were supported by the Deutsche Forschungsgemeinschaft (DFG), the Alexander-von-Humboldt-Stiftung, the Deutscher Akademischer Austauschdienst (DAAD), the Volkswagenstiftung and the Körber European Science Award, which are most gratefully acknowledged. A great many thanks are due to Ms. Barbara Reinhard, who took care of an almost endless succession of different versions of the manuscript with never-exhausted patience, and Ms. Doris Schäfer and Ms. Rosel Heger who handled the line drawings and the halftone photographs, respectively.

Darmstadt, February 1997

Ulrich Lüttge
Now, after 10 years, as I present the second edition of this book, there are no reasons to change the aims and the scope. However, during these ten years, international research efforts in physiological ecology of plants in the tropics have increased enormously in quantity and quality. In some fields advances were more substantial than in others. New approaches were made in remote sensing and, at the other end of the spectrum, in some areas molecular biology saw many developments regarding ecological performance of tropical plants, e.g. in understanding the adaptation of resurrection plants to the extreme habitat of inselbergs. This progress had to be covered in the second edition without too much of an increase in volume. Thus, it was again important to strive for a balance between detail and generality as advocated by Alexander von Humboldt who remains the spiritual mentor of the book. In this vein his suggestion in modifying the structure of the chapters was also followed when he writes:

_In an extended work where one strives for ease of understanding and overall clarity, the composition and layout in the arrangement of the whole are almost more important than the richness of the contents._

Therefore, to provide more convenient units for the reader, large chapters were broken down into smaller ones. Material on tropical forests, occupying about half of the entire volume of the book, is now arranged in five chapters covering structure and function under the influence of environmental cues and including epiphytes and mangroves as part of the tropical forest complex. Savannas are now treated in two chapters. Coastal Salinas have been combined with a new section on the Brazilian restingas in a chapter on coastal sand plains.

In spite of international agreements at the political level, not much has changed since the late 1980s regarding reducing the speed of the destruction of the original tropical environments. When Alexander von Humboldt wrote that

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1 In einem vielumfassenden Werke, in dem Leichtigkeit des Verständnisses und Klarheit des Totaleindrucks erstrebt werden, sind Composition und Gliederung in der Anordnung des Ganzen fast noch wichtiger als die Reichhaltigkeit des Inhalts. Kosmos, vol. IV, 1858
nature then appears greatest when, as well as the sensual impressions it is also reflected in the depth of thought.\textsuperscript{2}

he argued with a plea for stringent study and mathematical understanding. Now, as we are increasingly seeing the loss of the illusion that rationality prevents the destruction of nature, we may again have to think more about the former, “sensual impressions”. The description of the physiognomy of biotopes, again associated with the discussion of ecophysiological performance of plants in this book, may allude to this. In the preface ten years ago I commented on the fact that I present this text in English, not in my mother tongue. Besides linguistic unevenness, this may bear out different attitudes in thinking, as masterly expressed by Alexander von Humboldt, who himself was able to write in many different languages:

\textit{The tone of expression in its increased vividness will in no way be the same when involving either simple pure objectivity in the description of nature or the reflection of the surrounding nature embracing the feelings and innate character of man. In all literature these limitations are markedly different in accordance with the character of the language and the spirit of the people… Only at home – i.e. in the self assurance of the native mother tongue – can the correct balance of the timbre be unconsciously found.}\textsuperscript{3}

I hope I have, in the main, found the balance in this text and ask the reader to forgive any failures.

Again, I have to thank my students for much feedback, giving the book a realistic basis for coverage of the material. I am grateful that they have supported my lectures by their attendance, although I am now professor emeritus.

I am grateful to Dr. Dieter Czeschlik of Springer for his sustained confidence in the book and I warmly thank Ursula Gramm for her fine cooperation in its production.

Darmstadt, April 2007

\textit{Ulrich Lüttge}

\textsuperscript{2} Die Natur erscheint da am größten, wo neben dem sinnlichen Eindruck sie sich auch in der Tiefe des Gedankens reflectirt. Kosmos, vol. IV, 1858


Translated by myself from Alexander von Humboldt, Kosmos. Entwurf einer physischen Weltbeschreibung. Ottmar Ette and Oliver Lubrich, eds., Eichborn Verlag, Frankfurt am Main, 2004
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1.1 Historical Background of Ecophysiology

We aim

• to start by depicting habitats and plants physiognomically,
• to deduce problems from such observations in the field as are suited for physiological, biochemical and biophysical and perhaps even molecular experimentation in the laboratory, and
• to return from the laboratory to the field with increasingly sophisticated technologies for measurements and analyses applicable to field conditions.

With this we follow a great tradition, which was begun early in the last century, and which we may retrace from Mägdefrau’s History of Botany (1992) as follows.

The title of one of the best-known essays (1806) by Alexander von Humboldt is Ideas for a Physiognomy of Plants (“Ideen zu einer Physiognomik der Gewächse”). He realized that the physiognomy of vegetation is determined by environmental conditions and that the distribution of plants depends on the climate and, thus he became the founder of plant geography (von Humboldt ed 1989). The selective pressure exerted by variation in environmental factors then also became the most essential aspect for explanation of natural selection in Charles Darwin’s theory of evolution (Darwin 1859). However, it was Ernst Haeckel who coined the term ecology in 1866. Stephen J. Gould (1977), the sharp American essayist in phylogeny, caricatured it as follows:

“Ernst Haeckel, the great popularizer of evolutionary theory in Germany, loved to coin words. The vast majority of his creations died with him half a century ago, but among the survivors are ‘ontogeny’, ‘phylogeny’, and ‘ecology’. The last is now facing an opposite fate – loss of meaning by extension and vastly inflated currency. Common usage now threatens to make ‘ecology’ a label for anything good that happens far from cities or anything that does not have synthetic chemicals in it”.

However, Ernst Haeckel’s own original definition of ecology was already wide and may, in fact, encompass much of the current application of the term, since he
wrote that ecology is “... the entire science of the relations of the organism to its surrounding environment, comprising in a broader sense all conditions of its existence”.

Andreas Franz Wilhelm Schimper (1856–1901) founded *Plant Geography on a Physiological Basis* with this title of his famous text published in 1898, and he coined the term tropical rainforest. Simon Schwendener (1829–1919) suggested that the relations between the environment and the morphological traits of plants are best studied in areas providing extreme conditions. His advice has found many followers to date. It was, however, Ernst Stahl (1848–1919) who introduced experimentation to ecological research and thus founded physiological ecology. He also discovered the role of stomata in transpiration and photosynthesis. Among the late scientists of the twentieth century Arthur George Tansley (1871–1955), Otto Stocker (1888–1979), Arthur Pisek (1894–1975), Heinrich Walter (1898–1989), Bruno Huber (1899–1969) and Michael Evenari (1904–1989) all stimulated the development of physiological ecology. Physiological ecology primarily addresses itself to autecology, i.e. ecological relations of properties and performance of individual plants or species, but must also develop with synecology, i.e. consideration of integration of plant functions at the community level (Lüttge and Scarano 2004), which was already made clear by the early pioneers such as Arthur George Tansley who

1 "... die gesamte Wissenschaft von den Beziehungen des Organismus zur umgebenden Außenwelt, wohin wir im weiteren Sinne alle Existenzbedingungen rechnen können."
“made it clear that synecology and autecology are subsumed in the study of the community by methods firstly descriptive and appreciative, and secondly, analytic and experimental” (quoted from Godwin 1977).

1.2 The Tropics

Applying the approach of physiological ecology to understanding ecological functions and relationships in the tropics requires that we first must define what we mean by tropics.

Fig. 1.2A,B Diurnal (A) and annual temperature cycles (B) at a station in the warm tropics (Manaos at the Amazonas, Brazil) and in the cold tropics (Quito at 2,660 m a.s.l. in the Andes, Ecuador) and at stations in the temperate zone (Paris and Milan, respectively). The diurnal cycles in A are given for the warmest months as indicated by solid lines (July, September and July for Manaos, Quito and Paris) and the coldest months are depicted by dotted lines (June, November and January for Manaos, Quito and Paris). (After Lauer 1975)
Volkmar Vareschi (1980) has listed several possible definitions of the tropics, which partially overlap but give different emphasis:

- geodetically the tropics are limited by the lines of latitude 23° 27′ north and south of the equator, i.e. the Tropic of Cancer and the Tropic of Capricorn respectively;
- climatologically the tropics are the zones of equal day and night length; they are not basically characterized by high temperature and moisture; depending on altitude, warm and cold tropics can be distinguished, and depending on the precipitation regimes in the region between the equator and the two lines of latitude at 23° 27′ north and south, wet and dry tropics can be distinguished (Lauer 1975; Fig. 1.1);

**Fig. 1.3A–C** Global distribution of savannas (A) and tropical rainforest (B) and optimum carbon fixation (C). (After Vareschi 1980, A, C with permission of R. Ulmer; Walter and Breckle 1984, B with permission of S.-W. Breckle and G. Fischer-Verlag)
1.3 Tropical Forests and Savannas: General Importance

- phyto-geographically the tropics are indicated by the distribution of palms;
- eco-geographically the tropics are the zone in which the climatic effects of day-night cycles are far more important than those of seasonal cycles; day-night cycles of temperature are much larger than in the temperate zone in both the coldest and the warmest months, but annual cycles of mean monthly temperature are almost absent in the tropics (Fig. 1.2);
- botanically the tropics are contained in a well-separated pantropical floristic province;
- in terms of the biology of productivity, the tropics are the zones of optimal carbon fixation and photosynthetic capacity with $> 600 \text{ g m}^{-2} \text{ year}^{-1}$, which globally corresponds well to the occurrence of tropical rainforest in a broader sense (Fig. 1.3).

1.3 Tropical Forests and Savannas: Their Emotional, Commercial, Ecological and Scientific Importance

Forests and savannas are the ecosystems which cover the largest areas in the tropics (Fig. 1.3). Notwithstanding the wide public concern about destruction and decline of tropical forests, it appears that it is deeply ingrained in the nature of man to be frightened by the unknown in the darkness of dense and repellent forests. There were incidents of natural catastrophes in which falling trees and landslides with forests threatened man, as a consequence of which a call arose to remove the forests altogether. The contrast in our emotional reactions towards forest and savanna, respectively, is vividly expressed by Alexander von Humboldt (1982) in his *Journey to South America*:

“If one has spent many months in the dense forests along the Orinoco, if one got used there to seeing the stars only near the zenith like looking upwards from the bottom of a well as soon as one leaves the bed of the river, then wandering over the steppes\textsuperscript{2} has something pleasant and attractive in it. The new pictures which one perceives give deep impression; like the Llanero one enjoys the feeling of being able to look around so well. However, this comfort does not last long. If, wandering for eight to ten days, one gets used to the games of mirages and the brilliant green of *Mauritia* bushes, which appear mile after mile, one feels the desire for more variable impressions, one longs for the sight of the huge trees of the tropics…”\textsuperscript{3}

\textsuperscript{2} Note that A. von Humboldt did not yet distinguish between “steppes” and “savannas”, which we now consider as the grasslands of temperate and tropical zones respectively (Vareschi 1980; Walter and Breckle 1984).

\textsuperscript{3} “Hat man mehrere Monate in den dichten Wäldern am Orinoko zugebracht, hat man sich dort daran gewöhnt, daß man, sobald man vom Strome abgeht, die Sterne nur in der Nähe des Zenit und wie aus einem Brunnen heraus sehen kann, so hat eine Wanderung über die Steppen etwas Angenehmes, Anziehendes. Die neuen Bilder, die man aufnimmt, machen großen Eindruck, wie dem Llanero ist einem ganz wohl, ‘daß man so gut um sich sehen kann’. Aber dieses Behagen ist nicht von langer Dauer. Ist man nach acht- oder zehntägigem Marsch gewöhnt an das Spiel der Luftspiegelung und an das glänzende Grün der Mauritiabüsche, die von Meile zu Meile zum Vorschein kommen, so fühlt man in sich das Bedürfnis mannigfaltigerer Eindrücke, man sehnt sich nach dem Anblick der gewaltigen Bäume der Tropen…”.
Commerically it is important to remember that most tropical countries have to sustain increasingly large populations, savannas serving agriculture and forests providing resources, which are, however, renewable only to a limited extent. Although original CO₂ sequestration and hence gross primary productivity of tropical forests is high, due to high rates of respiration and the rapid degradation of litter in the tropical forests, net CO₂ uptake and net productivity is much reduced. It may even be lower than in a beech forest of the temperate zone (Fig. 1.4).

Large-scale deforestation proves to be irreversible (Medina 1991). Previous land use determines successions and recovery. In the Central Amazon it was found that sites which had been clear cut without subsequent use were dominated 6–10 years later by the pioneer genus *Cecropia* and had a high diversity, while sites used for pasture before abandonment were dominated by the pioneer genus *Vismia* and had a lower diversity. Seed source, effects on soil and mineral depletion lead to a more rapid return of primary forest species if deforestation is not followed by the use as pastures before abandonment (Mesquita et al. 2001). Therefore, it is possible to reconcile utilization and preservation of tropical ecosystems if human activities are directed in the right way, as vividly summarized by Whitmore (1990). For example, there are two types of shifting agriculture (slash-and-burn agriculture; Fig. 1.5). One of them is destructive and unsustainable. It is an invasive system, where fields are used until they are exhausted even for regrowth of secondary forest. The other is a cyclic system, where clearings are used for cultivation for 1–2 years and then left to recover so that they can be reused in due course during the cycle, without the need for further clearing of forest. This is a sustainable mode of shifting agriculture. Figure 1.6 shows the recovery of above-ground biomass of a wet tropical forest after a slash and burn activity. Clearly, full recovery to a level comparable to mature original forest may take 100–200 years if the magnitude of disturbance has not been too

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**Fig. 1.4** Comparison of gross and net productivity of a tropical rainforest in Thailand and a 60-year-old beech forest in Denmark. (After data from Larcher 1980)
large. However, if short-term cultivation after slash-and-burn action is followed by fallow periods of 20 years or longer, recovery mechanisms of forest ecosystems remain intact, and long-term cyclic utilization under low population pressure remains possible.

Scientifically, sustainable schemes of silviculture have been developed for tropical areas and should be extended and enforced, including appropriate methods of logging and timber removal (Whitmore 1990). Afforestation and timber plantations are established on degraded sites and may reduce the pressure on good natural forest. Trees exotic to the native tropical environments are frequently used for such aforesations. In Ethiopia the introduction of *Eucalyptus* historically has been
praised for having saved the country economically (Zewde 1992). In Brazil the total area covered by plantations of *Eucalyptus* has increased 8-fold during 30 years in the last century (Fig. 1.7). Ecologists have underlined the detrimental effects of exotic tree plantations on the indigenous environment. The tremendous difference in ecological quality between a more or less undisturbed woodland and an exotic timber plantation may become immediately clear at a glance (Fig. 1.8). However, there are also great advantages where degradation of ecosystems leaves no other choice. Some of the disadvantages and advantages are compared in Table 1.1: (i) potential harmful effects on soil properties are juxtaposed by experience with propagation of exotic tree species and silviculture, (ii) displacement of local native vegetation and fauna must be compared with improved productivity, (iii) susceptibility to epidemic diseases and pests can be counterbalanced by various nurse effects of exotic tree plantations.

An appropriate forestry management can back up the advantages and an exotic *Eucalyptus* plantation does not need to look as sterile as that of Fig. 1.8B (see Fig. 1.9C,D). This is supported by the case story of a *Eucalyptus saligna* plantation.

![Area covered by plantations of *Eucalyptus* in Brazil from 1965 to 1995 (DaSilva et al. 1995)](image)

Table 1.1 Comparison of disadvantages and advantages of exotic tree plantations

<table>
<thead>
<tr>
<th>DISADVANTAGES</th>
<th>ADVANTAGES</th>
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<tbody>
<tr>
<td><strong>MANAGEMENT</strong></td>
<td></td>
</tr>
<tr>
<td>Harmful effects on physical, chemical, biological</td>
<td>Experience with propagation and silviculture</td>
</tr>
<tr>
<td>soil properties</td>
<td></td>
</tr>
<tr>
<td><strong>PRODUCTIVITY AND DIVERSITY</strong></td>
<td></td>
</tr>
<tr>
<td>Displacement of local native vegetation</td>
<td>Initial fast growth and wood production</td>
</tr>
<tr>
<td><strong>COMMUNITY RELATIONS</strong></td>
<td></td>
</tr>
<tr>
<td>Susceptibility to epidemic diseases and pests</td>
<td>Nurse effects</td>
</tr>
<tr>
<td></td>
<td>• microclimate</td>
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<tr>
<td></td>
<td>• reduction of erosion</td>
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<tr>
<td></td>
<td>• enhancement of litter and humus production</td>
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in Ethiopia in a region where some remnants of original native forest of *Podocarpus falcatus* are still preserved, but where large areas are deforested and deteriorated (Feyera et al. 2002; Lüttge et al. 2003; Fetene and Beck 2004; Lemenih and Teketay 2004; Fritzsche et al. 2006). Figure 1.9A shows the *Eucalyptus* forest in the background of an old solitary female tree of *P. falcatus*, the seeds (Fig. 1.9B) of which are dispersed by birds. As given by the data on ground cover, light penetration and
Fig. 1.9A–D Forest of *Eucalyptus saligna* and *Podocarpus falcatus*, Shashemene-Munessa State Forest, Ethiopia. A Female tree of *P. falcatus* with *Eucalyptus* forest in the background. B Seeds on *P. falcatus*. C,D Various stages of young growth of *P. falcatus* inside the *Eucalyptus* forest

the number and density of naturally regenerated native woody species summarized in Table 1.2, the *E. saligna* plantation can be favourably compared with the adjacent native forest and the nurse effect of *E. saligna* is evident. The *Eucalyptus* is coppiced regularly about every 7 years which gives a certain advantage to regenerating native woody species. Moreover, physiological data comparing *E. saligna* and *P. falcatus*, the major native tree the regeneration of which is of greatest concern, also show that the *Podocarpus* can compete well with the *Eucalyptus* within the plantation. Photosynthetic electron transport rates are not pronouncedly lower in *P. falcatus* than in *E. saligna* in the plantation, but the *Eucalyptus* needs very much more water as shown by its higher transpiration rates, $J_{H_2O}$, and leaf conductance for water vapour, $g_{H_2O}$, and its lower water use efficiency given by the higher $\Delta^{13}C$ value of its leaves inside the plantation (for explanation of the latter see Sect. 2.5). Indeed, *P. falcatus* can readily regrow from seeds inside the *Eucalyptus* plantation (Fig. 1.9C,D). This suggests how an original native forest can be regenerated making use of the nurse function (Table 1.1) of an exotic tree plantation. In the case described here, *P. falca-
Table 1.2 Comparison of a plantation of *Eucalyptus saligna* and an adjacent native forest (A) and of some ecophysiological data of the *Eucalyptus* and of the major and most conspicuous native tree, the dioecious gymnosperm *Podocarpus falcatus* (B) in the Shashemene-Munessa State Forest, eastern escarpment of the Great Rift Valley, Ethiopia (7° 13′ N, 8° 37′ E). ETR<sub>1000</sub> = apparent photosynthetic electron transport rate at an irradiance of 1,000 µmol m<sup>−2</sup> s<sup>−1</sup> obtained from instant measurements at ambient irradiation. ETR<sub>max</sub> = maximum apparent photosynthetic electron transport rate obtained from measurements of light dependence curves (see Sect. 4.1.1, Box 4.6); for J<sub>H2O</sub> and g<sub>H2O</sub> of *E. saligna* the first number is of the adaxial and the second number of the abaxial leaf surface. (Data from Feyera et al. 2002, Lüttge et al. 2003, Lemenih and Teketay 2004)

<table>
<thead>
<tr>
<th></th>
<th><em>E. saligna</em> plantation</th>
<th>Native forest</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Range of ground cover (%)</td>
<td>11–100</td>
<td>25–100</td>
</tr>
<tr>
<td>Naturally regenerating native woody species (number/ha) in relation to age of plantation</td>
<td></td>
<td></td>
</tr>
<tr>
<td>11 years</td>
<td>3,575</td>
<td></td>
</tr>
<tr>
<td>22 years</td>
<td>10,100</td>
<td></td>
</tr>
<tr>
<td>27 years</td>
<td>18,650</td>
<td></td>
</tr>
<tr>
<td>Light penetration (% of full sunlight)</td>
<td>12–51</td>
<td>1–77</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>E. saligna</th>
<th><em>P. falcatus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>B</td>
<td></td>
<td></td>
</tr>
<tr>
<td>ETR&lt;sub&gt;1000&lt;/sub&gt; (µmol m&lt;sup&gt;−2&lt;/sup&gt; s&lt;sup&gt;−1&lt;/sup&gt;)</td>
<td>97</td>
<td>77</td>
</tr>
<tr>
<td>ETR&lt;sub&gt;max&lt;/sub&gt; (µmol m&lt;sup&gt;−2&lt;/sup&gt; s&lt;sup&gt;−1&lt;/sup&gt;)</td>
<td>87</td>
<td>76</td>
</tr>
<tr>
<td>J&lt;sub&gt;H2O&lt;/sub&gt; (mmol m&lt;sup&gt;−2&lt;/sup&gt; s&lt;sup&gt;−1&lt;/sup&gt;)</td>
<td>2/6</td>
<td>1</td>
</tr>
<tr>
<td>g&lt;sub&gt;H2O&lt;/sub&gt; (mmol m&lt;sup&gt;−2&lt;/sup&gt; s&lt;sup&gt;−1&lt;/sup&gt;)</td>
<td>67/200</td>
<td>37</td>
</tr>
<tr>
<td>Δ&lt;sup&gt;13&lt;/sup&gt;C (‰)</td>
<td>23.1</td>
<td>20.7</td>
</tr>
</tbody>
</table>

*tus* was never seen to germinate in the open secondary grassland but many seedlings and young trees were found in the plantation (Fig. 1.9C,D).

The ecological and scientific importance of savannas and forests in the tropics will be major topics of this book. There is a large diversity of unique grassland and forest ecotypes, which require physiognomic classification and understanding at the ecophysiological level. This is a prerequisite for maintaining or, perhaps more pessimistically, for reattaining an equilibrium between commercial necessities including agriculture and forestry and the preservation of unique natural environments. It must be noted, though, that no measures, even the most sophisticated schemes of sustainable land use based on scientific understanding of tropical biotopes and their components will be effective if man does not succeed in mastering the major dominating problem which is his own unlimited reproduction. Particularly in the tropics, increasing human population is the one major factor continuing to put pressure on the environment.

### 1.4 The Destruction of Tropical Forest

Of particularly wide public concern is the ongoing destruction of tropical rainforest. Estimations of the current destruction vary to some extent due to the application of different definitions of what actually is meant by tropical rainforest. This applies
both to the question of what are the tropics (see above, Sect. 1.2), and to the question of what is rainforest. (The latter is discussed in Sects. 3.1. and 3.2.) Thus, in analyzing the problem, one may find oneself confronted with different quantitative estimates.

For example, by taking evergreen and semi-evergreen forests with:

- no less than 100 mm rain in any month during 2 out of 3 years;
- an average yearly temperature of 24 °C without any occurrence of frost;
- an altitude of < 1,300 m above sea level, excepting Amazonia with < 1,800 m and SE-Asia with < 750 m,

and combining 13 critical and 3 very critical regions (as described in Fig. 1.10), respectively Myers (1988), arrives at the data given in Fig. 1.10, or globally at the following numbers:

- forest preserved in 1980: \(10 \times 10^6\) km\(^2\), covering 6–7% of the total land surface of the earth;
- disturbed: \(0.1 \times 10^6\) km\(^2\) per year;
- destroyed: 0.08 to 0.09 \(\times 10^6\) km\(^2\) per year.

---

**Fig. 1.10A, B** Original and remaining forest in 13 critical regions. **A** Madagascar, Atlantic coast of Brazil, West Ecuador, Columbian Chocó, West Amazonian Highlands, Rondonia/Acre in Brazilian Amazonia, montane forests in Tanzania/Kenya, Eastern Himalaya, Sinharaja Forest in Sri Lanka, Malaysian peninsula, NW-Borneo, Philippines and New-Caledonia, and in three particularly critical regions: **B** Madagascar, Atlantic coast of Brazil and West Ecuador. (After data of Myers 1988)
Using somewhat different definitions of tropical forests, Jacobs (1988) arrives at the following figures for the annual destruction:

- tropical rainforest in a narrow sense: $0.15 \times 10^6$ km$^2$ per year;
- wet tropical forest: $0.24 \times 10^6$ km$^2$ per year.

Unfortunately no significant improvements have been achieved to date on this tragic situation documented in the late 1980s. For example, in Brazil the Atlantic rain forest is now reduced to 7.5% of its original area (Myers et al. 2000), the Amazon area in the year 2004 experienced the highest deforestation rate ever and only 16% is still unharmed (Fearnside 2005). The major remaining areas covered with wet tropical forest are in the Zaire basin, in West Brazil and Amazonia, in the Guayana highlands and in New Guinea.

Some important global problems relate to the destruction of tropical forest with regard to

- the CO$_2$ budget of the atmosphere;
- the water balance;
- the nutrient balance;
- biodiversity,

the first two and the last of which are also causing considerable public anxiety.

Scientifically, the effects on CO$_2$ budgets remain a subject of debate because it is not clear whether alternative CO$_2$ fixation processes in terrestrial ecosystems will offset or even over compensate reductions due to loss of forest. Secondary vegetation may prove to be an increasingly strong CO$_2$ sink, and increasing CO$_2$ in the atmosphere may be coupled to higher ecosystem productivity (Medina 1991; Plant, Cell and Environment 1991). The relations of CO$_2$ with mineral nutrition, especially nitrogen, with guard cell sensing and transpiration and respiration, with temperature, with plant acclimation, and with the respective functions of forests and oceans as CO$_2$ sinks are highly complex non-linear interactions in feedback networks and simple conclusions are not possible (Plant, Cell and Environment 1999).

The water balance of large areas may be severely impaired by deforestation. For equatorial forests in Amazonia it has been shown by stable-isotope techniques (see Sect. 2.5) that 50% of total incoming rainfall was lost again by evapotranspiration from the forest. Thus, deforestation not only increases total runoff of water but also disturbs recirculation, as observed in the Amazon basin, leading to lower total rainfall and more pronounced seasonality (Medina 1991).

These observations also have implications for nutrient supply: due to the rapid turnover of nutrients in tropical forests (see Sect. 3.4.4) and problems of erosion, deforestation causes major destruction of soil systems and affects nutrient budgets.

Tropical humid forests are known to be the most diverse ecosystems in the world (see Sects. 3.2.1 and 3.3.1). They are thought to support more than 50% of all plant and animal species. Deforestation leads to loss of diversity, which has not been fully assessed by census to date.

In conclusion, we are not able to predict the actual nature of all the changes that may result from the more or less complete destruction of these forests (Whitmore 1990). The theory of deterministic chaos (Sect. 3.3.3) suggests that long-term
predictions about the behaviour of complex systems with feedback relations showing non-linear behaviour are intrinsically impossible (Hastings et al. 1993; Schuster 1984). However, it is equally clear that if we do not succeed in preserving these forests, we shall lose one of our greatest treasures.

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Chapter 2
Large-Scale Sensing and Diagnosis in Relation to the Tropical Environment

2.1 Approaches

In the discussion of “global change” it has become increasingly important to develop means allowing large-scale conclusions about the conditions and the behaviour of ecosystems or biomes. Indeed, techniques for examination and detailed structural analysis of the surface of our globe are continuously advanced, allowing the integration of observations in space and time. This is, of course, applicable throughout the globe. However, it is particularly relevant for the tropical environment, with extended tracts of ecosystems like savannas and forests (see Sect. 1.3), which are often difficult to penetrate on the ground.

Among the techniques applicable to the study of large-scale effects of plant life we must distinguish between those where the analytical method itself directly covers wide spaces and areas, such as remote sensing (Sect. 2.3), and those where it is the method of sampling, which can be developed to cover extended areas and thus, indirectly, affords comprehension at large-scale levels. In the former case only a smaller choice of analytical techniques mainly based on the use of radiation will be available, while in the latter case almost any analytical method may prove useful depending on availability of suitable samples. Clearly, there are many approaches for large-scale sensing and diagnosis of the environment, some of which shall be discussed below.

2.2 Climatic Relations and Vegetation Modeling

In the first volume of his “Kosmos” published in 1845 Alexander von Humboldt (Humboldt 2004) vividly defined climate as follows:

“The term climate in its most general meaning defines all changes in the atmosphere, which perceptibly affect our organs: temperature, humidity, changes of barometric pressure, calm state of the air or effects of changeable winds, the magnitude of electrical charge, the cleanliness of the atmosphere or its mixing with gaseous exhalations adverse to a smaller or larger
extent, and finally the degree of habitual transparency and clarity of the sky; which is not only important for an increased heat radiation of the soil, the natural development of plants and the ripening of fruits, but also for the sensations and the entire spiritual temper of man.”

Consequently, Walter and Breckle (1983) argue that “the climate . . . is the only primary factor, which affects the other factors like the soil and the vegetation and to a lesser degree also the fauna, but which in turn is influenced by them only to a limited extent in the range of micro-climate”. Thus, Heinrich Walter developed the concept of biomes and the technique of the Klimadiagramm (Sect. 2.2.1) and more recently global vegetation modeling is based on climatic factors (Sect. 2.2.2).

### 2.2.1 The Klimadiagramm

As the primary producers of biomass, plants determine the physiognomy and character of large ecological units and provide the basis for all other life. This has contributed greatly to the practice of using patterns of vegetation for a coarse global division of the geo-biosphere in ecological terms. On the other hand, Walter and Breckle (1983) argue that the large naturally occurring communities of flora and fauna, or “biomes”, are best delineated on the basis of the climatic conditions under which they occur, since in global terms a coarse division of geographical regions is given by the large climatic zones, from which Walter and Breckle (1983) then derived their term zono-biomes. Thus, we also obtain the large zones of vegetation in a three-dimensional climatic gradation (Ehrendorfer 1991):

- from the equator to the poles (temperature gradient);
- from the oceans to the continents (oceanity or continentality according to the degree of annual balance of temperature);
- in the altitudinal zones in high mountains.

This possibility of separating large-scale vegetation units according to the climate leads to the practical question of whether one can make predictions on plant distribution in extended areas based on simple models.

One simple technique, which has proven extraordinarily successful, is the Klimadiagramm of Walter (1973). In his autobiography Walter (1982) describes vividly how the idea developed when he was first confronted with the problem of a large-scale interpretation of vegetation in Anatolia (Turkey) in 1954. The Klimadiagramm (Box 2.1) essentially uses simple data which are readily available from all weather conditions.

---

1 “Der Ausdruck Klima bezeichnet in seinem allgemeinsten Sinne alle Veränderungen in der Atmosphäre, die unsere Organe merklich affiziren: die Temperatur, die Feuchtigkeit, die Veränderungen des barometrischen Druckes, den ruhigen Luftzustand oder die Wirkungen ungleichnamiger Winde, die Größe der electricen Spannung, die Reinheit der Atmosphäre oder die Vermengung mit mehr oder minder schädlichen gasförmigen Exhalationen, endlich den Grad habitueller Durchsichtigkeit und Heiterkeit des Himmels; welcher nicht bloß wichtig ist für die vermehrte Wärmestrahlung des Bodens, die organische Entwicklung der Gewächse und die Reifung der Früchte, sondern auch für die Gefühle und ganze Seelenstimmung des Menschen.”
stations, i.e. mean monthly temperatures and precipitation. They are plotted according to a precise scheme of scaling on the ordinate vs months on the abscissa: **humid periods** are indicated by areas on the graph, where the temperature curve is below the curve of precipitation; **arid periods** are delineated by the precipitation curve being lower than that of temperature. According to a precisely defined scheme, additional information can be built into the *Klimadiagramm*, so that depending on data availability each diagram may give a complete description of the climate at a given station.

**Box 2.1 Klimadiagramm after Walter (1973)**

- The months of the year are plotted on the abscissa.
- The mean monthly temperatures and precipitation are plotted on the ordinate, so that
  - at mean monthly precipitation between 0 and 100 mm one unit of scale corresponding to 10 °C gives 20 mm precipitation or the ratio of scalation is 1 °C:2 mm precipitation;
  - at mean monthly precipitation above 100 mm the precipitation scale is reduced to 1/10, and the ratio is 1 °C:20 mm precipitation.
- Humid periods are indicated by precipitation curves above temperature curves; they are marked by *vertical hatching* up to 100 mm and by *black colour* above 100 mm precipitation.
- Arid periods are indicated by precipitation curves below temperature curves, they are marked by *dotting*.
- According to a well-defined scheme, other details may be added to the *Klimadiagramm* as indicated in the examples given below.
Examples presented are for tropical stations in Africa with an arid, a perhumid and a seasonal climate: Moçâmedes at the Atlantic coast of Angola (15° 05′ S, 12° 09′ E), Djolu, Congo (00° 38′ N, 22° 37′ E) and Mpika, Muchinga Mountains, Rhodesia (11° 52′ S, 31° 26′ E). For further details see Walter and Lieth (1967) and Walter (1973).

For a large-scale evaluation of a certain area, or even an entire continent, one requires the diagrams of many stations covering the respective area. One can integrate them in a geographic information system, e.g. in the simplest way paste them on a map to obtain a good survey of the climatic structure of the area. Areas with humid, arid or seasonal climates are readily separated. An example is shown for
2.2 Climatic Relations and Vegetation Modeling

the predominantly tropical continent of Africa in Fig. 2.1. The humid belt along the equator is clearly separated from the more semi-arid and arid regions. The power of the approach can be seen by comparing the distribution of rainforest and savanna on the African continent (Fig. 1.3) with the more humid and more seasonal regions, respectively (Fig. 2.1).

Although we will have to draw attention to certain limitations of the Klimadiagramm technique later (Sect. 3.1), since arid and humid climates are strictly defined by precipitation and evaporation and not by precipitation and temperature as in the Klimadiagramm, we will make repeated use of the Klimadiagramm in this book.

Fig. 2.1 Klimadiagramm map of the African continent. Arid periods are dotted, humid periods are hatched or black. Arid, humid and seasonal regions are readily differentiated. Dashed horizontal line: equator. (Walter and Breckle 1984; with kind permission of S.-W. Breckle and G. Fischer-Verlag)
2.2.2 Vegetation Modeling Based on Irradiance and Water Budgets

Climatic conditions like irradiance and temperature affect the water-vapour pressure deficit of the atmosphere, and thus determine evapotranspiration or the loss of water vapour of the vegetation to the atmosphere. Irradiance and water

Fig. 2.2 A Global prediction of physiognomic vegetation types on the basis of ecophysiological models; compared with B actual observations. (Woodward 1987; with kind permission of the author and Cambridge University Press)
availability in turn are modulated by other climatic factors. Thus, it is possible to make model calculations of evapotranspiration from climatic data using basic plant-physiological principles of transpiratory water loss from leaves driven by the leaf/air water-vapour pressure-difference. Furthermore, there are close links between evapotranspiration and leaf area index (LAI), which is the total leaf area related to a unit of ground surface (see Sect. 3.4.1). The LAI is characteristically related to the physiognomy of plants and vegetation. Therefore, from LAI one may then obtain ecophysiological models of vegetation as dominated respectively by broad-leaved trees, shrubs and herbs (Woodward 1987). Large-scale presentations of the models’ results may then be compared with real observations (Fig. 2.2).

2.3 Remote Sensing Using Radiation

Remote sensing of the biosphere is based on the analysis of electromagnetic radiation (Hobbs and Mooney 1990). We may distinguish between measurements of reflection or absorption of radiation and fluorescence. Radiation is also used in gas analysis, but this is a somewhat different aspect (see Sect. 2.4).

2.3.1 Reflection and Absorption

The analysis of reflection, absorption and transmission of radiation by individual leaves, plants or by the vegetation canopy has become an important method in ecophysiology. The principle relations are shown in Fig. 2.3. The range of photosynthetically active radiation (PAR: 400 – 700 nm) is largely identical to that of the visible light. Here radiation absorption is dominating. Chlorophyll has an absorption minimum in the green range of the spectrum (550 nm), and this is identified by reduced absorption, and increased reflection and transmission (Fig. 2.3). In the infrared range of the spectrum (above 800 nm) radiation reflection and transmission are dominating. At very high wavelengths absorption increases again, although, this is not so relevant as solar emission contains little radiation above 2,000 nm.

The contrast between absorption of the radiation in the visible range and reflection in the infrared range of the spectrum by green plants has been used to develop a dimensionless vegetation index $Q$ related to reflection between 580 and 680 nm ($R_{680} - R_{580}$) and between 725 and 1,100 nm ($R_{1100} - R_{725}$), respectively, as follows:

$$Q = \frac{R_{1100} - R_{680}}{R_{1100} + R_{680}}$$ (2.1)

It results from this equation that at very low reflection between 580 and 680 nm and very high reflection between 725 and 1,100 nm, vegetation is dense and $Q$ tends towards +1. In contrast, at very high reflection between 580 and 680 nm and very
low reflection between 725 and 1,100 nm $Q$ tends towards $-1$, indicting sparse vegetation (Running 1990). The two values of $R$, $R_{580}^{680}$ and $R_{725}^{1100}$, can be measured from aeroplanes or meteorological satellites equipped with two sensors for the respective range of wavelengths. The results can be depicted on maps using false colours, which provide informative images at the global level. Formations with particularly dense vegetation (e.g. the tropical forests and the extended forest regions of the northern hemisphere) are readily distinguished from poorer areas like deserts, steppes and savannas (Malingreau and Tucker 1987).

Thus, analysis of reflection and absorption with the rough vegetation index obtained by comparing reflectance at two rather broad bands of wavelengths provides information on a given state of vegetation and, if followed in time, also about its dynamics. Although this type of analysis has been used successfully to predict harvests, it does not provide a real picture of the **physiological state and vitality of vegetation**. This can be improved by high-altitude aircraft or space based imaging spectroscopy with much higher spectral resolution of the solar radiation reflected from the Earth’s surface in contiguous narrow bands. A National Aeronautics and Space Administration (USA) Earth Observing (EO) device allows measurement of reflected radiance in 242 spectral bands from 0.4 to 2.5 µm at a spatial resolution of 30 m (Asner et al. 2004). The sampling of narrow bands of the optical spectrum allows deduction of more specific biochemical properties of canopies, e.g. by giving a photochemical reflectance index (PRI), an anthocyanin reflectance index, a spectroscopic water absorption index (Asner et al. 2004) and an index of nitrogen concentration (Asner and Vitousek 2005) in canopies. With spectrometers of particularly high resolution gross biochemical composition of vegetation utilizing the light absorption of quantitatively dominant organic compounds (e.g. sugars, cellulose, starch, lignin, protein) can also be measured (Wessman 1990).

The PRI uses the wavelength of 570 nm, which is affected only by chlorophyll absorbance, and the wavelength of 531 nm which is affected by both chlorophyll and carotenoid absorbance (Nichol et al. 2006). Carotenoid absorbance is modulated by
the epoxidation-state of components of the xanthophyll cycle which is related to the
dissipation of surplus photosynthetic excitation energy as will be explained below
in the context of light in tropical forests (Sect. 4.1.4). PRI is calculated in different
ways in the literature, i.e. as

\[
PRI = \frac{(R_{531} - R_{570})}{(R_{531} + R_{570})}
\]  

(2.2)

by Asner et al. (2004) and as

\[
PRI = R_{531} - \frac{R_{570}}{R_{531}} + R_{570}
\]  

(2.3)

by Nichol et al. (2006). It allows an assessment of photosynthetic light-use effi-
ciency (LUE) of canopies. Using (2.3) in a study of an experimental mangrove
canopy good positive and negative correlations were obtained between PRI and ef-
fective quantum yield of photosystem II and non-photochemical quenching of pho-
tosynthetic excitation energy, respectively (Fig. 2.4), which are directly related to
LUE as will be explained in more detail in Sect. 4.1.7. The anthocyanin reflectance
index is obtained as

\[
ARI = \frac{1}{R_{550}} - \frac{1}{R_{700}}
\]  

(2.4)

and it is interesting because anthocyanin is an indicator of newly formed foliage be-
fore the full development of chlorophyll pigments. A spectroscopic water absorption
index uses the localized sensitivity of two major canopy water-absorption features
(930 – 1,040 and 1,100 – 1,230 nm).

The disadvantage in the analysis of radiation reflection is that clear skies are
needed. An alternative is the use of micro-wave radiometry, since micro-waves
are not absorbed by clouds. They give information on the heat-radiation of surfaces,
which is also much influenced by vegetation.

In principle remote sensing by detection of radiation allows analysis of many
vegetation parameters on a large scale, e.g.

- the vegetation density on the land surface according to the leaf area index and the
  biomass;
- the density of plankton in the oceans;
- vegetation types and the structure and dynamics in ecosystems;
- photosynthetic activity and light-use efficiency;
- biochemical parameters of canopies;
- the productivity of agricultural and natural ecosystems;
- phenological cycles of growth;
- soil moisture;
- hydrology;
- changes by deforestation, fire, storm, erosion, pest infestations and other cata-
  strophic events.
In many of these examples analysis of temporal variations is essential, integrated by repeated observation. Another important aspect is the need for “calibration”, which may allow a more detailed interpretation of the radiation signals obtained in remote sensing. Due to the complex structure and dynamics of ecosystems, significant efforts are required for calibration, involving measurements on a hierarchy of levels with different resolution of area, e.g. on the ground, on measuring towers, in aeroplanes and helicopters and in satellites (Sellers et al. 1990). With better calibration, interpretation of finer detail and more sophisticated resolution will be possible from remote-sensing data. However, calibration or “ground truthing” itself is a great problem, especially in inaccessible tropical areas.

### 2.3.2 Fluorescence

A way different from PRI (Sect. 2.3.1) for obtaining information on the photosynthetic activity of vegetation is the analysis of fluorescence. The fluorescence from chlorophyll is not only directly related to the concentration of chlorophyll but is also inversely related to the **efficiency of photosynthesis**. This will be explained in more detail later in relation to photosynthetic light use in tropical environments (Sect. 4.1.7).
Remote fluorescence excitation is possible using powerful lasers. A laser-induced fluorescence spectrum is given in Fig. 2.5. The fluorescence maxima at 690 nm and 740 nm are particularly variable in response to stress as shown in Fig. 2.6 for some conditions studied in the laboratory. As plants senesce fluorescence decreases due to the degradation of chlorophyll (Fig. 2.6A). Conversely, when the photosynthetic process is impaired, e.g. by K⁺ deficiency, drought stress or herbicide action (Fig. 2.6B,C), fluorescence increases (Chapelle et al. 1984a). For a more sensitive analysis it has also been suggested that the ratio of fluorescence at the peak of 690 nm and in the far-red region at 730 or 740 nm should be used (Hák et al. 1990; Lichtenthaler et al. 1990).

Fig. 2.5 Laser-induced fluorescence spectrum of maize leaves (Chapelle et al. 1984b)

Fig. 2.6A–D Changes of laser-induced fluorescence due to various kinds of stress. A Senescence. B Potassium deficiency. C Drought. D Action of the herbicide DCMU (dichlorophenyl-dimethylurea) inhibiting photosynthesis. A, C, D soybean; B maize. (Chapelle et al. 1984a)
Thus, when used in remote sensing, fluorescence analysis allows large-scale diagnosis of stress effects by abiotic factors such as the availability of growth resources (e.g. water, mineral nutrients, photosynthetically active radiation etc.) or environmental pollutants and biotic factors, such as pests and pathogens. The resolution of analyses of laser-induced fluorescence of 685 nm during flights in meteorological aeroplanes flying at a height of 150 m and a nominal flight-speed of 100 m s$^{-1}$ is between 10 and 80 m. An example is given in Fig. 2.7 for a flight path of 6 km, resolving green and brown fields and forests.

Fig. 2.7 Profile of laser-induced fluorescence emission (wavelength of fluorescence 685 nm) along a flight path of 6 km above forests and fields. The bright profile gives fluorescence. The dark profile indicates terrain elevation and at the same time the different parts of the landscape, i.e. green fields, brown and freshly ploughed fields and trees. (After Hoge et al. 1983)
2.4 Gas Analysis

Another means of analyzing the effects of plant life across a range of scales is that of infrared gas-analysis (IRGA). It is of great importance because the method can measure the gas exchange of plants, particularly respiratory and photosynthetic CO₂ exchange (but not O₂!) and also transpirational loss of water vapour. Many molecules which play a role as environmental pollutants, such as sulfur dioxide, nitrogen oxides, ammonia and carbon monoxide can also be analyzed. Therefore, the IRGA is an important technique in ecophysiological studies encompassing photosynthesis as well as environmental control.

**Box 2.2  Infrared active and non-active gases**

*Infrared active*

<table>
<thead>
<tr>
<th>Gas molecules with two different atoms</th>
<th>Gas molecules with more than two identical atoms</th>
</tr>
</thead>
<tbody>
<tr>
<td>H₂O water vapour</td>
<td>O₃ ozone</td>
</tr>
<tr>
<td>CO₂ carbon dioxide</td>
<td></td>
</tr>
<tr>
<td>NH₃ ammonia</td>
<td></td>
</tr>
<tr>
<td>SO₂ sulphur dioxide</td>
<td></td>
</tr>
<tr>
<td>N₂O dinitrogen oxide</td>
<td></td>
</tr>
<tr>
<td>CO carbon monoxide</td>
<td></td>
</tr>
<tr>
<td>CH₄ methane</td>
<td></td>
</tr>
</tbody>
</table>

*Infrared inactive*

<table>
<thead>
<tr>
<th>Gas molecules with two identical atoms</th>
</tr>
</thead>
<tbody>
<tr>
<td>O₂ oxygen</td>
</tr>
<tr>
<td>H₂ hydrogen</td>
</tr>
<tr>
<td>N₂ nitrogen</td>
</tr>
</tbody>
</table>
An IRGA measures the specific absorption of **infrared radiation** with a characteristic absorption spectrum for a particular gas. It is caused by an uneven distribution of electrical charge in the gas molecules, i.e. a dipole moment, which can be excited by infrared radiation. This is present in gas molecules which are composed of two or more different atoms (Box 2.2). Moreover, gas molecules which are built up of more than two identical atoms also develop a dipole moment due to the oscillations of atoms against each other. For example in ozone, composed of three

![Diagram of IRGA](image)

**Fig. 2.8** The principle of infrared gas analysis (IRGA): The gas analyzer consists of four gas-filled chambers I–IV. The gas to be analyzed is passed through chamber II. It is often a gas stream modified during photosynthesis by leaves in a gas-exchange cuvette (G) under photosynthetically active radiation (PAR). The reference gas is contained in chamber I. An infrared radiation (IR) incident on both chambers is absorbed in correlation to the gas concentrations in the chambers. The radiation transmitted by chambers I and II heats up the gas contained in chambers III and IV below them. Depending on the intensity of the transmitted radiation, which is influenced in chamber II by the concentration in the measured gas, the gas in chambers III and IV is heated up to a larger or smaller extent. This causes a pressure difference which moves the membrane of a membrane condensor (M). The IR beams are chopped by a rotating disc (R), which interrupts the radiation in both chambers in an equal rhythm. Thus, synchronized changes of capacity and potential are obtained, which are amplified and rectified (V) and given out on a recorder, into a data logger (D) or on a digital read-out unit. With the appropriate choice of IR wave lengths corresponding to the IR absorption spectrum of the gas species studied, different gases can be analyzed. Since chambers III and IV also must contain the gas species to be measured, analysis of each gas species requires a separate specific analyzer. Cross-sensitivities for other gases in some cases may also have to be considered.
2.4 Gas Analysis

oxygen atoms (O$_3$), two of the atoms are always closer together and the distance to the third atom is larger (induced dipole moment). Conversely, gases with two identical atoms are not sensitive to infrared radiation, because even during oscillation of atoms the charge remains evenly distributed. (A list of important infrared active and non-active gas molecules is given in Box 2.2.)

For the same reason which allows their detection by IRGA, the infrared-active gases also contribute to the green-house effect, keeping the surface of the globe warm by absorbing infrared heat radiation which would otherwise radiate out into space. The most important gas in this respect is water vapour, without which the earth would be unbearably cold. The recent increase of other atmospheric gases like CO$_2$ and methane (CH$_4$) in the last hundred years is considered to threaten global temperature balance.

Figure 2.8 shows how photosynthetic or respiratory gas exchange of individual leaves or plants is measured in gas-exchange cuvettes. Studies at larger scales can be made by taking samples during meteorological flights with aeroplanes or balloons, which are later analyzed by IRGA-techniques. Such flights in the lower atmosphere are increasingly valuable in the investigation of large-scale ecological problems. An impressive example of the success of this approach is the study of gas exchange above the canopy of a tropical forest by measuring CO$_2$-concentrations. It has been demonstrated that high CO$_2$-concentrations build up above the canopy from respiration during the night and are decreased in photosynthesis during the day (Fig. 2.9).

Large areas can also be investigated by ground-based gas-analysis systems spanning a range from meters up to kilometers. Such an instrument, for example, is the Fourier-transformed-infrared-spectrometer (FTIR), which is equipped with a 60-cm

![Fig. 2.9](image-url) Vertical profiles of CO$_2$ concentrations in the atmosphere above a tropical forest based on the infrared analysis of gas samples taken at three different times during the morning. At 08.00 h CO$_2$ concentration is high due to nocturnal respiration of the plants; however, it gradually decreases in the course of the morning due to photosynthesis, and at 12.20 h it is clearly smaller than the average CO$_2$ concentration of the troposphere at a little more than 345 Pa/MPa. (After Matson and Harriss 1988)
telescope and appropriate computer technology, and using mirrors can provide trace-gas analyses over distances of up to 1.5 km (Fig. 2.10) (Gosz et al. 1988). Of course, this approach is difficult in denser and taller vegetation. New laser sensors, which operate not only in the infrared region of the spectrum but also in the visible and ultraviolet region, allow direct gas analyses from onboard aeroplanes (Matson and Harriss 1988; Matson and Vitousek 1990). Here, the troposphere at the surface of our planet is taken as kind of a gas-exchange cuvette to consider gas-exchange between the biosphere and the atmosphere. The example of Fig. 2.11 shows the separation of different atmospheric CO₂ concentrations above various tropical ecosystems along a 50-km-long path of a flight in the morning.

**Fig. 2.10** Infrared-radiation source (IR) and Fourier transform infrared spectrometer (FTIR), which together with telescopes and a mirror (or a network of mirrors) allow ground-based gas analysis over longer distances. (After Gosz et al. 1988)

**Fig. 2.11** Horizontal profile of CO₂ concentrations in the atmosphere above different ecosystems in the tropics based on measurements on board of a meteorological aeroplane along a flight path of a little more than 50 km between 08.30 and 08.43 h. The vegetation has increased the CO₂ concentration due to nocturnal respiration. The values above rivers are much lower and correspond to the average CO₂ concentration in the troposphere (see also Fig. 2.9). (After Matson and Harriss 1988)
2.5 Stable Isotope Analysis

Many chemical elements in nature occur in the form of several isotopes, which for a given proton content in the nuclei have slight differences in mass due to varied neutron contents. In most elements one of the isotopes quantitatively predominates, while the others have a much lower abundance.

Isotope techniques initially became well known through radioactive isotopes serving as tracers to follow the path of certain elements in complex metabolic reaction sequences and transport systems. Alternatively, radiocarbon dating uses the naturally occurring carbon isotope $^{14}$C, with a half-life of approximately 5,600 years, and provides a means of dating over relatively recent geological time scales. More recently, however, the analysis of stable isotopes has provided increasingly valuable information on spatial and temporal variations in ecological and palaeohistorical terms (Rundel et al. 1988; Máguas and Griffiths 2002). Table 2.1 provides information on those stable isotopes which currently promise to provide the most important information in ecology.

The differences in the physical and chemical properties of the various isotopes of an element depend on the relative differences in mass and therefore they are small. The exception is hydrogen with very light nuclei where the deuterium provides much greater isotope effects. However, the analytical methods are extraordinarily precise. The isotopes are analyzed using mass-spectrometry according to their mass to charge ratio. The results of the analysis of a gaseous sample are not expressed as absolute isotope contents but related to an internationally accepted standard. Let $x'$ be a rare and $x$ the most frequent isotope of an element, where

<table>
<thead>
<tr>
<th>Element</th>
<th>Isotope</th>
<th>Abundance (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hydrogen</td>
<td>$^1$H</td>
<td>99.985</td>
</tr>
<tr>
<td></td>
<td>$^2$H or D</td>
<td>0.015</td>
</tr>
<tr>
<td>Carbon</td>
<td>$^{12}$C</td>
<td>98.89</td>
</tr>
<tr>
<td></td>
<td>$^{13}$C</td>
<td>1.11</td>
</tr>
<tr>
<td>Nitrogen</td>
<td>$^{14}$N</td>
<td>99.63</td>
</tr>
<tr>
<td></td>
<td>$^{15}$N</td>
<td>0.37</td>
</tr>
<tr>
<td>Oxygen</td>
<td>$^{16}$O</td>
<td>99.759</td>
</tr>
<tr>
<td></td>
<td>$^{18}$O</td>
<td>0.204</td>
</tr>
<tr>
<td>Sulphur</td>
<td>$^{32}$S</td>
<td>95.00</td>
</tr>
<tr>
<td></td>
<td>$^{34}$S</td>
<td>4.22</td>
</tr>
<tr>
<td>Strontium</td>
<td>$^{86}$Sr</td>
<td>9.86</td>
</tr>
<tr>
<td></td>
<td>$^{87}$Sr</td>
<td>7.02</td>
</tr>
<tr>
<td></td>
<td>$^{88}$Sr</td>
<td>82.56</td>
</tr>
</tbody>
</table>
\( x' \) may be heavier or lighter than \( x \), one can obtain the isotope-ratio \( \delta x' \) in \( \text{‰} \) as follows:

\[
\delta x' = \left( \frac{(x'/x)_{\text{sample}}}{(x'/x)_{\text{standard}}} - 1 \right) \times 1000. \tag{2.5}
\]

Thus, in fact, one is operating with isotope-ratios, which provides the high precision in comparisons of different samples, expressed as a differential against the particular standard.

Isotope effects are a measure of the behaviour of individual molecules containing different isotopes of an element and occur during diffusion or transport in various media as well as in enzymatic reactions. The differences in the kinetic properties and in the behaviour of molecules with different isotopic composition in thermodynamic equilibria form the basis for many applications of the stable-isotope technique, including:

- geochemistry;
- hydrology;
- meteorology;
- paleoclimatology;
- biochemistry and physiology of metabolism;
- ecology and environmental research.

The technique originated from geochemistry. Its great importance in meteorology may be illustrated by considering water. The vapour pressure of water is proportional to the mass. Thus, heavy H\(_2\)O-molecules with the isotopes \( ^2\text{H} \) and \(^{18}\text{O} \) instead of \(^1\text{H} \) and \(^{16}\text{O} \) need higher temperatures to evaporate and are discriminated against. However, at higher temperatures the absolute H\(_2\)O content in the gas-phase is higher. During rain the heavier molecules then precipitate more readily than the lighter ones, and hence, evaporation and precipitation provide a climate effect on isotope composition of rain (Ziegler 1989):

- according to latitude;
  the content of heavy isotopes \( ^2\text{H} \) and \(^{18}\text{O} \) declines with increasing latitude following the temperature gradient;
- according to altitude;
  the content of \( ^2\text{H} \) and \(^{18}\text{O} \) declines with increasing altitude;
- according to seasons;
  at higher latitudes (> 30°) the rain contains more \(^2\text{H} \) and \(^{18}\text{O} \) in summer and less in winter;
- according to continentality;
  the \(^2\text{H} \) and \(^{18}\text{O} \) contents decrease with increasing distance from the coast;
- according to the amount of rain;
  the \(^2\text{H} \) and \(^{18}\text{O} \) contents decrease with increasing amount of rain falling.

This explains hydrological isotope effects. The isotope composition of groundwater, flowing surface-water, and recent precipitation is different. Thus, although no
fractionation occurs during uptake by plants, organisms which take up such water are also distinguished by their own isotope content. Although there are additional discrimination processes when water evaporates from leaves (enriching leaf $^2$H and $^{18}$O), a further fractionation occurs in favour of the heavy isotopes during incorporation into organic material. By analysis of the most recently produced biomass, allowing for certain exchange reactions one can conclude from which direction the last rain falls or one can determine the geographical origin of plants and food items (Smith 1975).

These climate effects have led to applications in palaeoclimatology. From the isotope composition of fossil water in subterranean water reservoirs, which have formed in geological periods, one can draw conclusions on the climate at that time. Analysis of small gas inclusions in layers of ice in glaciers, or of water from the ice itself, allow similar conclusions about the past. For example, in the ice of a glacier at 5,670 m a.s.l. in the Cordillera de Carabaya of the tropical Andes in Peru, relatively low levels of $^{18}$O [more negative values of $\delta^{18}$O, see (2.5)] indicate a warmer period between 1000 and 1500 A.D. This was correlated with lower accumulation of ice, although higher $^{18}$O levels (less negative $\delta^{18}$O), then represent a colder period from 1500 to about 1875 A.D. when ice-deposition was initially high (Fig. 2.12). Further opportunities are provided by the incorporation of water into organic constituents of plants, and the analysis of gross remnants of plants in peat accumulations or from the study of isotope composition of annual rings in old trees and wood.

When $\delta^{13}$C signatures of several ecosystem components such as the air, the plant biomass, fallen litter and the soil are studied systematically with a spatiotemporal resolution insights into the carbon dynamics, e.g. of tropical primary rainforests can be obtained (Buchmann et al. 2004). In extant current physiology of water relations of plants the isotope effects of evaporation and diffusion of water are useful for the study of transpiration and water use efficiency (WUE) dur-

![Fig. 2.12A,B $\delta^{18}$O-values (A) [see (2.5)] and accumulation of ice (B) for the past 1000 years in the glacier Quelcaya Cap, Cordillera de Carabaya, Peru ($13^\circ 56' S, 70^\circ 50' W$) related to values of the year 1980. (After Jones 1990; with kind permission by La Recherche)
ing photosynthesis. Because the major constraint for transpirational loss of water is the opening or closing state of stomatal pores \(^{18}\text{O}\)-isotope enrichment in the leaf biomass is a good measure of stomatal conductance integrated over the time of the life span of the leaf sampled and there is a significant positive relationship with mean transpiration rate (Sheshshayee et al. 2005). Since the opening/closing of stomata likewise determines diffusion of atmospheric \(\text{CO}_2\) into the leaves, the isotope \(^{13}\text{C}\) has been much used as an indicator for time integrated stomatal conductance of leaves, and in \(\text{C}_3\)-plants the variable rate of \(\text{CO}_2\)-diffusion via stomata primarily determines overall changes in \(^{13}\text{C}\)-discrimination during photosynthesis. Generally with a small conductance, i.e. when stomata are more tightly closed, if photosynthetic rate is maintained internal \(\text{CO}_2\)-concentration, \(p^i_{\text{CO}_2}\), tends to be low. With high conductance, i.e. when stomata are more opened, \(p^i_{\text{CO}_2}\) approaches the value of external \(\text{CO}_2\)-concentration, \(p^o_{\text{CO}_2}\). Overall carbon isotope discrimination, \(\Delta\), is then proportional to the ratio of \(p^i_{\text{CO}_2}/p^o_{\text{CO}_2}\) and, hence by indirect association also to leaf-conductance for water vapour, \(g_{\text{H}_2\text{O}}\), as follows:

\[
\Delta = a \frac{p^o_{\text{CO}_2} - p^i_{\text{CO}_2}}{p^o_{\text{CO}_2}} + b \frac{p^i_{\text{CO}_2}}{p^o_{\text{CO}_2}} = a + (b - a) \frac{p^i_{\text{CO}_2}}{p^o_{\text{CO}_2}} \%e .
\]  

(2.6)

In this relationship \(a\) gives \(^{13}\text{C}\) discrimination due to \(\text{CO}_2\)-diffusion in air (4.4\%e) and \(b\) the net fractionation caused by the carboxylation itself (ca. 27\%e, i.e. \(b - a\) is ca. 22.6\%e) so that (2.6) becomes

\[
\Delta = 4.4 + 22.6 \left( \frac{p^i_{\text{CO}_2}}{p^o_{\text{CO}_2}} \right) \%e .
\]  

(2.7)

From the measurements of the carbon isotope ratios in dry plant material, \(\delta_p\) (2.5), and in air, \(\delta_a\), \(\Delta\) is calculated as follows:

\[
\Delta = \frac{\delta_a - \delta_p}{1000 + \delta_p} \times 1000 \%e ,
\]  

(2.8)

where \(\delta_a\) and \(\delta_p\) are given in \%e. Determined by the contribution from respiratory \(\text{CO}_2\) the value for ambient air, \(\delta_a\), can vary between \(-10.5\) and \(-7.5\)\%e especially inside forests and depending on the height above ground. For normal bulk-air conditions, one assumes a \(\delta_a\) of \(-8\)\%e (Farquhar et al. 1989a,b; Broadmeadow et al. 1992; Ehleringer 1993; Guehl et al. 2004). Thus, we can summarize the proportionally of terms as follows:

\[
\Delta \sim \frac{p^i_{\text{CO}_2}}{p^o_{\text{CO}_2}} \sim g_{\text{H}_2\text{O}} \sim \frac{1}{\text{WUE}} .
\]  

(2.9)

However, this approach is increasingly subject to critique because \(^{13}\text{C}\)-isotope effects are also given by the activity of respiration as respiratory \(\text{CO}_2\) is enriched in \(^{13}\text{C}\) (Ghashghaie et al. 2001), the activity of photosynthesis and the developmen-
2.5 Stable Isotope Analysis

The internal conductivity of CO₂ within leaves is different in different plants, and the relationships of 2.9 are not allowing correct comparisons between species (Warren and Adams 2006). Δ may also vary in response to light gradients within canopies (Medina et al. 1991; Roux et al. 2001; Holtum and Winter 2005; Buchmann et al. 2004; see Fig. 3.31). Nevertheless, in comparisons of C₃ plants under critically comparable conditions the application of these equations still provides very useful information (Guehl et al. 2004).

Simultaneous analyses of ¹³C and ¹⁸O allow a distinction between effects of stomatal diffusion and photosynthetic capacity. A change of \( p_{\text{CO}_2}/p_{\text{CO}_2} \) as indicated by Δ can be due to a change of \( g_{\text{H}_2\text{O}} \) at constant maximum CO₂-assimilation, \( A_{\text{max}} \), or a change of \( A_{\text{max}} \) at constant \( g_{\text{H}_2\text{O}} \). The ¹⁸O signature mirrors accumulation of water in the photosynthetic organs and hence the contribution of stomatal regulation (Adams and Grierson 2001). If other effects on the ¹⁸O signature can be excluded – e.g. habitat influences such as differences in the ¹⁸O signature of the water available to the plants – the simultaneous analysis of \( \delta^{13} \)C and \( \delta^{18} \)O allows a distinction between effects of \( g_{\text{H}_2\text{O}} \) and \( A_{\text{max}} \) (Scheidegger et al. 2000). Positive correlations between \( \delta^{13} \)C and \( \delta^{18} \)O then indicate a dominant control by \( g_{\text{H}_2\text{O}} \) at relatively constant \( A_{\text{max}} \) where stomata operate in a broad range of opening and closing from high transpiration rates (low \( \delta^{18} \)O values) to low transpiration rates (high \( \delta^{18} \)O values). Strong variations of \( \delta^{13} \)C at low changes of \( \delta^{18} \)O, however, indicate that carbon gain is mainly under assimilatory and not under stomatal control.

Far reaching diagnoses as attained by applications of the stable-isotope technique in ecology may result from isotope effects of metabolism. Several enzymes discriminate against substrate molecules constituted of different isotopes leading to different isotope composition of products. An important example is the fixation of CO₂ for photosynthetic assimilation with discrimination occurring against the heavier isotope \(^{13}\)C as compared to \(^{12}\)C. The enzyme ribulosebisphosphate carboxylase (RuBPC), which directly leads to the formation of the C₃-compound phosphoglyceric acid in the light (C₃-photosynthesis), discriminates against \(^{13}\)CO₂ more strongly than another carboxylating enzyme, phosphoenol-pyruvate carboxylase (PEPC; Table 2.2), which forms the C₄-acid oxaloacetate by fixation of bicarbonate and leads to malate/aspartate (C₄-photosynthesis, Box 10.2). The latter enzyme (PEPC) also mediates dark fixation of CO₂ in plants with crassulacean acid metabolism (CAM, Box 5.1), where malic acid provides nocturnal CO₂ storage. In CAM, during the day, CO₂ is remobilized from malate and refixed and assimilated via RuBPC. Depending on the environmental conditions CAM-plants can also fix CO₂ in the light directly via RuBPC.

Due to the different extent of discrimination against \(^{13}\)CO₂ by the two enzymes during primary CO₂-fixation by the C₃- and C₄-plants, and by the variable expression of the two mechanisms in CAM-plants, carbon-isotope ratios (\( \delta^{13} \)C values) differ in the three types of plants. They are most negative (most depleted of \(^{13}\)C) in C₃-plants, less negative in C₄-plants and intermediate in CAM-plants (Fig. 2.13). Both C₄-photosynthesis and CAM are, in different ways, adaptations to reduced supply of water and contribute to the efficiency of plant water use. This means
Table 2.2 $^{13}$C-discrimination (‰) in various steps of the CO$_2$ fixation process (from Ziegler 1994)

<table>
<thead>
<tr>
<th>Step</th>
<th>$^{13}$C isotope discrimination</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diffusion of CO$_2$ in the gas phase</td>
<td>4.4</td>
</tr>
<tr>
<td>Dissolution of CO$_2$ in water</td>
<td>−0.9</td>
</tr>
<tr>
<td>Liquid phase diffusion of CO$_2$ or HCO$_3^-$</td>
<td>0.0</td>
</tr>
<tr>
<td>Hydration of CO$_2$</td>
<td>−7.0</td>
</tr>
<tr>
<td>Carboxylation of phosphoenolpyruvate relative to HCO$_3^-$</td>
<td>2.0</td>
</tr>
<tr>
<td>Carboxylation of phosphoenolpyruvate relative to CO$_2$</td>
<td>−5.0</td>
</tr>
<tr>
<td>Carboxylation of ribulose-bisphosphate</td>
<td>27</td>
</tr>
</tbody>
</table>

that in C$_4$- and CAM-plants, for each CO$_2$-molecule fixed, a smaller number of H$_2$O-molecules is lost via transpiration as compared to C$_3$-photosynthesis. Thus, in addition to the $^{13}$C-content, the $^2$H- and $^{18}$O-content of the plants is also affected. Within the different modes of photosynthesis there are subtleties dependent on the diffusive limitation imposed on evapotranspiration (see above) or in the relative utilization of RuBPC and PEPC in CAM, and generally in the use of water. All this is reflected in isotope composition. Thus, also various ecotypes of plants, like halophytes and xerophytes can be differentiated. It must be noted for the latter, however, that such comparisons are only allowed between C$_3$-species because these effects are highly overridden by the carbon isotope effects of CO$_2$ fixation by RuBPC and PEPC, respectively.

Another example from metabolism is represented by $N$-nutrition of plants. For nitrogen isotope effects the situation often is very complex and straightforward conclusions are difficult (Martinelli et al. 1999; Adams and Grierson 2001). Differences in nitrogen uptake mechanisms and in the pathways of assimilation and recycling of nitrogen in the plants can greatly affect $\delta^{15}$N values (Evans 2001). N-salts in the soil tend to enrich the heavier isotope $^{15}$N, as compared to atmospheric gaseous N$_2$, and
therefore one can recognize symbiotic N\textsubscript{2}-fixers (e.g. legumes with root nodules) by the lower 15N content. Analyses of the natural abundance of 15N in soils have also served to document forest-to-pasture chronologies and record changes of land-use pattern in the western Amazon Basin in Brazil (Piccolo et al. 1994).

The flow of various isotopes through the biomass of plants also affects the transfer into other compartments of ecosystems. This allows the study of food webs, habitat preferences in wandering animals, and even the analysis of eating and drinking habits in human populations and individuals. For the latter it usually suffices to analyze the organic matter of hairs or finger- and toenails.

Since the analysis of dry matter of the organisms is often sufficient, one can cover large geographic areas with sampling even from remote regions using simple equipment. Even collections in herbaria may be used. In this way, for example one can arrive at conclusions about the large-scale ecological distribution of modes of photosynthesis. C\textsubscript{4}-grasses dominate in tropical savannas, their relative abundance declines with increasing altitude (Tieszen et al. 1979; Medina 1982; see Sect. 10.1.1.2).

An impressive example, if not for a whole continent, is given for the rather large tropical island of Madagascar of 590,000 km\textsuperscript{2} (Kluge et al. 1991). Combining the Klimadiagramm method with the stable-isotope technique, the distribution of CAM among species of the genus Kalanchoë has been studied and related to climatic zones and vegetation types of the island. There are 52 species of Kalanchoë in Madagascar, of which all are either obligate or facultative CAM plants. There is high flexibility among the species to obtain a variable amount of carbon by direct CO\textsubscript{2} fixation via RuBPC, and this is reflected by increasingly negative $\delta^{13}$C values, whereas primary CO\textsubscript{2} fixation dominated by PEPC leads to less negative $\delta^{13}$C values. The large scale effects deduced from the analysis present a very close correlation of $\delta^{13}$C values in the dry matter of Kalanchoë species and climate and vegetation zones on the island. Less negative (CAM-like) values are dominant in the drier zones with evergreen dry forest, deciduous woodland, savannas and xerophilous thornbush, while more negative (C\textsubscript{3}-like) values prevail in the wetter zones with evergreen rainforest and montane forest (Fig. 2.14). The example illustrates the close relations between climate, vegetation types and prevalence of the water conserving CAM-mode of photosynthesis in a given genus. It even allows some views into the evolutionary history of the genus Kalanchoë. Comparisons of the phytogeographic distribution of C\textsubscript{3}- and CAM-species of Kalanchoë in Madagascar with the phylogeny of different subgenera based on morphological and molecular characteristics and the evolution of CAM in the CAM-species show that CAM has only evolved once (monophyletically) from the C\textsubscript{3}-species of the moister regions and that the more drought resistant CAM-species then have conquered the drier regions of the island (Kluge et al. 1991, 2001; Gehrig et al. 2001).

Large-scale isotope effects, however, may also result from transfer rates. Thus, respiration and photosynthesis of organisms determine the vertical $^{13}$CO\textsubscript{2}-gradient in tropical rainforests (Medina et al. 1986). Richey et al. (1990) have proposed to use $^{18}$O-analyses to assess the large-scale consequences of the destruction of tropical
Fig. 2.14A, B Climate zones related to Klimadiagramm distribution (A) and vegetation types (B) of Madagascar. The vegetation map (B) contains points indicating ranges of $\delta^{13}C$ values as explained in the inset. Note that the closed symbols marking the more negative $\delta^{13}C$ values are concentrated in the wetter regions, and the open symbols marking less negative $\delta^{13}C$ values are accumulated in the drier vegetation units. The inset also gives the frequency of $\delta^{13}C$ values for the samples collected on the island for three combinations of vegetation units as indicated. (After Kluge et al. 1991)
Fig. 2.14 (Continued)
rainforest in the Amazon region. Since C-, N- and S-compounds from biogenic and anthropogenic sources have different isotope composition, the pathways of pollutant emission can also be traced. The large global-cycles of a range of elements in the gaseous atmosphere, as well as regional environmental effects, can be diagnosed in this way.

Finally, interest has also been focussed on the element strontium, which is not subject to metabolism, in terms of mineral nutrition. The \(^{87}\text{Sr} / {^{86}\text{Sr}}\) ratios in the bed-rock develop in geological times. The different geochemical mobilization of the isotopes allows distinctions between nutrient supply of vegetation from the soil, water or dust in the atmosphere. This facilitates understanding of nutrient sources in ecosystems (Graustein 1989).

### 2.6 Mathematical Tools

Huge amounts of data become available in large-scale diagnostics. Networks of functional systems, sub-systems and supra-systems are emerging. The methods described in Sects. 2.2 – 2.5 reveal spatiotemporal pattern formation. We deal with multidimensional problems, which have to be summarized numerically or graphically and must be cast into a comprehensive presentation. This may possibly constitute the most important bottleneck. Hobbs and Mooney (1990) conclude their book on remote sensing of the biosphere functions with the statement, that even without the intensive further development of new sensors, the currently available technologies offer so much that the capacity for interpretation and application has been surpassed. The major problems do not appear to be with collection but with analysis and understanding of data.

The data mountains piling up require hardware and software technologies for storage and organization. Special statistical and mathematical procedures are essential to reduce the relevant information from the mass of data to an interpretable form, and the analysis of data needs the development of new mathematical approaches (Hütt 2001). Special geographic information systems with multi factorial mapping are designed to provide surveys related to space (Wallace and Campbell 1990). Image analyses use the concept of cellular automata and nearest neighbour algorithms to unravel spatiotemporal structures of patterns (Hütt and Lüttge 2002, 2005).

A particular problem of great fascination is the non-linear dynamics of all the ecosystems studied. In phytosociology unpredictability, e.g. in occupation of new habitats by species, is often readily interpreted as demonstrating that the distribution of plants and the development of diversity is stochastic. Taking the term stochastic in its strict mathematical meaning, this is by no means so simple. Stochastic white noise in empirical data time series can not readily be distinguished from the so-called deterministic chaos, which follows strict mathematical rules. A distinction between the two can only be made via sophisticated theoretical analyses requiring very detailed sets of time series data. These are rarely available, and
hence, it is hard to prove whether deterministic chaos or stochastic noise predominate.

Fig. 2.15A–C Comparisons of predictability in (A) random, (B) regular and (C) chaotic motion. (Modified after Schuster 1995)

Nevertheless, it is useful to consider briefly the possible implications of the theory of deterministic chaos in ecology. In random motion initially adjacent points are distributed with equal probability over all new allowed intervals (Fig. 2.15A). In regular motion initially adjacent points stay adjacent (Fig. 2.15B). In chaotic motion initially adjacent points become exponentially separated (Fig. 2.15C). Thus, regular motion and random motion show complete predictability and unpredictability, respectively. Chaotic motion offers some short term predictability (Schuster 1995). Although chaotic systems totally lack long term predictability their short term predictability is better than that of stochastic random processes. One can determine the error of such predictions, and with the appropriate algorithms one can
use them to regulate a system via a transputer so that the system is forced to stay in one of the chaotic paths (or trajectories) in time and space. Such fine regulation of chaotic systems, which offers opportunities for much more delicate manipulation than regulation of deterministic systems, is currently assessed in physics (Hübinger et al. 1993; Schuster 1995) and even explored for practical applications in engineering. Biological systems must obey physical laws. Conversely, we may also say that biological systems use physical laws to develop the diversity of life. It would be most surprising if the wide scope of possibilities inherent in deterministic chaos had not been used by life during evolution. It may be noted that with pure stochastic randomness life would be deprived of any significance and would be cast into meaninglessness. Conversely, pure deterministic regularity, allowing one to retrace all things accurately in the past and predict them precisely in the future for all (mathematical) infinity would cast life into tedious monotony. Only deterministic chaos, with its strict mathematical rules and yet high variability, with its unpredictability and yet delicate means of fine regulation, provides an opportunity for the adaptability, plasticity, diversity and beauty of life to unfold (W. Martienssen, quoted after a public lecture; Lloyd and Lloyd 1995).

Due to the pioneering contributions of R. May (May 1976) population dynamics has become one of the roots of the development of the chaos theory. Possibly the apparently simple logistic equation discussed by May (1976) may allow biologists a ready access to an intuitive comprehension of the theory of deterministic chaos. Let \( x_t \) be the size of a population at a certain state at time \( t \). We then want to know the size of the population at the next possible state in time, i.e. \( x_{t+1} \). It is obvious that the development of the population depends on its resources. These may be given by a growth factor \( r \) or more generally an external control parameter, such that \( x_{t+1} \) is proportional to \( r \cdot x_t \). However, it is not only evident from the exorbitant increase of the human population on the globe, but a general experience of population ecology, that increasing population densities also bear inhibitory mechanisms in themselves, i.e. \( x_{t+1} \) is also proportional to \( x_t \cdot (1 - x_t) \). Hence, the logistic equation for the development of the population \( x \) is

\[
x_{t+1} = r \cdot x_t \cdot (1 - x_t) .
\]

Subsequent population sizes can be calculated by recursions, where \( x_{t+1} \) is used in the place of \( x_t \) to obtain \( x_{t+2} \) and so forth.

However, the equation is only apparently simple. It describes one of several possible routes from order or regularity into chaos (Schuster 1995; Fig. 2.16). It shows that ordered predictability only occurs for a narrow range of the value of the control parameter \( r \). At low values of \( r \) there is a steady state, while at larger values of \( r \) a bifurcation (i.e. a branching or dichotomy) leads first to phase doubling and ordered oscillations between two states and then further bifurcations give four states. However, very tiny additional changes of \( r \) lead the way into the non-predictability of deterministic chaos. This is seen in computer simulations of (2.10), shown in Fig. 2.16. The lower diagram shows the initial steady state, effective for a large range of values of \( r \), then the first and second bifurcation leading to periods of 2 and 4 states, and with increasingly smaller increments of \( r \) there are then chaotic responses to tiny
The route from order to chaos via increasing periods by augmenting $r$ in the logistic recursion equation (2.10). The lower diagram shows the route from steady state via bifurcations (period 2, period 4) into chaos given by increasing $r$. The upper four diagrams give the calculated population sizes by iteration of (2.10) for the steady state, period 2 (two states), period 4 (four states) and chaos. (May 1976; Hastings et al. 1993)

Changes of $r$. The top four graphs show the results of iterative calculations of population sizes $x_t$. At low $r$ in the steady state the population is stable, at period 2 there are two and at period 4 there are 4 predictable states, while in chaos, prediction of subsequent population sizes from existing ones has become impossible.

This little excursion to population theory appeared useful to explain some basic implications of the chaos theory. Chaos is a property of non-linear dynamic systems and these are the rule and not the exception both in the living and non-living world. However, while the theory of deterministic chaos has already had some impact in population biology (May 1976; Hastings et al. 1993) it is intriguing that in ecology in general it has only been accepted very reluctantly (Linsenmair 1995; Stone and Ezrati 1996), or even been rejected in the exclusive distinction of deterministic and stochastic development of diversity. It is intriguing because population biology is a field so close to or even part of ecology. For example, we may consider the control parameter $r$ in (2.10) as an indicator of general resources or even as stress.
integrates functioning of diversity (Cramer 1993), we realize that this must occur only within a rather narrow window of stress conditions, as it is in fact borne out in experiments like those of Grime et al. (1987) and Tilman (1982) described in Sect. 3.3.2. Likewise, we are right back in the realm of deterministic chaos when we reject the climax theory of formation of stable steady state vegetation types and adopt instead the oscillating mosaic model with continuous dieback and renewal of “unpredictable irregularity” for tropical forests (Sect. 3.3.3). It is not unlikely that deterministic chaos, which certainly governs the ecology of populations, also determines the structure of tropical forests (as of other environments) with their oscillatory and non-linear behaviour.

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Chapter 3
Tropical Forests.
I. Physiognomy and Functional Structure

3.1 Separation of Different Types of Tropical Forests

In the tropics seasonality is determined by rainfall. Seasonality of rainfall is absent over only a very narrow zone 1° north and south of the equator (Fig. 3.1). Seasonality of rainfall is the most important factor determining the definition of different types of tropical forest. Hence, a detailed separation of types of tropical forests is obtained when they are related to Klimadiagramm graphs (after Walter 1973, see Sect. 2.2.1, Box 2.1), which depict the duration and severity of dry and wet seasons. Humid and arid climates, respectively, are defined by the difference between rainfall and evaporation. Positive values indicate a humid climate, where precipitation is larger than evaporation, and negative values mark arid climates with evaporation larger than precipitation. As we have demonstrated above (Sect. 2.2.1), the Klimadiagramm technique based on temperature and precipitation is highly successful in demonstrating the degree of aridity and humidity of individual stations as well as large areas. In contrast to data on temperature and precipitation, which usually are readily available from many weather stations, measurements of free evaporation are scarce. Other factors, especially wind, may significantly affect evaporation. Thus, where evaporation data is available, it can add much to the information provided by Klimadiagramm graphs. As seen in the examples of seven stations in Venezuela (Fig. 3.2) the results of Klimadiagramm graphs regarding the occurrence of humid seasons is roughly confirmed by the rainfall minus evaporation (R – E) index. However, the wet seasons generally appear somewhat shorter with the R – E index, and on the basis of this criterion small apparent humid seasons of the Klimadiagramm graphs disappear entirely (Fig. 3.2 diagrams 1 and 2). These seven stations carry different types of forest and represent a latitudinal transect from the wet continental areas close to the equator to the drier coastal regions in the north of Venezuela (Fig. 3.3). A very strong effect of latitude on the expression of tropical forest types is highly evident, which agrees with the predictions of Fig. 3.1.

Using India and Venezuela as examples comparison of forest types is made with a diagram of precipitation versus extension of dry periods (Fig. 3.4). The corresponding Klimadiagramm graphs for Venezuela are shown in Fig. 3.5. The major
types of forests distinguished in relation to the degree of seasonality which increases with increasing numbers of dry months per year and decreasing annual rainfall are:

- evergreen rainforest,
- seasonal rainforest,
- semi-evergreen moist and dry monsoon or trade-wind forest,
- drought-deciduous forest,
- thorn scrub and cactus forest.

Fig. 3.2 Diagrams for seven stations of a transect across Venezuela as shown in Fig. 3.3. The diagrams indicate the extensions of wet seasons according to the Klimadiagramm concept \((\text{thinner plus thicker vertical bars})\), i.e. where the rainfall curve is above the temperature curve; see Box 2.1), and the dry seasons according to the Klimadiagramm concept are \(\text{dotted as usual}\). The \text{thick line} gives free evaporation. The \(R - E\) index is positive where the rainfall curve of the Klimadiagramm is above the evaporation curve, and this indicates the extensions of the wet seasons according to the \(R - E\) index \((\text{thicker vertical bars})\). The \(R - E\) index is negative where the rainfall curve of the Klimadiagramm is below the evaporation curve and this indicates the extensions of the dry seasons according to the \(R - E\) index \((\text{left white in the diagrams})\). Annual precipitation \(P\); annual free evaporation \(E\). (After Medina 1983, with kind permission from Elsevier Science-NL, Sara Burgerhartstraat 25, NL-1055 KV Amsterdam, The Netherlands)
3.1 Separation of Different Types of Tropical Forests
Gradation of rainfall is also inherent in Beard’s distinction (Beard 1946, 1955) of forests according to \textit{altitude} (Fig. 3.6):

- low-land rainforest,
- lower montane rainforest,
- upper montane rainforest,
- elfin forest.

Some of the forest types will be discussed separately below.
3.2 Physiognomy of Different Types of Tropical Forests

3.2.1 Tropical Rain Forests

Tropical evergreen rainforests are said to contribute about 35% of global net primary production (Löscher et al. 2003). However, there is a problem of deciding what we define as “tropical rainforest”. This is best illustrated by eight maps of Venezuela presented by Vareschi (1980), where he depicts the distribution of rainforest in this tropical country according to the views of different authors (Fig. 3.7). In the two
Fig. 3.5A–F Klimadiagramm graphs for the different forest types distinguished in the diagram of Fig. 3.4B.
Fig. 3.6A–D Types of tropical forest at different altitudes. A Semi-evergreen lowland rainforest (East Venezuela). B Montane rainforest (northern range Trinidad). C Upper montane rainforest (cloud or fog forest; Rancho Grande, northern coastal range Venezuela). D Elfin forest (Serro Santa Ana, Paraguana Peninsula Venezuela)
extreme cases either almost $2/3$ of the whole country is covered by rainforest (upper left in Fig. 3.7) or there is no rainforest at all (lower right in Fig. 3.7); and there are gradations in between these extremes. In Brazil much of the Amazon basin is covered by rainforest. The Brazilian Atlantic forest also is a typical tropical rain forest. It belongs to the 25 biodiversity hot spots of the world. Of an original area of

![Fig. 3.7 Distribution of “rainforest” (black) in the tropical country Venezuela according to different authors. (Vareschi 1980, with kind permission of R. Ulmer)](image-url)
1,227,600 km² only 91,930 km² (7.5%) are remaining to date of which 33,084 km² (35.9%) are protected, and there are 20,000 plant species, 8,000 of which are endemic (Myers et al. 2000).

The purist’s definition of tropical rainforest requires that there should be no seasonality of rainfall whatsoever. Hence, the lack of any rainforest in Venezuela accords with the purist’s definition (Fig. 3.7, lower right). If one begins to broaden the definition, of course, it becomes a matter of taste how far this term may be extended. How long should rainless periods be and in how many successive years should they occur in order to retain the term “rainforest”? Accordingly, we then derive the gradations seen in the maps of Venezuela, shown in Fig. 3.7.

In addition to seasonality there are other features which characterize tropical rainforests. One of the most conspicuous is the extraordinary diversity of tree species. In contrast to the temperate and boreal zones, where forests can be named after dominant tree species, e.g. spruce, fir, pine, beech, oak, birch etc., there is no dominance of anyone particular tree species in tropical rainforests. One may encounter up to 300 tree species per ha, which represent about 1/3 of all plant species present. The most frequent tree species rarely represent more than 15% of all species of trees present (Jacobs 1988; Whitmore 1990). This phenomenon also makes it difficult to define the minimal quadrat of sampling plots in plant sociology. The minimal quadrat is given by the size of a plot in a system being studied above which the total number of species observed does not increase (see Sect. 3.3.1 and Fig. 3.15). Such minimal quadrats in tropical rainforests may be quite large and may never be attained.

3.2.2 Tropical Cloud and Elfin Forests

One of the best preserved tropical cloud forests is the forest of Rancho Grande on the northern coastal range of Venezuela (Fig. 3.6C). It is determined by the trade winds coming from a north-eastern direction (Fig. 3.8). Clouds build up over the Caribbean islands and dissolve as the wind moves south, where it then hits the coastal range of mountains on the South American continent. The hot wind cools down as it climbs upwards and on top clouds are formed almost continuously (Figs. 3.6C and 3.8). We find an altitudinal gradation of vegetation from cactus-forest, thorn scrub and dry forest to evergreen cloud forest. Clouds break up as the wind drives down the southern slopes and also move further south with the trade winds. In places, the constant exposure to the wind may lead to formation of elfin forest with dwarf trees similar to those on the top of Santa Ana Mountain on the Paraguana Peninsula of Venezuela, which are here dominated by Clusia multiflora and the palm Geonema paraguanensis about 1 m tall (Fig. 3.6D). In addition the reduction of growth and formation of dwarf forms may also be caused by reduced availability of nutrients, especially phosphorus, due to the lower mineralization rates at lower temperatures when altitude increases (Kitayama and Aiba 2002).
3.2.3 Floodplain Forests

Wetland ecosystems are found to be related to hyperseasonal and marsh savannas (Sect. 9.2, Fig. 9.10), but in addition we mention them here because we also find fresh water flooded sites in moist forests all over the world’s tropics (Esteves 1998) where all stages from open water to high forest can often be traced. We may distinguish between swamp forest which is permanently waterlogged and marsh forest which is flooded only seasonally (Richards 1996; Fig. 3.9). In Brazil the Central Amazon floodplains cover an area of more than 300,000 km² (Junk 1997) where we may distinguish nutrient poor bottomland floodplains along black water rivers (várzea) and nutrient rich periodically inundated riverine wetlands fed by white water rivers (igapó) (Esteves 1998). In Central Amazon floodplains in the pioneer species *Salix maritima* even the canopy can remain under water for months, while the canopy of the shade tolerant late successional species *Tabernaemontana juruana* always remains out of the water (de Simone et al. 2002).

Flooding leads to hypoxic and even anaerobic conditions (Richards 1996; Lobo and Joly 1998), which require morphological and anatomical as well as physiological adaptations. Phytohormones such as ethylene and auxin are involved in their regulation. At the morphological/anatomical level adventitious roots with lenticels above the water (Sect. 3.3.4.1) and root aerenchymas facilitate aeration of root tissues because plants subject to flooding have to rely on supply of oxygen from parts of the plants which are not flooded (Pimenta et al. 1998). There is adaptive hypertrophy of lenticels under the control of ethylene. In *Sesbania commersoniana* the height $\times$ length of the main root lenticels was $0.31 \times 1.56$ (mm $\times$ mm) in non-flooded controls and $0.44 \times 2.06$ (mm $\times$ mm) when flooded (Pimenta et al. 1998). The submerged roots may produce suberized and lignified barriers in the exodermis to reduce diffusion of oxygen from the root tissue to the ambient soil (de Simone et al. 2003a) although some loss of oxygen from the roots will also help to build up
Fig. 3.9 A, B Flooded forest Reserva Biologica Poço dos Antos, Rio de Janeiro State, Brazil. C *Euterpe oleracea* palm swamp, French Guyana
a partially oxidant atmosphere at the root periphery important for acquisition of nutrients and control of harmful reduced compounds at the root periphery (Lobo and Joly 1998). **White water** fed flood plains are rich and **black water** fed flood plains are poor in nutrients. **Symbiotic dinitrogen fixation** is frequent but is discussed in Sect. 10.2.3.2 in the context of savanna floodplains. The **reducing root environment** during long periods of flooding also may lead to formation of several harmful reduced compounds and especially dangerously high levels of reduced iron, Fe$_{2}^{2+}$, and manganese, Mn$_{2}^{2+}$, and stress due to uptake and storage of these metals in the plants (Lobo and Joly 1998; de Simone et al. 2003b). At the metabolic level **glycolysis and fermentation** with the production of ethanol or lactic acid serve anaerobic metabolic energy turnover (Lobo and Joly 1998; Pimenta et al. 1998; de Simone et al. 2002).

Trees and herbs may respond differently to flooding. There are basically two different response patterns among trees, deciduous tree species respond to the flooded period by complete defoliation and evergreen tree species are maintaining their foliage. Thus, Fernandez et al. (1999) found two different physiological reactions, (i) a decreasing rate of photosynthesis, stomatal closure and reduced leaf conductance for water vapour with flooding, and (ii) flood tolerance, where both photosynthesis and leaf conductance were independent of flooding. The C$_{4}$-photosynthesis grass *Echinochloa polystachya* on submerged Central Amazon floodplains showed the very high rates of photosynthesis of 30–40 µmol m$^{-2}$ s$^{-1}$ typical for C$_{4}$-photosynthesis (Sect. 10.1.1.2) but much lower rates of 17 µmol m$^{-2}$ s$^{-1}$ during shorter dry periods (Piedade et al. 1994).

### 3.2.4 Thorn Scrub and Cactus Forests

Examples comparing the physiognomy of a thorn scrub and a cactus forests are shown in Figs. 3.10 and 3.11. The term cactus forest was coined by Vareschi (1980). Cactus-forests represent an example of thornbush-succulent forests. This type of forest in Madagascar covers a small area in the south-west of the island (see Fig. 2.14) dominated by Didieraceae (11 species in 4 genera), Euphorbiaceae and other succulent and deciduous woody species (Fig. 3.12). It is also characteristic of the “Caatinga” formation in NE Brazil (Fig. 3.13A). In Venezuela there is the “Espiniar” in the area around Carora, where Vareschi (1980) distinguishes a thornbush-forest, with Mimosaceae (*Haematoxylon praecox*) and Caesalpiniaceae (*Cercidium praecox*) which has only one species of cactus, and a cactus-forest with 10 or more different species of cacti (Figs. 3.11 and 3.13B,C). However, both types of forest mutually intermingle and form a mosaic-like pattern. The term cactus forest relies on the acceptance of large columnar cacti as tree-like plants, and depends on the size of the area occupied by them. Alternatively or additionally, one may require the most important physiognomical aspect of a forest to be the formation of a closed canopy. The area around Carora in Venezuela, for which Vareschi originally coined the term, is dominated by columnar cacti of *Cereus lemairei*, *Ritterocereus griseus* and *Cephalocereus moritzianus*. However, it appears, that woody Mimosaceae, Cap-
Fig. 3.10A, B Types of dry tropical forest. A Drought deciduous forest (Falcon, Venezuela). B Cactus-forest (Carora, Venezuela)

paridaceae and Caesalpiniaceae like *Cercidium praecox* very much add to the impression of a closed canopy, which is certainly given when one is walking around in these forests. The floor of these forests is bare of vegetation or covered by a for-
bidding muddle of thorny cacti, particularly *Opuntia wentiana* and *O. caribea*. This may be due to a large extent to overgrazing by goats. At places where the access of goats is prevented, grasses are entering these cactus-forests, which then obtain a physiognomy more comparable to the equivalent thornbush-savanna in Africa.

The climate at the sites of these thornbush-succulent forests is strongly seasonal and very dry during most of the year. The *Klimadiagramm* of Carora (Fig. 3.14) for example only shows a pronounced wet period from September to December and a very short rainy season in May to June. The open canopy of these deciduous forests allows much penetration of full sunlight, and the plants are subject to stress by:

- high irradiance ($h\nu$),
- high temperature ($T$),
- scarcity of water or drought ($H_2O$),
- limited nutrient availability especially nitrogen ($N$).

The ecophysiological responses of plants in dry tropical forests will be discussed in Sect. 5.2).
Fig. 3.12 Thornbush-succulent forest in SW Madagascar with Didieraceae and Euphorbiaceae. (Photographs courtesy M. Kluge)
Fig. 3.13A–C Caatinga in the state of Ceará, Brazil (A), and thornbush-succulent forests near Carora, Venezuela (B, C)
3.3 Horizontal Structure and Diversity of Tropical Forests

3.3.1 Diversity and the Spatial Structure of the Environment

Considering the various types of forests in Sects. 3.1 and 3.2, diversity of tropical forests has already been alluded to and the high floristic diversity in tropical rainforests has been mentioned (Sect. 3.2.1). This leads to the problem that the minimum quadrats of plant sociology become very large. Minimum quadrats give the smallest possible area in which all species occurring in a habitat are present, as illustrated in Fig. 3.15. Whitmore (1990) has used such species to area diagrams to illustrate the concept of floristic $\alpha$, $\beta$- and $\gamma$-diversity referring to different levels in landscapes (Noss 1983) (Fig. 3.16) as first defined by Whittaker (1975), i.e. by taking the richness of species as given by the number of different species per minimum quadrat:
Fig. 3.15 Species/area curves for four tropical forests in Venezuela. A Cloud forest La Carbonera (minimal quadrat 2,500 m²); B moist trade-wind forest Rio Caura (minimal quadrat 1,100 m²); C and D cloud forest of Rancho Grande, C all species, D only trees with a stem diameter > 10 cm, for which the minimal quadrat has not been attained at 7,500 m². (After data of Vareschi 1980, from Lüttge 1995)

- at the level of communities or coenoses, α-diversity.
- at the level of ecosystems with different vegetation types, for example at ridges, on hillsides, in valleys etc., β-diversity.
- at the level of landscapes comprising several ecosystems, γ-diversity.

Another approach is the evaluation of diversity in the spatial structure of the physical environment in relation to environmental factors. Bell et al. (1993) have suggested the use of log–log regressions of environmental factors, such as edaphic variables, water chemistry and climate, vs distance over large spatial scales (10⁶ m). Plotting the log variance of environmental factors, e.g. the soil nitrogen, soil phosphorus etc., on log distance allows comparisons of both the heterogeneity of different environments with respect to that given factor and the different factors within a particular environment. With consideration of environmental factors, of course, ecophysiological aspects are introduced into the discussion of diversity. Varying ecophysiological behaviour of given genotypes is expressed as phenotypic plasticity. In the log–log analysis of regression of variance of environmental factors on distance by Bell et al. (1993) there was no indication that the variance of the physical environment tended to approach some maximal value as the distance increased. In contrast, it increased continuously with distance. Thus, the slopes of the log–log regressions provide a means to compare heterogeneity of environments and factors in relation to each other, i.e. slopes of the log–log regressions indicate the correlations of nearby sites between each other. Where nearby sites are highly correlated, selection will tend to favour specialization because dispersing offspring find conditions for growth similar to their parents. This leads to diversity of genotypes. On the other hand, where nearby sites show little correlation between each other, offspring tend to find conditions different to their parents. This favours plasticity.
3.3 Horizontal Structure and Diversity of Tropical Forests

Fig. 3.16 Floristic diversity related to species-area diagrams. (After Whitmore 1990, from Lüttge 1995). αβ... Species-poor community (low α-diversity) with low β-diversity, viz. few species, small minimal quadrat; αβ... species-poor community (low α-diversity) with high β-diversity, viz. few species, large minimal quadrat; αβ... species-rich community (high α-diversity) with low β-diversity, viz. many species, small minimal quadrat; αβ... species-rich community (high α-diversity) with high β-diversity, viz. many species, large minimal quadrat; γ... bi- (or multiphasic) curves indicating γ-diversity

3.3.2 Diversity and Plasticity and the Biological Stress Concept

Environmental factors direct us to the consideration of the role of stress, because any environmental factor can become a stress factor or stressor if its dosage is too high or too low. This is explained by the biological stress concept as described in Box 3.1. We may ask the questions as to how stress may be involved in regulating plasticity and diversity and whether in fact, plasticity and diversity are related.

In an experiment applying different degrees of stress to experimental microcosms, Grime et al. (1987) have demonstrated that high diversity is given only within a rather narrow range of stressed conditions. For conditions in the British Isles high species diversity occurred at stress intensities which allowed no less than 350 g m$^{-2}$ dry biomass, but no more than 750 g m$^{-2}$. At lower stress there is dominance of one or only a few robust and competitive species. At higher stress only a few highly adapted “specialists” survive as competition peaks in circumstances of abundance. In relation to plant nutrition, despite the abundance of resources available to vegetation established on fertile soil, plant growth results in the simultaneous development of depletion zones which creates circumstances of unequal access and traps subordinates in the depletion zones while supporting the monopoly by growth forms with the genetic potential for coarse-grained foraging (Campbell et al. 1991).
In a Malaysian rainforest it was shown that the species diversity of trees and vines strongly responded to combined phosphorus and potassium concentrations in the soil. Diversity was highest on soils with a medium P + K index, it declined towards both very poor soils and soils with more ample nutrient supply (Fig. 3.17). The relationship between diversity and environmental richness can also be demonstrated for tropical birds and mammals (Reichholf 1994).

**Box 3.1  The biological stress concept**

A good physical analogue for developing the terminology is a spring. **Stress** is put on the spring by **strain**. **Reversible stress** is brought about by strain in the elastic range of the spring material: **elastic strain**. **Irreversible stress** is due to strain beyond the elastic range of the spring material: **plastic strain**.

The biological stress concept was developed by Selye (1973), Levitt (1980) and Larcher (1987). Any external factor (biotic or abiotic) and internal factor can induce stress, i.e. become a **stressor**, if its dosage is too high or too low. The terminology of the biological stress concept is explained in the diagram giving four different possible cases for the development of a biological system with time (abscissa).

1. **Strong stress**

   Strong stress out of an **alarm phase** more or less rapidly leads into a phase of **exhaustion** followed by **acute damage** and death. The stress has negative effects, it is a **distress**.
Box 3.1  (Continued)

2. **Low stress followed by stress removal**
   Low stress leads into an alarm phase generating recovery mechanisms. In a recovery phase the system develops out of the conditions in which stress has negative effects, to conditions in which stress has positive effects and stimulates the system; stress is a eustress. The system stabilizes during a hardening phase and attains a resistance phase, in which it may remain, unless the degree of stress is changed or external or internal reserves required for resistance are exhausted. With respect to the latter, it is clear that time, i.e. the duration of stress application may be important. Upon stress removal the system enters a dehardening phase and returns to the normal level.

3. **Low stress followed by additional stress**
   The system first develops like that of case (2), but then additional stress is applied either by the original stress becoming stronger or by additional different stressor(s). The system now goes into the condition of distress, an exhaustion phase and chronic damage.

4. **Strong stress with acute damage followed by repair after stress removal**
   The system first develops like that of case (1), but then a stress-free period follows, and during a repair phase the system is restored and returns to the “normal” level.

(After Beck and Lüttge 1990.)

**Phenotypes** are the receivers and modulators of environmental input and producers of output performance at the community level. The development of phenotypes from genotypes is the real origin of complexity in biology (Schuster 1998; see also West-Eberhard 1986, 1989, 2003; Sultan and Bazzaz 1993; Solbrig 1994; Gehrig et al. 2001). Booth and Grime (2003) tried to test this using microcosms planted with different species, where each species was present in different microcosms at a different degree of genetic diversity. The genetic diversity was generated by planting mixtures of varying numbers of different clones of plants obtained from vegetative propagation. Stress was applied in the form of trampling and artificial grazing. In

![Figure 3.17](image.png)

**Fig. 3.17** Relationship between the diversity of trees and vines in a Malaysian rainforest (ordinate) and combined phosphorus and potassium concentrations in the soil ($P + N$ index on the abscissa). (After Tilman 1982)
this way it was attempted to relate genetic diversity to community diversity. Diversity declined in all of the microcosms, and there were no dramatic differences in the first 3 years of the 5 years experiment. However, in the last 2 years the decline of diversity was lower in the microcosms having the largest genetic diversity.

With regard to plasticity it appears that both high stress and low stress do not favour traits, which support such phenotypic variability. High stress favours specialized adaptations to the prevailing specific and strong stressor (e.g. frost near the poles or drought in deserts). Low stress allows the success of few species, which can competitively procure resources for development of their own biomass (e.g. nitrophilious plants in sites rich in nitrate and other nutrients). Only medium stress advances the unfolding of variability. Stress of medium intensity and high variability in time is typical for the environment of the tropical forests, where the important factors are:

- nutrients,
- water,
- CO₂,
- light,
- temperature.

None of these factors ever really becomes extreme, but their dynamic spatiotemporal variations and interactions cause stress in tropical forests and determine the struggle for existence between species (Richards 1996). This makes it important to study functional diversity and in this respect the observation of cross diversity by Guehl et al. (2004) is highly interesting. These authors have used the relation between $\delta^{13}$C-data and leaf conductance for water vapour, $g_{H₂O}$ (see Sect. 2.5) to assess water relations of functional types of rain forest trees, i.e. shade tolerant, hemi tolerant and heliophilic species. Differences in $\delta^{13}$C among species were primarily driven by $g_{H₂O}$, and there was some indication for the expected higher water use efficiency of heliophilic species. However, there was a non-linear pattern in the relations of $\delta^{13}$C and the gradient of shade tolerance and the results were not in full agreement with a simple concept of functional types, so that cross diversity among main functions or traits may reflect an important aspect in functional diversity.

Phenotypic plasticity must be considered in relation to co-occurrence of different genotypes within a population which are each adapted to a slightly different environment. Genetic variation is reflected in phenotypic plasticity (Booy et al. 2000). Plasticity itself can be considered as a trait, which is subject to selection (West-Eberhard 1986, 1989, 2003). However, plasticity per se is not adaptive. This much depends on the physiological costs of plasticity (van Kleunen and Fischer 2005). In any case, phenotypic plasticity offers material for selection, since selection is acting on the phenotypes. This is particularly important in systems, which are not strictly homeostatic (see Sect. 3.3.3), and where radiative movement of phenotypes followed by separation may be one of the bases for the development of genetic diversity (West-Eberhard 1986, 1989, 2003). Thus, the promotion of phenotypic plasticity by variable and medium stress may be one of the reasons for the extraordinarily high biodiversity of tropical forests (Lüttge 1995, 2005, 2007).
3.3.3 Diversity and the Chaos of Oscillating Mosaics

After assessing diversity and plasticity, this then leads us to the question: Is there homeostasis? The tropical rainforest is frequently considered to be a climax association. Ideally, climax associations are steady-states for vegetation, representing stable or homeostatic ecological equilibria, determined by the natural environmental factors in a given climatic zone. According to the climax theory (Clements 1936) independent of the starting conditions at a given location, progressive successions should always lead to the same final equilibrium or climax association. Only when there is an effect of external influences, such as natural or man-made catastrophes, are regressive successions elicited, which cause a deviation from the climax association. Of course, the latter involves changes of environmental conditions.

The question arises, however, as to whether the final steady state is really independent of the starting conditions. Can predictions be made? Is there only one possible final equilibrium? Or are there several different possible ecological states? Is it then possible that small initial deviations from the mean climatic conditions (e.g. mean annual precipitation and temperatures) might divert the development of succession towards very different end points?

In fact, the straightforward application of the climax theory to large ecosystems has been challenged by Remmert (1985, 1991), using the very example of the tropical rainforest. He strongly underlines the dynamic nature of rainforests (see also Whitmore 1990) and in his view the tropical rainforest is subject to a continuous cycle of series of successional states. It represents a diverse cyclically changing mosaic pattern (see also Watt 1947). This can be illustrated by considering the dynamics of gaps or chablis in the tropical rainforest (Orians 1982; van der Meer and Bongers 1996). In the original French meaning chablis are clearings in forests due to storms. In wet tropical forests tall falling trees with their large crowns cause two adjacent gaps, one beneath the original location of the crown and the other one at the site of impact on the ground (Fig. 3.18).

When this is set in the context of floristic diversity, destruction such as the formation of chablis, as well as the introduction of roads may increase diversity because $\beta$-diversity is introduced (Sect. 3.3.1). Gaps and chablis are reinvaded by vegetation, and with various successional stages the forest is restored (Fig. 3.19). Thus, such chablis are sites of destruction and renewal, which at any given time may comprise 3 – 10% of the total forest area (Jacobs 1988). Larger clearings also result from shifting agriculture (Fig. 3.20) and other human activities.

In the renewal of forest in natural clearings resulting from falling trees, hurricanes, earthquakes, volcanic eruptions, fires and landslides, or in farms abandoned due to exhaustion of nutrients or the take-over of weeds and pests there is no predetermined pattern. As Jacobs (1988) comments “... the selection is one of unpredictable irregularity". There is a plethora of environmental factors affecting regeneration and to which the unpredictability of proximal species regeneration will be related to. It depends among others on the extent of diversity in adjacent vegetation and the age of the surrounding communities, the light climate (Torquebiau 1988), the availability and viability of propagules, seed and seedling bank compo-
Fig. 3.18 A.B Formation of gaps or chablis by falling trees. Subsequently the crown gap fills more rapidly than the gap created by the impact. (After Jacobs 1988). C Fallen tree in a forest of Sierrania Páru, Venezuela
Fig. 3.19 Reinvasion of a chablis. (After Jacobs 1988)
Fig. 3.20  Slash and burn agriculture (see also Fig. 1.5)
sition (Dalling et al. 1998; Massey et al. 2006), dispersal limitation and dormancy parameters (Dalling et al. 1998), differences in growth and mortality rates among species with different carbon allocation patterns (Newell et al. 1993; Dalling et al. 1998), edaphic specialization and soil resources (Phillips et al. 2003; Palmiotto et al. 2004; Valencia et al. 2004). With such unpredictability we are not naturally facing a stochastic development of diversity. This would be an *a priori* unjustified simplification. However, we are right back in the realm of **non-linear dynamics and deterministic chaos** (Sect. 2.6; Solé et al. 1994; Solé and Manrubia 1995a,b; Manrubia and Solé 1996; Levin and Muller-Landau 2001), where we may recall one of the most characteristic implications of the chaos theory, namely that even the slightest differences in the starting conditions – or the many factors affecting gap dynamics – may lead to the most dramatic differences in subsequent development (see also Fig. 2.15C).

### 3.3.4 Diversity and Life Forms

Diversity is also given by the variability of life-forms. The life-form concept is defined rather loosely. Many attempts have been made to categorize the diversity of plant types by distinction of life forms which are morphologically more or less conspicuous. Life forms represent morphological adaptations to environments or towards a given stress factor or set of stress factors. An original example illustrating an approach to such a classification is RAUNKIAER’s crisp distinction of five life forms of vascular plants according to the life time of shoots and the position and protection of regenerating buds, namely:

- the **phanerophytes** with regenerative buds higher than 50 cm above ground,
- the **chamaephytes** with buds closer to the ground (10–50 cm above ground),
- the **hemicryptophytes** having a close contact of the buds with the ground,
- the **cryptophytes** with below ground regenerative organs (rhizomes, onions, bulbs, storage roots etc.),
- the **therophytes** or annuals.

These life forms are particularly conceived for analysis of vegetation in mesic and temperate climates as they describe strategies for over-wintering. However, they may also be used to describe adaptation to regular seasonal drought periods and, thus, are useful with respect to the tropical environments. Moreover, of course, the distinction between trees (macrophanerophytes), shrubs or bushes (microphanerophytes) and herbs of different forms inherent in these definitions is always applicable. However, this scheme is hardly sufficient to come to grasp of diversity in a tropical forest.

Vareschi (1980) has noted that as a basis for schemes defining different life forms, morphological modifications of any of the major plant organs could be chosen, e.g. life forms based on roots, shoots, leaves, flowers or propagules. Another approach would be to derive life forms which use morphological modifications at the whole
plant level with distinct mechanistic relations. Both shall be illustrated here by giving a few specific examples.

### 3.3.4.1 Root Categories

Root categories of trees frequent in tropical forests are stilt roots and buttress roots (Fig. 3.21). It has been debated whether such roots have mainly mechanical functions or serve aeration and O₂-supply to below ground root tissues. Presumably both are important. Buttress roots, in particular, may function like ropes with effective anchoring of the trunk to the ground (Mattheck 1992) and it was shown experimentally that they indeed have a clear anchorage function (Crook et al. 1997). In addition, the increase in above-ground root surface brought about by these root types may facilitate aeration. In wet tropical soils, where gas diffusion is limited and where vigorous soil-respiration will lower O₂-concentration, this may be a particularly important aspect. Indeed, immediately below ground the buttress roots show much branching and produce many fine absorptive roots, which can be supplied with O₂ via pores in the bark of the above ground buttress (Fig. 3.21E,F). Stilt roots also are often covered with lenticels facilitating gas exchange with the atmosphere (Fig. 3.21G,H).

### 3.3.4.2 Leaf Categories

The most variable plant organ in form is the leaf. Vareschi’s (1980) leaf analyses of plants in the cloud forest of Rancho Grande in Venezuela reveal more than 300 forms, most of which are reproduced in Fig. 3.22 for the sake of their graphic attractiveness. **Raunkiaer’s size classes of leaves** offer a more systematic approach, where leaves are distinguished by their area:

- **megaphyll** > 1,500 cm²
- **macrophyll** 1,500 – 180 cm²
- **mesophyll** 180 – 20 cm²
- **microphyll** 20 – 2 cm²
- **nanophyll** 2 – 0.2 cm²
- **leptophyll** < 0.2 cm²

Table 3.1 gives an idea of the percentage distribution of leaf sizes in a rainforest and an evergreen bushland. It shows that larger leaves predominate in the rainforest whilst smaller leaves are found in the bushland. Naturally, the leaf shape is an essential additional feature of diversity (Fig. 3.22). It is difficult, however, to delineate distinct categories, and without any mechanistic basis this approach may devalue the use of life form classifications. Vareschi (1980) lists about 18 leaf forms according to shape and special surface features, in addition to Raunkiaer’s size classes, and then derives a diversity coefficient, \( C_d \) as follows:

\[
C_d = n \cdot f,
\]  
(3.1)
3.3 Horizontal Structure and Diversity of Tropical Forests

Fig. 3.21A–H Root types of trees in tropical forests. Giant buttress roots in a rain forest in French Guyana (A,B). Buttressed tree in the cloud forest of Rancho Grande, northern coastal range of Venezuela (C). Stilt roots of Pandanus (D) in Queensland, Australia. Buttresses with absorptive roots in a rain forest in French Guyana (E,F). Palm in a forest of the Gran Sabana, Venezuela (G,H), with lenticels clearly seen in H.
Fig. 3.21 (Continued)
where $n$ is the number of species occurring and $f$ the number of leaf categories. The lowest possible value of $c_d$ is 1 (one species only occurring). In mesic environments with few species and low leaf form diversity it may be several tens or hundreds, whereas in tropical environments under favourable conditions it may reach up to 20,000.
Table 3.1 Percentage distribution of leaf sizes in an evergreen rainforest in Brazil and an evergreen bushland at Port Henderson Hill, Jamaica (Medina 1983)

<table>
<thead>
<tr>
<th></th>
<th>Rainforest macropanaphytes</th>
<th>Bushland micropanaphytes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of species</td>
<td>49</td>
<td>43</td>
</tr>
<tr>
<td>Macrophyll</td>
<td>2</td>
<td>–</td>
</tr>
<tr>
<td>Mesophyll</td>
<td>75</td>
<td>16</td>
</tr>
<tr>
<td>Microphyll</td>
<td>16</td>
<td>74</td>
</tr>
<tr>
<td>Nanophyll</td>
<td>2</td>
<td>7</td>
</tr>
<tr>
<td>Leptophyll</td>
<td>4</td>
<td>2</td>
</tr>
</tbody>
</table>

3.3.4.3 Stem Characteristics

Conspicuous life forms based on stem characteristics are the fleshy and woody stem succulents (Sects. 8.2.3.2.1 and 10.1.2.2, respectively) and the xylohemicryptophytes with their xylopodia or lignotubers (Sect. 10.1.2.2).

3.3.4.4 Whole Plant Modifications

Very typical special life forms of vascular plants in tropical forests are epiphytes, hemi-epiphytes and lianas to which a special chapter (Chap. 6) is devoted.

Another example are the myrmecophytes (ant plants). The symbiosis between plants and ants plays a particularly important role in the tropical environment. It is frequently found in epiphytes (see Sect. 6.6.3) but also in terrestrial plants, where the genera *Tococa* (Melastomataceae), *Cecropia* (Moraceae) and woody Leguminosae are the best known ant plants. In the Sira-mountains of Peruvian Amazonia, Morawetz and Wallnöfer (1992) counted that 4.4% of all species were genuine myrmecophytes. The ant plants prefer disturbed sites, which may be naturally due to land-slides; 86% of all genuine myrmecophytes (38 species) were found in such sites, while only 14% (6 species) regularly occurred in the primary forest.

The plants provide hollows, so-called *domatia*, where the ants find protected spaces for nests, e.g. in the inflated leaf bases of *Tococa* (Fig. 3.23A), the hollow stems of *Cecropia* (Fig. 3.23B) and thorns and leaf petioles of many Leguminosae (Caesalpiniaeae, Mimosaceae). In addition the ants may receive nutrition in the form of nectar from extra floral nectaries or various food bodies (Webber et al. 2006) and special nutritive appendices containing fat and oils, protein and carbohydrates, e.g. the *elaiosomes* (appendices of seeds) or the *Müller-bodies* of *Cecropia* which are made up of glycogen and not the usual plant-storage carbohydrate starch.

It is thought that in return the ants provide to the plants protection from phytophagous animals especially insects (Davidson and Epstein 1989; Duarte Rocha and Godoy Bergallo 1992). It has also been observed that ants keep their host plants free of epiphytes. A most astonishing story has been reported by Morawet et al. (1992). The *Myrmecochista* ants of *Tococa occidentalis* systematically and rapidly kill all angiosperms coming closer than 4 m to their host plants. *T. occidentalis* is
Fig. 3.23A, B Ant-nest plants. A Tococa sp. with ant nests in the inflated leaf bases (arrows). B Cecropia sp. with ant nests in the hollow stem

A light demanding species and its growth and proliferation is stimulated by the ants’ clearing of the surrounding competitors. Thus, after an initial *T. occidentalis*-plant has been colonized by the ants, pure *T. occidentalis* stands with a diameter of several
meters (10 – 30 m) may then develop, around which the ants even maintain a “safety corridor” (Fig. 3.24). Using their mandibles the ants cut the veins of the leaves of the competing plants. In the case of palmate leaves they attack the point at the base, where all veins join; pinnate venation is destroyed by cutting the first and second order veins at the base; the veins of monocotyledons (e.g. palms) are cut one by one along the entire leaves. After cutting the veins the ants inject a poisonous excretion from their abdomen. Apical meristems are also attacked. In this way the plants die rather rapidly. Although the ants can effectively kill 10 – 50 m tall trees, they do not usually attack such emergent trees at some distance of their host plants which may then form a closed canopy 10 – 25 m above the stand of *T. occidentalis*. As the light demanding *T. occidentalis*-plants die away back in the shade, the stand deteriorates and the ants emigrate to start a new cycle elsewhere.

### 3.4 Vertical Structure

Stratification, meaning the vertical structure of tropical forests, is directly linked to local action of specific environmental factors, such as light, temperature, humidity, CO₂ and minerals, the vertical distribution of which can be described. The vertical structure of tropical forests is determined by several more or less distinct and typical canopy layers. In simplified terms one may distinguish three major layers:

- a layer of emerging giant trees up to 60 – 80 m tall,
- an intermediate main canopy layer up to 24 – 26 m,
- a lower canopy layer,

(Whitmore 1990), as shown in the schematic transect of Fig. 3.25. More realistic transects of actual forests often show a larger complexity, and there is also much diversity of vertical structures among forest types.
The abundant plant life in these various strata determines vertical gradients of many important environmental factors such as:

- light intensity and spectral composition,
- temperature,
- air humidity,
- CO₂-concentration,
- mineral nutrients.

### 3.4.1 Irradiance

Due to absorption by the foliage intensity of irradiance may decrease exponentially from the main canopy layer down to the forest floor, which often obtains only a few per cent of the intensity received by the upper canopy or by a large forest clearing (Fig. 3.26). One consequence of such light gradients in tropical forests is that the maximum heights individual trees may reach are negatively correlated with shade tolerance and that there is a positive correlation of maximum height with light saturated rates of photosynthesis which are usually higher in sun plants (Sect. 4.1.1) (Davies et al. 1998).

Light-absorption by the canopy of forests may be treated according to Lambert–Beer’s law, which is well known from photometry. The ratio of the light intensity $I$
of a beam passing through a sample solution of a thickness $d$ and the light intensity of the incident light beam $I_0$ is given by

$$\frac{I}{I_0} = 10^{-\varepsilon dc}, \quad (3.2)$$

where $\varepsilon$ is the molar extinction coefficient and $c$ the concentration of the sample. In analogy, the situation for canopies may be written as

$$\frac{I_l}{I_0} = e^{-kLAI_0 - \varepsilon}. \quad (3.3)$$

Here $I_0$ is the light intensity outside the canopy and $I_l$ the intensity at level $l$, $LAI_0 - \varepsilon$ is the leaf area index between the top of the canopy, $o$, and level $l$, and $k$ is a constant. The leaf area index is dimensionless and is given by a projection of all foliage onto a certain level $l$ or onto the ground; it thus is the ratio of

$$[\text{total foliage area above a unit area at layer } l] : [\text{unit area}],$$

and a typical value for tropical rainforests is 8.

Light-absorption by the canopy not only reduces light intensity but also changes the light quality or spectral composition. In the red region of the spectrum absorption by photosynthetic pigments changes the red:far red ratio (R:FR) so that phytochrome regulated processes, which respond to this ratio are affected (Sect. 4.2.2). In a low-land rainforest in Costa Rica R:FR was found to be 1.23 in a large clearing but only 0.42 on the forest floor (Chazdon and Fetcher 1984) and in rain forests in French Guiana R:FR values of 0.10 to 0.15 were recorded (Bongers et al. 2001).

The degree to which the canopy is closed above the forest floor or leaves openings for light penetration can be determined by quantitative image analysis of photographs taken around noon with wide-angle or fish-eye lenses pointing upwards...
3.4 Vertical Structure

from the ground (Fig. 3.27). In addition to the diffuse light filtering through the canopy foliage, the forest floor may also obtain light in the form of **light flecks**. Light flecks occur when movements of leaves in the wind or the changing angle of the sun allow direct light penetration for intermittent periods of time. These light flecks may provide up to 80% of the total irradiation received by the forest floor, and their intensity ranges from 10 to 70% of full sunlight. They are important for photosynthetic productivity (see Sect. 4.2.1). Figure 3.28 shows that for short periods lower strata in tropical forests may obtain quite high irradiance, which may at times exceed that received by strata higher up. Thus, the gradual decline of irradiance from the top of the canopy to the ground shown in Fig. 3.26 does not always correspond to the actual situation.

**Fig. 3.27** Vertical fish-eye camera view from the floor to the canopy of a rain forest in Panamá. (Photograph Bettina Engelbrecht)

**Fig. 3.28** Daily course of irradiance at different strata of a wet tropical forest in northern Australia on an almost cloudless day; i.e. 36 m = above the canopy, 22 m and 10 m = increasingly lower levels inside the forest. (After Doley et al. 1987)
3.4.2 Temperature and Air Humidity

Diurnal variations of soil temperature and air temperature 1.5 m above the ground within a forest in Surinam in comparison to small and large clearings are shown in Fig. 3.29. There is strong dampening of daily changes of temperature inside the forest, where it remains much cooler than in the gaps and clearings.

Relative air humidity (RH) is related to temperature. Hence, the water-vapour pressure saturation deficit of the atmosphere at the top of the canopy and at various levels inside the forest shows a similar pattern (Fig. 3.30). It is close to zero at all levels at sunrise, shows a maximum at 14.00 h and decreases inside the forest from the higher to the lower strata. Since water-vapour pressure deficit of the atmosphere determines the driving force for transpiration, it constitutes a highly important ecophysiological factor. High RH also increases the CO₂-sensitivity of stomata and there is acclimation of stomatal responses which may play a role for photosynthesis in the lower strata of tropical forests (Talbott et al. 2003).

![Fig. 3.29A,B](image)

**Fig. 3.29A,B** Daily course of soil temperature at 2 cm depth (A) and air temperature 1.5 m above the floor (B) in a forest in Surinam. Comparisons between the closed forest and clearings are made for the hot and dry season. (After Jacobs 1988)

![Fig. 3.30](image)

**Fig. 3.30** Daily course of water-vapour pressure saturation deficit of the atmosphere at different strata of a forest in Surinam during the dry season; i.e. above the canopy and at increasingly lower levels inside the forest as indicated. (After Jacobs 1988)
3.4 Vertical Structure

3.4.3 Carbon Dioxide

Carbon-dioxide concentration in the atmosphere inside forests is influenced by photosynthesis and respiration of the organisms living in the forests including soil respiration (Buchmann et al. 1996). Daily averages of CO₂-concentration at the soil surface may be quite large, i.e. up to 1,000 ppm, due to the respiration of plant roots and soil organisms. One meter above the floor of two forests of the upper Rio Negro Basin in Venezuela, daily average CO₂-concentration was still 508 and 541 ppm respectively, and then showed little decline for up to 20 m (Medina et al. 1986). More detailed analyses of the diurnal and seasonal dynamics of the vertical profile of CO₂ concentration in a tropical rain forest are shown in Fig. 3.31A. Clearly at times plants within the canopy may photosynthesize at CO₂-concentrations well above

![Figure 3.31A–C](image)

**Fig. 3.31A–C** Vertical gradients of CO₂ and carbon isotope signatures. **A** CO₂ concentrations of the air at different levels above the soil surface in a tropical rain forest of French Guiana, where closed symbols are for the early morning and open symbols for midday, when the vegetation has already reduced the CO₂ levels by photosynthesis, and circles and triangles are for the wet and the dry season, respectively. **B** δ¹³C values of the air (symbols as for A). **C** Depletion of δ¹³C in the leaf biomass in three lowland tropical forests, where the open and closed symbols for French Guiana are for the dry and the wet season, respectively. The δ¹³C values of the leaves at the top of the vertical profile were taken as a reference (zero depletion) to calculate the intra-canopy depletion of δ¹³C with decreasing height above the ground. (Modified after Buchmann et al. 2004)
the average CO$_2$-concentration in the atmosphere outside the forests. It is seen in Fig. 3.31B,C that there are also vertical gradients of $\delta^{13}$C of the air and of the leaf biomass (Buchmann et al. 2004; see also Sect. 2.5).

### 3.4.4 Mineral Nutrients

#### 3.4.4.1 Inorganic Nutrient Cycling

When we consider inorganic nutrient cycling in tropical forests we must include, of course, the soil. It is frequently assumed that the major portion of minerals in wet tropical forests is bound in the living biomass. This is not always true and the soil may contain a considerable fraction of the minerals in the ecosystem. It is often the soil which is the most vulnerable part in tropical forests. Exposed by unbalanced logging systems or methods of shifting agriculture it may rapidly become oxidized and eroded. With vegetation and soil we obtain a conspicuous vertical structure (Figs. 3.32 and 3.33). Mineral nutrients show variability over the horizontal strata of forests, because interaction with leaves and stems causes precipitation to become enriched in nutrients and the throughfall of rain and the stemflow in the forests show much higher concentrations of most mineral ions than the rain water itself (Table 3.2).

An example of inorganic nutrient cycling in a wet tropical forest is given in Fig. 3.32. Input of minerals to the soil is via rain, canopy leaching with throughfall and stemflow (see also Table 3.2) and via litter fall (see also tables on page 232 and Fig. 10.2, page 277 in Richards 1996).

### Table 3.2 Mineral nutrients in rainwater, throughfall and stemflow. (A) Average nutrient concentration in rainwater and annual input in several tropical locations throughout the world. (Data from Medina and Cuevas 1994) (B) Values measured in a forest in Central-America. (Data from Junk and Furch 1985)

<table>
<thead>
<tr>
<th>Nutrient</th>
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<th>B</th>
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<tr>
<td></td>
<td>Nutrient concentration in rainwater (µmol/l)</td>
<td>Annual input via rainwater (mmol/m$^2$)</td>
</tr>
<tr>
<td></td>
<td>Rainwater</td>
<td>Throughfall</td>
</tr>
<tr>
<td>Na</td>
<td>n.d.</td>
<td>n.d.</td>
</tr>
<tr>
<td>K</td>
<td>1.0</td>
<td>20</td>
</tr>
<tr>
<td>Ca</td>
<td>11.1</td>
<td>200</td>
</tr>
<tr>
<td>Mg</td>
<td>8.2</td>
<td>152</td>
</tr>
<tr>
<td>NH$_4^+$-N</td>
<td>25.9</td>
<td>493</td>
</tr>
<tr>
<td>NO$_3^-$-N</td>
<td>9.3</td>
<td>196</td>
</tr>
<tr>
<td>PO$_4^-$-P</td>
<td>0.7</td>
<td>15</td>
</tr>
<tr>
<td>SO$_4^2-$-S</td>
<td>21.8</td>
<td>424</td>
</tr>
</tbody>
</table>
Tropical forests frequently have a nutrient limitation of some sort. Although the soil is often poor in mineralized nutrients the vegetation is luxuriant and so highly rich in species. As in savannas (Sect. 10.2.2), phosphorus is often the most problematic element. Mycorrhizal symbioses between plant roots and fungi are important (Medina and Cuevas 1994; Béreau et al. 2004) and there is feedback between the essential controlling steps of retranslocation and mineralization in tropical rain forest ecosystems dominated by ectomycorrhizal trees (Chuyong et al. 2000).
P/N-ratios in canopy leaves of tropical humid forests range from 15 to 35 (mol/mol) × 10³ (Medina and Cuevas 1994) similar to those in plants of savannas. Nitrogen cycles for a semideciduous forest are shown in Fig. 3.33. Nodulation and atmospheric dinitrogen fixation is nutrient limited in tropical forests (Souza Moreira et al. 1992). In a rainforest in French Guyana, however, 43% of the Leguminosae were fixing N₂, the contribution of N₂-fixation to their nitrogen nutrition averaged 54%, and overall the N₂-fixing species are important for the performance of the ecosystem increasing its nitrogen-biomass by 10% (Domenach et al. 2004). N₂-fixation capacity of the rain forest trees is controlled and

Fig. 3.33 Compartmentation and annual turnover of nitrogen in a semideciduous forest in Ghana. (From the Ecology of Neotropical Savannas by Guillermo Sarmiento. Copyright © 1984 by the President and Fellows of Harvard College. Reprinted by permission of Harvard University Press (Sarmiento 1984))
limited by low phosphorus and high nitrogen levels in the soil (Pons et al. 2007; Sect. 10.2.3.2.2).

Roots, which often form very dense mats, are mainly restricted to the upper 0.1 – 0.3 m of the soil, and frequently the soil layer itself on top of the bed rock is rather thin. **Soil respiration**, which is very high in wet tropical forests has a typical rate of 4 µmol CO₂ m⁻² s⁻¹ (Buchmann et al. 2004) and corresponds to 600 – 670 g organic matter m⁻² year⁻¹, of which 67 – 82% is due to respiration within root mats. **Rates of mineralization** of organic litter are high and **recirculation of minerals** is rapid. Phosphorus in the soils of humid tropical forests is correlated with the litter fall mass (Silver 1994). Rapid recirculation is important for avoiding nutrient leaching (Chuyong et al. 2000). Litter turnover may support seedling growth (Brearley et al. 2003) and is essential for the development of photosynthetic capacity (Santiago and Mulkey 2005).

**Ants** play a role in biomass turnover and mineralization. In myrmecophytes the ants may contribute to **nutrition** of their hosts (see Sect. 6.6.3). In *Tococa guianensis* it was observed that one of the two adjacent domatia at the base of each leaf (see Fig. 3.23A) is used for nesting and the other for dumping excrement and debris. By radioactive tracer studies the inner surface of the domatia has been shown to be absorptive of low molecular substrates like amino acids and phosphate, in contrast to the surfaces of the leaf lamina. Thus, it is highly likely that nutrients are absorbed from the rotting material in the trash-domatium (Nickol 1992). On the other hand, in contrast to other reports in the literature that in *Cecropia* (Fig. 3.23B) 93% of its nitrogen is supplied by ants, a recent study suggested that it is only ≤ 1% (Fischer et al. 2003).

**Leaf-cutter ants** (Fig. 3.34) are a special case. (In the following text I follow the monograph of Wirth et al. 2003.) Herbivory in general can enhance nutrient cycling by, e.g.

- enhancing the leaching rate of nutrients from foliage,
- increasing the rate of litter fall,
- stimulating nutrient cycling and turnover within plants,
- promoting activities of decomposer organisms.

### Table 3.3 Selection of some quantitative data on the activity of leaf-cutter ants, *Atta colombica*, extracted from Wirth et al. (2003) and Herz et al. (2006)

<table>
<thead>
<tr>
<th>Metric</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nest size (m²)</td>
<td>A few to about 100</td>
</tr>
<tr>
<td>Dry leaf mass collected (kg per year)</td>
<td>273 ± 161 (SD)</td>
</tr>
<tr>
<td>Average</td>
<td>85 – 470</td>
</tr>
<tr>
<td>Leaf area collected (m² per year)</td>
<td>2700</td>
</tr>
<tr>
<td>Average</td>
<td>835 – 4550</td>
</tr>
<tr>
<td>Leaf area (m²) collected per ground area (ha) per year</td>
<td>1217</td>
</tr>
<tr>
<td>Dry biomass (kg) collected per ground area (ha) per year</td>
<td>132</td>
</tr>
<tr>
<td>Foliage loss of host plants (%)</td>
<td>8 – 40</td>
</tr>
</tbody>
</table>
Leaf-cutter ants are a special case because they collect an enormous amount of plant biomass and carry it into complicated underground chamber systems where they cultivate fungi. Some quantitative data are compiled in Table 3.3. The loss of foliage by the host plants of up to 40% can reduce their fitness. However, there is also compensatory feedback. Leaf-cutter ants prefer to collect leaf pieces from the upper canopy. Partial defoliation causes an increase in the frequency and variability of light flecks and may result in higher rates of photosynthesis due to increased light penetration and incident irradiance on the remaining parts of tree crowns. Thus, herbivory by leaf-cutter ants appears to have little effect on whole forest canopy photosynthesis although it may considerably reduce photosynthesis locally. The effects on nutrient flow in the forests are patchy because the ants, *Atta colombica* as the species of the case study of Wirth et al. (2003), bury the nitrogen rich exhausted fungal substrate or refuse from their fungi gardens in large refuse chambers below the fungus chambers of their nests at a depth of 7 m below the surface and only partially on the soil surface. Only deep rooting trees may have access to the former but fine roots of nearby plants may penetrate the latter. The refuse is enriched in nitrogen because the ants prefer to collect the more N-rich young leaves and use more the carbon than the nitrogen. The carbon/nitrogen ratios are 22 in canopy foliage and 36 in normal leaf litter, 21 in the leaf harvest of the ants and only 16 in the refuse dump from the ant’s fungi gardens. In the study area of Wirth et al. (2003) on Barro Colorado Island, Panamá, in locations covering less than 0.5% of the area populated by leaf-cutting ants nitrogen flux is therefore about 20–30 times higher than in the rest of the forest. Hence, while a large scale benefit of plant nutrition from leaf-cutter ants is debatable local positive effects on plant growth and fitness are evident.
3.4.4.2 Nutrient Partitioning

Different partitioning of inorganic nitrogen assimilation between the roots and shoots of trees is observed in pioneer and mature phase trees of tropical forests. In gaps the mineralization of a large mass of fresh litter, e.g. from fallen trees, may lead to higher availability of NO$_3^-$-N (not NH$_4^+$-N) and PO$_4$-P (Denslow et al. 1998). Thus, rapidly growing pioneer or colonizing tree species, which are exposed to high irradiation, exhibit a large capacity to assimilate nitrate in their leaves, where light energy can be directly used in photosynthetic nitrate reduction (Aidar et al. 2003). Partitioning of NO$_3^-$-assimilation between roots and shoots is strongly related with average daily photosynthetically active radiation rather than the availability of NO$_3^-$ in the soil (Stewart et al. 1992). Leaves of shaded species have low levels of nitrate reductase and show little capacity to utilize nitrate, even when it was readily available, and primarily assimilate ammonia (Stewart et al. 1988, 1990; Fredeen et al. 1991; Fredeen and Field 1992; Denslow et al. 1998).

3.4.4.3 Flushing of New Leaves and Longevity of Mature Leaves Related to Nutrient Budgets

An interesting phenomenon, which may also be related to nutrient budgets is leaf flushing. New leaves and shoots expand from their buds very rapidly to attain a size close to that of mature leaves, much before they reach their final rigidity and pigmentation. In fact they hang down from the branches as if wilted, and often are coloured brightly yellow or red (Fig. 3.35). The development of chloroplasts and the photosynthetic apparatus is delayed which are both particularly nitrogen-demanding. This can be considered to be an adaptation to conditions of high fungal and herbivore damage to the expanding leaves. Damage may be 100 times higher to young than to mature leaves. Mature leaves are better protected (Kursar and Coley 1992a,b; Schlindwein et al. 2006). Costs of damage to the newly flushed leaves remains low since not so many resources have been invested in them. Resource allocation to leaves becomes beneficial when they mature and establish photosynthetic productivity in return. Delayed greening is observed in many species (Kursar and Coley 1992b; Miyazawa and Terashima 2001) and occurs mainly in shade tolerant species and not in gap-requiring species. In the shade a late development of photosynthesis is less disadvantageous than in high light (Kursar and Coley 1992b). It would be interesting to know if the bright colour of freshly flushed leaves even functions in attracting herbivores to these “cheap” leaves, thus protecting the “expensive” mature leaves. In a tropical dry-deciduous forest and a dry-thorn forest in India, phenological strategies have also been observed in relation to leaf flushing. Flushing occurs in the dry season and reaches a peak before the onset of the rains. Herbivorous insects emerge with the rains and attain a peak biomass during the wet months, so that early leaf flushing and maturation provides protection (Murali and Sukumar 1993).

Nutrient availability also affects the structure and longevity of leaves of forest trees. Leaf longevity may vary in different tropical forest tree species from about
18 months to several years (Richards 1996). It is highly plastic and can respond to light (Osada et al. 2001). Small leathery leaves ("scleromorphic microphylls") are developed on infertile soils due to N- but mainly P-deficiency (Medina and Cuevas 1989; Medina et al. 1990). Such leaves are more durable and better protected from herbivory (Choong et al. 1992) than large, thin leaves. Thus, nutrient investment in leaf structure provides a return in the form of photosynthetic products for a longer period of time. Deciduous and evergreen species coexist in tropical dry forests. They differ greatly in their investments of resources for leaf construction and maintenance. In deciduous species, with roots occurring under relatively nutrient-rich conditions, leaves can have a potentially high nitrogen-use efficiency (CO$_2$-assimilation related to leaf N-content; see Sect. 4.1.2). Conversely, in evergreen species with lower nitrogen-use efficiency, the long residence time of nitrogen is favourable because roots occur in nutrient-poor soil microhabitats (Sobrado 1991). Both deciduous and evergreen species preserve nitrogen resources. Reserves of nitrogen are maintained in the twigs in drought-deciduous species and in the older leaves in evergreen species, providing some nitrogen for the reconstruction of new leaves following drought and during leaf exchange respectively (Sobrado 1995). In conclusion, plant species obviously allocate resources either to obtain a high photosynthetic assimilation rate from large and fragile leaves for a brief time or to provide a resistant physical structure which results in a lower rate of CO$_2$ assimilation over a longer time (Reich et al. 1991). Thus, mineral nutrition influences the lifespan of leaves.

Fig. 3.35A,B Leaf-flushing. A in a mango tree, B in Brownea sp.
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Simone O de, Müller E, Junk WJ, Richau K, Schmidt W (2003b) Iron distribution in three central Amazon tree species from white water-inundation areas (várza) subjected to different iron regimes. Trees 17:535–541


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Chapter 4
Tropical Forests.
II. Ecophysiological Responses to Light

4.1 Light Responses of Photosynthesis

Although gradients of several different environmental factors are noticeable in tropical forests (Sect. 3.4), intensity of irradiance is most highly variable and appears to play the most prominent role in determining the ecophysiological comportment of forest plants. At the top of the canopy and in larger clearings in full sun-light intensity of photosynthetically active radiation (PAR) at 400 – 700 nm wavelength may range from well above 1,000 up to 2,500 µmol m$^{-2}$ s$^{-1}$ photons. On the forest floor there may be less 5 µmol m$^{-2}$ s$^{-1}$ photons (see Figs. 3.26 and 3.28). Thus, light can become a stress factor from both too much (when it causes overenergization of the photosynthetic apparatus and hence photoinhibition or even photodestruction), or too little (when it becomes limiting as an energy source of photosynthesis). Focussing of light by leaf epidermal cells may increase irradiance intensity in the mesophyll of under story plants of tropical forests (Vogelmann et al. 1996). However, the major responses are those of the photosynthetic machinery.

4.1.1 Light-Response Characteristics of Sun and Shade Plants

The photosynthetic utilization of light by plants is described quantitatively by light-response curves (Fig. 4.1), which are distinguished by several cardinal points as follows (see also Box 4.1). In darkness (zero PAR), there is net-CO$_2$ release due to respiration. As light intensity increases, net-CO$_2$ release is gradually reduced until the light-compensation point is attained, where net-CO$_2$ exchange is zero because photosynthetic CO$_2$-uptake just balances respiratory CO$_2$-release. Above this point, net-CO$_2$ uptake increases until light saturation is reached. The light-saturation point often is hard to determine precisely, because light saturation is approached gradually. Hence, half saturation of photosynthesis is often quoted alternatively or additionally. The slope of the nearly linear part of the curve below saturation gives the apparent quantum yield (mol CO$_2$ per mol photons) of photosynthesis.
Plants may be genetically determined for growth at low or high light intensity. In this case we can distinguish genuine shade and sun species. However, there are also ontogenetic and developmental modifications, where light exerts a signalling function rather than being only the energy source of photosynthesis, and plants may acclimate or adapt ecophysiology to low and high irradiance, respectively (see Sect. 4.3.2). The potential for light acclimation is species specific and may involve major structural and functional changes in the photosynthetic apparatus (Bailey et al. 2001). Thus, there may be shade and sun forms of given species. Plants surviving in
Box 4.1 Light-response characteristics

- **Light-response curves and their cardinal points**

- **Distinctive characters of sun and shade plants**

<table>
<thead>
<tr>
<th></th>
<th>Shade plants</th>
<th>Sun plants</th>
</tr>
</thead>
<tbody>
<tr>
<td>Respiration</td>
<td>Low</td>
<td>High</td>
</tr>
<tr>
<td>Light compensation point</td>
<td>Low</td>
<td>High</td>
</tr>
<tr>
<td>Half saturation point</td>
<td>Low</td>
<td>High</td>
</tr>
<tr>
<td>Light saturation point</td>
<td>Low</td>
<td>High</td>
</tr>
<tr>
<td>Maximum rate of photosynthesis</td>
<td>Low</td>
<td>High</td>
</tr>
<tr>
<td>Quantum yield</td>
<td>High</td>
<td>Low</td>
</tr>
</tbody>
</table>

the understory or below canopy of tropical rainforests may experience opening and closure of the canopy several times during their lifetime. Understory species of *Miconia* (Melastomataceae) responded to canopy openings by production of new sun-leaves rather than acclimation of old shade-leaves, which could significantly increase maximum assimilation rates (Newell et al. 1993). Individual plants may also have both shade- and sun-leaves when part of the foliage is shaded and exposed respectively. Then we may define such plants as shade or light tolerant, but not shade or light demanding.

All of these various aspects are very important for plant life in tropical forests with their highly variable light climates. Comparisons of light response curves and their cardinal points provide distinctive characters for shade and sun species or phenotypes (Box 4.1). Shade plants usually have lower rates of respiration but the activity of the alternative cyanide resistant pathway of mitochondrial electron transport not producing ATP is low and therefore the ATP/O₂ efficiency of respiration is higher than in sun plants as required due the lower overall energy input at low irra-
diance in the shade (Noguchi et al. 2001b). Shade plants have lower rates of photosynthesis at light saturation and together with the lower rates of respiration this leads to lower light compensation and light saturation points, but higher quantum yields than in high light or sun plants. In Fig. 4.1 this is illustrated by the comparison of sun and shade plants (Fig. 4.1A) and pioneer, climax and understory trees and shrubs (Fig. 4.1B).

The different light-use characteristics of sun and shade plants are very important for understanding the distinct stages in the dynamics of tropical forests (Sects. 3.3.3 and 4.3.2). They distinguish pioneer species from climax species, and from plants of the under-growth. During growth (Sect. 4.3.2), pioneer species show the characteristics of sun plants, understory species that of shade plants (Eschenbach et al. 1998), and the dominant trees of later successions (climax species) show an intermediate behaviour as they may be extremely sun exposed in the upper canopy and shaded in the lower canopy layer (Fig. 4.1B, Tables 4.1 and 4.2). Thus, the pioneer species Cecropia peltata needs much higher light intensities for light saturation of photosynthesis and has much higher rates of maximum photosynthesis than the shade plant Croton glabellus, and a comparison of the light-response curves of dominant climax trees in the upper canopy, i.e. Cordia alliodora and Goethalsia meiantha, with

Table 4.1 Values for cardinal-points of light-response curves of sun and shade plants in general and of plants in tropical forests. (After Lüttge 1985)

<table>
<thead>
<tr>
<th>Plant type</th>
<th>Light-compensation point (µmol photons m(^{-2}) s(^{-1}))</th>
<th>Light saturation of CO(_2)-uptake (µmol photons m(^{-2}) s(^{-1}))</th>
<th>Rate of CO(_2)-uptake at light saturation (µmol m(^{-2}) s(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sun plants</td>
<td>20 – 30</td>
<td>400 – 600</td>
<td>10 – 20</td>
</tr>
<tr>
<td>Shade plants</td>
<td>0.5 – 10</td>
<td>60 – 200</td>
<td>1 – 3</td>
</tr>
<tr>
<td>Tropical rainforest</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Upper canopy</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sun types</td>
<td>12</td>
<td>250 – 370</td>
<td>13 – 19</td>
</tr>
<tr>
<td>Shade types</td>
<td>6 – 12</td>
<td>125 – 185</td>
<td>6 – 10</td>
</tr>
<tr>
<td>Lower canopy</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shade types</td>
<td>6 – 12</td>
<td>125</td>
<td>4 – 5</td>
</tr>
<tr>
<td>Herbs</td>
<td>2.6 – 6</td>
<td>25 – 37</td>
<td>1.3 – 1.9</td>
</tr>
</tbody>
</table>

Table 4.2 Maximum rates of photosynthesis of plants in various stages of succession dynamics, and daily rates of photosynthesis in various strata, of an Australian rainforest (Doley et al. 1988)

| Species of early stages of forest successions | 15   |
| Tree species of later stages of forest successions | 4 – 15 |
| Undergrowth species                          | 1 – 3 |

<table>
<thead>
<tr>
<th>Daily rates (mmol CO(_2) m(^{-2}) day(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaves of upper canopy level</td>
</tr>
<tr>
<td>Leaves at the fringe of a large clearing</td>
</tr>
<tr>
<td>Leaves of the undergrowth</td>
</tr>
</tbody>
</table>
4.1 Light Responses of Photosynthesis

Fig. 4.2 Leaf-internal CO₂-partial pressures ($p_{iCO_2}$) and CO₂-assimilation ($A$) to leaf conductance to water vapour ($g_{H2O}$) ratios of five tropical rainforest tree species in artificial stands under common conditions in French Guiana. *Closed circles*: Pioneer species (*Jacaranda copaia, Goupia glabra, Carapa guianensis*); *open circles*: late successional species (*Dicorynia guianensis, Eperna falcata*). (After data of Huc et al. 1994)

that of the understory shrub *C. glabellus* in Fig. 4.1B shows the distinct differences between sun and shade plants with respect to all the features listed in Box 4.1.

Pioneer and late successional rainforest species also regulate their leaf gas exchange in different ways. Shade plants have lower leaf conductance to water vapour, $g_{H2O}$, than sun plants which leads to lower gas exchange and growth (Bonal et al. 2000; Sack et al. 2005). Thus, pioneer species operate at lower $A/g_{H2O}$ ratios (CO₂-assimilation $A$), i.e. with a greater stomatal aperture and higher internal CO₂-partial pressures ($p_{iCO_2}$) as compared to trees found in the later stages of succession (Huc et al. 1994; Fig. 4.2).

4.1.2 The Photosynthetic Apparatus: Pigments, Enzymes and Nitrogen

It is very often observed in the tropics, that individual plants of a given species growing in deep shade inside a forest and exposed to full sun-light in an open habitat respectively, form morphologically very different phenotypes, which are also strongly distinguished by pigmentation. For example, this is frequently found among rosettes of bromeliads, e.g. in the genera *Bromelia* and *Ananas* which belong to genetically identical clones propagating vegetatively by formation of ramets. In *Bromelia humilis* shade plants are much larger than sun plants; they have long and slender leaves, whereas sun plants overall have a more stunted appearance (Fig. 4.3). The most conspicuous difference is leaf colour, which is dark green in the shade plants, brightly yellow in the sun plants and light green in intermediate forms.

What is behind this pronounced difference in pigmentation? Addressing this question requires a reminder of the basic structure of the photosynthetic apparatus situated in the thylakoid membranes of the chloroplasts (Box 4.2). The major
Fig. 4.3 Phenotypes of *Bromelia humilis*, from left to right yellow/exposed form, intermediate light green/exposed form and dark green/shaded form

**Box 4.2 Structure and function of the photosynthetic apparatus**

A. Scheme of a chloroplast with outer membrane (envelope), inner membrane, the stroma (= plastoplasm or “cytoplasm” of the chloroplast), stromal and granal thylakoids and thylakoid interior.
There are four important integral proteins or protein complexes in the thylakoid membrane:

- **Photosystem II** (PS II) with antenna and reaction-centre pigments; it occurs only in the appressed regions of granal thylakoids.
- The **cytochrome b6,f-complex**.
- **Photosystem I** (PS I) with antenna and reaction-centre pigments; it occurs in the stroma thylakoids.
- The **NADP-reductase** (NADP = nicotinamide-adenine-dinucleotide-phosphate).
- The **F_{0}F_{1}-ATPase** or coupling factor.

When PS II and PS I are excited by the absorption of photons (hv), H$_{2}$O is split into oxygen, protons and electrons (e$^{-}$), electrons flow from PS II via membrane-bound plastoquinone (Q) and mobile plastoquinone (PQ) to the **cytochrome-b6,f-complex** and plastocyanine (PCy) at the lumen side of the membrane, and from PCy further to PS I, ferredoxin at the stroma side of the membrane and to the **NADP-reductase**, which finally generates the reducing equivalents needed for CO$_{2}$ reduction. If they are not utilized in CO$_{2}$ reduction, the systems of this electron-transport chain may become overreduced, and damage may result if the excitation energy cannot be dissipated in other ways.

Electron transport is associated with charge separation and simultaneously leads to establishment of a **proton-electrochemical gradient** across the thylakoid membranes between the lumen (∼pH 5) and the stroma (∼pH 8). This is the driving force for the movement of protons through the **ATPase** which is coupled to ATP synthesis providing the energy needed for CO$_{2}$ assimilation.
It is sufficient that one of the antenna pigments absorbs a photon ($h\nu$) and is excited. Transfer of the excitation energy between antenna pigments always eventually leads to excitation of the reaction center. The larger the light trap the more probable is excitation of the reaction centre.

components are the pigments of the two photosystems (photosystem I and II), the thylakoid proteins embedded in the membrane lipid-bilayer and the cofactors of the photosynthetic electron-transport chain. Pigments are the chlorophyll $a$ of the light harvesting complex (light trap) and accessory antenna pigments such as chlorophyll $b$, carotenoids and xanthophylls. Thylakoid-proteins are the various elements of the electron-transport chain (redox-chain), the ATP-generating coupling factor ($F_0F_1$-ATPase) and chlorophyll-protein light harvesting complexes.

Since proteins as well as chlorophyll and cytochrome molecules contain much **nitrogen**, this element plays a prominent role in constructing the photosynthetic apparatus in the thylakoids. Given that the components of the photosynthetic apparatus acclimate to changing light climate then nitrogen supply is important for these processes. Thus, it is appropriate to determine the **N-costs of thylakoid membranes**, which can be expressed in units of mol N:mol chlorophyll. For example, in *Alocasia macrorrhiza*, a shade tolerant species native to tropical rainforest understories in Australia, this was 45 mol N/mol chl under natural shade, and 56 mol N/mol chl in *Pisum sativum* grown at high irradiance (Evans 1988). A general comparison of shade plants and sun plants reveals a number of characteristics, as follows:
D. Photosynthetic Pigments

Chlorophyll a

\[
\begin{align*}
\text{Phytyl-residue:} & \quad \text{a hydrophobic tail} \\
\text{System of} & \quad \text{conjugated} \\
\text{double bonds} & \quad \text{in Chl b}
\end{align*}
\]
The reaction-centre pigment chlorophyll $a$ and antenna pigments chlorophyll $b$ and carotenoids. The essential feature of the light absorbing pigments are systems of conjugated double bonds.

(Schemes after Lüttge et al. 2005)

- **Shade plants contain more chlorophyll $b$ or have smaller chlorophyll $a:b$ ratios.**

The larger relative amount of antenna pigments assures that low photosynthetically active photon flux densities (PPFDs) or light intensities are used efficiently, i.e. at low flux densities photons are absorbed effectively and the excitation energy can be transferred to the light trap reaction center chlorophyll (Box 4.2C). This explains
the higher quantum yield of shade plants (Sect. 4.1.1, Fig. 4.1, Box 4.1). At a given nitrogen availability chlorophyll \( a : b \) ratios increase with increasing irradiance (Kitajima and Hogan 2003).

- **Shade plants have lower rates of electron flow along the redox-chain in the thylakoids related to chlorophyll.**

This is a consequence of the larger chlorophyll content of the photosystems.

- **Shade plants have less soluble protein in relation to chlorophyll but shade plants have larger total N-contents in their biomass.**

The soluble proteins of leaves include ribulose-bis-phosphate carboxylase/oxygenase (RuBISCO, see also below or RuBPC in Sect. 2.5). This enzyme-protein is responsible for photosynthetic CO\(_2\)-fixation. It is the single major protein and hence N-containing compound in plant leaves. The lower protein/chlorophyll ratio in shade plants is due to the higher chlorophyll content and lower content of RuBISCO. However, generally shade plants have larger total N-contents in their biomass, and chlorophyll \( a : b \) ratios increase with decreasing N-availability especially under high irradiance conditions (Kitajima and Hogan 2003). An over production of RuBISCO may occur for an N-reserve and then there is a weak correlation of N-contents and RuBISCO and maximal rate of photosynthesis (Warren et al. 2000).

- **Shade plants have larger photosystem II/photosystem I ratios.**

This is related to the change of the spectral composition of light passing through the canopy, where the shorter-wave length red-light is filtered out to a larger extent than the longer-wave length red-light (see Sect. 4.2). The chlorophyll of photosystem II (PS II) is excited by somewhat shorter wavelengths (P-680 for absorption at \( \lambda = 680 \) nm) than that of photosystem I (PS I; P-700). Since both photosystems must co-operate in photosynthesis, shade plants need more PS II in relation to PS I.

- **Shade plants have larger chloroplasts and more grana formation.**

Experiments to elucidate these relationships have often been made with tropical plants, since the contrast between deep shade in the dark rainforests and full sun exposure in clearings and open habitats with small solar inclination throughout the year is more pronounced in the tropical environment. Figure 4.4 shows the results of a study, where *Alocasia macrorrhiza*, which has a large capacity for photosynthetic acclimation to different light environments, was adapted to various light intensities during growth, i.e. from very low PPFDs up to 800 \( \mu \text{mol m}^{-2} \text{s}^{-1} \). The photosynthetic capacity, the activity of RuBISCO, the content of cytochrome \( f \) – an important element of the photosynthetic electron-transport chain (Box 4.2) – and the chlorophyll \( a:b \) ratio increased considerably with light acclimation. The amount of trap chlorophyll of PS I showed no change, but PS II increased slightly at high growth irradiance up to 800 \( \mu \text{mol m}^{-2} \text{s}^{-1} \). Thus, in this particular experiment a considerably larger PS II/PS I ratio was not seen in the shade grown plants. Total chlorophyll content decreased. There was a small decrease of quantum yield. It may be noted additionally, however, that a cost-benefit study which includes modelling and simulation suggests that shade leaves not necessarily have a lower photosynthetic capacity.
than sun leaves when leaf mass rather than area (as in Fig. 4.4) is used as a basis, although the higher investment in CO₂-fixation-cycle enzymes and electron-transport carriers per unit of leaf surface in shade plants remains evident (Sims and Pearcy 1994; Sims et al. 1994). Thus, by and large the differences between low- and high-light grown *Alocasia* plants are in conformity with the general distinctions between shade and sun plants made above, despite the general observation that *A. macrorrhiza* is a typical understory rainforest plant in Australia, and still more pronounced effects may be observed with plants showing a greater phenotypic plasticity at still higher irradiance.

A study with the low and high-light grown phenotypes of *Bromelia humilis* (see Fig. 4.3) also corroborates these basic relationships, and emphasizes the modulation by nitrogen nutrition (Fetene et al. 1990; Table 4.3). In the low-light plants,

---

**Fig. 4.4** Components and photosynthetic functions of leaves of the tropical understory plant *Alocasia macrorrhiza* grown under varying light intensities up to 800 μmol m⁻² s⁻¹ photons (λ = 400 – 700 nm). (After Chow et al. 1988; see Anderson and Thomson 1989)
Light responses of photosynthesis

Table 4.3 Effects of light intensity and nitrogen on photosynthesis and leaf parameters of *Bromelia humilis* (Fetene et al. 1990)

<table>
<thead>
<tr>
<th>Irradiance during growth [µ mol photons m(^{-2}) s(^{-1})]</th>
<th>High (700 – 800)</th>
<th>Low (20 – 30)</th>
</tr>
</thead>
<tbody>
<tr>
<td>+N Light-saturated rate of photosynthesis (µ mol O(_2) m(^{-2}) s(^{-1}))</td>
<td>14.0 ± 3.5</td>
<td>8.3 ± 2.0</td>
</tr>
<tr>
<td>−N Light-saturated rate of photosynthesis (µ mol O(_2) m(^{-2}) s(^{-1}))</td>
<td>16.7 ± 2.6</td>
<td>6.9 ± 2.5</td>
</tr>
<tr>
<td>Apparent quantum yield (mol O(_2) mol(^{-1}) photons)</td>
<td>0.077 ± 0.010</td>
<td>0.042 ± 0.002</td>
</tr>
<tr>
<td>+N Light compensation point (µ mol photons m(^{-2}) s(^{-1}))</td>
<td>0.085 ± 0.015</td>
<td>0.041 ± 0.003</td>
</tr>
<tr>
<td>−N Light compensation point (µ mol photons m(^{-2}) s(^{-1}))</td>
<td>25 ± 4</td>
<td>40 ± 5</td>
</tr>
<tr>
<td>Total chlorophyll (µ g g(^{-1}) FW)</td>
<td>99 ± 10</td>
<td>725 ± 19</td>
</tr>
<tr>
<td>Chlorophyll a/b ratio</td>
<td>2.61</td>
<td>2.83</td>
</tr>
<tr>
<td>Nitrogen-use efficiency at light saturation of photosynthesis (mol CO(_2) mol(^{-1}) leaf N)</td>
<td>2.35</td>
<td>2.32</td>
</tr>
</tbody>
</table>

Chlorophyll levels were high as compared to the high-light plants and increased by additional N-nutrition. The chlorophyll \(a : b\) ratio was higher in the high-light plants. The different construction of the photosynthetic apparatus was reflected in a development of the typical cytological structure of sun- and shade-plant chloroplasts, respectively (Fig. 4.5). Low-light grown plants developed characteristically large, globular, shade-acclimated chloroplasts, with extensive grana-formation and hence appressed thylakoid membranes (Box 4.2). The number of thylakoid membranes per granum was threefold larger in low-light than in high-light grown plants, and the ratio of appressed to non-appressed thylakoid membranes was 3.5 – 5.0 and 1.0 – 1.5 respectively. Chloroplasts of high-light plants grown without N had only poorly developed thylakoids. Light compensation points were higher in the high-light plants of *B. humilis* (Table 4.3). It was most noteworthy, however, that with extra N-nutrition the low-light plants could attain similar light saturated rates of photosynthesis as the high-light plants and that the high-light plants almost reached the apparent quantum yield of the low light plants. Expressed on a leaf-nitrogen basis net photosynthetic CO\(_2\)-fixation was similar in low and high-light grown plants independent of whether additional N as supplied. This demonstrates the optimisation of nitrogen use, but it also suggests an interaction with other factors, since the ratio of net-CO\(_2\)-fixation to nitrogen levels was not constant but rather low at low N-levels and higher at high N-levels.

Maximum assimilation rates related to nitrogen levels of leaves give the nitrogen-use-efficiency (NUE), which is an important parameter relating the functioning of the photosynthetic apparatus to mineral nutrition. In general, assimilation vs leaf-nitrogen curves are linear over certain ranges of N-levels (Fig. 4.6; Nielsen et al. 1997). Often they do not appear to extrapolate to the origin, and thus, show reduced NUE at low N-levels. At higher N-levels there may be N-saturation of assimilation (see *Diplacus* in Fig. 4.6B). Therefore, Evans (1988) has evaluated the general
N-relationships of sun and shade plants somewhat critically. While a correlation between assimilation and N-levels is clearly given, other factors like characteristics of individual species (Fig. 4.6) and growth conditions must also be involved. This may include irradiance during growth since with spinach and peas (unlike in the experiment of Table 4.3), there was an effect of light intensity on NUE.

**Fig. 4.5A–D** Chloroplast ultrastructure of *Bromelia humilis* grown in low light with N (A) or without N (B) and in high light with N (C) or without N (D). (Fetene et al. 1990)
Reich et al. (1994) have presented a detailed investigation of these relations performed in two open and disturbed sites and three late successional forest types in the Amazon basin, which differed in light climate and nutritional status (Fig. 4.7). Photosynthesis-N relations are steepest and intercepts on the $x$-axis (N-levels) are highest in the disturbed open habitats with high resource acquisition and rapid plant growth (lines a and b in Fig. 4.7A,B), which also have the highest rates of photosynthesis (sun plants). Among the other sites, under N-limitation curves were steeper (lines d and e in Fig. 4.7A) than when P plus Ca were more deficient (line c in Fig. 4.7A). This was somewhat less clearly seen, when leaf N was expressed on a leaf area basis (Fig. 4.7B) as compared to the leaf mass basis (Fig. 4.7A), so that besides species and site characteristics a certain effect of the basis of data expression, i.e. mass or leaf area is also noted.
4.1.3 The Origin of High-Irradiance Stress and General Plant Responses

The biological stress concept has shown us that stress can result from low or high dosage of any particular environmental factor (Box 3.1). In sun plants increased chlorophyll $a/b$ ratios and a comparatively small size of chlorophyll $a$ and $b$ binding antennae (Sect. 4.1.2) contribute to protection from too high irradiance (Krause et al. 2001). Conversely shade plants, or phenotypes considered in Sects. 4.1.1 and 4.1.2, are adapted to low irradiance stress typical of the interior of dense forests. Stress by high irradiance might generally appear to be more characteristic of open habitats like savannas. However, it is also found in deciduous and semi-deciduous dry forests and in the upper canopy of wet forests. Moreover, in view of the very high
light intensities of some light flecks (Sect. 4.2.1), it may even be a particular problem for the shade-adapted plants in the understory of moist forests. Finally, shade plants of the forest floor may be suddenly exposed to high irradiance when gaps are created by falling trees. Hence, it is necessary to address of how plants avoid damage from excess irradiation. Strategies of avoidance include vertical leaf angles and small lamina areas (He et al. 1996) and chloroplast movements (Augustynowicz and Gabryś 1999; Gorton et al. 1999).

With respect to excess absorbed irradiance first it is necessary to recall the various states of excitation and relaxation of chlorophyll in the photosystems (Box 4.3). Excitation to the 2nd singlet level follows absorption of photons of blue light, while red light causes excitation to the 1st singlet level. Relaxation from the 2nd singlet state occurs by emission of heat, while there are several ways of relaxation from the 1st singlet state to the ground level. The normal means of energy dissipation in photosynthesis is photochemical work (Box 4.3), i.e. the eventual reduction of CO₂ fixed via RuBISCO. This, however, under certain circumstances may become a limiting process, e.g. due to:

- low intercellular CO₂-concentrations in leaves due to high CO₂-fixation rates following over saturation of the photosynthetic apparatus by PPFD,
- closure of stomata to reduce transpirational loss of water in response to high irradiance and heat with the concomitant consequence of low intercellular CO₂-concentrations,
- general over excitation of the photosynthetic apparatus and over reduction of the redox-elements of the photosynthetic electron-transport chain (see Box 4.2).

**Box 4.3 Light absorption, chlorophyll excitation and relaxation**

A. Absorption spectra of the reaction-centre pigment chlorophyll a and the antenna pigments chlorophyll b and carotenoids (see Box 4.2).
Box 4.3 (Continued)

B. Ground state and excitation states with substates (*horizontal lines*) and relaxation of chlorophyll:

Absorption of the more energy-rich blue-light quanta (shorter wave-lengths) leads to the **second and third excited singlet state** (half-life $10^{-14} - 10^{-15}$ s). Absorption of the less energy-rich red-light quanta (longer wavelengths) leads to the **first excited singlet state** (half-life $10^{-9} - 10^{-11}$ s). Relaxation can occur by transition between systems, and energy is dissipated as **heat**. Transition from the first singlet state to the **triplet state** (half-life $10^{-4} - 10^{-2}$ s) is only probable when the whole system is overexcited. Relaxation from the first singlet state to the ground state in addition to energy dissipation as heat can occur by emission of light as **fluorescence**. Relaxation from the triplet state to the ground state is possible by the emission of light as **phosphorescence**. Energy transfer from the first singlet state and the triplet state can lead to **photochemical work**, i.e. CO₂-assimilation or photorespiration in the case of the first singlet state and formation of oxygen radicals and **photodamage** in the case of the triplet state.

Overall there is a set of several means of dissipating excitation of chlorophyll *a* in photosystem II (see Boxes 4.3 and 4.4):

- PS II **photochemistry**, due to CO₂ or O₂ binding,
- relaxation by emission as **heat** (Sect. 4.1.4),
- relaxation by emission as **fluorescence** (Sect. 4.1.7),
- relaxation by **energy transfer** to photosystem I,
- transfer of excitation from the 1st singlet state to the **triplet state**, which is correlated with a change of electron spin from antiparallel to parallel.

One valve for dissipation of surplus energy is photochemical work. Increased contents of electron-transfer-chain components and RuBISCO are, of course, protec-
4.1 Light Responses of Photosynthesis

tive (Ramalho et al. 1999). A photochemical work different from CO₂ assimilation is **photorespiration**. This is possible, since RuBISCO (ribulosebisphosphate carboxylase/oxygenase) not only reacts with CO₂ but also with O₂ and can oxygenate ribulosebisphosphate to form phosphoglycolate, which is metabolized in the photorespiratory reaction cycle. However, this still may be of limited capacity to avoid adverse effects of overenergization, which leads to **photoinhibition**. The primary site of photoinhibition is photosystem II. It can be protected by energy dissipation as heat which is correlated with chlorophyll fluorescence. These are important functions which need to be treated in separate sections (Sects. 4.1.4 and 4.1.7, respectively).

Energy transfer to photosystem I is also called **spill over**. Intact photosystem II in higher plants is located in the appressed thylakoid regions of chloroplast grana (Box 4.2) but for spill over the peripheral light harvesting complexes of photosystem II get phosphorylated by a specific kinase and are transferred to the stroma region of the thylakoids. This is a reversible process highly regulated by irradiance and the redox state of plastoquinone, PQH₂ (see Box 4.2).

The triplet state is much more stable, i.e. it has a much longer half-life, than the two singlet states. Therefore, it may lead to the formation of **reactive oxygen species and oxygen radicals** with the subsequent destruction of pigments, lipids and membranes. Radical scavengers or antioxidants are a number of redox substances, such as dihydroascorbate, reduced glutathione and for the chloroplast especially tocopherol (Krieger-Liszkay and Trebst 2006) and the enzymatic reactions of superoxide dismutases. The xanthophyll cycles of chloroplasts also are mechanisms for the scavenging of highly reactive singlet oxygen (Sect. 4.1.4).

### 4.1.4 Dissipation of Excitation Energy in the Form of Heat: The Role of Xanthophylls

Dissipation of surplus excitation energy in the form of heat is mediated by cycles of xanthophylls. The **zeaxanthin cycle** is one of the most important photoprotective mechanisms in photosynthesis (Demmig-Adams et al. 1996; Gilmore 1997; Gilmore and Govindjee 1999). It binds harmful singlet activated oxygen (\(\text{^1O}_2\)) and is a futile cycle in terms of energy turnover. The basic metabolic reactions are shown in Box 4.4. The xanthophylls of the zeaxanthin cycle are peripherally associated with the light harvesting complex of photosystem II, LHCII (Horton and Ruban 2005). Singlet activated oxygen is bound in the formation of the epoxides antheraxanthin and violaxanthin from zeaxanthin, which also requires redox energy in the form of NADPH + H⁺. The zeaxanthin cycle only functions when a trans-thylakoid proton gradient, \(\Delta p\text{H}\), is built up by photosynthetic electron transport. The \(\Delta p\text{H}\) otherwise used to power photophosphorylation is the primary controlling factor of the zeaxanthin cycle. \(\Delta p\text{H}\) and the electrons are used for deepoxidation and the return of the cycle to zeaxanthin when the originally harmful oxygen is eventually reduced to water and the energy of redox equivalents, electrons and \(\Delta p\text{H}\) across the thylakoid
Box 4.4 Xanthophyll-cycles

The **zeaxanthin-cycle** scheme was originally proposed by Hager (1980) and later forcefully propagated by Demmig-Adams (1990), Demmig-Adams and Adams (1992) and Pfündel and Bilger (1994). The turnover in the cycle involves detoxification of singlet activated oxygen ($^1\text{O}_2$) and energy dissipation, namely binding of activated oxygen by oxidation of zeaxanthin to violaxanthin (epoxidation) and dissipation of the energy of photosynthetic electron transport by rereduction (deepoxidation) to zeaxanthin. The epoxidase is located on the stroma side and the de-epoxidase on the thylakoid-lumen side of the thylakoid membrane, and the pH optima of the epoxidase (pH 7.5) and the deepoxidase (pH 5.2) correspond to the prevailing conditions in the chloroplast stroma and the thylakoid interior, respectively. The deepoxidase is mobile within the thylakoid lumen at neutral pH but becomes membrane-bound when the pH drops and a pH gradient is established across the thylakoid membrane by photosynthetic electron flow (Hager and Holocher 1994); it has a narrow pH optimum at pH 5.2 and is presumed to be activated by the photosynthetic electron transport via acidification of the luminal pH (Büch et al. 1994). Ascorbate is a cofactor in the deepoxidation reaction (not drawn in the cycle itself).

An additional xanthophyll-cycle is the **lutein/lutein-epoxide cycle**. While zeaxanthin has two $\beta$-ionon rings and can form two epoxides, lutein has one $\alpha$-ionon ring and only one $\beta$-ionon ring, and therefore, can form only one epoxide. The deepoxidase is the same as in the zeaxanthin-cycle (violaxanthin deepoxidase), while the epoxidase either is the same as the zeaxanthin epoxidase or a homologous enzyme (Matsubara et al. 2001, 2003).

membranes is effectively dissipated as heat. The zeaxanthin cycle directly protects PSII rather than PSI but may indirectly protect also PSI by restricting electron flow (Barth et al. 2001).

As an alternative, or in addition, to their function in the futile zeaxanthin cycle, xanthophylls may be involved in directly affecting the **structure of the light-harvesting complex** itself (Horton et al. 1994) and thus diverting excitation by absorbed photons from the reaction centre of photosystem II (PSII). Zeaxanthin can bind to the internal binding site of the xanthophyll lutein in LHCII (Horton and Ruban 2005). Zeaxanthin binds in dependence of $\Delta$pH at the thylakoid membrane (Gilmore 1997; Gilmore and Yamasaki 1998; Gilmore et al. 1998; Gilmore and Govindjee 1999) causing conformational changes of the system, possibly involving aggregation of the light-harvesting complex of PSII, which may be facilitated by an absence of violaxanthin and/or a presence of zeaxanthin and converting the reaction centre of PSII into a centre dissipating heat (Bilger and Björkman 1994; Horton et al. 1994; Gilmore et al. 1996; Horton and Ruban 2005) through charge separation of a chlorophyll-zeaxanthin heterodimer (Holt et al. 2005). This mechanism operates under prolonged and very extreme excessive light, while the zeaxanthin cycle responds to much lower and variable levels of excess light (Gilmore et al. 1996).
Independent of the zeaxanthin-cycle, zeaxanthin can also directly function as an antioxidant and prevent lipid oxidation removing epoxy groups from fatty acids, where violaxanthin formation provides protection against lipid peroxidation (Schindler and Lichtenthaler 1996; Baroli et al. 2003).

Thus, three possible xanthophyll mechanisms are listed by Schindler and Lichtenthaler (1996), namely:

- reaction of zeaxanthin with highly reactive oxygen species and the futile energy dissipating zeaxanthin cycle,
- aggregation/dissociation of the light-harvesting complex,
- reaction of zeaxanthin with reactive oxygen species.
An additional xanthophyll-cycle is the lutëin/lutëin epoxide cycle (Box 4.4). Lutëin is an intrinsic component of the light harvesting complex of PSII. It facilitates enhanced photoprotection through its superior singlet and/or triplet chlorophyll quenching (Matsubara et al. 2005). The lutëin cycle operates in parallel to the zeaxanthin-cycle in some plants, e.g. in mistletoes (Sect. 6.5) and the tropical Fabaceae Inga (Matsubara et al. 2001, 2003, 2005).

Over energization of the photosynthetic light harvesting apparatus is always a potential danger and ecophysiologically the xanthophylls provide an important protective machinery for many circumstances. Plants permanently exposed to full sunlight have effective protective mechanisms (Krause et al. 2006) and young leaves develop them to a higher degree than mature leaves (Krause et al. 1995). Zeaxanthin-cycle dependent energy dissipation is an extremely flexible process and can kinetically respond within seconds to minutes. Via adaptive changes of pool sizes of the xanthophylls time-scales of days up to seasons can be covered (Demmig-Adams et al. 1996). Ecophysiologically the zeaxanthin-cycle, for example, is operative in the light-exposed phenotypes of bromeliads in the tropics, zeaxanthin was only detected in the yellow high-light plants of Bromelia humilis (see Fig. 4.3) and not in the shade plants (Fetene et al. 1990) and also plays a significant role in Guzmania monostachia (Maxwell et al. 1994, 1995). A survey of several other sun and shade plants including tropical rainforest species also showed that sun plants possessed larger xanthophyll pools and greater maximal zeaxanthin and antheraxanthin contents than shade plants. Sun plants displayed a greater maximal capacity for photoprotective energy dissipation via the pigments than plants acclimated to very low irradiance, and in sun leaves the reduction state of PSII at full sun light remained at a much lower level than in shade leaves (Demmig-Adams and Adams 1994; Gilmore 1997). In the vertical light gradients in tropical forests levels of zeaxanthin-cycle pigments increase from the forest floor to the canopy (Logan et al. 1996). Xanthophyll pool size and zeaxanthin-cycle activity are also enhanced when photosynthesis is under nitrogen limitation (see Figs. 4.6 and 4.7) (Tóth et al. 2002; Cheng 2003).

### 4.1.5 Damage and Repair of Reaction Centres of Photosystem II: The D$_1$-Protein

Turnover in the xanthophyll-cycle can be very rapid. Alternatively to energy dissipation as heat and especially in the absence of xanthophyll-cycle associated photoprotection (Thieie et al. 1997) a slower process develops, which is irreversible when protein biosynthesis is inhibited. It is due to a functional dissociation between the reaction centres and antennae of photosystem II (see Box 4.2; Demmig-Adams and Adams 1993). The reaction centres of photosystem II are built up of one copy each of a D$_1$- and a D$_2$-protein. The destruction of these proteins prevents coupling of excitation and electron transport via the light trap reaction centres because in the light harvesting complex of PSII (LHCII) excitation is passed to plastoquinone (Q) via the D$_1$-protein. Repair needs protein synthesis (Box 4.5). The D$_1$-protein is al-
ways destroyed by light even at rather low intensities. Repair is most effective at low irradiance (30 µmol m$^{-2}$ s$^{-1}$). The D$_1$-protein is always under turnover, but at high irradiance and without photoprotection repair mechanisms are too slow resulting in damage of D$_1$ in the LHCII (Tyystjärvi and Aro 1996; He and Chow 2003), where light stress is amplified by high temperature stress (Königer et al. 1998). However, this damage which is slowly reversible in the turnover of D$_1$-protein destruction and resynthesis (Box 4.5) is also a mechanism of photoprotection as it inhibits over reduction of the photosynthetic electron transport chain.

**Box 4.5 Damage and repair of the reaction centres of photosystem II in light-stress and recovery cycles**

Under high light intensities (HL) the D$_1$-protein is first modified reversibly and recovery needs low light intensities (LL); (1). Under further stress the D$_1$-protein is damaged irreversibly (2) and repair needs protein synthesis (3). The turnover of the D$_2$-protein is slower although it also can be damaged irreversibly by light stress (Schäfer and Schmid 1993; Critchley and Russel 1994).

4.1.6 Conclusion: Summarizing Mechanisms of Dissipation of Photosynthetic Excitation Energy

In summary, the photosynthetic excitation energy not used by reduction and assimilation of CO$_2$ can be dissipated by a suite of protective and destructive mechanisms:

- the oxidase function of RuBISCO, photorespiration,
- the separation of peripheral and core parts of PSII, spill-over,
- capture of $^1$O$_2$ and dissipation of excitation energy as heat,
• reversible damage of the D1-protein of LHCII,
• irreversible photodestruction.

The second to the fourth of these mechanisms imply photoinhibition of photochemical work of either CO2-assimilation or photorespiration (Box 4.3), and the fourth one includes photodestruction. This makes us realizing difficulties and ambiguities in our nomenclature: What is “inhibition” and what is “damage”, what is a reaction for “protection” and what is “destruction”? The differences between acute and chronic damage may be gradual and the quantitative relationships between various ways of energy dissipation in relation to dynamics of photoprotective forces remain a conundrum (Osmond and Grace 1995). In terms of the stress-concept (Box 3.1) reversible and irreversible photoinhibition of CO2-assimilation, represent elastic and plastic strain, respectively.

4.1.7 Dissipation of Excitation Energy in the Form of Fluorescence: A Tool in Plant Ecophysiology

From the first singlet excited state chlorophyll can relax directly to the ground state by emission of light. The wavelength of this light is shifted somewhat towards the far red range of the spectrum as compared to the wavelength optimum of 680 nm of the excitation of chlorophyll a of PSII (P680). This is called chlorophyll fluorescence. The intensity of this energy-dissipation is low and fluorescence does not contribute to photoprotection under high irradiance stress. However, as a pathway alternative to photochemical work and the non-photochemical processes of harmless thermal dissipation of energy via the xanthophylls and oxidative photodestruction (Sect. 4.1.6) fluorescence of chlorophyll a of PSII is an excellent indicator of the state of PSII and its operation. Emission of fluorescence is most readily measured in a non-invasive way by photometric techniques, where the yield and quenching, respectively, of fluorescence are analyzed. As fluorescence is a reaction competing with photochemistry and with non-photochemical processes the magnitude of fluorescence quenching quantitatively represents:

• photochemical work, i.e. transfer of electrons from excited photosystem II to plastoquinone (“photochemical quenching”) and effective functioning of the mechanism leading to photosynthetic CO2-assimilation,
• energization of thylakoid membranes with xanthophyll mediated thermal energy dissipation (“non-photochemical quenching”),
• reversible and irreversible photoinhibition.

This has led to the development of sophisticated analyses of fluorescence signals, which allow to distinguish between photochemical competence and the balance between reversible and irreversible photoinhibition, as explained in Box 4.6. The method has become a powerful tool in plant-ecophysiology and as an essentially non-invasive and a non-destructive method it is also potentially suitable for remote sensing, and hence, for the ecophysiological survey of large tropical forest
and savanna areas (see Sect. 1.3). Fluorescence analysis is based on the KAUTSKY-effect explained in Box 4.6. H. KAUTSKY worked in the early 1930s and had to use elaborate optical equipment at 73 K. Currently we use pulse amplitude modulated spectrophotometers, we can work at ambient solar radiation and

![Graph showing light response curves of ΔF/Fm', ETR and NPQ](image)

**Fig. 4.8** Light response curves of $\Delta F'/F_m'$, ETR and NPQ (for explanation see Box 4.6) given by plotting momentary measurements of chlorophyll fluorescence of *Podocarpus falcatus* trees obtained during day-courses at two different sites, i.e. in a natural forest (*left*) and in a plantation of *Eucalyptus saligna* (*right*) of a montane forest in Ethiopia (see also Sect. 1.3) vs incident irradiance (PAR). (From Lüttge et al. 2003)

**Box 4.6 Fluorescence analysis**

A. Fluorescence induction kinetics (KAUTSKY effect)

In the first second after excitation fluorescence of photosystem II is induced and rises from the fluorescence ($O$) of the dark-adapted leaf obtained at very weak excitation energy to $I$, where all primary electron acceptors ($Q$ in Box 4.2B) are reduced, and after a small shoulder further to $P$, where the plastoquinone pool ($PQ$ in Box 4.2B) is also reduced.
Box 4.6   (Continued)

The high fluorescence obtained at \( P \) after the first second is quenched as the electron-transport capacity at the acceptor side of photosystem I and other fluorescence-quenching processes are activated.

B. Fluorescence analysis

In a pulse modulated-fluorescence-analysis system the following kinetics are obtained during induction after a period of darkness (the example given was obtained from a leaf of *Clusia multiflora*):

> Arrowheads pointing upwards and downwards respectively, indicate switching on and off of light, namely:

- \( m \) weak measuring light,
- \( p \) a single pulse of saturating actinic light,
- \( a \) actinic light with regular light-saturating pulses.
4.1 Light Responses of Photosynthesis

**Box 4.6** (Continued)

Symbols in the graph have the following meaning:

- $F_o$ minimal fluorescence yield of dark-adapted sample in weak measuring light,
- $F_m$ maximum fluorescence yield of the dark-adapted sample,
- $F_v$ maximum variable fluorescence,
- $F'_o$ minimal fluorescence yield of the light-adapted sample,
- $F'_m$ maximum fluorescence yield of the light-adapted sample.

Calculations which can be made include the following:

1. $F_v/F_m$ as a measure of potential quantum yield of photosystem II after dark adaptation, which is lowered by photoinhibition,
   \[
   F_v/F_m = (F_m - F_o)/F_m.
   \]

2. $\Delta F/F'_m$ as a measure of effective quantum yield,
   \[
   \Delta F/F'_m = (F'_m - F)/F'_m.
   \]

3. ETR = $0.86 \times 0.5 \times (\Delta F/F'_m) \times$ PPFD as an empirical approximation of the relative electron transport rates, where PPFD is incident photosynthetic photon flux density, the factor 0.86 accounts for an average light absorption of leaves of 86% (unless measured specifically) and the factor 0.5 for equal distribution of absorbed photons to PSII and PSI.

4. The quenching coefficient for photochemical quenching of fluorescence, $q_P$
   \[
   q_P = (F'_m - F)/(F'_m - F'_o).
   \]

5. The quenching coefficient for non-photochemical quenching of fluorescence, $q_N$
   \[
   q_N = 1 - (F'_m - F'_o)/(F_m - F_o).
   \]

6. The extent of non-photochemical quenching, NPQ,
   \[
   NPQ = (F_m - F'_m)/F'_m.
   \]

(Refs.: Genty et al. 1989; van Koten and Snel 1990; Schreiber and Bilger 1993; Bilger et al. 1995; Maxwell and Johnson 2000)
Among the parameters explained in Box 4.6 potential quantum yield of PSII, $F_v/F_m$, is extremely useful in ecophysiology as it allows to distinguish between acute and chronic photoinhibition. A dark adapted sample where all elements of the electron transport chain are oxidized (“open”) shows maximum $F_v/F_m$ upon a saturating light pulse. This is close to 0.83, because maximally 83% of the light are used (Björkman and Demmig 1987). If $F_v/F_m$ is lower than that, the sample is under photoinhibition. Then one can study the time of darkening needed to restore it to close to 0.8 (Thiele et al. 1998). If the photoinhibition indicated by $F_v/F_m$ was reversible within several tens of minutes one was observing acute photoinhibition due to built up of an electrochemical gradient at the thylakoid membranes and xanthophyll type energy dissipation. If it was not reversible before several hours, destruction of D1-protein must have been involved. If it was not reversible for an extended period, e.g. overnight, there has been irreversible photodamage and photoinhibition was chronic.

Effective quantum yield of PSII, $\Delta F/F_m’$, and apparent electron transport rate, ETR, indicate the activity of photochemical work. $\Delta F/F_m’$ decreases with increasing light intensity as an increasingly less proportion of the incident irradiance is used for photosynthesis, and ETR increases up to light saturation. In this way for example from actual momentary measurements at varying irradiance, e.g. during the course of a day, light saturation curves can be obtained and non-photochemical fluorescence quenching can also be related to irradiance (Fig. 4.8). In Fig. 4.9 light-response curves of net CO₂-uptake and photochemical quenching of a sun and a shade leaf are compared. The CO₂-uptake curves show the typical characteristics of sun and shade types (see Fig. 4.1). Photochemical quenching is high in both cases at low PPFD and decreases much more rapidly with increasing light intensity in the shade leaf than in the sun leaf, suggesting increased over reduction of the photosynthetic electron transport chain.
4.2 Varying Irradiance on the Forest Floor and in Gap Dynamics

4.2.1 The Response to Light Flecks

Light flecks were already mentioned in relation to the vertical structure of forests (Sect. 3.4.1) describing the dynamics of light penetrating through the forest canopy. The importance of such dynamics is illustrated by modelling canopy photosynthesis with steady state and dynamic models, respectively, where the former overestimate carbon gain by 13.4% at open sites and even by 86.5% at low light environments of the understory (Stegemann et al. 1999; Timm et al. 2002, 2004). Clearly, light flecks must be important in any type of forest. However, in the very dark, moist tropical forests the dynamics of the responses of photosynthesis to light flecks play an essential role in fulfilling the energy demands of photosynthesis in lower canopy layers and particularly on the forest floor.

A prerequisite for photosynthetic utilization of the irradiance of rapidly formed and transient light flecks are swift and co-ordinated reactions of stomata as well as the biophysical and biochemical machineries of CO₂-assimilation. Figure 4.10 shows that CO₂-uptake, stomata-limited leaf conductance for water vapour (gH₂O) and intercellular CO₂-concentration (pCO₂) in the leaves of Claoxylon sandwicense and Euphorbia forbesii respond within minutes to a stepped increase of irradiance from low to high intensity. Both species occur in the understory of a Hawaiian forest (Pearcy 1983). In C. sandwicense, a tree with C₃-photosynthesis, gH₂O...
showed an immediate linear increase, which continued for more than 50 min; net CO₂-uptake first increased very rapidly and then more gradually in correlation with \( g_{H2O} \); \( p'_{CO2} \) decreased initially in response to increased availability of light energy for photosynthesis and then increased again slightly as stomata opened more widely (increased \( g_{H2O} \)) allowing CO₂-uptake from the atmosphere. *E. forbesii*, performing C₄-photosynthesis (see Box 10.2, Sect. 10.1.2), responded in a somewhat different fashion. There was a slight delay in stomatal opening, but then maximal stomatal conductance was attained within 15 min. After an initial decline, \( p'_{CO2} \) was stabilised at an intermediate level while CO₂-uptake reached a high, constant rate.

Are these responses sufficient to allow the plants to make efficient use of short light flecks? Interestingly there is an effect of **accelerating CO₂-uptake with time**, when very short light flecks are imposed repeatedly over short periods. Figure 4.11 shows, for the two species discussed above, that CO₂-uptake during artificial light flecks increases gradually when subsequent light flecks of a duration of 1 min are alternated with low background intensity for about 90 s. Conditioned or induced leaves have a considerably higher light use efficiency in light flecks than uninduced ones which is decreasing as light flick length increases (Fig. 4.12; Valladares et al. 1997). The **intensity of this background light** is also important in maintaining the conditioning effect, which leads to increasing efficiency in the use of light flecks. As shown in Fig. 4.13, the efficient use of 5-s light flecks at 500 µ mol photons m⁻² s⁻¹ increases considerably when the background light intensity following each light flick is increased from 0 to 10 µ mol photons m⁻² s⁻¹. At very high intensities the irradiance of light flecks is used more effectively when there are **interruptions** by low intensity background irradiation. This is explained by after effects of the high

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**Fig. 4.11A, B** Response of CO₂-uptake of: A *C. sandwicense*; B *E. forbesii* during 1-min light flecks (PPFD = 510 µ mol photons m⁻² s⁻¹) on a background of 22 µ mol photons m⁻² s⁻¹, which was presented to the plants for 2 h prior to the first light fleck and which interrupted the individual light flecks. **Arrows** indicate increase (↑) and decrease (↓) of PPFD respectively. (Pearcy et al. 1985)
4.2 Varying Irradiance on the Forest Floor and in Gap Dynamics

Fig. 4.12 Light use efficiency (LUE) during light flecks as a function of light fleck duration (log scale on the x-axis) in induced (closed symbols) and uninduced (open symbols) leaves of three tropical rain forest understory shrub species. (After data of Valladares et al. 1997)

Fig. 4.13 Efficiency of the utilization of 5-s light flecks (PPFD = 500 µmol photons m$^{-2}$s$^{-1}$) on a background irradiance of PPFD varied between 0 and 10 µmol photons m$^{-2}$s$^{-1}$ given for 60 s after each light fleck. In each case, leaves had been conditioned to reach a steady-state CO$_2$ assimilation at 500 µmol photons m$^{-2}$s$^{-1}$ before applying the series of light flecks (Kirschbaum and Pearcy 1988b)

irradiance light flecks, namely post irradiance CO$_2$ fixation (Kirschbaum and Pearcy 1988a; Leakey et al. 2005).

What is the nature of these conditioning processes, which include induction, the use of short-time high irradiance and the apparent after-effects during low background irradiation? The nature and mechanism of the important after effects are understood looking at a 20-s light fleck experiment with the tropical shade-plant Alocasia macrorrhiza where CO$_2$ and O$_2$ gas exchange were recorded simultaneously before, during and after the light fleck (Fig. 4.14). At the beginning of the light fleck, O$_2$ evolution increased very rapidly, and during the first second it attained about twice the rate of steady state CO$_2$-uptake. Subsequently it dropped again and matched the rate of CO$_2$-uptake after 2.5 s. This suggests that light-dependent elec-
electron transport, indicated by photosynthetic O$_2$ evolution, may proceed rapidly to fill up pools of reduced compounds in a very short initial period after stepped increase in irradiance, before it becomes limited by reactions of CO$_2$-reduction. Biophysical light-reactions of photosynthesis (Box 4.2B) are extremely fast. Therefore, in light flecks the slower processes of induction are the biochemical reactions of CO$_2$-fixation and assimilation as well as stomatal responses. Among them, the regeneration of ribulose-bis-phosphate the CO$_2$-acceptor in photosynthesis, is comparatively fast. It was found to be 60 – 120 s under transient light conditions as typical for light flecks, while light-activation of the activity of the carboxylase (RuBISCO) and stomatal reactions occurred in the range of 10 – 30 min (Sassenrath-Cole and Pearcy 1992). On the other hand, the mechanisms which show slower induction are also subject to slower decay and may remain active during intermittent light flecks. At the end of a light fleck, when there is a stepped decrease of irradiance, O$_2$-evolution drops immediately as photosynthetic electron transport stops. However, CO$_2$-uptake declines only gradually showing an after effect of the high irradiance during the light-fleck due to a surplus of reduced compounds formed during high PPFD. In this way the consequence of after effects is that high light of light flecks can be used more effectively when the high irradiance is not continuous because this allows a more efficient use of the intrinsic potential for reduction built up during absorption of light at high intensity. Thus, this phenomenon explains the particular efficiency of short duration light fleck utilisation as a co-ordination of more rapid responses (photosynthetic electron transport) and more sluggish processes (photosynthetic CO$_2$ assimilation), with both adjusted to some extent in series so that each process may not be entirely simultaneous. Of course, the light flecks must be short, if this is to be relatively important quantitatively. The different time constants of the processes involved also explain the conditioning to intermittent light (Fig. 4.11). Thus, the specific dynamics of transients after light intensity is stepped up and down, make light flecks a quantitatively more important energy
source for forest-floor photosynthetic carbon assimilation than one might expect from their intensity and duration alone. The dynamics of fluctuating light, stomatal conductance and biochemical activation and pools of key photosynthetic intermediates are also convincingly simulated by mathematical models (Kirschbaum et al. 1997). Another factor which is also involved is respiration the activity of which is regulated by ATP-demand of the plants during light fleck dynamics (Noguchi et al. 2001a).

One may also ask whether light fleck responses are different in shade and sun plants, since one might expect that the latter are less dependent on intermittent light. Indeed, such differences have been observed. They are largely based on stomatal dynamics. Stomatal relations are very important as the induction of photosynthesis during dynamic light flecks depends on stomatal opening and CO₂ availability to the mesophyll. When stomata are already open at low background irradiance induction may be faster than when first a stomatal opening movement of guard cells is required (Valladares et al. 1997).

Responses of plants to light flecks are also species specific (Leakey et al. 2005). Species dependence of stomatal responses are also seen in Fig. 4.10. A comparison of two dipterocarp rain forest tree species showed that one species could use light flecks quickly and the other more slowly but instead performed photosynthesis continuously at low light (Zipperlen and Press 1997). In species of *Piper*, acclimation of stomatal responses to different light intensities was observed, which was important for the performance of the plants in varying light environments (Tinoco-Ojanguren and Pearcy 1992). A comparison of *Piper auritum*, a pioneer tree, and *Piper aequale*, a shade tolerant shrub of Mexican tropical forests, showed that differences in induction of photosynthesis could be accounted for by differences in stomatal behaviour. The shade tolerant shrub, *P. aequale*, had the larger and more rapid response of stomatal conductance (gH₂O) to light flecks, which was shown to improve carbon gain during subsequent light flecks for shade adapted plants. Conversely, low-light acclimated plants of the pioneer tree, *P. auritum*, showed even slower and smaller conductance responses than sun-acclimated plants, and there was no significant improvement in use of subsequent light flecks (Tinoco-Ojanguren and Pearcy 1993a,b). Another comparison was provided by Poorter and Oberbauer (1993), who studied saplings of a climax tree species, *Dipteryx panamensis*, and a pioneer tree, *Cecropia obtusifolia*, in a rainforest of Costa Rica. The results of their comparative investigation are compiled in Table 4.4. Remembering the differences in general photosynthesis characteristics of these groups of plants (Sect. 4.1.1) it appears that the climax-tree saplings exploit temporal variation in light availability by refining the speed of the induction response. In contrast, the pioneer species adjust by realising higher rates of light-saturated photosynthesis under high irradiation.

Different light fleck responses have also been reported in relation to leaf-longevity (Kursar and Coley 1993). In shade-tolerant species with short lived leaves (1 year) induction to attain 90% of maximum photosynthetic rates took 3–6 min, while 11–36 min were needed in long-lived leaves (> 4 years). In this case, however, RuBISCO activation seemed to be the time-limiting factor.
Table 4.4 Comparison of the responses of saplings of two Costa Rican rainforest tree species to light flecks in situ (Poorter and Oberbauer 1993)

<table>
<thead>
<tr>
<th>Character</th>
<th><em>Dipteryx panamensis</em></th>
<th><em>Cecropia obtusifolia</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Induction time needed to reach 90% of light-saturated rate of photosynthesis in the morning</td>
<td>16 min</td>
<td>10 min</td>
</tr>
<tr>
<td>Daily average induction time needed</td>
<td>Shorter than in <em>C.o.</em></td>
<td>Longer than in <em>D.p.</em></td>
</tr>
<tr>
<td>Duration of maintenance of high levels of induction</td>
<td>Longer than in <em>C.o.</em></td>
<td>Shorter than in <em>D.p.</em></td>
</tr>
<tr>
<td>Behaviour when grown in shaded sites as compared to bright sites</td>
<td>Faster rates of induction</td>
<td>No difference in rates of induction</td>
</tr>
<tr>
<td></td>
<td>No difference in light-saturated rates of photosynthesis</td>
<td>Lower light-saturated rates of photosynthesis</td>
</tr>
</tbody>
</table>

On the forest floor plants heat up in light flecks and this much adds to sudden light stress (Leakey et al. 2003, 2005). Thus, light flecks may not only have beneficial effects and it can not be generalized that light fleck activity is directly associated with greater carbon gain (Leakey et al. 2005). It is an intriguing question if the plants adapted to life in the deep shade of forest floors do not get under severe problems of photoinhibition and photodamage when subjected to high irradiance in the light flecks. Shade leaves of some plants do not appear to be photoinhibited during light flecks, they have a limited xanthophyll-cycle strategy and use increased synthesis of D1-protein (Schiefthaler et al. 1999). However, mostly it is observed that there is photoinhibition due to NPQ but no photodamage. This is managed because of the short time constants of zeaxanthin functions (Sect. 4.1.4). With the rise and fall of the transthylakoid ΔpH in relation to incident irradiance xanthophyll-cycle dependent energy dissipation is engaged rapidly during light flecks preventing photooxidative damage and disengaged rapidly after light flecks pass (Demmig-Adams et al. 1996; Logan et al. 1997; Watling et al. 1997; Adams et al. 1999).

### 4.2.2 Light Quality: Signalling Functions of Light

As already mentioned above (Sect. 3.4.1), light quality changes in relation to horizontal and vertical structure of forests.

Ultraviolet light (UV) is interesting because blue light and UV may exert signalling functions. Shade adapted tropical tree seedlings can gradually adapt to UV (Krause et al. 2003b) and UV radiation may be attenuated by UV absorbing substances and plant cuticles (Krauss et al. 1997). Often, however, natural UV-A and
UV-B radiation may cause photoinhibition and photodamage particularly in shade leaves exposed to full sunlight (Krause et al. 1999, 2003a).

Most interesting in relation to signalling, however, is the other end of the spectrum because filtration by canopies eliminates the red light (R) from the solar spectrum much more effectively than the far-red light (FR). Sunlight has a mean R/FR ratio of 1.2 but under green canopies the ratio may be reduced to levels below 0.5 (Vázquez-Yanes and Orozco-Segovia 1993). This affects all processes regulated by the phytochrome system. Irradiation with red light generates the active PFR form of phytochrome, which elicits various photomorphogenetic responses. Far-red light inactivates the phytochrome, shifting the phytochrome equilibrium towards the inactive P_R-form (Box 4.7). The light intensities required in phytochrome effects are often extremely low. It is the signalling function of light, which is sensed by the phytochrome system and not its function as an energy source.

Box 4.7 The reversible phytochrome system
4.3 Seedlings: Germination, Establishment and Growth

4.3.1 Regulation of Seed Dormancy and Germination

Among the many processes governed by phytochrome (Sect. 4.2.2) one of the most well known is the germination of the seeds of “light-germinators”, i.e. positive phoblastic seeds. In this way phytochrome also plays an important role in the regulation of succession and regeneration in tropical forests, because light dependence of seed germination is one of the most fundamental differences between pioneer species and late successional or climax species, where competition is not only explained by the substrate and energy aspects of irradiance but also its signalling functions (Aphalo et al. 1999).

Only seeds of late successional and climax species can germinate and establish seedlings under deep canopy shade. These seeds germinate very soon after dispersal and also remain alive in the soil only for a short time. The mean ecological longevity of seeds in the tropical rainforest may be one of the shortest of any plant community (Vázquez-Yanes and Orozco-Segovia 1993). The advantage of this behaviour lies in the fact that seeds are more threatened by predators and parasites in the soil environment of the tropical rainforest with continuous moisture and high temperature, than are seedlings. Thus, the seed banks in rainforest soils are depleted of seeds of late succession and climax species. On the other hand, seedlings may grow extremely slowly and a persistent nursery of small plants is built up, i.e. a seedling bank instead of a seed bank. Flores (1992) has studied two species of the cloud forest of the northern coastal range of Venezuela and his observations give a good idea about the actual longevity of tree seedlings after germination:

- Aspidosperma fendleri (Apocynaceae), an emergent species, which grows its crowns above the canopy (see Fig. 3.25),
  - germination time 5 days,
  - longevity of cotyledons 2 months,
  - longevity of 1st leaf pair 2 years.

- Richeria grandis (Euphorbiaceae), a canopy species,
  - germination time 20 days,
  - longevity of cotyledons 2.5 years,
  - longevity of leaves 3 years.

The small plants remain in a state of slow growth until a canopy gap provides an opportunity for stimulation of growth (see Sect. 4.3.2). The survival of the seedlings is independent of photosynthetic parameters and largely determined by morphological characteristics which are likely to provide protection from and enhance defence against herbivores and pathogens, i.e. dense and tough leaves, a well established root system and a high wood density. Furthermore, reserves of non-structural carbohydrates in stems, roots and storage cotyledons support long-term survival of seedlings of shade tolerant species enabling them to cope with periods of biotic and abiotic
stress (Myers and Kitajima 2007). Seedlings in gaps proved to be more resistant to herbivory than seedlings in the undergrowth of tropical forests (Blumwald and Peart 2001). Seedling survival of 13 tropical tree species was found to be negatively correlated to relative growth rate (RGR), i.e. both low RGR of plants raised in the shade and high RGR of plants in the sun, and to leaf area ratio and positively correlated to root/shoot ratios and wood density (Kitajima 1994; Fig. 4.15). Fast growing pioneer plants need lower stem support and afford a lower wood density, but this reduction of support costs is related to higher mortality rates (Fig. 4.15E; King et al. 2006).

In contrast to late successional species seeds of woody pioneer species are capable of dormancy. They are often the most abundant components of the soil seed bank in tropical forests (Vázquez-Yanes and Orozco-Segovia 1993). Dormancy may be enforced by hard seed coats which are impermeable to water and oxygen and need many weeks for breakdown by weathering and microbial action. However, germination is mainly determined by light.

Light may act via temperature effects, especially via temperature alternations, which are required by some seeds for germination. Canopy gaps and clearings lead to greater fluctuations of soil surface temperatures due to direct insolation (see Fig. 3.29). Often, however, germination is regulated by light quality and the involvement of the phytochrome system rather than by light intensity. A higher proportion of red light activates and a higher proportion of far-red light inactivates phytochrome and the reversibility of phytochrome effects may be important in excluding reactions to short light flecks (Sect. 4.2.1) and sensing true light gaps. The photoreversibility of phytochrome mediated germination within certain time limits may be essential to prevent germination resulting from light flecks (Vázquez-Yanes and Orozco-Segovia 1993).

The sophisticated regulation of dormancy and germination, respectively, is most frequent among pioneer species and gap colonizers, with germination inhibited under closed canopies and stimulated in clearings.

### 4.3.2 Growth of Seedlings

Seedling growth depends on availability of water (Sect. 5.1) and nutrients (Sect. 3.4.4) but most drastically on light (Medina 1998; Poorter 1998). After germination and establishment of seedlings often forming nurseries of slow growing plants (Sect. 4.3.1), further growth will depend very much on photosynthesis, the light powered fixation of CO₂ and reduction to organic material, as well as allocation of photosynthetic products (Zipperlen and Press 1996; Scholes et al. 1997). This, of course, applies to both pioneer and climax species. Both may differ though, in responses to light intensity, which are representative of sun and shade plant characteristics (see Sect. 4.1.1).

However, in some cases the differences in photosynthetic capacity related to light intensity between seedlings of pioneer and climax species, or between mature early and late successional species, has been found to be surprisingly small (Riddoch...
Fig. 4.15 Seedling mortality rate during the first year in the shade of 13 tropical tree species related to relative growth rate (RGR) in shade and sun (A,B), leaf area ratio (LAR) (C), root : shoot ratio (D) and wood density (E). (After Kitajima 1994)
Fig. 4.16 Leaf-anatomy of seedlings of a pioneer or early succession tree, *Nuclea diderrichii* (A,B), and a late succession tree *Entandrophragma angolense* (C,D), grown at high light (A,C) and at low light (B,D). The white bars denote 50 µm. (Riddoch et al. 1991)
et al. 1991). Huber (1978) examined photosynthetic characteristics, e.g. the light compensation point (Sect. 4.1.1), of 54 vascular plant species in Rancho Grande (Venezuela). He found that by this criterion the majority of the species growing in the lower forest strata did not belong to extreme shade-adapted plant types, but possessed a wide capacity for response to the highly variable irradiance in this montane cloud forest. It may be noted generally that a schematic distinction of pioneer sun plants/shade plants in this context is too simple. Changes can occur during development (Turnball 1991; Agyeman et al. 1999; Kyereh et al. 1999; Poorter et al. 2005). Mature shade leaves of seedlings can substantially acclimate to full sunlight employing mechanisms of energy dissipation, UV absorbing substances etc. (Krause et al. 2004). Availability of water and nutrients, especially nitrogen (Sect. 4.1.2) play a role in this (Castro et al. 1995; Bungard et al. 2000).

Complex regulation is involved. For a fluctuating tropical environment with frequent disturbance by typhoons and canopy opening a trade off between acclimation ability and plasticity has been considered (Yamashita et al. 2002). Strauss-Debenedetti and Bazzaz (1991) have suggested that plasticity and acclimation should be distinguished as follows:

- **late successional species** often cannot acclimate to high light intensities when transferred from low-light to high light (**low acclimation**) but may grow well if kept continuously under low and high light respectively (**high plasticity**),
- **pioneer species** may grow at low and high light and show a considerable stimulation after transfer from low light to high light (**high plasticity and high acclimation**).

The expression of low-light and high-light forms of a species may also be determined by the **phytochrome** system (Smith et al. 1993), but in particular **blue-light photoreceptors** are also involved in this regulation (Lichtenthaler et al. 1981; Humber and Senger 1984; see Lüttge et al. 1986). Leaf-anatomical features often show pronounced differences; sun leaves are thicker than shade leaves and have additional layers of palisade parenchyma. In a comparison of young seedlings of the tropical trees *Nauclea diderrichii* (De Wilde.) Merrill, a pioneer species, and *Entandrophragma angolense* (Welw.) C. DC., a climax species, both from West Africa, differences in acclimation and photosynthetic capacity at high light intensity were only small. However, there were marked morphogenetic effects on leaf anatomy in plants grown in the sun and in the shade respectively, in the pioneer species *N. diderrichii* but not so much in the climax species *E. angolense* (Fig. 4.16).

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5.1 Drought in Moist Tropical Forests

Seasonality of rainfall (Sect. 3.1) can lead to the formation of tree rings in wet tropical forests (Worbes 1999; Dünisch et al. 2003). Seasonal drought may occur regularly in these moist forests and not only in dry tropical forests. In Central and South America it can be enforced by southern oscillation or El Niño events (Engelbrecht et al. 2002). After extreme dry periods tropical rain forests may even be threatened by fire (van Nieuwstadt and Sheil 2005, Sect. 10.3). Along the 65 km across the isthmus of Panamá, where B. ENGELBRECHT and colleagues have studied tree seedling performance in relation to drought stress in the moist forests there is a gradient of forest formation due to a moisture gradient from the drier Pacific to the wetter Atlantic side (Fig. 5.1A). The number of days when no precipitation reaches the forest floor (days with lower than 3 mm rain) range from 20 to more than 90 in the moist forests across the isthmus (Fig. 5.1B).

Responses of tree seedlings were studied in detail because they were expected to be the most drought sensitive life stage of trees in the moist forests due to their shallow roots and limited access to soil water. However, it was found that once established seedlings were remarkably tolerant to severe drought events and desiccation and wilting (Engelbrecht et al. 2002; Tyree et al. 2002). Three cases could be distinguished where effects of drought on survival of seedlings and growth were not correlated:

- drought had little effect on both growth and survival in well adapted species,
- drought had little effect on survival but a strong effect on growth in species which shed their leaves under dry conditions and are facultatively deciduous,
- drought strongly affected survival in species where the surviving individuals show an intermediate growth reduction

(Engelbrecht and Kursar 2003). Among the factors of environmental pressure of light, herbivory and pathogens soil moisture proved to be the main one determining seedling survival or mortality (Engelbrecht and Kursar 2003; Engelbrecht et
Fig. 5.1A, B Rainfall gradient across the isthmus of Panamá. A Annual rainfall from the drier Pacific (0 km) to the wetter Atlantic (60 km) side of the isthmus. B Number of times (y-axis) in 27 years when years with 20 to about 90 days occurred where the daily precipitation was below 3 mm (x-axis) so that due to interception by the canopy and evaporation no rain water reached the ground. (A: by courtesy of B. Engelbrecht, B: Tyree et al. 2002, by permission of Oxford University Press)

Fig. 5.2 Relation of drought resistance to lethal leaf water potential in wilted leaves. Low and high lethal leaf water potential are related to low and high mortality, respectively. (Figure by courtesy of B. Engelbrecht and T.A. Kursar; for details see Tyree et al. 2003)

Differences of species in their responses to drought could be basically explained by tolerance of wilting and desiccation and there was a linear relation between lethal leaf water potential and drought resistance (Fig. 5.2; Tyree et al. 2003). Thus, via the effects on the seedlings drought has an important impact on
plant population dynamics (Engelbrecht and Kursar 2003) and species distribution (Engelbrecht et al. 2005) in the forest types along the isthmus of Panamá.

Species may react to drought stress by adaptive reduction of leaf area (Phillips et al. 2001; Sobrado 2003). Stomatal regulation plays a role. Among 110 species of mature trees in a 12-year-old tropical rainforest mesocosm model, Rascher et al. (2004) found functional diversity with different reactions of different species, with leaf fall, reduced maximum rates of photosynthetic electron flow and stomatal closure. Tropical evergreen rainforest species show isohydric regulation where stomata are sensitive to vapour pressure deficit and respond to short term water stress (Cunningham 2004) and stomatal responses to humidity are based on sensing the transpiration rate itself (Meinzer et al. 1993).

5.2 Drought in Dry Tropical Forests

“From wet to dry” species in the tropics face increasing problems of water availability (Holbrook and Franco 2005). The dominating ecophysiological stress parameters in dry tropical forests are strong seasonal drought ($H_2O$) and high irradiance ($h\nu$, see Chapter 4 for a detailed discussion) with strong interactions between them and with other environmental parameters, i.e.

1. $h\nu \leftrightarrow T$: Absorption of radiation by leaves leads to heating.
2. $H_2O \leftrightarrow h\nu$: Heating and drying of the atmosphere, increases the leaf-air water-vapour pressure gradient and thus leads to increased transpirational water loss.
3. $H_2O \leftrightarrow T$: Water loss can be controlled by closure of stomata, but this then reduces transpirational cooling by evaporation, and leaves heat up further.
4. $H_2O \leftrightarrow N$: Soil water deficit reduces the availability of $N$; the transpiration stream serves distribution of nutrients in the plant.

In their adaptations plants combine phenological, structural, physiological and biochemical responses.

5.2.1 Leaf Shedding and Hydraulic Architecture

In dry tropical forests some trees may have access to deep water sources and can maintain their water-use during drought. These trees do not have a great seasonal variation in their leaf fall (Meinzer et al. 1999). In other trees leaf shedding is an avoidance strategy in terms of the biological stress concept and like for savannas (Sect. 10.1.2.1) phenological cycles play an important role. Many dry tropical forest trees shed leaves at the onset of the dry season. A reduction of hydraulic conductance of the leaves precedes senescence and possibly causes senescence (Sobrado 1993; Brodribb and Holbrook 2003). Trees may flush new leaves before the onset of the rainy season protecting the young growth from herbivory (see Sect. 3.4.4.3)
by insects which emerge with the rains (Murali and Sukumar 1993). However, this is an overall somewhat simplified picture. In fact, there is a large range of phenological behaviours. A co-occurrence of tree species with phenological patterns ranging from deciduous to completely evergreen is often observed, and one can find species that are leafless for as much as 6 months standing near to ones that retain full crown foliage despite the near absence of rainfall for many months (Brodribb and Holbrook 2005; Diaz and Grandillo 2005). Leaves may be shed throughout the year and trees shed and flush leaves almost every month in a pattern associated with sporadic rainfall events (Diaz and Grandillo 2005). The phenological variability of leafless and fully leaved trees occurring side by side is not necessarily due to different rooting depths but can be explained by differences in the capability to use small episodic rainfall events especially with water wetting the leaf surfaces rather than coming from the soil (Diaz and Grandillo 2005).

Hydraulic architecture needs to be adapted. By shedding leaves drought-deciduous species avoid significant plant water loss during the driest and hottest months but they must cope with larger seasonal water potential fluctuations in their leaves and require a higher water transport efficiency which leads to seasonal occurrence of xylem embolisms (Sobrado 1993). The principle differences seen when deciduous dry rainforest trees are compared with evergreen ones are the following:

- deciduous species have larger xylem vessel diameters,
- therefore, deciduous species have lower wood density,
- deciduous trees are more vulnerable to xylem vessel cavitation or embolism blocking water transport,
- deciduous species have a higher water storage capacity.

These correlations can be found to be borne out in nature (Sobrado 1993; Choat et al. 2005). However, on the other hand there is also an overwhelming functional diversity and variation in hydraulic strategies, such as stem and leaf specific conductance and vulnerability to embolism, among dry forest species co-occurring side by side (Brodribb et al. 2002, 2003). In some deciduous species drought-induced embolism is avoided prior to leaf shedding, whereas in others leaf shedding and xylem embolism are closely linked (Brodribb et al. 2002), where leaf hydraulic conductance and water potential are not correlated with leaf life spans (Brodribb and Holbrook 2005). Xylem cavitation of leaf veins can elicit a feed forward signal to stomata causing stomatal closing responses that may lead to depression of gas exchange (Brodribb and Holbrook 2004) and are one of the reasons for a midday-depression (see Sects. 5.2.2.1 and 10.1.2.3).

Among various other physiological reactions a high emission of isoprene gas has been noted, which may be linearly related to irradiance up to $2,500 \mu \text{mol m}^{-2} \text{s}^{-1}$ and constitute considerable parts of the entire carbon budget of the plants (Lerdau and Keller 1997). It is under the control of the endogenous circadian biological clock (Wilkinson et al. 2006). As a hydrophobic gas this has been discussed in relation to reduction of evaporative water loss. However, isoprene may also function as an antioxidant (Peñuelas et al. 2005; Affek and Yakir 2002) protecting against excessive light and damage by heat and reducing oxidative stress (Sect. 4.1.2) (Sharkey and Yeh 2001).
In nutrient poor habitats of dry forests low soil water may amplify nutritional problems because more than actual nutrient availability water may control uptake of nutrients (Rentería et al. 2005). Before leaves are shed nutrients such as nitrogen are remobilized in the senescing leaves and stored in twigs, the N-resources of which may provide some N for later reconstruction of the canopy (Sobrado 1995). RuBISCO activity may be reduced by water stress (Parry et al. 2002).

5.2.2 Ecophysiological Responses of Plants with C\textsubscript{3}-Photosynthesis and Crassulacean Acid Metabolism (CAM)

In their reactions to the interacting stress effects of drought and high irradiance the plants must optimise responses to the particular limitations given. This may lead to disadvantages; for example closing stomata at low water availability and high irradiance reduces water loss but also causes increased heating; CO\textsubscript{2}-uptake is prevented and this leads to the dangers of photoinhibition (Sect. 4.1.7). C\textsubscript{3} and CAM-plants may respond by stomatal closure in the middle of the days when challenged by high irradiance, heating and transpiratory loss of water peaks, but this has very different implications in both modes of photosynthesis.

5.2.2.1 The Midday Depression of C\textsubscript{3}-Plants

The C\textsubscript{3}-bromeliad Pitcairnia integrifolia grows in the thornbush-forest of Trinidad and smaller adjacent islands. Its performance on a clear and very hot day demonstrates the implications of the strategy of midday stomatal closure in C\textsubscript{3}-photosynthesis (Lüttge et al. 1986; Fig. 5.3). Photosynthetic CO\textsubscript{2}-uptake rose after dawn as light-intensity increased and reached the highest rate at about 09.00 h. During this time temperature increased from about 23 °C to about 36 °C, but leaf temperature remained very close to air temperature. Beyond that point stomata began to shut and had fully closed by noon, when leaf conductivity to water vapour, $g_{H2O}$, was zero (not shown in Fig. 5.3). At this time, and until about 15.00 h irradiance had attained its highest level around 2,000 µmol photons m\textsuperscript{-2} s\textsuperscript{-1} and leaf temperature now increased much above air temperature with the highest value close to 52 °C and almost 8 °C higher than air temperature. If inhibition of CO\textsubscript{2}-uptake was only due to stomatal closure, one would have expected intercellular CO\textsubscript{2}-concentration ($p_i CO_2$) to have remained at low levels during this period. However, $p_i CO_2$ rose and this shows that there were likely to be photoinhibitory responses occurring as well as the well documented change in carboxylation efficiency at this time. Later in the afternoon, when irradiance and temperatures declined again, stomata re-opened and $p_i CO_2$ dropped, but CO\textsubscript{2}-uptake only reached less than a third of the rate attained in the morning. Hence, strain during the hottest time of the day was only partially elastic and had a strong plastic component. Only during the subsequent night water
uptake and rehydration as well as possible repair mechanisms may restore photosynthetic capacity.

The phenomenon of reduced gas exchange during the hottest time of the day is called **midday-depression**. It is very frequent among trees, shrubs and herbs in hot

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**Fig. 5.3** Daily course of CO\(_2\) uptake (\(J_{CO_2}\)), intercellular CO\(_2\) concentration (\(p_{CO_2}^L\)), leaf temperature (\(T_L\)), air temperature (\(T_A\)) and solar irradiance (\(L\)) for a plant of *Pitcairnia integrifolia* in Trinidad and photograph of a plant with the head of the porometer attached, which was used for measurements. (Lüttge et al. 1986)
and arid regions (Schulze et al. 1974, 1975a,b; Tenhunen et al. 1980, 1981, 1984; Pathre et al. 1998) and also frequently observed among trees in savannas and cerrados (Sect. 10.1.2.3, Figs. 10.10–10.13). The midday-depression may be smaller or larger. Gas exchange may be totally absent during this time by full stomatal closure. Moreover, recovery in the afternoon, as shown for example in Fig. 5.3, may be expressed to different extents and with increasing drought it may not occur at all. Usually nocturnal rehydration may provide more effective recovery but this as well will be reduced as drought becomes increasingly severe.

In addition to mechanisms of stress tolerance, there are also means of stress avoidance. P. integrifolia for example may roll its leaves, exposing only the lower abaxial surface to the sun. This surface is densely covered by silvery trichomes. Bromeliad trichomes have evolved for absorption of water and nutrients (Sect. 6.4). The trichomes of P. integrifolia are non-absorbent and composed of dead cells which effectively reflect the light. Compared to white paper (100% reflectance) the reflectance of the abaxial leaf surface with scales was found to be 46.5% but only 19.8% when the scales were removed. As an alternative role of the non-absorbent bromeliad trichomes functioning as a water repellent has been discussed rather than reflection of excessive light and reduction of photoinhibition (Pierce et al. 2001).
5.2.2.2 CAM: Escape from the Dilemma Desiccation or Starvation

Choosing between limiting the effects of any one stress represents a daily “damage limitation exercise” such that plants with C3-photosynthesis face the dilemma of desiccation or starvation, when under water stressed conditions. With the midday-depression, the strategy is to try to avoid desiccation by stomatal closure at the expense of CO2-supply for photosynthesis. Desiccation is always more rapid and is the more immediate danger than starvation. One escape from this dilemma is provided by the evolution of crassulacean acid metabolism (CAM) (Box 5.1), where CO2 is fixed during the night, when water-vapour pressure saturation deficit of the atmosphere is much lower than during the day, and hence stomatal opening has a smaller effect on the water budget of the plants. The CO2 fixed is stored in chemical form of organic acids mainly as malic acid, remobilized again during the day and made available for photosynthesis, so that the plants can utilize the light energy of solar irradiance for CO2-assimilation behind closed stomata.

![Phylogenetic tree of plant families with Crassulacean acid metabolism](image)

**Fig. 5.4** Phylogenetic tree of plant families with Crassulacean acid metabolism
This mode of photosynthesis was first discovered in plants of the genus *Kalanchoë* (see Sect. 2.5), which belong to the family of the Crassulaceae, and hence the name. However, it has evolved independently several times, i.e. polyphyletically, since there are CAM-performing taxa on almost all branches of the phylogenetic tree of vascular plants (Fig. 5.4). Among the plants of the thornbush-succulent forests many are CAM-plants, i.e. the cacti in the new world (Figs. 3.11B and 3.13), the succulent Euphorbiaceae in the old world, the Didieraceae (Fig. 3.12) and many of the rosette plants in the Bromeliaceae (which may cover the whole floor of neotropical dry forests like the rosettes of *Bromelia humilis* in Fig. 3.10A), Agavaceae and Liliaceae, to name the major ones.

However, CAM may not only operate in the simple day-night fashion described above. In fact it provides an enormous range of plasticity in form and function, allowing responses to environmental conditions to be optimised (see also Sect. 2.5). The best way of describing these options is by reference to the four phases of CAM according to the nomenclature introduced by Osmond (1978; see Box 5.1). Phase I represents nocturnal stomatal opening with CO₂-uptake, fixation and storage as malic acid, whereas during phase III daytime stomatal closure with CO₂-remobilization and assimilation occurs. Phases II and IV are transitional phases in the early morning and in the afternoon. Phase IV often plays an important role, because when CAM plants are well watered it may be quite extensive. Then CAM plants take up CO₂ directly from the atmosphere and assimilate it directly by the C₃-mode of photosynthesis via RuBISCO. This can make a major contribution to their productivity.

Conversely, water stress may become so severe that even CAM plants face the dilemma of desiccation or starvation. Then, stomata may be closed even during the night, and CAM represents an option for survival by recycling CO₂ internally. The CO₂ evolved nocturnally during respiratory metabolism is refixed and stored as malic acid; the day-time remobilization and reassimilation, using solar radiation, recycles carbohydrate reserves for the subsequent night (Box 5.1). Under severe drought stress cacti, for instance, keep stomata closed continuously for many months (see also Sect. 8.2.3.2.1). By CO₂-recycling they do not gain carbon, but very little is lost and solar energy can be used to maintain metabolism and remain competent until water is available again. At the same time, with totally closed stomata, the plants lose only a little water via cuticular transpiration. Water storage tissues in cacti and other succulents also provide reserves and help to overcome drought periods.

In a drought deciduous forest in western Mexico, Lerdau et al. (1992) studied the performance of the arborescent cactus *Opuntia excelsa*. In the dry season, when trees had shed their leaves, the cactus had a competitive advantage, as there was no light limitation. However, a factor associated with plant size, possibly water status, limited carbon gain during the dry season. Larger individuals were able to utilize water stored in their trunks and main branches (see also Sect. 8.2.3.2.1). Light availability in the forest understorey constrained CO₂-assimilation of the cactus in the wet season.

Daytime CO₂-remobilization from nocturnally stored organic acids behind closed stomata also participates in controlling photoinhibition which would be amplified
Box 5.1 Crassulacean acid metabolism (CAM)

In CAM plants there are two ways of primary CO$_2$ fixation, namely via the enzymes phosphoenolpyruvate-carboxylase (PEPC) and ribulosebiphosphate-carboxylase oxygenase (RuBISCO). In its typical performance CAM has four phases (Osmond 1978):

- **Phase I:**
  Nocturnal dark fixation of CO$_2$ via PEPC generating malic acid, which is translocated into the vacuole by proton pumps (H$^+$-ATPase and H$^+$-pyrophosphatase – PP$_i$ase – transporting protons) and an inward rectifying malate anion channel (transporting malate$^{2-}$) at the tonoplast.

- **Phase II:**
  A transition phase in the early morning, after light energy becomes available, with primary CO$_2$ fixation partially via PEPC and RuBISCO, respectively.

- **Phase III:**
  Efflux of non-dissociated malic acid from the vacuole, malate decarboxylation and refixation of the CO$_2$ via RuBISCO behind closed stomata.

- **Phase IV:**
  Opening of stomata in the afternoon, when nocturnally accumulated malic acid is consumed, and primary CO$_2$ fixation via RuBISCO.

CAM may play a role as a water-conserving mechanism at different levels of drought stress.

- In the typical performance dominating nocturnal CO$_2$ uptake reduces transpirational loss of water related to CO$_2$ acquired and thus increases water-use efficiency, because the evaporative demand on leaves with open stomata is smaller in the dark than in the light.

- At increased drought stress first phase IV and then also phase II are eliminated, and stomata remain closed for the whole light period, further restricting transpirational loss of water.

- At still more severe drought, stomata may also be partially or totally closed during the dark period. In this situation the CO$_2$ fixed nocturnally for the accumulation of malic acid partially or totally may come from internal sources, i.e. mainly respiration (CO$_2$ recycling). This further reduces transpirational loss of water but also limits carbon acquisition.

The scheme of CAM (►) shows the key reactions in metabolism. With PYR pyruvate; PEP phosphoenolpyruvate; OAA oxaloacetate; MAL malate; $P_i$ inorganic phosphate; $[\text{CH}_2\text{O}]$ carbohydrate and transport across the tonoplast: with MC malate transporter; the H$^+$-ATPase and H$^+$-PP$_i$ase, and passive malic acid efflux.

Net CO$_2$ exchange by the CAM-plant Kalanchoë daigremontiana (►►) with increasing drought stress: o—o well-watered; +—+ low and ●—● high drought stress. Phases I to IV are indicated. Phase II and IV CO$_2$ exchange is expressed only in the well-watered plant; onset of phase I CO$_2$ exchange is delayed in the severely stressed plant (Smith and Lüttge 1985).
when internal CO₂-levels at high irradiance were low as in the midday depression of C₃-plants (Sect. 5.2.2.1) (Osmond 1982; Adams and Osmond 1988; Griffiths 1989). In fact, internal CO₂-levels ($p_{iCO_2}$) behind closed stomata during the light period of CAM may be very high and reach up to a few percent (Cockburn et al. 1979; Kluge et al. 1981; see Lüttge 1987, 2002). However, in correlation with the internal CO₂-concentrating mechanism of organic acid remobilization from the vacuoles and the

Fig. 5.5 Chlorophyll-fluorescence variables (see Box 4.6 for explanation) in Clusia minor in the C₃ state (---) and in the CAM state (-- · · · phase II, · · · · · · phase IV, —— phase III). (Haag-Kerwer 1994)
related high rates of CO₂-reduction, high internal oxygen concentrations also build up, i.e. close to 40% or twice the atmospheric O₂-concentration (Lüttge 2002). Thus, other protective mechanisms of energy dissipation (Sects. 4.1.4 and 4.1.6) must also be active.

Experiments measuring chlorophyll fluorescence in the neotropical facultative CAM-tree *Clusia minor*, which can perform both CAM and C₃-photosynthesis (Sect. 6.6.2.3), have shown that photoinhibition, if it occurs, is most likely to be observed during phase IV of CAM, when stomata are open and plants fix CO₂ via RuBISCO rather than in phase III. Light response characteristics of chlorophyll-fluorescence variables (see Box 4.6) in phases II and IV were similar to those observed with *C. minor* in the C₃-state and very different to those of phase III of CAM (Haag-Kerwer 1994; Fig. 5.5).

When nocturnal accumulation of malic acid occurs from recycled CO₂ alone (100% recycling), this is an extreme case. However, stomata may only be partially closed during the night and malic acid accumulation may be due to both recycled CO₂ and CO₂-uptake from the atmosphere. Since the stoichiometry of CO₂-fixed to malic acid formed is unity, recycling can be calculated in absolute terms as

\[
\text{malic acid accumulated minus CO₂ taken up}
\]

or in relative terms (% recycling) as

\[
\frac{\text{malic acid accumulated minus CO₂ taken up}}{\text{malic acid accumulated}} \times 100.
\]

The degree of recycling may then depend on the severity of drought stress. This is illustrated in Fig. 5.6 by a study of *Aechmea aquilega* and its higher altitude coun-

![Fig. 5.6 Net nocturnal CO₂ uptake from the atmosphere and internal CO₂ recycling of Aechmea (A. aquilega at the three lower altitudes and A. fendleri at the highest altitude) in relation to altitude and precipitation in Trinidad. (After data of Griffiths et al. 1986)
terpart *Aechmea fendleri* along a gradient of altitude and precipitation in Trinidad. *A. aquilega* grows both terrestrially and epiphytically from very dry deciduous thornbush-forests to quite wet forests, and *A. fendleri* is epiphytic in wet forests. Figure 5.6 shows that with increasing altitude and precipitation total CO₂-uptake by the *Aechmeas* increased and relative CO₂-recycling decreased considerably.

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Chapter 6
Tropical Forests. IV. Lianas, Hemi-Epiphytes, Epiphytes and Mistletoes

6.1 The Conquest of Space:
Cryptogams and a Diversity of Life Forms of Vascular Plants

Perhaps epiphytism could be thought to be primarily the utilization of any possible surface for holdfast and establishment, i.e. a conquest of space with epiphytes found in aquatic and terrestrial habitats made up of various combinations of lower and higher plants. In aquatic habitats, i.e. lakes, rivers and the sea, there are always algae growing on each other. This not only applies to unicellular and filamentous forms and their colonies, but also to macroalgae like kelp and red algae. In the mesic terrestrial climate many lower plants are epiphytic, like mosses and lichens and also some forms of small pleurococcoid aerial green algae as well as cyanobacteria (blue green algae). In the tropics lower plants may constitute massive formations of epiphytic biomass, e.g. the bryophytes the biomass of which increases with altitude (Freiberg and Freiberg 2000) in upper montane cloud forests (“moss-forests”, Fig. 6.1). Even the surfaces of leaves of plants in such forests may harbour a diverse flora or phyllosphere with bacteria, cyanobacteria, fungi, green algae, bryophytes and lichens and occasional seedlings of vascular plants (Ruinen 1961, 1974; Coley et al. 1993; Freiberg 1998) (Fig. 6.2).

Life forms of vascular plants that evolved in the conquest of space are lianas, hemi-epiphytes and the mistletoes, where the latter not only compete for space but also combine epiphytism with parasitism. In the temperate zone we have climbers and vines often especially in moist gallery forests, but if we exclude the parasites of the mistletoes among the vascular plants the fern Polypodium vulgare is the only known epiphyte, and moreover, it is only facultatively epiphytic. In contrast, the popular view of tropical rainforests is determined by the image of an abundant flora of epiphytes, vines and lianas, climbers with hanging and host-strangling shoots and curtains of aerial roots (Fig. 6.3).

This image, although intuitively correct, needs to be carefully differentiated. Growth of lianas, climbers and vines is particularly rich at the perimeter of forests, along rivers, roads and around clearings. They are often light-demanding plants. Epiphytes are often although not generally found to be more abundant in montane
rainforests and in cooler upper montane fog and cloud forests, where air moisture is always high, than in the hot lowland rainforests (Freiberg and Freiberg 2000).

Remembering that vascular plants evolved from aquatic ancestors during the conquest of land and that then they were subject to many new kinds of stress with respect to water and nutrient relations, it may not be surprising that there is very little
Fig. 6.2A, B Epiphylls. **A** On a leaf of *Clusia* sp., with cyanobacteria, algae, mosses and lichens (Sierra Maigualida 05°30' N, 65°15' W). **B** On a leaf in a cloud forest above Lake Coté (Costa Rica) with mosses and a higher-plant seedling.

fossil record of epiphytism. Epiphytism must be a fairly recent development among vascular plants. Most epiphyte diversity dates from the Pliocene-Pleistocene (Benzing 1989a, 1990; Lüttge 1989). Against this background, when plants may even live in the air, this may be considered a rather extreme case of the conquest of space. The
Fig. 6.3A–C Rainforests with epiphytes and lianas. A Plate from Martius’ Flora Brasiliensis (Martius 1840–1906). B A cloud forest above Lake Coté, Costa Rica. C Curtain of aerial roots of a strangler fig (*Ficus*) (Queensland, Australia)
so-called atmospheric bromeliads constitute such life forms. They have given up any contacts with substrates supplying water and nutrients other than from the atmosphere. They may hang down from the branches of phorophytes (see Fig. 6.15D below) or may even get holdfast on wires of fences or telephone lines (Fig. 6.4).
Table 6.1  Taxonomic diversity of epiphytes. (Data from Kress 1989)

<table>
<thead>
<tr>
<th>Number of taxa</th>
<th>% epiphytes of total taxa of vascular plants</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>23,466</td>
</tr>
<tr>
<td>Genera</td>
<td>879</td>
</tr>
<tr>
<td>Families</td>
<td>84</td>
</tr>
<tr>
<td>Orders</td>
<td>44</td>
</tr>
</tbody>
</table>

Evolution of epiphytism has clearly occurred many times and has been polyphyletic, since taxonomic diversity of epiphytes is quite substantial (Table 6.1). The best-known families with epiphytes are headed by the Orchidaceae, although the Araceae, Piperaceae and Bromeliaceae are also important, and epiphytic taxa are abundant among ferns. In some tropical forests up to 50% of all leaf biomass may be due to epiphytes, and of the known species of lianas 90% are native to the tropics. The meagre fossil record of epiphytes (Mägdefrau 1956) does not offer support for the discussion of evolution. The upper Devonian arborescent horsetail, *Pseudoborina ursina* about 360 million years ago had a stem diameter of 0.12 m and carried an epiphyte *Codonophytum epiphytum*. The phylogenetic relationships, however, are uncertain. In Permian formations in Germany from about 260 million years ago leafy organs resembling basket forming mantle leaves of extant epiphytic ferns of the genera *Platycerium* and *Polypodium* are preserved. However, these extant fern genera are leptosporangiate, and such forms did not exist at that time. The most original extant pteridophytes are two species each of the genera *Psilotum* and *Tmesipteris* and all of them are epiphytes. They belong to the Psilotatae and are often considered as relicts of evolution. Although they are very similar to the earliest land plants, i.e. the Psilophytae, which first conquered land and died out again in the middle Devonian 360 million years ago, the exact phylogenetic relationships again are not clear. From the very poor palaeontological record alone one may readily conclude that epiphytism of vascular plants is a very recent event in geological history.

6.2 Cryptogams

6.2.1 Bacteria and Cyanobacteria

Microclimate and, foremost, the moisture and availability of liquid water is the most important parameter determining the frequency and biodiversity of epiphylls (Freiberg 1999). Bacteria may make the cuticle of leaves more permeable for water as they secrete surfactants and extracellular enzymes (Schreiber et al. 2005). Coverage of the host leaves by mats of cyanobacteria can have adverse effects on light utilization by the leaves. However, it has been suggested that nitrogen fixation by the epiphyllic cyanobacteria may also supplement nutrients available to the host (Ru-
Dinitrogen \((\text{N}_2)\) reduction in the phyllosphere mainly depends on light and water. Maximum rates measured are \(5 \text{nMN m}^{-2} \text{ leaf surface s}^{-1}\) (Freiberg 1998). In a premontane tropical rainforest in Costa Rica N-supply by N\(_2\)-fixation in the phyllosphere was calculated as 2 to 7 kg N ha\(^{-1}\) year\(^{-1}\) (Freiberg 1994) but the higher values (30 to 60 kg N ha\(^{-1}\) year\(^{-1}\)) which have been presented in the literature for other areas are discussed critically (see also Sect. 10.2.3.2.1).

### 6.2.2 Bryophytes and Lichens

As shown above (Sect. 6.1, Fig. 6.1) bryophytes and lichens may constitute a considerable floristic diversity and biomass among the epiphytes in tropical rainforests, especially in the cloud forests at higher elevations with their cooler nights (Seifriz 1924; Sipman 1989). Epiphyllous liverworts are involved in a reciprocal transfer of nitrogen with their host leaves, where the amount of nitrogen obtained by the epiphyllous liverworts from the host leaves varies between 1\% and 57\% of their entire demand, and vice versa host leaves obtain mostly up to 2.5\% of their nitrogen demand from leachates of the epiphylls (Wanek and Pörtl 2005).

Green and Lange (1994) have provided a comparison of photosynthesis in mosses and lichens. A major difference between the two groups is the effect of water relations on photosynthesis. In mosses, the CO\(_2\)-exchange surface is external, and the mosses have special water storage volumes, i.e. special cells – often dead cells – and capillary structures, which are separated from the gas exchange areas. Therefore bryophytes may constitute most important water stores in the epiphytic habitat (Freiberg 1997). Lichens have an internal CO\(_2\)-exchange surface with the phycobionts embedded in a relatively compact fungal tissue, and any water storage will tend to hinder gas exchange either within the compact tissue or at the outer lichen surface. Therefore, as compared to mosses, lichens tend to have lower maximal water content on a dry weight basis and there is the risk that high thallus water content impairs CO\(_2\)-uptake and assimilation. This difference between the two groups possibly explains the particular dominance of bryophytes in very wet habitats, while lichens can also be very successful in dry habitats. Bryophytes are also well adapted to the large variation of temperatures in their montane, cloud and elfin forest habitats. They show constitutive temperature resistance to both rather cool temperatures often encountered in these habitats and quite hot temperatures that may occur during light fleck events (Lösch and Mülders 2000).

Floristics, taxonomy and habitat occupation by tropical lichens has been well studied (Galloway 1991). Less work is available on their ecophysiology. However, ecophysiological studies have investigated lichens in the temperate rainforests, e.g. in New Zealand (Green and Lange 1991; Green et al. 1991; Lange et al. 1993) and also in forests of the wet tropics (Lange et al. 1994; Zotz and Winter 1994a). Lange et al. (1994) have studied the gas exchange, water relations and potential productivity of the cyanobacterial basidiolichen *Dictyonema glabratum* living epiphytically,
saxicolously and terrestrially in a lower montane tropical rainforest in Panamá with an annual precipitation of 4,000 – 4,500 mm and a mean annual temperature of 21 – 22 °C (Fig. 6.5). This lichen occurs both in shaded and exposed sites, and it is quite frequent in this forest. It has a rather unusual ecophyiological behaviour with respect to water saturation of its thallus and a number of additional traits, which explain its high productivity in the habitat.

Normally photosynthetic net CO₂-uptake is impaired in lichen thalli including lichens in tropical forests (Lange et al. 2000, 2004) when they are oversaturated with water due to diffusion limitation from surface water or blocked air channels in the mycelium (e.g. see Sect. 11.2.2 and Fig. 11.22). However, not in all lichens water saturation inhibits CO₂-diffusion. The reasons are not known. It is not related to a formation of secondary chemical lichen compounds and must be due to morphological features (Lange and Green 1997; Lange et al. 1997). *D. glabratum* maintains maximum rates of net-CO₂ uptake when it is fully hydrated up to a water content of 1,000% of its dry weight (Fig. 6.6). This allows maximum benefit from the heavy rain storms occurring in the habitat. The lichen also possesses a mechanism for concentrating internal inorganic carbon by energy dependent transport, which occurs in many algae and also higher water plants (see Griffiths 1989; Badger et al. 1993). This mechanism allows photosynthesis at elevated intracellular CO₂-levels. In corticulous crustose green algal lichens in the understory of a lowland tropical rainforest periods of thallus suprasaturation with water are reduced by the presence

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**Fig. 6.5** The lichen *Dictyonema glabratum* (syn. *Cora pavonia*) growing epiphytically on a 6-m-tall bush in a lower montane tropical rainforest in Panama. (Photograph courtesy B. Büdel; see Lange et al. 1994)
6.2 Cryptogams

Fig. 6.6 Net photosynthesis of the lichen *Dictyonema glabratum* in relation to water content in percent of dry weight. (Lange et al. 1994)

![Net photosynthesis graph](image1)

Fig. 6.7 A daily course of net CO₂ exchange and water content of the lichen *Dictyonema glabratum* with air temperature and light intensity (PPFD) in its natural habitat in a lower montane rainforest in Panamá; measured on 23 September 1993 by Lange et al. (1994)

![Daily course graph](image2)

of water-repelling surface structures of the hyphae of the mycobiont as well as the production of a hydrophobic fungal protein, hydrophobin (Lakatos et al. 2006).

Net CO₂-exchange on many days is typically bimodal with a peak in the morning, when thalli are wetted from dew and early fog, and another peak after midday when heavy showers may occur (Fig. 6.7). In between, the thallus may dry out and CO₂-uptake ceases. In fact, drying out occurs for a few hours almost every day, and similar to most lichens, *D. glabratum* is also desiccation tolerant (Sect. 11.4.2). However, unlike many other lichens it does not reactivate photosynthetic CO₂-fixation immediately after rewetting following desiccation, but it needs a recovery period of
about 60 min. Thus it appears that lichens of the very moist lower montane rainforest show subtle changes in rehydration and reactivation characteristics as compared to lichens from temperate or arid habitats (Sect. 11.4.2).

Another important trait is the thermophily of *Dictyonema glabratum*. It has been noted above that epiphytic mosses and lichens are particularly abundant in forests at higher elevations. The better supply of water in the epiphytic habitat by dew and fog may only be one reason for this distribution. An even more critical factor may be the reduction of respiration at lower night temperatures because respiration is a critical factor in the net productivity of lichens in the tropics where respiratory losses may be substantial. Indeed, the cooler nights much reduce respiration and thus nocturnal loss of carbon, which is a considerable factor in overall productivity, may be decisive for the general preponderance of epiphytic mosses and lichens in cloud and fog forests in the tropics. In *Dictyonema glabratum* respiration increases only slightly with temperature up to 22 °C, but then increases sharply with higher temperatures. Net photosynthesis increases up to 22 °C and then declines in parallel with increasing respiration, so that gross photosynthesis calculated from net photosynthesis and respiration remains at a constant high level up to 40 °C. The balance of net photosynthesis is positive up to 35 °C (Fig. 6.8). In fact the maximum rates of net CO₂-uptake in *Dictyonema glabratum* are quite high even in comparison to sun plants among vascular epiphytes (see below: Table 6.6). On a thallus area basis the highest rate observed in the field was 8 µ mol m⁻² s⁻¹. Calculations have suggested that the annual relative production under the habitat conditions of *Dictyonema glabratum* in Panamá is 2.28, i.e. a gain of 2.28 g of carbon per 1 g of initial thallus carbon. Thus, even with leaching of carbon under the influence of regular heavy rain which is frequently observed in lichens (Bruns-Strenge and Lange 1992), *Dictyonema glabratum* must retain sufficient surplus to allow rapid growth.

**Fig. 6.8** Net photosynthesis, dark respiration and calculated gross photosynthesis of the lichen *Dictyonema glabratum* in relation to temperature at a light intensity (PPFD) of 150 µ mol m⁻² s⁻¹ and at high thallus water content. (Lange et al. 1994)
This behaviour of a tropical rainforest lichen is quite remarkable in comparison to the slow growth otherwise observed among lichens. The observations of Lange et al. (1994) put the **biomass production of lichens** and its ecological importance in tropical fog and cloud forests in a new perspective. Other lichens may have similar capacities for high productivity (Zotz et al. 1998; Lange et al. 2000, 2004). Lichens with cyanobacteria as phycobionts are particularly frequent in the moist tropics (Büdel et al. 2000). In the **cyanobacterial lichens dinitrogen fixation** is an additional advantage. If we average maximum rates of net photosynthesis given by Lange et al. (2000, 2004), a superior performance of cyanobacterial lichens compared to green alga lichens is observed with rates in µmol m\(^{-2}\) s\(^{-1}\) of 5.3 ± 1.9 (11) and 3.0 ± 1.1 (3), respectively (SD with number of measurements including different species). In the balance of overall productivity, however, it must be noted that maximum rates are only possible for short periods each day (Fig. 6.7) and respiratory losses are significant (Fig. 6.8; Lange et al. 2000, 2004). In the deep shade of the understorey of tropical rain forests lichens may also make effective use of light-flecks (Lakatos et al. 2006; Sect. 4.2.1).

### 6.3 Lianas, Climbers, Vines and Hemi-Epiphytes

Lianas, climbers and vines are rooted in the soil and use other plants, especially trees, as support for growth away from the ground (Holbrook and Putz 1996a). It is mostly assumed that the particular advantage of this habit is to allow these plants to escape from deep shade and to reach the upper canopy of forests. This implies that their seeds would germinate in the shade and seedlings initially would grow upwards and develop in the shade. In the tropics, lush growth of lianas and climbers, however, is mostly found adjacent to clearings and in sites disturbed by man, and it appears that these forms need high irradiance for establishment and development. Lianas in fact can slow down successions in the reinvansion of gaps (Sect. 3.3.3), in that they suppress climax species, and thus, support the growth of pioneer species (Schnitzer et al. 2000). Growth of saplings of trees is not only inhibited by lianas via competition for light but also below ground via competition in the root medium (Schnitzer et al. 2005).

The plants climb using **tendrils** formed from modified leaves or parts of leaves, shoots or adventitious roots. Shoots wind around branches or form coils, which are then modified by the **secondary thickening**, so that the wood develops in the form of bands (Fig. 6.9), or it is fragmented to individual strands forming rope- or cable-like structures which are resistant to torsion.

Some species in the aroid genera *Philodendron* and *Monstera* and the Cyclanthaceae *Asplundia* begin their life with rooting in the soil and climbing up a phophyte, but later their old roots degenerate. By growing at the tip and continuously degenerating the base of their shoots, they literally crawl up their hosts. Hence, they begin as lianas and later become epiphytes. They have been termed **secondary hemi-epiphytes**. However, this term is not all that convincing; strictly they are sec-
Fig. 6.9 Spirally twisted flat and band-like shoots of lianas

ondarily epiphytes. Moreover, in some cases aerial adventitious roots can be formed again, which may hang down from these plants like curtains (Fig. 6.3C) and establish contact with the ground for a second time. Thus, secondary hemi-epiphytes would become primary hemi-epiphytes, a term used for plants which start their life epiphytically but subsequently establish soil-contact.

The latter include the stranglers, a true group of “murderers”. Among them is a genus with an extreme plasticity, namely Clusia (Clusiaceae, Order Theales) (see also below: Sect. 6.6.2.3). Clusia-seedlings may get established terrestrially and grow directly as independent trees. However, these plants, like other stranglers, may begin their seedling stage as humus epiphytes, using accumulations of humus in knotholes or between branches of phorophytes for establishment (Fig. 6.10A). Alternatively, they germinate in epiphyte gardens together with several other epiphytic species (Fig. 6.10B–D), where tanks of bromeliads or nest and basket-forming ferns provide the required substrate. Then, adventitious roots develop, some of which grow positively gravitropically to the ground whilst others are attached to the host tree (Fig. 6.11). First they may only compete with their host for light. Subsequently, after rooting in the ground, they also compete for nutrients in the soil. Eventually they strangle and kill their host. Their adventitious roots surrounding the trunk of the host tree hinder the secondary thickening and clamp the phloem in the bark with the sieve tubes, the tender pathways for long distance transport of assimilates. Prevented from adequate partitioning of supplies, the phorophyte dies. It seldom falls
Fig. 6.10A–D Epiphytic seedlings of *Clusia rosea* in humus accumulation of tree forks (A) in an epiphytic garden (B), and inside tanks of the bromeliad *Aechmea lingulata* (C, D). In D the tank of *A. lingulata* has been cut open showing the accumulated humus and the root system of a *Clusia* seedling.
Fig. 6.11 Adventitious root-system of the strangler *Clusia rosea*

down. The roots of its ungrateful visitor often form a veritable net with anastomoses via parenchyma bridges, and inside this hollow cylinder of adventitious roots the stem of the former host rots away. Thus, the originally epiphytic strangler becomes an independent tree with a **pseudostem** of adventitious roots. Such behaviour is not only observed by *Clusia*, of course, but equally by other genera with stranglers, e.g. *Ficus* species (Fig. 6.12). Other species of *Ficus*, i.e. *F. pertusa* and *F. trigonata* live in palm trees. They generate negatively gravitropic roots which suspend them in the crowns of the palms, where they find humus between the leaf bases (Putz and Holbrook 1986). A most successful form is represented by *Ficus bengalensis*. The original aerial roots of a single plant, after gaining ground-contact, may form an entire forest of pseudostems. Walter and Breckle (1984) described an individual, which was only 26 m tall but had an average crown diameter of 170 m, a crown circumference of 530 m and a crown area of 22,000 m². (See also *Ficus microcarpa* in Fig. 6.12C.)

By clasping other plants lianas are saving investment in thick stems which would provide independent support for their heavy plant biomass. Only the first shoots produced after germination are self supporting and their Young’s modulus is high indicating higher stiffness or lower elasticity, then the shoots start to climb which is associated with anatomical changes and a decreasing Young’s modulus (Rowe and Speck 1996; Speck 1997). The reduction of supporting tissues in lianas is also true for their leaves which are found to have a lower leaf mass per unit leaf area and this is also beneficial for optimising nitrogen use in relation to photosynthesis of
fast growing lianas (Kazda and Salzer 2000). Using the support by their host plants lianas can afford to have very wide xylem vessels reducing friction for the transpiration stream and facilitating transport over long distances (Ewers et al. 1990). Vessels of up to 0.7 mm in diameter have been observed. The xylem sap readily
flows out of these wide vessels when they are cut open. Wandering around one may serve oneself from such lianas for a cool drink. Vareschi (1980) reports on a 1 m long piece from which 205 ml of water were collected within 3 min.

Thus, lianas and hemi-epiphytes evidently develop a particular hydraulic architecture to support a huge leaf biomass via relatively thin shoots. The theoretical expectation is that compared to free standing trees (Zotz et al. 1997):

- lianas and hemi-epiphytes show significantly higher specific stem conductivity, $K_s$,
- lianas and hemi-epiphytes show less wood cross-section per unit leaf area, i.e. lower Huber-values, $H_v$,
- lianas and hemi-epiphytes tend to have less conductive stems per unit leaf area, $K_l$.

A quantitative comparison between free standing trees of three species and hemi-epiphytes of four species of Ficus, respectively, and the hemi-epiphyte Clusia uvitana has been presented by Patiño et al. (1995), where Ficus species are C_3-plants and C. uvitana is a C_3/CAM-intermediate species (Table 6.2). The ranges of $K_s$ values for the hemi-epiphytic and the terrestrial Ficus species overlap, but as expected much higher maximum values are reached in the hemi-epiphytes. However, for the hemi-epiphytic C. uvitana the $K_s$ value is much lower. As also expected $K_l$ values are lower in hemi-epiphytic Ficus species than in free standing trees, but the values for C. uvitana are still much lower. The Huber-values, $H_v$, are similar in both the C_3 and C_3/CAM-hemi-epiphytes and as expected lower than in the free standing trees. The differences in $K_s$ and $K_l$ values between the hemi-epiphytes with the different modes of photosynthesis show that in addition to hemi-epiphytism hydraulic architecture is also related to the performance of CAM and that due to the water saving mechanism of CAM (Sect. 5.2.2.2, Box 5.1) C. uvitana can afford lower specific stem conductivity, $K_s$, and lower leaf specific conductivity of stems, $K_l$.

The wide vessels of lianas are potentially prone to cavitation and embolism which would lead to loss of conductivity. However, Andrade et al. (2005) observed that maximum sap flow densities in co-occurring lianas and free standing trees were comparable at a similar stem diameter. In the tropical vine-like bamboo Rhipido-

### Table 6.2 Hydraulic architecture parameters of free standing trees and hemi-epiphytes of the genus Ficus and the hemi-epiphyte Clusia uvitana (rounded up values from Patiño et al. 1995)

<table>
<thead>
<tr>
<th></th>
<th>Free standing trees</th>
<th>Ficus Hemi-Epiphytes</th>
<th>C. uvitana Hemi-Epiphyte</th>
</tr>
</thead>
<tbody>
<tr>
<td>Specific stem conductivity $K_s$ (kg s$^{-1}$ m$^{-1}$ MPa$^{-1}$)</td>
<td>11 to 14</td>
<td>7 to 34</td>
<td>1.1</td>
</tr>
<tr>
<td>Cross section per unit leaf area $H_v \times 10^4$</td>
<td>2.0 to 6.1</td>
<td>1.0 to 2.2</td>
<td>1.4</td>
</tr>
<tr>
<td>Conductive stem per unit leaf area $K_l$ (kg s$^{-1}$ m$^{-1}$ MPa$^{-1}$)</td>
<td>23 to 52</td>
<td>7 to 23</td>
<td>1.5</td>
</tr>
</tbody>
</table>
**Box 6.1 Some basic principles of water relations of plants**

The water potential \( \psi \) is defined as

\[
\psi = \frac{\mu_{\text{H}_2\text{O}} - \mu_{\text{H}_2\text{O}}^0}{V_{\text{H}_2\text{O}}},
\]

where \( \mu_{\text{H}_2\text{O}}^0 \) is the chemical potential of pure water, \( \mu_{\text{H}_2\text{O}} \) the actual chemical potential of water in a solution and \( V_{\text{H}_2\text{O}} \) the partial molar volume of water.
ψ is best explained using an osmotic system of two chambers separated by a **semipermeable membrane** each having a vertical tube. The solvent particles (\(\bullet = \text{H}_2\text{O}\) molecules) can pass the semipermeable membrane, whereas the solute particles (\(\circ = \text{solute}\) molecules) cannot permeate.

The difference of **osmotic pressure** between the solutions of the two chambers, \(\Delta \pi\), drives water across the semipermeable membrane from the chamber of the lower osmotic pressure, \(\pi\), to the chamber of the higher \(\pi\). The flow of water is a **volume flow** \(J_v\). The associated volume change leads to the ascent of solution in the vertical tube of the chamber with the higher \(\pi\). The column of solution exerts a **hydrostatic pressure** on the solution, \(\Delta P\), which counteracts the osmotic water flow driven by \(\Delta \pi\). At thermodynamic equilibrium

- \(\Delta P = \Delta \pi\) and \(\Delta \psi = 0\),

i.e. there is no water potential difference between the two chambers since at any given time

- \(\Delta \psi = \Delta P - \Delta \pi\).

All parameters have the physical unit of a pressure. \(\pi\) is related to the **solute concentration**, \(c\), as follows

- \(\pi = c \cdot R \cdot T\),

where \(T\) is the temperature in Kelvin and \(R\) the universal gas constant.

In plant cells \(P\) is built up at the elastic **cell walls** and is called **turgor pressure**.
Box 6.1  (Continued)

Measurements of \( \psi \) can be made by psychrometric techniques or using a pressure chamber. In the latter case a plant shoot or leaf is tightly sealed in the chamber, with the cut stem or petiole protruding to the outside. When pressure is exerted on the air in the chamber, xylem sap is expressed from the cut end. The equilibrium pressure, where the sap just reaches the cut end, can, with certain precautions, be related to the water potential of the stem or leaf.

\( P \) can be measured by inserting small glass capillaries into cells which are adjoined to a pressure transducing read-out system (pressure probe). Often it is also calculated from \( \psi \) and \( \pi \), but this needs to be interpreted with care.  
\( \pi \) is obtained from psychrometry or freezing point determinations of cell sap. Plasmolysis studies are also applied. 
(See textbooks, e.g. Nobel 1983; Lüttge et al. 2005.)

6.4 Epiphytes

As noted above, the only vascular epiphyte in the mesic climate, the fern Polypodium vulgare, is a facultative epiphyte. This means that there are gradations between the terrestrial and epiphytic habit (Gessner 1956; Richards 1996). In the tropics many species, e.g. among bromeliads and aroids, grow equally well terrestrially and epiphytically (Fig. 6.13; see also Table 6.4).

Benzing (1989a) has conceived five different schemes alternatively classifying epiphytes in categories based on:
I. relationships to the host (or “phorophyte”),
II. growth habit,
III. humidity,
IV. light
V. phorophyte-provided media

(Table 6.3). The epiphytic life form is effectively encompassed in categories I and II. The other three categories refer to the three major stress factors of epiphytic plant life (see Sect. 6.6). The entire system of five schemes is very useful as it offers a good summary of the great morphological and ecophysiological diversity among epiphytes and their associates. On the other hand, it suffers from the general problem of attempts of this kind of casting the diversity of life into schematic systems. Thus, the study of case stories may prove more appealing.

One of the most exciting case stories is offered by the Bromeliaceae (for monographs see Martin 1994; Benzing 2000). They operate with tanks and epidermal scales or trichomes. The tanks are made up by densely overlapping leaf-bases of the rosette-forming bromeliads and depending on life form there is a gradation in effectiveness of water storing capacity. The scales are epidermal structures which developed increasing complexity during the evolution of bromeliads. They consist of living basal or foot cells, stalk cells, which may be living or dead in the mature stage of the trichomes, and the actual scales comprised of dead cells (Fig. 6.14).
Fig. 6.13A,B The bromeliad *Aechmea lingulata* growing both terrestrially (A) and epiphytically (B). (St. John-Island, US Virgin Islands, Lesser Antilles)

Fig. 6.14A,B Schemes of scales of bromeliads. A Top view. B Cross-section the living cells of the scale dotted and with a nucleus. The black line along cells in B indicates cutinization of the epidermal cells and the outer walls of the trichome stalk cells which allows entry of solutes into the leaves only via a specific pathway enforcing membrane passage and cytoplasmic control over the solutes taken up. (After Sitte 1991 with permission of G. Fischer-Verlag)
### Table 6.3
Five different schemes alternatively classifying epiphytes. (After Benzing 1989a,b)

<table>
<thead>
<tr>
<th>Section</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>I. Relationships to the phorophyte</strong></td>
<td></td>
</tr>
<tr>
<td>1. Autotrophs, using the phorophyte only for support</td>
<td></td>
</tr>
<tr>
<td>1.1 Accidental</td>
<td></td>
</tr>
<tr>
<td>1.2 Facultative</td>
<td></td>
</tr>
<tr>
<td>1.3 Hemi-epiphytic</td>
<td></td>
</tr>
<tr>
<td>1.3.1 Primary</td>
<td></td>
</tr>
<tr>
<td>1.3.1.1 Strangling</td>
<td></td>
</tr>
<tr>
<td>1.3.1.2 Non-strangling</td>
<td></td>
</tr>
<tr>
<td>1.3.2 Secondary</td>
<td></td>
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<tr>
<td>1.4 Genuinely epiphytic</td>
<td></td>
</tr>
<tr>
<td>2. Parasites</td>
<td></td>
</tr>
<tr>
<td><strong>II. Growth habit</strong></td>
<td></td>
</tr>
<tr>
<td>1. Trees</td>
<td></td>
</tr>
<tr>
<td>2. Shrubs</td>
<td></td>
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<tr>
<td>3. Suffrutescent to herbaceous forms</td>
<td></td>
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<tr>
<td>3.1 Tuberous</td>
<td></td>
</tr>
<tr>
<td>3.1.1 Storage, woody and herbaceous</td>
<td></td>
</tr>
<tr>
<td>3.1.2 Myrmecophytic, mostly herbaceous</td>
<td></td>
</tr>
<tr>
<td>3.2 Broadly creeping: woody or herbaceous</td>
<td></td>
</tr>
<tr>
<td>3.3 Narrowly creeping: mostly herbaceous</td>
<td></td>
</tr>
<tr>
<td>3.4 Rosulate, herbaceous</td>
<td></td>
</tr>
<tr>
<td>3.5 Root/leaf tangle, herbaceous</td>
<td></td>
</tr>
<tr>
<td>3.6 Trash-basket, herbaceous</td>
<td></td>
</tr>
<tr>
<td><strong>III. Humidity</strong></td>
<td></td>
</tr>
<tr>
<td>1. Poikilohydrous (mostly lower plants)</td>
<td></td>
</tr>
<tr>
<td>2. Homoiohydrous</td>
<td></td>
</tr>
<tr>
<td>2.1 Hygrophytes</td>
<td></td>
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<tr>
<td>2.2 Mesophytes</td>
<td></td>
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<tr>
<td>2.3 Xerophytes</td>
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<tr>
<td>2.3.1 Drought-endurers</td>
<td></td>
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<tr>
<td>2.3.2 Drought-avoiders</td>
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<tr>
<td>2.4 Impounders</td>
<td></td>
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<tr>
<td><strong>IV. Light</strong></td>
<td></td>
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<tr>
<td>1. Exposure types</td>
<td></td>
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<tr>
<td>2. Sun types</td>
<td></td>
</tr>
<tr>
<td>3. Shade-tolerant types</td>
<td></td>
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<tr>
<td><strong>V. Phorophyte-provided media</strong></td>
<td></td>
</tr>
<tr>
<td>1. Relatively independent of rooting medium</td>
<td></td>
</tr>
<tr>
<td>1.1 Atmospheric forms</td>
<td></td>
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<tr>
<td>1.2 Twig and bark inhabitants</td>
<td></td>
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<tr>
<td>1.3 Forms creating substitute soils or attracting ant colonies</td>
<td></td>
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<tr>
<td>2. Utilizing preexisting specific rooting media</td>
<td></td>
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<tr>
<td>2.1 Humus-dependent</td>
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<tr>
<td>2.2.1 Shallow humus forms</td>
<td></td>
</tr>
<tr>
<td>2.2.2 Deep humus forms</td>
<td></td>
</tr>
<tr>
<td>2.2.3 Ant-nest garden and plant catchment inhabitants</td>
<td></td>
</tr>
<tr>
<td>2.2 Parasites</td>
<td></td>
</tr>
</tbody>
</table>
By the structure of tanks and scales we may distinguish four different life forms of bromeliads (Table 6.4):

- **Type I: Soil Root.**
  Some bromeliads which are obligately terrestrial do not form tanks; often these forms are highly xeromorphic; they may be densely covered with scales; however the scales do not function in water and nutrient absorption but may rather serve reflection of light (see Sect. 5.2.2.1, Figs. 5.3 and 6.15A).

- **Type II: Tank Root.**
  Other obligately terrestrial bromeliads have rudimentary tanks, which have limited water and litter collecting capacity; the scales make only minor contributions to water and solute uptake; however, in addition to the soil-roots, plants of this type develop stem-borne “tank-roots” growing up between the overlapping leaf bases into the tanks (Figs. 4.3 and 6.15B).

- **Type III: Tank-Absorbing Trichome.**
  The roots are conditionally absorbent but mostly have only mechanical functions for holdfast in these epiphytic forms and may even secrete a cement-like lipopolysaccharide (Brighigna et al. 1990), the tanks effectively collect rain water and decomposing debris; scales are found most densely on the leaf bases in the tank, where they serve water and nutrient uptake (Figs. 6.13 and 6.15C).

- **Type IV: Atmospheric-Absorbing Trichome.**
  Tanks in these forms are mostly absent and only occasionally poorly developed;

### Table 6.4 Life-forms of Bromeliaceae, their characterization and distribution among the three subfamilies Pitcairnioideae, Bromelioideae and Tillandsioideae. (After Pittendrigh 1948; Smith et al. 1986a; Smith 1989; Benzing 2000; note that the latter author has recently separated two different groups out of type III and distinguishes five types)

<table>
<thead>
<tr>
<th>Designation of life-form</th>
<th>Root system</th>
<th>Tank</th>
<th>Epidermal trichomes</th>
<th>Growth habit</th>
<th>Taxa</th>
</tr>
</thead>
<tbody>
<tr>
<td>Type I</td>
<td>Absorbent soil roots</td>
<td>Lacking</td>
<td>Unspecialized and non-absorbent</td>
<td>Obligately terrestrial</td>
<td>Great majority of Pitcairnioideae/many Bromelioideae</td>
</tr>
<tr>
<td>Type II</td>
<td>Absorbent soil roots and tank roots</td>
<td>Rudimentary</td>
<td>Relatively unspecialized</td>
<td>Obligately terrestrial</td>
<td>All terrestrial Bromelioideae</td>
</tr>
<tr>
<td>Type III</td>
<td>Usually only mechanical</td>
<td>Well developed</td>
<td>Specialized and absorbent; concentrated on leaf base</td>
<td>Most obligately (some facultatively) epiphytic</td>
<td>All the epiphytic Bromelioideae, majority of Tillandsioideae</td>
</tr>
<tr>
<td>Type IV</td>
<td>Exclusively mechanical</td>
<td>Often entirely lacking</td>
<td>Specialized and absorbent; often cover entire shoot</td>
<td>Obligately epiphytic (or saxicolous)</td>
<td>Tillandsioideae: Several species of <em>Vriesea</em>, otherwise species exclusively <em>Tillandsia</em></td>
</tr>
</tbody>
</table>
Fig. 6.15A–D Life forms of bromeliads. A Type I, soil root, *Pitcairnia integrifolia*, Trinidad. B Type II, tank root, *Bromelia humilis*, Falcon, Venezuela. The basal leaves were removed and the rosette was turned upside down for photography, so that the tank roots growing upwards between the leaves can be seen. C Type III, tank-absorbing trichome, *Tillandsia fasciculata*, Cerro Santa Ana, Paraguana Peninsula, Falcon, Venezuela. D Type IV, atmospheric-absorbing trichome, *Tillandsia usneoides*, Merida, Venezuela
the entire leaf surface is covered by highly specialized scales, which provide the only route for uptake of water and minerals from rain and dust in the atmosphere; in some forms roots are lacking entirely (Figs. 6.4 and 6.15D).

These life forms of bromeliads provide an interesting example of how the vegetative plant form has been shaped by evolution towards epiphytism; and in this case, particularly driven by the need for water and nutrient acquisition in the epiphytic habitat.

6.5 Mistletoes

Mistletoes growing on bushes and trees are not literally epiphytes, which originally use the phorophytes only as a holdfast. Mistletoes are true parasites. They largely belong to two families of the Order Santalales, namely the Loranthaceae (∼900 species and 65 genera) and the Viscaceae (∼400 species). Mistletoes occur ubiquitously in the temperate zone, in arid regions as well as in the wet tropics (Sallé et al. 1993). The majority of mistletoe taxa occur in the tropics. Although ecophysiology of mistletoes is increasingly well studied (Popp and Richter 1997), apparently it is not known why they have such a particularly high diversity and biomass in the tropics (Benzing 1990).

When germinating on the host trees, haustoria of mistletoes penetrate through the bark and join the host cambium, where they form a cambium themselves, which keeps pace with that generating the secondary thickening of the host so that the haustoria gradually become incorporated in the host’s wood (Sallé et al. 1993). Via the haustoria the mistletoes establish vascular contacts with the host. Very few mistletoes have phloem connections, since the contacts are predominantly apoplastic between the xylem elements of host and parasite. Thus, the standard view is that mistletoes are hemi-parasites on the xylem and transpiration-stream taking only water and nutrients from the host, while they are photosynthetically competent and capable of their own assimilation. The idea that mistletoes might have evolved from terrestrial root hemi-parasites sucking the xylem of host roots has been discussed (Benzing 1990).

In order to direct part of the transpiration stream from the host to their own shoot system for water and nutrient supply, mistletoes need to establish the required driving force. Indeed, it has been shown that they have a more negative leaf-water potential (see Box 6.1) and a larger leaf-conductance for water vapour and hence a higher transpiration rate, than the host leaves (Schulze et al. 1984; Ziegler 1986; Richter et al. 1995; Popp and Richter 1997). The difference between the leaf conductances in mistletoes and in their hosts respectively, can also be demonstrated by carbon-isotope analysis, because in C3-plants the variable rate of CO2-diffusion via stomata primarily determines overall changes in 13C-discrimination during photosynthesis, i.e. more negative δ13C-values indicate higher life time stomatal conductance, gH2O, higher average internal CO2-partial pressures \( p_{\text{CO}_2}^i \), and lower water use efficiency, WUE (Sect. 2.5). Lüttge et al. (1998) measured 21 host mistletoe pairs in Brazil and
found that consistently \( \delta^{13}C \)-values were more negative in the mistletoes than in the host leaves documenting higher transpiration rates and \( g_{H_2O} \) of the mistletoes and their operation at higher \( p^i_{CO_2} \) (Table 6.5). The higher transpiration rates also contributed to higher transpirational cooling of the mistletoe leaves as compared to the host leaves (Table 6.5), which certainly is an additional advantage of the parasites in hot and dry sites.

If mistletoes have similar or lower CO\(_2\)-assimilation rates as compared to host leaves, this also implies that the mistletoes may have considerably lower water-use-efficiencies (WUE = CO\(_2\) assimilated : H\(_2O\) transpired) at the expense of the host. Net CO\(_2\) uptake is generally considered to be lower in mistletoes as compared to their hosts (Popp and Richter 1997). However, in the study of Lüttge et al. (1998) photosynthetic capacity assessed from measurements of chlorophyll fluorescence parameters (Box 4.6) in mistletoe leaves proved to be similar to that of host leaves. Only in very exposed open sites photosynthetic capacity of mistletoe leaves was inferior, but that was due to a pronounced sun-type expression of host plant leaves. Mistletoes may even grow on mangrove associates like *Conocarpus erectus* (Orozco et al. 1990; see Chap. 7) and true mangroves, where they must establish a water potential gradient large enough to allow movement of water downhill from the salt-loaded halophilic host to their own leaves, but it is also observed that increasing drought and salinity stress may make hosts less suitable for invasion by mistletoes (Miller et al. 2003).

The view that mistletoes exclusively are parasites for water and nutrients, needs to be modified since carbon gain of mistletoes from the host can be significant (Richter et al. 1995; Escher et al. 2004). Studies of partitioning of dry matter and mineral nutrients (Pate et al. 1991a,b), which included analyses of carbon-isotope ratios (see Sect. 2.5; Marshall and Ehleringer 1990), showed that 24% (Pate et al. 1991a) to 62% (Marshall and Ehleringer 1990) of the mistletoe carbon may be derived from the host, and a tabulation of Popp and Richter (1997) even lists values up to 87%. This is not yet the ceiling though, because a fully holoparasitic heterotrophic Loranthaceae mistletoe, *Tristerix aphyllus*, has been discovered, which grows on the tissue of cactus stems (Kraus et al. 1995). First the transfer of carbon-compounds from the hosts to the mistletoes is partially due to the fact, that under various circumstances the xylem sap itself may also carry organic compounds. Second the mistletoe tissue may take up organic material from the host phloem by phloem unloading via apoplastic pathways and active membrane-transport, where the mistletoe becomes a sink for source substrates from the host. The involvement

<table>
<thead>
<tr>
<th>( \delta^{13}C ) (‰)</th>
<th>( p^i_{CO_2} ) (Pa/MPa)</th>
<th>( T_{leaf} ) (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>-3.25 ± 1.59 (21)</td>
<td>52 ± 25 (21)</td>
<td>-2.0 ± 1.4 (17)</td>
</tr>
</tbody>
</table>
of active, membrane-controlled transport can make acquisition of both mineral ions and organic compounds by the mistletoe from the host a highly selective process (Pate et al. 1991b; Rey et al. 1991; Escher et al. 2003). Phloem mobile mineral nutrients can also arrive in the mistletoes via the internal phloem-xylem-circulation of the host (Bannister et al. 2002).

An interesting morphological feature of mistletoes, related to parasite-host nutrient relations, is the often observed strong resemblance between parasite and host leaves (Ehleringer et al. 1986; Fig. 6.16). The mimicry of host leaves is common

Fig. 6.16 The Loranthaceae Phthirusa ovata (recognisable by its inflorescence) in a host tree, Brazil
since mistletoes often have higher nitrogen contents than their hosts, and hence reduces the likelihood of mistletoe herbivory. Mimicry is absent when mistletoes are poorer in N than the host.

6.6 Stressors Driving Ecophysiological Adaptation of Epiphytes and Hemi-Epiphytes

The major factors, which limit epiphytic life and thus may become stressors (Box 3.1), are:

- light,
- water,
- mineral nutrients.

Light (Sect. 6.6.1) is highly variable, similar to the situation of other species operating in different strata of the forest canopy (see Sect. 3.4.1). Water (Sect. 6.6.2) and mineral nutrients (Sect. 6.6.3) are particularly difficult resources to obtain by epiphytes having no roots in the soil and therefore availability of water may be considered the major constraint in the epiphytic habitat.

6.6.1 Light and the Evolution of Plants to Epiphytism

A generally encountered view assumes that climbing and epiphytism in plants is a struggle for light in an escape from the darkness of forest floors. This goes back to A.F.W. Schimper, who concluded his observations in forests of the American tropics with the hypothesis that epiphytic bromeliads evolved from shade adapted terrestrial forms (Schimper 1888). However, as we have already mentioned above (Sect. 6.1), lianas and vines are most frequently light demanding plants of pioneer successions. Epiphytes occupy sites of variable light exposure. Studies of the distribution of epiphytic orchids on phorophytes in a West African rainforest have shown that only a small percentage of the total number of species are found in the upper canopy, and most species dwell within the crowns of trees (Fig. 6.17).

Pittendrigh (1948) grouped the epiphytic bromeliads of Trinidad in three categories according to their light demand:

- an exposure group,
- a sun group,
- a shade tolerant group.

Using stable carbon isotope analysis (Sect. 2.5), Griffiths and Smith (1983) have determined the distribution of C3-photosynthesis and CAM among these 40 species. They related the mode of photosynthesis to Pittendrigh’s light-demanding categories and the annual precipitation at the sites where they occur in Trinidad. The result of
Fig. 6.17 Distribution of epiphytic orchids on trees in a West African rainforest. Numbers of species found in the different zones of the phorophyte related to total orchid species counted. The zones of the phorophyte are: A the basal part of the stem up to 3 m above ground level; B the stem up to the first ramifications; C, D and E the canopy divided into three equal parts along the length of the branches from inside to outside. (Goh and Kluge 1989, after Johansson 1975)

the survey is depicted in Fig. 6.18 (see also Fig. 6.23). At the wettest site (> 6.4 m precipitation per year) the shade group is not represented at all, with one species of the exposure group, six species of the sun group and only one CAM species being present. At somewhat lower annual precipitation, the sun group prevails with a total of eight species and three CAM species among them. Under intermediate precipitation, only C3 species comprise the exposure and shade groups. However, at the driest sites one finds only CAM plants of the exposure and sun groups. Thus, CAM among epiphytic bromeliads is clearly correlated with reduced water availability and sun exposure which exacerbates drought stress.

Together with the development and specialization of epidermal trichomes (see Sect. 6.4, Table 6.4, Fig. 6.14), which can be considered as an evolutionary trait (Mez 1904; Tietze 1906), Pittendrigh (1948) used the abundance and distribution of species in the three categories for consideration of the evolution of epiphytism among bromeliads. He suggested that epiphytic bromeliads did not evolve from shade demanding ancestors of the forest floor but rather were derived from terrestrial ancestors of open habitats originally adapted to sun exposure and at least temporary drought.

The observation that CAM occurs only among bromeliads of the sun and exposure groups supports this interpretation because phylogenetically CAM is considered to be rather an advanced physiological trait. The family of the Bromeliaceae
6.6 Stressors Driving Ecophysiological Adaptation of Epiphytes and Hemi-Epiphytes

Fig. 6.18 Distribution of epiphytic Bromeliaceae of the exposure group (Ex), the sun group (Su) and the shade-tolerant group (Sh) with C_3 photosynthesis (open parts of the bars) and CAM (closed parts of the bars) in Trinidad related to annual rainfall. (After Griffiths and Smith 1983)

Fig. 6.19 Scheme of putative phylogenetic relationships within the Bromeliaceae based on the taxonomic distribution of CAM and C_3 photosynthesis at the level of individual genera and molecular systematics. The scheme shows that both the epiphytic habit (E) and CAM must have arisen more than once during evolution of the present-day forms. Within the Bromelioidae there are indications of a progressive loss of CAM in some genera. T = terrestrial, E = epiphytic forms, C_3 = plants with C_3-photosynthesis. (Smith 1989; Crayn et al. 2000, 2004)
is monophyletic. Among the three subfamilies most likely the Bromeliioideae and possibly the Tillandsioideae are monophyletic while the Pitcarnioideae are poly-
phyletic (Crayn et al. 2000, 2004; Horres et al. 2000). The family comprises about
2800 species (Luther and Sieff 1998). Martin (1994) has identified the photosyn-
thetic pathway of 249 species of which 69% show CAM capacity with various de-
grees of CAM expression. CAM and epiphytism have evolved independently and
diphyletically several times within each subfamily (Fig. 6.19; Smith 1989; Crayn
et al. 2000). From a terrestrial C3 ancestor epiphytism evolved first. In the branch
giving rise to the Tillandsioideae from the epiphytic C3 plants CAM evolved, so that
this subfamily is exclusively epiphytic with both C3 and CAM species. In the branch
starting from the terrestrial C3 plants CAM evolved giving rise to the exclusively
terrestrial Pitcarnioideae with both C3 and CAM plants. From the branch starting

Table 6.6  Cardinal points of light-response curves of various epiphytes compared to genuine sun
and shade plants. Epiphytes were related to sun and shade plants respectively, by evaluating all
of the three given criteria (light-compensation point, light-saturation of photosynthesis, rate of
photosynthesis at saturation) together, because coordination is not simple when using single criteria
individually. (After Lüttge 1985)

<table>
<thead>
<tr>
<th>Plant type or species</th>
<th>Light compensation point (µ mol photons m(^{-2}) s(^{-1}))</th>
<th>Light saturation of photosynthesis (µ mol photons m(^{-2}) s(^{-1}))</th>
<th>Rate of photosynthesis at saturation (µ mol CO(_2) or O(_2) m(^{-2}) s(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sun plants(^a)</td>
<td>20–30</td>
<td>400–600</td>
<td>10–20</td>
</tr>
<tr>
<td>Epiphytes:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Platycerium grande</em> (C3 fern)(^b)</td>
<td>20</td>
<td>(\gg 520)</td>
<td>(&gt; 3)</td>
</tr>
<tr>
<td><em>Anthurium hookeri</em> (C3 aroid)(^b)</td>
<td>5–40</td>
<td>180–375</td>
<td>1–6</td>
</tr>
<tr>
<td><em>Kalanchoë uniflora</em> (C3/CAM Crassulaceae)(^b)</td>
<td>25–75</td>
<td>275–500</td>
<td>0.5–4</td>
</tr>
<tr>
<td><em>Phalaenopsis violacea</em> (CAM orchid)(^c)</td>
<td>16–20</td>
<td>180–200</td>
<td>4–8</td>
</tr>
<tr>
<td><em>Phalaenopsis grandifolia</em> (CAM orchid)(^c)</td>
<td>14–20</td>
<td>240–260</td>
<td>6–8</td>
</tr>
<tr>
<td>Shade plants(^a)</td>
<td>0.5–10</td>
<td>60–200</td>
<td>1–3</td>
</tr>
<tr>
<td>Epiphytes:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Aglaochora heracleum</em> (C3 fern)(^b)</td>
<td>5</td>
<td>160</td>
<td>3</td>
</tr>
<tr>
<td><em>Pyrrosia longifolia</em> (CAM fern)(^b)</td>
<td>8</td>
<td>100–150</td>
<td>1–2</td>
</tr>
<tr>
<td><em>Pyrosoia lanceolata</em> (C3 fern)(^b)</td>
<td>15</td>
<td>200–300</td>
<td>–</td>
</tr>
<tr>
<td><em>Drymoglossum piloselloides</em> (CAM fern)(^b)</td>
<td>8</td>
<td>300–500</td>
<td>–</td>
</tr>
<tr>
<td><em>Nepenthes × hookeriana</em> (C3 carnivorous plant)(^b)</td>
<td>5–10</td>
<td>150–225</td>
<td>3–5</td>
</tr>
</tbody>
</table>

\(^a\) Data as given also in Table 4.1
\(^b\) Data for glass-house grown plants (Lüttge et al. 1986)
\(^c\) Data for field-plants in Singapore (Goh and Kluge 1989).
from terrestrial CAM plants epiphytism evolved giving rise to the exclusively CAM Bromelioidae with both terrestrial and epiphytic species.

In conclusion, at least for the bromeliads, Schimper’s idea of epiphyte evolution towards light from shade demanding understorey plants is most probably not valid. It was more likely to have represented a conquest of space by plants already adapted to the ecophysiological problems of exposed nutrient-poor habitats. The shade-adapted epiphytic bromeliads are mostly shade-tolerant and not shade-demanding, and they probably constitute a later development.

However, Schimper’s hypothesis may still apply to the evolution of epiphytism in other groups of plants. Where this is the case, one would expect to find not only shade-tolerant but also clearly shade-demanding species. This can be assessed by comparing the cardinal points of light-dependence curves, which distinguish shade and sun plants (see Sect. 4.1.1, Table 6.6). By the criteria of light-compensation point, light-saturation and maximal rates of photosynthesis at least some epiphytic ferns and orchids are found to be typical shade plants, while other ferns and orchids, Kalanchoë uniflora and Nepenthes appear to be sun types. Mechanisms of protection from photodamage involving zeaxanthin and antioxidants, such as tocopherol (Sects. 4.1.3 and 4.1.4) have been studied in various epiphytic ferns (Tausz et al. 2001).

6.6.2 Water

6.6.2.1 Acquisition of Water Shaping Life Forms of Epiphytes and Hemi-epiphytes

The availability of water is the most pronounced problem for epiphytes and hemi-epiphytes which have no root-soil contact (Zotz and Hietz 2001). Rada and Jaimez (1992) compared terrestrial and epiphytic plants of the facultatively epiphytic Araceae Anthurium bredmeyeri growing close to each other in a tropical Andean cloud forest. The epiphytic plants were affected to a greater degree by the decrease in water availability during the dry season. They showed a larger decrease in leaf conductance and lower leaf water potentials during the dry season than the terrestrially growing plants as well as a reduction in stomatal densities in new leaf growth. Clearly, the water factor can have a large influence on life form of epiphytes.

Most of the lower plant epiphytes, i.e. aerial algae, lichens, bryophytes and even some ferns, are poikilohydrous and desiccation tolerant (Table 6.3: III 1; see also Sect. 11.4.2). They are truly resistant to drought stress, because they can dry out without suffering damage, overcoming drought periods in a non-hydrated state and becoming viable again when water can be absorbed from precipitation. Of the lichens only those, which have green algae as the photoautothrophic symbionts, are able to acquire their water and reactivat e photosynthesis from the water vapour in the gas phase (Lange et al. 1986, 1988). This also holds for pleurococcoid aerial green algae (Bertsch 1966). However, lichens having cyanobacteria as symbionts require water in liquid form to reactivat e photosynthesis.
Tillandsoid trichomes have no effect on leaf boundary layers and any associated reduction in transpirational water loss (Benz and Martin 2006). Some atmospheric bromeliads may take up water from the gas phase of the atmosphere by equilibration of the hygroscopic cell walls of the dead scale cells in the trichomes which densely cover their surface. Thus, one may observe a peak of water-vapour uptake when the relative air humidity (RH) increases at the beginning of the night (Fig. 6.20). However, this is matched again by a loss of water vapour at the beginning of the day when RH decreases and therefore the bromeliad leaf cells do not have a net gain of water from this mechanism (Schmitt et al. 1989).

In consequence, angiosperm epiphytes have developed a range of other adaptations which often are equally related to the nutrient “stress” factor (Sect. 6.6.3), e.g. formation of tanks or humus collecting baskets, in which they effectively create their own soil with a limited water storage capacity. Water demanding animals like small frogs may even live in tanks of bromeliads (Fig. 6.21), which in some species

Fig. 6.20A–C Night-day cycle of water-vapour exchange by plants of Tillandsia recurvata L. A Water-vapour exchange of normal living plants shows a peak of net uptake (negative values of $J_{H_2O}$) as the dew-point temperature ($T$) decreases and relative air humidity ($RH$) increases at the onset of the dark period, and a peak of net release (positive values of $J_{H_2O}$) with the opposite changes of $T$ and $RH$ at the beginning of the light period. B These peaks are also observed with plants killed in boiling water. They are restricted to passive hygroscopic equilibration of dead structures. C Subtraction of $J_{H_2O}$ by the dead plants from that of the living plants shows true transpirational water-vapour loss, which is much higher throughout most of the dark period in this CAM bromeliad than during the light period. (Schmitt et al. 1989, from Lüttge 1989)
can impound 5–10 l of water. Water storage tissues in leaves and stems may also be prominent, so that leaf and stem succulence occurs in most bromeliads (Horres and Zizka 1995), orchids and the epiphytic cacti (Fig. 6.22). In this relation it has been underlined that independent of age plant size of epiphytes matters a lot because availability and especially storage capacity of water is highly size dependent and this has effects on many other functions including allocation and partitioning of nutrients and area based photosynthetic capacity. Identical environmental conditions impose different degrees of stress on co-occurring smaller and larger plants (Zotz and Andrade 1998; Schmidt and Zotz 2001; Schmidt et al. 2001; Zotz et al. 2001, 2004; Zotz and Hietz 2001).

### 6.6.2.2 CAM and Water Relations Parameters

The pre-eminent role of water in limiting the life of epiphytes has resulted in the frequent occurrence of CAM, the mode of photosynthesis which conserves water (see Sect. 5.2.2.2). At Barro Colorado Island, Panamá, 25% of the epiphyte flora are CAM plants (Zotz and Ziegler 1997). Some authorities have counted about 13,500 species of epiphytes with CAM. This corresponds to 57% of all epiphyte species, while only 10% of all vascular plants are CAM species. The advantage of CAM for epiphytic life is:
Fig. 6.22A–C Stem succulent epiphytic cacti (A Epiphyllum, B Selenicereus inermis growing through a termite nest), and adaxial water storage tissue of a leaf succulent bromeliad (C)
6.6 Stressors Driving Ecophysiological Adaptation of Epiphytes and Hemi-Epiphytes

- water saving, i.e. a high water use efficiency,
- provision of an osmotic driving force for water uptake by nocturnal acid accumulation,
- flexibility in the mode of carbon acquisition.

See Sect. 5.2.2.2.

A census of epiphytic bromeliad species in Trinidad has related the frequency of bromeliad epiphytes and the relative number of CAM species to annual rainfall and the prevailing type of forest (Fig. 6.23). Very dry deciduous seasonal forest sustains low epiphytic bromeliad biomass and the small number of species are CAM plants. The abundance of the epiphytic bromeliad species is highest in the evergreen seasonal forest and the lower montane rainforest (Fig. 6.23). This is consistent with the general observation that epiphyte richness is highest at mid elevation, e.g. at 1,000 m a.s.l. in a Costa Rican study covering the altitudinal range from 0 to 2,500 m a.s.l., and strongly correlated to rainfall and not to temperature and light in the canopy (Cardelús et al. 2006). In the Trinidadian study the relative contribution of CAM species to the total number of species declines rapidly as forests get wetter and the water saving function of CAM becomes less important. A decrease of CAM epiphytes with increasing altitudes as seen in Fig. 6.23 is frequently described (Earnshaw et al. 1987; Hietz et al. 1999).

Table 6.7 summarizes some water-relation parameters (Box 6.1) of epiphytes. Since most of those studied to date are also CAM-species, it is difficult to decide

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![Fig. 6.23](image-url) Relations between total number of epiphytic bromeliad species, the relative number of CAM species among them, annual rainfall and prevailing forest types in Trinidad. (Smith 1989)

whether these are typical properties of epiphytes or general characteristics of CAM plants. The high relative water content of epiphytes as compared to various C₃-crop plants and trees is noteworthy. A high relative water content is a typical feature of CAM-plants and is associated with high water-storage capacity and succulence (Fig. 6.24). For the epiphytic ferns and orchids of Australia, Winter et al. (1983) could demonstrate correlations between succulence and CAM expression (Fig. 6.24). The highest osmotic pressures (\( \pi \)) of epiphytes in Table 6.7 are somewhat above 20 bar; in C₃-desert plants they may reach 100 bar. The lowest, i.e. most negative, water potentials (\( \psi \)) of epiphytes are at \(-10 \) bar, in C₃-desert plants values below \(-150 \) bar may be found. Hence, the cell sap of epiphytes is diluted, i.e. osmotic pressures are relatively low (see also Martin et al. 2004), the water potential is high and the turgor pressure (\( P \)) is low. In this respect epiphytic C₃- and CAM-bromeliads are little different, and also terrestrial CAM-plants show values in this range. The epiphytic C₃/CAM intermediate \( \textit{Clusia uvitana} \) in a rainforest in Panama has leaf water potentials in the same range, i.e. \(-7 \) to \(-9 \) bar (Zotz et al. 1994).

\textit{Clusia} (see Sect. 6.6.2.3) and \textit{Ficus} are genera of hemiepiphytes and stranglers, with very similar habits, but the latter has been studied much less in terms of physiological ecology of photosynthesis and water relations. This is astonishing because \textit{Ficus} appears to be as successful in tropical forests as \textit{Clusia}. Both have very different strategies though. Most species of \textit{Clusia} have CAM-capacity but as far as it is known to date all species of \textit{Ficus} are obligate C₃-plants. Holbrook and Putz (1996b) have made interesting intraspecific comparisons of water relations in the life forms of epiphytes and terrestrial trees in the genera \textit{Ficus} and \textit{Clusia}. They found that in five species of \textit{Ficus} the epiphytic life forms as compared to terrestrial trees had:

- several-fold higher specific leaf area (m\(^2\) g\(^{-1}\)), which may also be taken as higher degree of “succulence”,
- two- to fourfold lower stomatal densities, which may be discussed in relation to the need of reduced transpiration at lower availability of water in the epiphytic habitat,

<table>
<thead>
<tr>
<th>Plants</th>
<th>Relative water content(^a)</th>
<th>( \psi )</th>
<th>( P ) (bar)</th>
<th>( \pi )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Epiphytic CAM plants (ferns, orchids, bromeliads)</td>
<td>0.80 to 0.94</td>
<td>(-0.8 ) to (-9.9 )</td>
<td>2.0 to 10.0</td>
<td>1.7 to 23.4</td>
</tr>
<tr>
<td>Terrestrial CAM plants</td>
<td>0.93 to 0.96</td>
<td>(-2.4 ) to (-7.9 )</td>
<td>1.4 to 5.4</td>
<td>4.8 to 12.0</td>
</tr>
<tr>
<td>Epiphytic C₃ bromeliad</td>
<td>(- )</td>
<td>(-2.0 ) to (-3.8 )</td>
<td>2.3 to 3.9</td>
<td>5.2 to 6.1</td>
</tr>
<tr>
<td>Terrestrial crop plants</td>
<td>0.58 to 0.75</td>
<td>(- )</td>
<td>(- )</td>
<td>(- )</td>
</tr>
<tr>
<td>North American trees</td>
<td>0.60 to 0.85</td>
<td>(- )</td>
<td>(- )</td>
<td>(- )</td>
</tr>
</tbody>
</table>

\(^a\) Ratio of the volume of intracellular water (i.e. inside the plasmalemma) at incipient plasmolysis to the volume of intracellular water at maximum turgor pressure.
6.6 Stressors Driving Ecophysiological Adaptation of Epiphytes and Hemi-Epiphytes

Fig. 6.24 Correlation between δ\textsuperscript{13}C values as a yardstick for CAM expression (see Sect. 2.5) and leaf thickness indicative of the degree of succulence for Australian epiphytic ferns and orchids. (Winter et al. 1983)

- osmotic pressures (\(\pi\)) about 6 bars lower,
- a bulk modulus of cell wall elasticity (\(\varepsilon\)) about 50% lower.

We must note that cell wall elasticity is inversely related to \(\varepsilon\), i.e. the higher \(\varepsilon\) the more elastic and the lower \(\varepsilon\) the stiffer is the cell wall. With the relationship of

\[
\Delta P = \varepsilon \frac{V}{\Delta V},
\]

where \(\Delta P\) and \(\Delta V\) are turgor pressure and volume changes, respectively, and \(V\) is cell volume, it then follows that a given change in volume (\(\Delta V\)) leads to a lower change in pressure when \(\varepsilon\) is larger or cell walls are stiffer, i.e. in the epiphytic \textit{Ficus} plants a larger volume of water can be lost before turgor is lost than in the terrestrial trees. As a result leaves of the more succulent epiphytes and the conspecific less succulent trees of \textit{Ficus} species lost turgor at approximately the same relative water content.

With the water potential

\[
\psi = P - \pi
\]

(see Box 6.1) at \(P = 0\), or zero turgor, \(\psi = -\pi\), and this is substantially higher (less negative) in the epiphytes due to the lower osmotic pressure \(\pi\). These observations agree with the general trends for higher succulence, higher \(\psi\) and lower \(\pi\) in epiphytes (see above and Table 6.7).

In contrast to \textit{Ficus} species, in \textit{Clusia} differences in all of these water relation parameters between epiphytes and trees were very small. Thus, while \textit{Clusia} has instantaneous plasticity of responding to changing water supply and evaporative
demand by photosynthetic options (C₃-CAM transitions) *Ficus* shows intrinsic developmental changes during the transformation from epiphyte to tree which is associated with improved acquisition of water.

In CAM plants water relation parameters $\psi$, $P$ and $\pi$ also oscillate together with the day-night malic acid rhythm. Figure 6.25 describes an experiment with the atmo-

![Figure 6.25](image-url)

Fig. 6.25 Experiment showing the capacity of cells of the atmospheric CAM bromeliad *Tillandsia usneoides* for water uptake during a day-night cycle. Plants were weighed (initial FW) dipped for 10 min into water, dried superficially and then weighed at intervals to determine the point where rapid evaporation of surface water is completed and water is only lost from the living cells by transpiration, which allows to estimate water uptake by extrapolation (A). It is seen that osmotic pressure $\pi$ (B) and malate levels (C) increase during the night, and increased water uptake (D) and turgor pressure (E) measured directly with an intracellular pressure probe are associated with this. (see Lüttge 1987)
spheric CAM-bromeliad *Tillandsia usneoides*, showing that nocturnal accumulation of malic acid provides an osmoticum, which may drive cellular water uptake. It can be seen that cell-sap osmotic pressure (\(\pi\)) increases together with malic-acid levels. Water uptake, measured after dipping the plants for a short period into water as shown in Fig. 6.25A, clearly increased during the night together with \(\pi\), and this also led to an increase in turgor pressure. It should be noted, that while atmospheric bromeliads could occur in rather dry habitats, they are often found at sites where fog forms during the later part of the night and in the early morning. Water from condensed fog and dew is then available at times when malic-acid concentration in the cells is high and can lead to osmotic uptake of water.

### 6.6.2.3 CAM and Flexibility: The Case Study of *Clusia*

A major advantage of CAM in habitats where there are large short term and seasonal variations in water availability is the inherent flexibility in this mode of carbon acquisition. The different expression of the four CAM phases (see Box 5.1) in constitutive CAM plants already allows highly variable responses. If water supply were to range from very severe to moderate and low drought stress, there may be, respectively total stomatal closure and CO₂-recycling (also called CAM-idling), predominant nocturnal opening of stomata (Phase I) or increasing use of phase IV and phase II CO₂-uptake during the daytime hours. There may even be continuous CO₂ uptake day and night under well watered conditions. In addition there are species which are true C₃-CAM intermediates. They can switch from C₃ photosynthesis to CAM as drought stress increases, and back again when the stress is released. Among the epiphytic bromeliads *Guzmania monostachia* is such a C₃-CAM intermediate and it is the only one in the Bromeliaceae family (Maxwell 2002; Maxwell et al. 1994, 1995, 1999). However, there are other taxa with C₃-CAM-intermediate epiphytes. The epiphytic fern *Pyrrosia confluens* and the Crassulaceae *Kalanchoë uniflora* belong to this group (Griffiths 1989) as well as species of *Peperomia* (Sipes and Ting 1985; Ting et al. 1985; Holthe et al. 1987). The plants showing the most flexible response, however, are in the hemi-epiphyte and strangler genus *Clusia*. A separate book is monographically devoted to *Clusia* (Lüttge 2007a) and it is only briefly used here as case study. Each of the photosynthetic modes mentioned above are expressed in *Clusias*:

- pure C₃-photosynthesis,
- pure CAM,
- C₃/CAM-intermediate behaviour with environmentally controlled reversible changes between the two modes of photosynthesis,
- night time stomatal closure with fixation of respiratory CO₂ and vacuolar malate accumulation plus day-time stomatal opening and reduction of CO₂ both from the atmosphere and the nocturnally stored malate (CAM-cycling),
- stomatal closure around the clock and only recycling of respiratory CO₂ (CAM-idling),

(see Fig. 6.26).
Fig. 6.26A–I Modes of photosynthetic CO₂ exchange in Clusia.
Left panel. Comparison of four species under identical conditions in a phytotron, Clusia venosa with C₃ photosynthesis (A), Clusia minor with CO₂ uptake day and night (B), Clusia major and Clusia alata both with CAM but differing in the development of phase IV (C,D).
Center panel. Clusia minor in a growth chamber with C₃ photosynthesis under well-watered conditions at high irradiance (1,700 µmol photons m⁻² s⁻¹) and medium leaf/air water vapour pressure difference (ΔW = 6.6 mbar⁻¹) (E); CAM with the well-expressed four phases (I–IV) under drought stress at low irradiance (400 µmol photons m⁻² s⁻¹) and high ΔW (13.5 mbar⁻¹) (F); and CO₂ uptake day and night under well-watered conditions, low irradiance (400 µmol photons m⁻² s⁻¹) and low ΔW (3.4 mbar⁻¹) (G).
Right panel. Clusia rosea in the field with C₃ photosynthesis (H) and CAM with an extended phase II in the first half of the day (I).
Black bars on the abscissa indicate the dark periods. (Lütte 1991)

Variability of ecophyiological response is observed:

- between different species under given environmental conditions (Fig. 6.26, left panel),
- for a given species under different environmental conditions (Fig. 6.26, center and right panels),
- even for the two different leaves of a given node in the same plant when they are kept under different conditions (Fig. 6.27).

The rapid changes between C₃-photosynthesis and CAM, that may be performed by Clusia are determined by the external control parameters:

i) water relations,
ii) day/night temperature regime,
iii) light.
In an experiment with a plant of *C. minor* rewatered after a period of several days of drought, it was possible to get two opposite leaves at a given node to perform C₃-photosynthesis and CAM respectively, at the same time. One leaf, when maintained in an atmosphere with a low leaf-air water vapour pressure difference (ΔW or VPD), i.e. kept under a low transpiratory demand, switched to C₃-photosynthesis a few hours after watering with CO₂ uptake.
markedly reduced in the subsequent night. The other leaf, kept at high VPD, continued to perform CAM with the four phases clearly noticeable, as both leaves had done during the drought period before watering (Fig. 6.27).

ii) By varying the temperature regime, it was found that a certain day-night temperature difference was important for expression of CAM in *C. minor* (Fig. 6.28). The shift between CAM and C3-photosynthesis was fully reversible when the temperature regimes were changed between equal day/night temperature and day/night temperature differences (Fig. 6.29).

iii) In well-watered plants a drastic increase in light intensity led to an elimination of nocturnal dark-CO2-fixation and an increase in daytime C3-photosynthesis. Obviously, this represents an optimal use of high light energy provided that water is not limiting (Fig. 6.30).

*Clusia* spp. are also remarkable in several other ways:

- showing the highest nocturnal acid accumulation ever observed for CAM plants (Table 6.8),
- accumulating large amounts of citric acid during the dark period additionally or alternatively to malic acid (Table 6.8).

The latter observation also requires a comparative evaluation of the relative ecophysiological advantages of malic and citric acid accumulation during CAM (Table 6.9). Consideration of intermediary metabolism suggests that different compartmentation and different contributions of mitochondrial and cytosolic reactions may both be involved. Citric acid accumulation, in contrast to malic acid accumulation, does not lead to a net gain of carbon, although it contributes to carbon recycling. However, carbon recycling via citric acid may be favourable because daytime breakdown of citric acid may possibly result in the liberation of more CO2 than

![Fig. 6.29A–C](image)

*Fig. 6.29A–C* Change of *Clusia minor* from C3 photosynthesis to CAM and back to C3 photosynthesis as a day/night temperature difference of 10 °C is introduced and removed again. Gas exchange after seven days at 25/25 °C day/night (A) followed by five days at 30/20 °C (B) and by four days at 25/25 °C (C). *J*$_{CO2}$ net CO2-exchange, $g_{H2O}$ leaf conductance for water vapour. (Haag-Kerwer et al. 1992)
6.6 Stressors Driving Ecophysiological Adaptation of Epiphytes and Hemi-Epiphytes

Fig. 6.30 Elimination of dark CO$_2$ fixation ($D$) and stimulation of light CO$_2$ fixation ($L$) in a well-watered plant of *Clusia minor* by transfer from lower to high irradiation ($h\nu$). (Data from Schmitt et al. 1988)

Table 6.8 The highest nocturnal acid accumulation (mmol titratable H$^+$/l) and the highest nocturnal citrate accumulation (mmol citrate/l) observed in CAM. These records were measured in epiphytes (*Aechmea nudicaulis*) and hemi-epiphytes (*Clusia species*)

| Titratable acidity          |  |
|-----------------------------|  |
| *Aechmea nudicaulis*        | Field Trinidad, March 1983 | 625$^a$ |
| *Clusia rosea*, phytotron   |  | 1120$^c$ |
| *Clusia minor*              | Field, Trinidad, March 1990 | 1410$^{b}$ |

| Citrate                      |  |
|-----------------------------|  |
| *Clusia minor*              | Field Trinidad, March 1990 | 125$^b$ |
| *Clusia rosea*, phytotron   |  | 200$^c$ |

Data from $^a$ Smith et al. 1986b, $^b$ Borland et al. 1992, $^c$ Franco et al. 1992

that of malic acid, and the availability of this internal CO$_2$ could prevent photoinhibition (see Sect. 4.1.7) more effectively when light intensity is high. In fact it has been observed for four different *Clusia* species that the ratio of malic acid : citric acid accumulated during the dark period decreased in response to drought stress, relatively favouring carbon recycling via citrate. Since citrate accumulation does not contribute to C-acquisition, naturally it also does not help to improve water-use-efficiency (WUE). It also adds less to changes in cell-sap osmotic pressure than malate accumulation, because only one mole of citrate is formed per mole of hexose consumed. However, citrate is known to be an effective buffering sub-
Table 6.9 Comparative evaluation of the ecophysiological advantages of nocturnal accumulation of malate ($\Delta$ malate) and citrate ($\Delta$ citrate) respectively, in CAM. (Franco et al. 1992; Haag-Kerwer et al. 1992)

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<tr>
<th></th>
<th>$\Delta$ malate</th>
<th>$\Delta$ citrate</th>
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<tbody>
<tr>
<td>Carbon acquisition</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>H$_2$O-saving during C acquisition</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>$\Delta\pi$ with possible H$_2$O acquisition</td>
<td>Yes</td>
<td>Limited</td>
</tr>
<tr>
<td>Nocturnal recycling</td>
<td>CO$_2$</td>
<td>Carbon skeletons</td>
</tr>
<tr>
<td>Daytime recycling</td>
<td>CO$_2$</td>
<td>CO$_2$</td>
</tr>
<tr>
<td>Buffering capacity</td>
<td>Small</td>
<td>Large</td>
</tr>
<tr>
<td>Ecophysiological functions</td>
<td>H$_2$O-saving; preventing photoinhibition to some extent</td>
<td>Effectively preventing photoinhibition</td>
</tr>
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6.6 Stressors Driving Ecophysiological Adaptation of Epiphytes and Hemi-Epiphytes

This may sustain the very high nocturnal vacuolar acid accumulation observed in *Clusia* with day-night changes of titratable proton levels of more than 1 M (Table 6.8).

The diversity of the hemi-epiphyte and strangler *Clusia* in the tropics has presented us with many unexpected observations and stimulating new reflections on the nature of ecophysiological adaptations. Even individual species can occur as the life forms of free standing terrestrial trees, stranglers, hemi-epiphytes and epiphytes. There are ca. 350–400 species of *Clusia* occupying a wide range of habitats, e.g. coastal rocks and sand dunes, savannas, gallery forests, open shrub land, dry low land forest, secondary shrub forest, dry montane karstic limestone forest, montane rain forest, upper montane rain forest, cloud and elfin forest, rock outcrops (inselebergs; see Sect. 11.3.2; Fig. 6.31, see also Fig. 3.6D), and again individual species may be found in several of these types of sites (Table 6.10). Perhaps *Clusia* is so successful because of the high degree of physiological plasticity. This also makes it suitable for reclamation of tropical land by afforestation and as an ornamental tree even in the center of cities.

**Fig. 6.31A–E** Habitat diversity of *Clusia*. **A** *Clusia fluminensis* on sand dunes in the restinga formation on the Atlantic coast near Rio de Janeiro, Brazil. **B,C** *Clusia rosea* on granite rocks on the British Virgin Island Virgin Gorda (Lesser Antilles), with aerial adventitious root systems in the rock furrows in **C**. **D** *Clusia* sp. Gran Sabana, Venezuela, with an epiphytic bromeliad *Catopsis berteroniana*. **E** *Clusia rosea* in montane rainforest on the US Virgin Island St. John (Lesser Antilles)
### Table 6.10 Ecological amplitude of individual species of *Clusia, C. multiflora (C. mu.), C. parviflora (C.p.), C. rosea (C.r.), C. fluminensis (C.f.), C. minor (C.mi.), C. criuva (C.c.)* with their modes of photosynthesis indicated (From Lüttge 2007b)

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<tr>
<td></td>
<td>C3</td>
<td>C3</td>
<td>CAM</td>
<td>CAM</td>
<td>C3/CAM</td>
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<td>Coastal rocks</td>
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<td>Secondary shrub forest</td>
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<tr>
<td>Dry montane karstic limestone forest</td>
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<td>●</td>
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<td>●</td>
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<td>●</td>
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<tr>
<td>Montane rain forest</td>
<td>●</td>
<td>●</td>
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<td>Upper montane rain forest</td>
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<tr>
<td>Cloud forest/fog forest/elfin forest</td>
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<td>Inselberg</td>
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#### 6.6.3 Mineral Nutrients

Some special adaptations to the poor nutrient supply in the epiphytic habitat have already been mentioned above in the discussion of life forms of epiphytes (Sects. 6.3 and 6.4) and in relation to water stress (Sect. 6.6.2). They include the use of humus accumulation in trees (Fig. 6.10A) and morphological features of the plants for collecting humus such as the formation of baskets and nests (Fig. 6.10B) as well as tanks (Figs. 6.15 and 6.10C,D). Scales (epidermal trichomes) of bromeliads (Fig. 6.14) and the velamen radicum of aerial roots of aroids and orchids serving atmospheric nutrition also belong to the specialised plant structures formed for nutrient and water uptake (Goh and Kluge 1989; Reinert 1998). The velamen is a multilayered peripheral structure, which is readily infiltrated by water from throughfall or stemflow (Fig. 6.32).

It has even been argued that the successful trapping of rain and throughfall, enriched by leachates from leaves and stems, is nutritional piracy, depriving...
Fig. 6.32A–F Velamen radicum in epiphytic orchids. A Velamen of a *Dendrobium* species. V velamen; Ex exodermis; C cortex. B Detail from A showing the dead velamen cells with the typically perforated walls. C Detail from A showing the exodermis with an aeration cell (AC). D Surface view of an aerial root of *Vanda tricolor* with dry velamen. The air-filled velamen cells appear homogeneously whitish. E The same detail as in D; however, after wetting the velamen. With the exception of the pneumatophodes (PN), the velamen cells are filled with water and thus appear dark. F Cross-Sect. through the water-imbibed velamen of *Vanda tricolor* in the region of the pneumatophode (PN) and aeration cells (AC). The air-filled cells of the pneumatophode appear white. (Goh and Kluge 1989)
host trees of resources which otherwise would reach their rooting medium (Benzing 1989a,b, 1990). A comparison of the nitrogen content in leaves of facultative epiphytes at adjacent sites, showed significantly lower N-levels in two aroid species growing epiphytically as compared to their terrestrial counterparts. N-content was similar in two tank-forming bromeliads, whereas in seedlings of *Clusia* low N-content was also related to growth directly on the phorophyte and not to growth inside bromeliad tanks (Fig. 6.33). Epiphytes, especially in the Orchidaceae, may form mycorrhizas (Reinert 1998). The fungal hyphae penetrate the epiphytes as well as the decaying bark of the host phorophyte. This is evidently piracy of a more overt kind and the tree effectively becomes the pedosphere of the epiphyte (Ruinen 1953; Johannson 1977; Benzing 1982; Benzing and Atwood 1984). An interesting example of counter-piracy is found when phorophytes produce adventitious canopy roots which exploit the nutrient debris collected within the epiphyte cover (Nadkarni 1981).

Analyses of the stable isotope $^{15}$N have been used to trace several possible sources of nitrogen and processes of nitrogen acquisition in tropical epiphytes as compared to associated soil rooted trees (Stewart et al. 1995; Reinert 1998; Hietz et al. 1999; Wania et al. 2002). The relations are complex. N-isotope signatures of epiphytes vary with canopy position and the related water supply. The variations

![Fig. 6.33](image-url)

*Fig. 6.33* Comparison of nitrogen levels in cohabitant epiphytic and terrestrial-life-forms of two aroid and two bromeliad species and of *Clusia rosea*. Data show N content in leaves of epiphytic minus leaves of terrestrial plants of the same species (numbers are $p$ values of a $t$ test for statistically significant differences or n.s. = non-significant). (Ball et al. 1991)
are attributable in part to altered $^{15}$N-discrimination during N-acquisition, i.e. atmospheric deposition, leachates and biological dinitrogen fixation, and to changes in partitioning of N isotopes within the plant. Epiphytes may make considerable use of biological N$_2$-fixation by cyanobacteria and free living N$_2$-fixing bacteria of the phyllosphere (see Sect. 6.1) including their own leaves. Brighigna et al. (1992) described the trichome layers of bromeliad leaves as a favourable habitat for microbes including N$_2$ fixing bacteria.

Two additional strategies involve interactions with animals, one of which is predatory and the other one symbiotic, namely:

- **carnivory**,  
- **mutualism with ants**.

Carnivory by plants is quite frequent in the tropics and subtropics (Fig. 6.34). In the plant kingdom, carnivory is generally assumed to be a mechanism for the acquisition of mineral nutrients, especially N, P and S, by photosynthetically autotrophic plants living in nutrient-poor habitats such as peat bogs (Schmucker and Linnemann 1959; Lüttge 1983). Hence, one would assume that carnivorous plants would be rather frequent in the canopy habitat. However, this is not the case. Carnivorous plants have developed special organs for the capture of prey, glands for digestion and absorp-
tion of low molecular compounds obtained from the prey, and mechanisms for the attraction of small animals such as showy and colourful appendages and production of scent and nectar (see also Sect. 10.2.3.3). Thus, in cost/benefit analyses the rarity of carnivorous plants in epiphytic habitats can be explained by the high costs for investment and maintenance of these complex attraction and capture mechanisms (Givnish et al. 1984; Ellison 2006). Since other factors, particularly water and often light, are equally limiting, a cost-benefit analysis suggested carnivory would not be effective under these circumstances.

On the other hand, there are a few examples of carnivorous plants among climbers and epiphytes. The pitcher plant genus of *Nepenthes* is native in the Malayan archipelago and an exclusively tropical genus (Fig. 6.34). There are 71 species of *Nepenthes* altogether, among which a few are purely terrestrial, but 6 are epiphytic and many are climbers (Fig. 6.35). The pitchers attract prey by their shiny and often

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**Fig. 6.35** *Nepenthes gracilis* (Malaysia)

**Fig. 6.36** *Nepenthes*. A Pitcher cut open showing the velvety covering with loose wax particles in the upper part and the gland zone below. B Part of the upper pitcher region with wax particles and protrusions. C Scale-covered gland
6.6 Stressors Driving Ecophysiological Adaptation of Epiphytes and Hemi-Epiphytes
colourful rim, which also bears nectaries towards the inside of the pitcher opening. Small animals, predominantly insects, having fallen over the slippery collar into the pitcher lumen, rapidly drown in the digestive fluid produced by glands on the bottom, which contains a protease secreted by the plant and other enzymes provided by microorganisms participating in prey digestion. Escape via the pitcher walls is prevented by downward pointing scale-like tissue over the glands (Fig. 6.36C), modified stomata with protrusions towards the pitcher lumen and a lubrication with small and loose wax particles in the upper part of the pitcher (Gorb and Gorb 2006; Fig. 6.36A,B). Substances obtained from the digested prey are absorbed via the gland cells.

Some of these traits are also shared by tanks of bromeliads. They often contain dead and putrefying insects and may absorb substances like amino acids from such prey via their scales. In some cases, such as the epiphytic bromeliad *Catopsis berteroniana*, there is also wax at the adaxial leaf surfaces lubricating the tank interior (Benzing 1989b). However, these plants have no glands and do not secrete digestive enzymes, so that at most there is only the initial development towards the carnivorous syndrome (see also Sect. 10.2.3.3).

A more sophisticated example is *Utricularia*. Many species in this genus are aquatic, forming small bladders from modified leaves along the stems. The bladders are tightly closed by a trap-door, and actively transport ions across the trap wall into the outer medium to drive the osmotic loss of water from the trap lumen. This creates tension in the bladder-walls, which sets the bladder trap. Small animals trigger the opening of the trap door by touching the antennae-like protuberances and are swept into the trap as the tension in the trap wall is released (Fig. 6.37). The animals are then digested inside the bladders. In the tropics, *Utricularia* species often live

![Fig. 6.37 Schematic drawing of a longitudinal section of a trap of *Utricularia*. i Bladder lumen; o outer medium; D trap door; M trap mouth; SH sensitive hairs of the trap door = trigger hairs; A, antenna. Dotted arrow opening and closing of the trap door; the tissue beneath the trap door prevents opening from the inside. H₁, H₂, H₃ various types of gland hairs serving prey digestion and transport functions. (After Schmucker and Linnemann 1959)](image)
Fig. 6.38A–C Utricularia humboldtii in the tanks of Brocchinia tatei. A Inflorescence of U. humboldtii emerging from a tank of B. tatei. B Outer tank leaves removed to show the basal system of U. humboldtii bladders on stems and leaves with petioles and lamina emerging from the tank. C Larger and smaller U. humboldtii-bladders
Fig. 6.39A–D Ant-house epiphytes. A, B The orchid *Schomburgkia humboldtiana* with pseudobulbs cut open in B to show the ants nest. C The bromeliad *Tillandsia flexuosa* epiphytic on the cactus *Pilosocereus ottonis*, where ants are nesting in the inflated basal part of the tank. D The Asclepiadaceae *Dischidia rafflesiana* with adventitious roots in modified leaves.
epiphytically between mosses on stems of trees. Most cunning is *Utricularia humboldtii*, which lives inside the tanks of the bromeliad *Brocchinia tatei* (Fig. 6.38).

Another tropical habitat which is often nutrient limited are the savannas. We will refer to carnivorous plants again below, when we discuss their role and their contribution to nutrient turnover in this habitat (Sect. 10.2.3.3).

In *symbiotic mutualisms of epiphytes with ants* (Huxley 1980) we may distinguish two forms, which among other benefits, provide mineral nutrition to plants, namely (Davidson and Epstein 1989; Benzing 1989b, 1990):

- ant garden epiphytes,
- ant house epiphytes.

Ants frequently construct nests in trees using various materials which are rich in nutrients (forming an ant-nest “carton”). Seeds of plants may germinate directly from such a nutritive carton. Since the plants offer various goods in return, such as nectar, fruits and seeds, the ants often disperse and plant the seeds of their epiphytes in ant gardens. Conversely, plants themselves may also provide nesting facilities for ants, e.g. cavities in various parts of the plant body or hollow stems (Figs. 3.23 and 6.39; Sect. 3.3.4.4). Among the epiphytes there are many *myrmecophytic* species with such ant houses, e.g. orchids with ant nests in pseudobulbs and bromeliads with inflated tank leaves (Fig. 6.39A–C). The ants carry soil and other decaying material into the nests and add their faeces, which gives a debris from which the host plants may absorb nutrients. The pitchers of some species of the Asclepiadaceae *Dischidia* are most sophisticated, since adventitious roots grow into the soil and debris accumulated by ants inside these containers. In effect, epiphytic *Dischidias* literally construct their own flower pots (Fig. 6.39D). A study with the Malaysian *Dischichia major* using stable isotopes to trace sources of N and C (Sect. 2.5) has shown that 29% of the host nitrogen is derived from debris deposited into the leaf pitchers by ants and that 39% of the carbon assimilated by the host is derived from ant-related respiration (Treseder et al. 1995). Ant respiration may increase the CO2 concentration in the pitcher lumen above atmospheric levels. Since the host has stomata on the inner pitcher-wall surface this can be directly used for CO2-fixation even in the dark in this obligate CAM-plant.

In many cases these plant-ant interactions are true symbioses with obligate mutualism, since the partners are no longer successful individually. The epiphytic plants benefit nutritionally and may be protected from herbivores, while the ants obtain nest-sites and various items of food.

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Chapter 7
Tropical Forests. V. Mangroves

7.1 Phytogeography

Mangroves are a characteristic and important type of tropical and subtropical forests, with a unique capacity to tolerate large short-term changes of salinity. The name comes from the Spanish “mangle” for Rhizophora, a mangrove genus, and the English “grove”. Mangroves may also be considered as “tide-forests”, since their ecology is determined primarily by the tides at the three typical sites where they occur (Fig. 7.1):

- coastal mangroves,
- estuarine mangroves and
- coral mangroves,

i.e. mangroves along the coastlines, in river estuaries and around coral reefs and coral islands. However, salinity in mangroves is not only influenced by the tides, but also by the climate. At high tide salinity in the rooting medium of mangroves, of course, will be determined by sea water. At low tide, however, it will be higher or lower depending on the climatic conditions, i.e.

- humid climate with rainfall frequently diluting and leaching salt,
- arid climate with salt normally concentrated,

so that in any case mangrove sites are characterized by conditions of very variable salinity, which may even change rhythmically. Climate impacts on mangrove trees are also reflected in an annual cyclicity. Although as tropical trees mangrove trees lack distinct growth rings, high resolution profiles of stable carbon isotope ratios ($\delta^{18}O$, $\delta^{13}C$) in the wood of the stems reveal a seasonal cyclicity related to physiological processes under the environmental driving forces of salinity and water.
Fig. 7.1 Continued
potential of soils and other factors such as relative air humidity (Verheyden et al. 2004, 2005).

Mangroves delimit most tropical coast-lines and also extend into the subtropics (Fig. 7.2), such that 60–75% of all tropical coast-lines are occupied by mangroves (Popp 1991). The area covered by mangroves is 140,000 km², which is about 0.1% of the total land surface of the earth. The total global biomass of mangroves is estimated to be 8.7 gigatons dry weight (Twilley et al. 1992). There are about 50–75

<table>
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<th>Table 7.1</th>
<th>Na⁺ and Cl⁻ levels in different mangrove species collected from all over the world. (Popp et al. 1984)</th>
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<td>Melaleuca sp.</td>
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Cl⁻ in seawater
Fig. 7.2 Global distribution of mangroves with numbers indicating the approximate number of tree and shrub species in the mangrove vegetation. (After Vareschi 1980, with kind permission of R Ulmer)

Fig. 7.3 Co-occurring mangrove species in the Morocoy Park of Venezuela (see Fig. 7.1A,B): *Avicennia germinans, Laguncularia racemosa, Rhizophora mangle*
different species of mangroves in 20–26 genera in 16–20 families (Ellison 2002), some of which are depicted in Fig. 7.3 and listed in Table 7.1. Floristic diversity is poor in the Americas (1–5 tree species) and also in Africa (four species in West Africa, eight species in East Africa and Madagascar) but quite respectable in Asia (about 25 species in India and 30 species in SE-Asia), although in general terms mangroves are floristically much poorer than other tropical forests.

7.2 Site Characteristics and Contrasts in Salinity

Mangroves are characterized by their trees. Trees in mangrove forests may become quite tall although often mangroves have a scrub-like physiognomy (e.g. compare Fig. 7.1B and F). The woody mangrove species are frequently distributed in a banded zonation pattern oriented in parallel to the shore line. This pattern is correlated with the frequency and duration of tidal immersion modulating the degrees of salinity stress, and it is also influenced by dispersal of propagules, competition among mangrove species and herbivory (Ball 2002). Taller trees are formed in the

Fig. 7.4 The mangrove fern *Acrostichum aureum* (Costa Rica)
fringe forest near the water’s edge and dwarf forms further inland at higher elevation in the intertidal zone (Cheeseman and Lovelock 2004; Lovelock et al. 2006a; see also Sect. 7.6). Lin and Sternberg (1992a,b, 1993) have compared scrub and tree life-forms of the mangrove species *Rhizophora mangle* with trees in the fringe forest at lower levels (24 cm above sea level) and the scrub formation at higher levels (60 cm a.s.l.). The scrub form is associated with high salinities occurring at the higher levels during the dry season. In the rainy season, the scrub mangroves can also take up fresh water from rain, and *R. mangle* is therefore a facultative halophyte. However, frequent stress is caused by the changes in salinity following shifts between flooding by ocean water and fresh water introduced by rain. Such variations can lead to a significant decrease in photosynthesis and plant growth in the scrub mangroves, in contrast to constant salinity which maintains the salt load in the substratum.

On the silty substrate of mangroves the undergrowth of vascular plants is usually poor (Ball 1996) although the vigorous growth of large terrestrial ferns of the genus *Acrostichum* often is a striking feature (Fig. 7.4). These “mangrove ferns” are shade-tolerant plants, which, however, have their maximum development and productivity under full exposure. *Acrostichum aureum* is quite salt tolerant, although perhaps somewhat less than the mangrove trees. However, the gametophytes are only resistant to mild salinity stress and can survive the full salinity of sea water only for short periods, so that establishment is a problem and the fern remains restricted to the landward side of mangrove swamps (Medina et al. 1990; Li and Ong 1998; Sun et al. 1999).

### 7.3 Morphological Characteristics of the Mangrove Tree Life Form

At the littoral habitats the wood of the trunks of mangrove trees needs to resist particularly strong winds as well as the pressure of tides. The major stress factors related to morphological characteristics of the mangrove tree life form, however, are **salinity** and the additional stress of low O\(_2\)-partial pressure resulting from the inundation of the silty **hypoxic substratum** in which they root. This causes particular demands on morphology of roots for aeration and hydraulic architecture for lifting water to the shoots against the low water potential of the saline substratum.

#### 7.3.1 Hypoxia in Inundated Swampy Soils, Root Morphology and Aeration

The root systems of mangrove trees are most remarkable. In comparison to other tropical forest communities root biomass is greater in mangroves (Ball 1996). Highly conspicuous is the diverse range of strangely shaped bizarre root systems
above the soil surface. They must have evolved to provide anchorage as well as aeration in the silty muddy soils. With respect to the latter function they have been named **pneumatophores**. Diffusion of gases is highly limited in the inundated soil. Therefore, only contact of the root system with the atmosphere or with the sea water, depending on tidal level allows gaseous exchange. Figures 7.5 and 7.6 show a variety of some of the most frequently observed aerial root systems with stilt roots, planks and buttresses and finger-or knee-like protrusions above ground.

The root aeration provided by these pneumatophores is reinforced by a physiological mechanism. The exposed parts of these roots usually have **lenticels**, which

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**Fig. 7.5A–C** Root types of mangroves. A Stilt-, B Buttress-type roots. C Knee- or finger-like pneumatophores. (Vareschi 1980, with kind permission of R. Ulmer)

**Fig. 7.6A–D** Stilt roots of *Rhizophora mangle* (A–C) and finger-like pneumatophores of *Avicennia germinans* (D)
7.3 Morphological Characteristics of the Mangrove Tree Life Form

A

B

C

D
are openings in the bark where gas but not water can penetrate. The influx of water is prevented by surface tension in the intercellular spaces of the lenticels. A pneumatophore aerenchyma may occupy as much as 70% of total root volume (Curran 1985). During high tide, root respiration reduces the O\textsubscript{2}-concentration in the intercellular spaces of the root aerenchyma to a hypoxia of as little as 4–8% (Kitaya et al. 2002). Photosynthetically active cells at the surface of the pneumatophores can feed some O\textsubscript{2} into the aerenchyma for root respiration (Aiga et al. 1995; Kitaya et al. 2002), but pneumatophore photosynthesis is decreased with flooding due to reduced irradiance (Kitaya et al. 2002). Thus, the low O\textsubscript{2}-concentration in the submerged pneumatophores of only a quarter to less than half of the atmospheric concentration causes considerable O\textsubscript{2} gradients along the roots and gas-pressure deficits in the aerenchyma to minus 1.7 kPa (Chiu and Chou 1993; Skelton and Allaway 1996; Youssef and Saenger 1996; Lösch and Busch 1999), because the O\textsubscript{2} consumed in respiration cannot be reabsorbed readily from the sea water, while the CO\textsubscript{2} liberated can be dissolved as bicarbonate and released. At low tide, when the roots establish contact with the air again, the pressure deficit effectively leads to air being sucked into the root air spaces via the lenticels. Hypoxia (see also Sect. 3.2.3) is an additional stress to salinity in mangrove trees and, in view of the energy costs of salinity tolerance (e.g. salt exclusion, K\textsuperscript{+}/Na\textsuperscript{+}-selectivity, see Sects. 7.4 and 7.6), such mechanisms for the control of hypoxia at the root level are quite important in addition to ventilation from the photosynthesizing shoot via the aerenchyma.

### 7.3.2 Hydraulic Architecture and Xylem Sap Flow

For assessment of water potential gradients in plants as driving forces for xylem sap flow in trees Scholander and coworkers introduced the pressure chamber technique. In view of the particular situation of mangroves in their saline substratum they devoted much of their pioneering work to mangrove trees, where xylem tensions of 3.8–5.2 MPa were recorded and accepted as sufficiently exceeding the osmotic pressure of sea water (2.5 MPa) to produce the driving force for sap ascent and a transpiration stream according to the cohesion-tension theory (Scholander 1968; Scholander et al. 1965, 1966). Conversely, Zimmermann et al. (1994a, 2002) argue that the balancing pressure used in the pressure chamber technique overestimates xylem tension. Using staining techniques they detected high-molecular-weight polymeric polysaccharide-mucilage in the xylem vessels of *Rhizophora mangle*. They argue that such mucilage would tend to strongly support gas bubble formation, which would prevent stable xylem tensions larger than 0.1 MPa. Moreover, the mucilage would hinder a mass flow of water. Xylem conductivity would decrease with saps of extreme salinities controlled by swelling and shrinking of pectin-based hydrogels in the pit membranes (López-Portillo et al. 2005), but also reduced leaf conductivity for water vapour with increasing salinity is involved due to stomatal regulation (Sobrado 2001). Zimmermann et al. (1994a, 2002) observed sap flow rates in mangrove trees of 0.05–0.14 mm s\textsuperscript{-1} which they consider to be quite low.
They suggest then, that sap ascent is driven by gravity-independent streaming at gas/water interfaces (given by the gas bubbles) as well as a gradient of chemical activity of water established by the potentially highly hygroscopic mucilage attracting and holding the water. This raised much dispute in relation to the standard cohesion-tension theory of sap flow in the xylem (Zimmermann et al. 1994b; Tyree 1997; Lösch 1998; Wei et al. 1999a,b), and although this is not the place to get involved in detail in this controversy it is noteworthy that mangroves are important players in this game. Thus, Becker et al. (1997) note that xylem clogging by mucilage in mangroves cannot be generalized and they report sap flow rates in mangrove trees of $0.09–0.16 \text{ mm s}^{-1}$, which they think are not that low and compare well with those of other tropical trees. We may conclude with Becker et al. (1997) that “like plants of other vegetation types, mangrove species will probably exhibit a range of transpirational behaviours in response to their saline habitat once they have been more fully investigated”.

Hydraulic architecture plays a large role in such comparisons (Ball 1996). Sobrado (2000) found that the hydraulic systems of the three mangrove species *Avicennia germinans*, *Laguncularia racemosa* and *Rhizophora mangle* were comparable to the lowest end of the range reported for tropical trees. Wood and bark anatomy are adapted to water availability, salinity and oxygen supply in relation to the frequency and duration of flooding periods (Yáñez-Espinoza et al. 2001). Specific hydraulic conductivity of leaves declines with increasing salinity (Lovelock et al. 2006b). Under salinity stress controlled by the phytohormone auxin trees tend to form xylem vessels with smaller diameters which also applies to mangroves (Junghans et al. 2006). Mangrove species of the Rhizophoraceae have smaller vessel diameters than non-mangrove species of the same family (Janssonius 1950).

### 7.3.3 Vivipary

Some mangrove species are viviparious (Fig. 7.7). After fertilization they develop from the zygotes as embryos and then seedlings, which grow out of the flowers and fruits and remain for some while on the mother plant. Once liberated the viviparious seedlings can establish directly in the sediment at low tide or float in the sea water and are dispersed. Establishment appears to be particularly important since traits related to it appear to be stronger predictors of distribution than those associated with dispersal (Clarke et al. 2001). In general, however, advantages of vivipary are not clear since it is observed in only some mangrove tree taxa (e.g. *Rhizophora mangle*).

### 7.4 Exclusion, Inclusion and Excretion of Salt

Mangroves, like all other halophytes (which are plants growing in saline habitats), utilize strategies where they function as
Fig. 7.7 Vivipary in *Rhizophora mangle*

- **salt excluders** or
- **salt includers** with intracellular **salt dilution** (succulence) and **compartmentation**,

and in addition operate with

- **salt excretion**

(Popp et al. 1993).

**Salt exclusion** normally only affords resistance against mild or intermediate salinity stress, mainly for osmotic reasons (see Box 6.1). In order to maintain **osmotic balance** and keep a water potential gradient from the substratum to the plants, salt excluding plants would have to synthesise alternative organic solutes, which would consume energy and tie-up a large amount of important resources in terms of carbon skeletons, nitrogen and sulphur (see Box 7.1). Thus, the alternative is **salt inclusion** whereby the salt itself is used as a readily available and “cheap” osmoticum. In species which have special **salt glands** on their leaves, surplus salt may be eliminated by **salt excretion**.

The relative effectiveness of these mechanisms is illustrated by comparing salt levels in the leaves and in the xylem sap of mangrove species with and without salt.
glands (Fig. 7.8). Species with salt glands appear to have higher salt concentrations in the xylem sap than species without salt glands. Analyses in the field suggest that *Rhizophora mucronata*, is a salt excluder as shown by the rather low Cl\(^-\)-levels in the xylem sap while *Aegialitis annulata* is a salt includer as indicated by the larger xylem sap Cl\(^-\)-concentration. In contrast to the salt excluder, *A. annulata* has salt glands and is capable of salt excretion. Irrespective of the large differences in xylem sap salt concentrations adult leaves had similar salt levels in both species. Hence, the different strategies for dealing with salt, whether by exclusion at the root level or excretion at the leaf level and dilution via succulence (see below) lead to the same salt level in leaves.

However, the distinction between salt excluders and salt includers is only relative. There is always some control of salt uptake at the root level. This is the case in all mangroves, and the salt concentration in the xylem sap is always much smaller than in seawater, where the Cl\(^-\) concentration is over 500 mM (Scholander 1968; Fitzgerald and Allaway 1991). The levels of Na\(^+\) and Cl\(^-\) in the xylem sap of the examples shown in Fig. 7.8 are five to more than ten times less than those of seawater, in contrast to the levels in leaves. Table 7.1 gives a compilation of NaCl-levels in 23 different mangrove species collected from all over the world. Generally, the salt concentrations in the leaves were similar to that of seawater. Deviations of tissue contents of Na\(^+\) and Cl\(^-\) from the average contents of these ions in sea water are small and mostly not larger than ca. \(\pm 100\) mM although in some cases deviations of ca. \(\pm 200\) mM and ca. \(\pm 400\) mM have been reported (Table 7.1). This is
due to accumulation of salt from the lower concentrations in the xylem sap into the leaf cells which is fast during leaf expansion but continues gradually in mature and senescing leaves (Cram et al. 2002). However, a comparison of salt concentrations in the xylem sap and in the sea water rooting medium shows that strictly speaking at the root level all mangroves are salt excluders. This can add to salinization of the substratum, which, may have ecophysiological implications for photosynthetic CO₂-uptake and transpiration (Passioura et al. 1992; see Sect. 7.5.1). Salt accumulation in the leaves almost equally affects both ions Na⁺ and Cl⁻ with a small tendency to a larger Cl⁻ accumulation. While the average Cl⁻/Na⁺-ratio in sea wa-

Fig. 7.9A, B Cross-sections of a young (A) and a mature (B) leaf of the mangrove Sonneratia sp. The mature leaf is much thicker, having a much larger water content to area ratio (= leaf succulence) due to enlargement and high vacuolization of the inner mesophyll cells. (Lear and Turner 1977, with kind permission of University of Queensland Press)
7.4 Exclusion, Inclusion and Excretion of Salt

ter is ca. 1.2, the Cl−/Na+ -ratios of the mangrove trees shown in Table 7.1 average at 1.4 ± 0.2, with the exception of the three species where the salt content was ca. 400 mM less than that of sea water.

Many mangrove tree species can also grow in fresh water and behave as facultative halophytes. As in other halophytes, up to a certain level salinity stimulates growth, but high salinities inhibit growth to different extents in different mangrove species (Ball 1996, 2002). The optimum salt concentration for growth may be well below the NaCl-concentration of sea water, e.g. in the mangrove tree *Avicennia germinans* it was found to be at 170 mM and higher concentrations (680 and 940 mM) were inhibitory (Suárez and Medina 2005). Thus, there is a range of comportments from moderate to high salt tolerance and obligate halophily (Ball 1996).

Salt accumulation as a consequence of salt inclusion and the concentrating effect of transpiration has important correlates at the cellular level, namely salt compartmentation and dilution. Salt is sequestered (compartmented) in the cell sap vacuoles where it can be diluted by osmotic uptake of water. However, this requires an increased volume if the overall salt concentration were to be maintained at a constant level. Therefore, such salt dilution is associated with succulence (“salt succulence”), with the formation of large central vacuoles. This supports maintenance of water relations and turgor pressure according to the relationship

\[ \Delta \psi = \Delta P - \Delta \pi, \]  

(7.1)

where \( \psi \) is water potential, \( P \) turgor potential and \( \pi \) osmotic potential (see Box 6.1). Succulence of mangrove leaves may increase as leaves age (Cram et al. 2002), and

![Fig. 7.10 Cl− content (mol m−2 leaf surface) and Cl− concentration (mol l−1 tissue water at saturation) in leaves of the mangrove *Laguncularia racemosa* related to the degree of succulence. The latter is given by the ratio of the leaf-water content at water saturation and the surface of both sides of the leaves (kg m−2). (After Biebl and Kinzel 1965, from Kinzel 1982, with kind permission of the author and R. Ulmer)
this is mainly due to an enlargement of leaf cells, providing larger vacuoles in which salt can be accumulated and diluted to some extent (Fig. 7.9). Thus, the total chloride content of leaves, when expressed on a leaf area basis, increases considerably, whereas chloride concentration remains rather constant as succulence increases. This clearly demonstrates the dilution effect enabled by succulence (Fig. 7.10). An anatomical disadvantage of salt succulence is a reduction of CO₂-diffusion within the leaves to the chloroplasts decreasing photosynthetic capacity (Parida et al. 2004a).

**Box 7.1 Compatible Solutes**

As for all halophytes, the cytoplasm, the enzymes and membranes of mangrove cells are as equally sensitive to higher Na⁺-concentrations as those of glycophytes (Ball and Anderson 1986; Sommer et al. 1990). Due to their large hydration shells, Na⁺ ions disturb the molecular water structures, i.e. the specific arrangement of the dipole molecules of H₂O at the surfaces of proteins and membranes. This leads to the requirement for compartmentation. The NaCl taken up is sequestered in the vacuoles, where it is accumulated and may be effectively diluted as shown above. However, an osmotic balance is required in the cytoplasm because turgor pressure (Eq. 7.1) can only build up at the plasmalemma/cell wall boundary. The tonoplast membrane itself does not offer enough elastic resistance, and there can-
not be a gradient of $\pi$ across the tonoplast, i.e. $\pi_{\text{cytoplasm}}$ must equal $\pi_{\text{vacuole}}$. To this end, halophytes normally synthesise small organic molecules which serve as osmolytes, and are also called compatible solutes, as they both serve as cytoplasmic osmotica and are compatible with water structures. Their function in stabilizing cytoplasmic water structures is based on their molecular electron and charge distribution being similar enough to water-dipoles to be compatible with maintenance of cytoplasmic structures. Box 7.1 presents a variety of compounds, which are known to function as compatible solutes. Sorbitol, mannitol and pinitol are particularly frequent among mangroves (Popp 1984; Popp and Polanía 1989; Richter et al. 1990). Accumulation of compatible solutes in the cytoplasm alone is much more efficient in terms of resources and energy needed than if organic molecules were used throughout the whole cell as osmotica to withstand salt stress of the medium. In succulent tissues the relative volume of the cytoplasm is only 1–2% of the total cell volume, so that vacuolar salt accumulation accompanied by cytoplasmic accumulation of compatible solutes is a very cost effective mechanism of osmotic adjustment.

Fig. 7.11A–F Development of the salt gland hairs of the mangrove *Avicennia marina*. A–E various stages of development. F Mature salt gland (Fahn and Shimony 1977, with kind permission of the author and Linnean Society). A Terminal cell; Ba basal cell; C cuticle; E epidermal cell; S secretory cell; St stalk cell; W cell wall
Fig. 7.12 Leaves of *Avicennia germinans* with salt crystals (*above*) and dissolving salt at high air humidity (*below*)
The mechanism of salt excretion by glands has been studied extensively in non-tropical halophytes (Lüttge 1975). It is an energy dependent, active transport process, moving ions against large gradients of their electro-chemical potential. Figure 7.11 shows the development of the glandular hairs of the mangrove *Avicennia marina* (Fahn and Shimony 1977). The mature salt gland is covered and encircled by a cuticle, so that an apoplastic, cell-wall route of salt excretion is not available (Fitzgerald and Allaway 1991). The salt is moved via basal cells, often called “collecting cells”, and stalk cells to the secretory cells, which excrete it into a subcuticular space at the head of the gland. Water follows osmotically. The pressure of the excreted fluid increases in the subcuticular space, and the salt is eventually released through pores in the cuticle opening under the hydrostatic pressure. During hot and dry days numerous salt crystals form on the leaves as the excreted salt solution dries (Fig. 7.12). Conversely, in the early morning, when air humidity is high, the excreted salt on the leaf surface hygroscopically absorbs water and a salty “rain” may drip down from the mangrove trees.

Excretion is also under adaptive regulation. With increases of xylem osmolality due to drought in *Avicennia germinans* (Sobrado 2002) or salinity in *Laguncularia racemosa* (Sobrado 2004) excretion tends to rise exponentially (Fig. 7.13), and at

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Fig. 7.13 Osmolality of xylem sap (triangles) and rates of salt excretion (circles) by *Laguncularia racemosa* in relation to salinity (in ‰ sea water strength). Open and closed symbols are observations in the field and in the laboratory, respectively. (After data of Sobrado 2004)
the same time leaf conductance for water vapour decreases hyperbolically providing a trade-off between enhancement of salt excretion and control of water loss (Sobrado 2002, 2004).

7.5 Photosynthesis

7.5.1 CO₂-Exchange and Stomatal Conductance

Measurements of gas exchange of mangrove trees in relation to the degree of sub-stratum salinity are summarized in Fig. 7.14, where for comparison the units of reference of different authors were unified so that salinity is roughly indicated as that of 1/10, 1/2 and 1/1 of sea water. (This also applies to Sect. 7.5.2 below.) An effect of salinity on net CO₂-uptake ($J_{CO_2}$) is not very pronounced up to 1/2-strength of sea water; only Avicennia corniculatum seems to be more sensitive than Avicennia marina and the 19 species averaged. Full strength (1/1) sea water then reduces $J_{CO_2}$ as stomatal conductance of the leaves ($g_{H_2O}$) is also declining, but these effects are not dramatic. Internal CO₂-partial pressure ($p_{iCO_2}$) remains between 150 and 250 Pa/MPa. The increase of $p_{iCO_2}$ in A. corniculatum, while stomata partially closed (reduced $g_{H_2O}$) and $J_{CO_2}$ strongly decreased at 1/1-strength sea water can be explained by photoinhibition (see Sect. 7.5.3) preventing fixation of internal CO₂. In any of the cases shown in Fig. 7.14 comparatively high rates of photosynthesis are still maintained at full strength sea water. These rates compare well with rates of glycophytic C₃-plants and even C₄-plants in the absence of salinity (Table 7.2), which underlines the strong capacity of mangroves to perform effectively under high salinity.

Comparative studies of Conocarpus erectus and Avicennia germinans during the rainy season and the dry season offer additional insights into the success of man-

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7.5 Photosynthesis

**Fig. 7.14** Net CO₂-uptake ($J_{\text{CO}_2}$), leaf conductance for water vapour ($g_{\text{H}_2\text{O}}$) and leaf internal CO₂ partial pressure ($p_i^{\text{CO}_2}$) of the mangrove tree species *Avicennia marina* and *Avicennia corniculatum* (after Ball and Farquhar 1984a,b) and of 19 different species studied in the field in Australia and Papua New Guinea (after Clough and Sim 1989) at approximately 1/10-, 1/2- and 1/1-strength sea water as indicated in the columns. (From Lüttge 2002)

Groves under strongly varying conditions of salinity. *C. erectus* is not a true mangrove, but rather a mangrove associate or ally. It does not grow as close to salt-water lagoons and estuaries or tidal plains as the mangroves *sensu strictu*. However, at places its distribution overlaps with that of mangroves, for instance in alluvial sand plains at the Caribbean coast of Venezuela. There are various sizes of vegetation islands on these sand plains (see Sect. 8.2.1), where *C. erectus* and *A. marina* are found in close proximity (Fig. 7.15). In the rainy season the sand plains may be flooded by fresh water to a depth of 0.5 m, but in the dry season they dry out becoming hypersaline and covered with a crust of salt (Sects. 8.2.1 and 8.2.3.4). These two species were found here growing on the same vegetation island, and Fig. 7.16 shows that in the rainy season, both species had similar CO₂-uptake rates, $J_{\text{CO}_2}$, but that *A. germinans* operated at considerably lower conductance, $g_{\text{H}_2\text{O}}$, and internal CO₂-concentration, $p_i^{\text{CO}_2}$, than *C. erectus*. In the dry season, $J_{\text{CO}_2}$ in the morning was similar to that measured in the wet season for *A. germinans*. There was a midday depression (see Sects. 5.2.2.1 and 10.1.2.3), which was followed, however, by considerable recovery in the afternoon; $p_i^{\text{CO}_2}$ was similar to that in the wet season although $g_{\text{H}_2\text{O}}$ was somewhat reduced. Conversely, CO₂-uptake in *C. erectus* in the dry season was greatly reduced, with only a small peak in the morning, and $g_{\text{H}_2\text{O}}$ and $p_i^{\text{CO}_2}$ were low throughout the day. It is evident that with similar $J_{\text{CO}_2}$ for both species in the rainy season, the smaller reduction of $J_{\text{CO}_2}$ in the dry season allowed *A. germinans* to maintain productivity under salinity-stress and drought better than
Fig. 7.15A,B *Avicennia germinans* (A) and *Conocarpus erectus* (B) on an alluvial sand plain at the Caribbean coast of Venezuela

the mangrove-associate *C. erectus* as the true mangrove maintained similar rates of \( J_{CO_2} \) to *C. erectus* at lower \( p_{CO_2}^{i} \) in the rainy season and then \( J_{CO_2} \) in *C. erectus* was greatly reduced as \( p_{CO_2}^{i} \) declined in the dry season (Fig. 7.16).

Although *C. erectus* does not grow close to the shoreline or reach the tidally inundated mud plains, it may grow around sand dunes. It is then subject to salinity from salt spray and develops very thick succulent leaves at the windward side of the
bushes, while leaves on the sheltered side are non-succulent (Fig. 7.17). The non-succulent leaves protected from the salt spray have higher $J_{CO_2}$ and transpiration, $J_{H_2O}$, during the second part of the day than the salt-exposed leaves (Fig. 7.18). Similar observations were described by Naidoo et al. (2002) who compared the mangrove associate *Hibiscus tiliaceus* with the true mangroves *Avicennia marina*.

---

**Fig. 7.16A,B** Leaf conductance for water vapour, $g_{H_2O}$, net CO$_2$-uptake, $J_{CO_2}$, and internal CO$_2$ partial pressure, $p_{iCO_2}$, in leaves of the same plants of *Avicennia germinans* (A) and *Conocarpus erectus* (B) studied during the rainy season (○) and the dry season (●). (After Smith et al. 1989)
and Bruguiera gymnorrhiza at sites with low and high salinities, respectively, and found that H. tiliaceus showed better photosynthetic performance than the mangroves at the low salinity site and vice versa at the high salinity site.
7.5 Photosynthesis

7.5.2 Water Use Efficiency

In relation to salinity and osmotic stress of mangrove trees water-use-efficiency (WUE) is of great interest. The WUE\(_\text{ratio}\), as defined by \(J_{\text{CO}_2}/J_{\text{H}_2\text{O}}\), decreases with salinity only slightly in \(A. \text{marina}\) and more pronouncedly at 1/1-strength sea water in \(A. \text{corniculatum}\). WUE\(_\text{ratio}\) is not only affected by substrate salinity but also by leaf-to-air water vapour pressure difference (VPD) with considerable decreases as VPD increases (Fig. 7.19). However, Ball (1986) argues that notwithstanding these reductions of WUE\(_\text{ratio}\) the values observed remain exceptionally high. Indeed, the WUE\(_\text{ratio}\) values summarized for all conditions of salinity and VPD given in Fig. 7.19 are higher than in glycohytic C\(_3\)-plants as well as C\(_4\)-plants, and most remarkably they are in the same range as obtained for the highly water saving nocturnal CO\(_2\)-uptake by CAM plants (Table 7.2).

Since stomatal control affects \(J_{\text{CO}_2}\) and \(J_{\text{H}_2\text{O}}\) and hence WUE\(_\text{ratio}\) a calculation of intrinsic WUE, WUE\(_\text{intrinsic}\), is performed to include a consideration of the driving forces for \(J_{\text{CO}_2}\), i.e. the difference between external, \(p_{\text{CO}_2}^a\), and internal, \(p_{\text{CO}_2}^i\), CO\(_2\)-partial pressure, and for \(J_{\text{H}_2\text{O}}\), i.e. VPD, and also the CO\(_2\)-compensation point of photosynthesis, \(\Gamma\),

\[
\text{WUE}_{\text{intrinsic}} = \frac{p_{\text{CO}_2}^a - p_{\text{CO}_2}^i}{p_{\text{CO}_2}^a - \Gamma} \tag{7.2}
\]
Fig. 7.19 Water-use-efficiency ratios (\(W_{\text{UERatio}}\)) of \textit{Avicennia marina} and \textit{Avicennia corniculatum} at approximately 1/10-, 1/2- and 1/1-strength sea water salinity and different leaf-to-air vapour pressure differences (VPD) as indicated by the numbers (in Pa/kPa) in the graphs. (After Ball and Farquhar 1984a; from Lüttge 2002)

and since

\[
p_i^{\text{CO}_2} = p_a^{\text{CO}_2} - \frac{1.6 J_{\text{CO}_2}}{g_{\text{H}_2\text{O}}} \tag{7.3}
\]

\[
g_{\text{H}_2\text{O}} = \frac{J_{\text{H}_2\text{O}}}{\text{VPD}} \tag{7.4}
\]

\[
p_a^{\text{CO}_2} - p_i^{\text{CO}_2} = 1.6 W_{\text{UERatio}} \text{ VPD}, \tag{7.5}
\]

intrinsic water use efficiency is obtained as

\[
W_{\text{UERatio}} = \frac{1.6 W_{\text{UERatio}} \text{ VPD}}{p_a^{\text{CO}_2} - \Gamma}. \tag{7.6}
\]

(The factor 1.6 accounts for the ratio of diffusivities of water vapour to \(\text{CO}_2\) in air.) The results show that \(W_{\text{UERatio}}\) increases with increasing salinity and VPD (Fig. 7.20) and suggest improved use of water as stomata partially close and VPD increases. This supports the conclusions reached from considering \(W_{\text{UERatio}}\) (Fig. 7.19), because assuming constant \(p_a^{\text{CO}_2}\) and \(\Gamma\) (denominator in (7.6)) \(W_{\text{UERatio}}\) for the values in Fig. 7.19 in \textit{A. marina} at all salinities would increase from 6 Pa/kPa to 24 Pa/kPa VPD by a factor of 1.3 to 1.5 and in \textit{A. corniculatum} at 1/10- and 1/2-strength sea water by a factor of 1.25. At 1/1-strength sea water and VPD from 6 Pa/kPa to 12 Pa/kPa the increase in \(W_{\text{UERatio}}\) would be by a factor of 2.

Hence, in terms of both \(W_{\text{UERatio}}\) and \(W_{\text{UERatio}}\) mangrove trees prove well equipped for economic water use in their habitats which are characterized by high salinity and solar radiation leading to high VPD. With respect to the role of VPD it is also necessary to mention leaf and air temperatures which in addition to atmospheric water vapour partial pressure are essential determinants of VPD. Reduced transpiration with increased WUE would reduce transpirational cooling (Sect. 5.2.2.1). Leaf angle position towards solar radiation and morphological characteristics of
leaves are additional attributes in optimization of these relations by mangrove trees (Ball 1996).

The relationships discussed above may be interpreted as illustrating the compromise of the desiccation-starvation dilemma (see Sect. 5.2.2). Since the flow of salt into the leaves is proportional to salinity and transpiration, control of transpiration also reduces the salt load and the danger of serious water deficits and salt toxicity in the leaves. The reduction of CO₂-gain, which also follows partial stomatal closure, is partially offset by effective CO₂-fixation at low $p_{\text{CO₂}}^i$, whilst maintaining high WUE (as noted by Ball 1986). Interestingly, it was also observed that of all the mangroves studied, the salt-excreting species (*Avicennia marina*) afford the highest rates of CO₂-uptake and water-vapour conductances, although the salt load of leaves may be similar in excreting and non-excreting species (Fig. 7.14).

### 7.5.3 High Irradiance, Photoinhibition and Oxidative Stress

Kitao et al. (2003) observed a correlation of light saturated electron transport rates (ETR$_{\text{max}}$) of mangrove trees in a gradation from pioneer species, to intermediate species and shade tolerant climax species (Table 7.3). [This is also a good example for the potential of ETR$_{\text{max}}$-analyses for the assessment of intrinsic photosynthetic capacities of plants adapted to various sites (Sect. 4.1.7).]

**Photoinhibition** has manifold protective functions as well as potentially being irreversibly destructive (Sect. 4.1.7). As shown by measurements of potential quantum yield of photosystem II ($F_v/F_m$ of PSII, see Sect. 4.1.7) mangroves are often highly resistant against photoinhibition. Cheeseman (Cheeseman 1994; Cheeseman et al. 1991) did not observe photoinhibition in *Rhizophora mangle* under water stress in the greenhouse and in *Bruguiera parviflora* in the field. Under extremely challenging conditions $F_v/F_m$-values of $\sim 0.8$ were detected in *Rhizophora stylosa* (Cheeseman et al. 1997). Sobrado (1999) studied *Avicennia germinans* during the rainy and the dry season at a site with high salinity (30–50‰) in the wet season,
60‰ in the dry season) and at a site with low salinity (5 – 15‰ and 40‰ in the wet and dry season, respectively; where 30 – 35‰ correspond to 0.52 – 0.55 M NaCl, i.e. the salinity of sea water). Predawn values of \( F_v/F_m \) were \( \sim 0.75 \) under all conditions indicating only very mild chronic photoinhibition not reversible over night. Similar predawn values of \( F_v/F_m \) were measured with *Avicennia marina* under 1/1-strength sea water salinity and hyper-salinity of 2/1-strength sea water (Sobrado and Ball 1999), and there was no evidence for pronounced chronic photoinhibition under severe salinity. The shade tolerant plants of Table 7.3 showed very slight chronic photoinhibition after darkening of 5 h or longer (\( F_v/F_m = 0.78 \)). Thus, mangrove tree chloroplasts must be well protected against chronic photoinhibition and photodestruction.

On the other hand, during high insolation mangrove trees certainly can become subject to acute photoinhibition, which is not reversible after short periods of darkening. Björkman et al. (1988) reported a large decrease of \( F_v/F_m \) for various mangrove species at high solar radiation in the field. In the different seasons and sites where Sobrado (1999) did not observe chronic photoinhibition as mentioned above she detected \( F_v/F_m \) values as low as 0.45 – 0.55 at midday, i.e. severe acute photoinhibition, which then was largely reversible over night. This may be related to the protective functions of acute photoinhibition where excess photosynthetic excitation energy is dissipated in a harmless way, mainly in the form of heat (see Sect. 4.1.4). The involvement of xanthophylls in this protective process has been shown in mangroves (Christian 2005). The depression of \( F_v/F_m \) in mangrove-tree leaves at midday was found to be correlated with the concentration of zeaxanthin per unit leaf area (Lovelock and Clough 1992). This was not seen, however, in a study, where the performance of *Avicennia marina* was compared at 1/1- and 2/1-strength sea water salinity. The hyper saline condition reduced net photosynthetic CO\(_2\)-uptake (\( J_{CO_2} \)) from 7.6 to 4.3 µmol m\(^{-2}\) s\(^{-1}\) and stomatal conductance for water vapour from 123 to 53 mol m\(^{-2}\) s\(^{-1}\). Despite the much reduced CO\(_2\)-assimilation under the hyper saline regime, xanthophyll pool sizes and epoxidation states as well as non-photochemical energy dissipation (i.e. not connected to CO\(_2\)-assimilation)

<table>
<thead>
<tr>
<th>Mangrove trees</th>
<th>ETR(_{\text{max}}) (µmol m(^{-2}) s(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pioneer species</td>
<td></td>
</tr>
<tr>
<td>Sonneratia alba</td>
<td>95</td>
</tr>
<tr>
<td>Rhizophora stylosa</td>
<td>90</td>
</tr>
<tr>
<td>Intermediate species</td>
<td></td>
</tr>
<tr>
<td>Bruguiera gymnorrhiza</td>
<td>60</td>
</tr>
<tr>
<td>Rhizophora apiculata</td>
<td>55</td>
</tr>
<tr>
<td>Shade-tolerant climax species</td>
<td></td>
</tr>
<tr>
<td>Xylocarpus granatum</td>
<td>40</td>
</tr>
</tbody>
</table>
were similar in both sets of plants, i.e. at 1/1- and 2/1-strength sea water salinity. This suggests that in the hyper saline regime more excitation energy may have been dissipated via photorespiration. Other alternative electron sinks may have been also involved. In any case, under the conditions of this study there was no increased xanthophyll-cycle dependent photoprotection or non-photochemical dissipation of excess excitation energy despite the 43% decrease in CO₂-assimilation rate with the doubling of the salinity level.

Over energization of the photosynthetic apparatus also causes oxidative stress due to the formation of reactive oxygen species (ROS, see Sect. 4.1.3). Protection mechanisms comprise the ascorbate/glutathione cycle and antioxidative enzymes, such as superoxide dismutases (SODs) and others, which are found to be active in mangroves (Cheeseman et al. 1997; Takemura et al. 2002; Parida et al. 2004b). Comparing the mangrove species *Rhizophora stylosa* and *Rhizophora mangle* with pea (*Pisum sativum*), Cheeseman et al. (1997) found that total SOD activities were 38 and 6 times higher, respectively, in the two mangrove species than

![Figure 7.21](image)

**Fig. 7.21** Salinity dependent accumulation of polyols and correlated increase of potential quantum yield of photosystem II (*Fₐ/Fₘ*) after 30 min of dark adaptation in gametophytes of the mangrove fern *Acrostichum aureum*. (Closed circles total polyols, open circles D-pinitol; errors are SE) (A), correlation of polyol and Na⁺ concentration in the tissue (B, C), gametophytes grown under the external salinities indicated by the abscissa in (B) and then transferred to 340 mM NaCl for two days. Hardening by growth at increased salinity (A) is demonstrated by increased *Fₐ/Fₘ* (B) and this is correlated to tissue polyol concentration (C). (After Sun et al. 1999, from Lüttge 2002)
Another interesting observation is that polyols, which are the dominating compatible solutes in mangroves (Box 7.1) may have an additional function as effective radical scavengers (Orthen et al. 1994). Li and Ong (1998) and Sun et al. (1999) studied this in the gametophytes of the mangrove fern Acrostichum aureum. Polyol concentration was strongly correlated with Na$^+$ accumulation in the tissue as determined by substrate salinity (Fig. 7.21A). This involves hardening to salinity stress as it is seen when the gametophytes grown at up to 150 mM NaCl are transferred to 340 mM NaCl for two days and then, $F_v/F_m$ is measured at an irradiance of 400 µmol m$^{-2}$s$^{-1}$ following 30 min dark adaptation (Fig. 7.21B) where high $F_v/F_m$ is correlated with cyclitol content (Fig. 7.21C).

Different strategies in niche occupation are also involved. Lovelock and Clough (1992) give an example for mangroves of the Daintree River in Australia (17°S, 147°E). In Rhizophora there is stress avoidance as leaves are oriented nearly vertically and thus reduce light absorption. Bruguiera parviflora has small horizontal leaves, which are rich in xanthophylls functioning in dissipation of excitation energy. Larger horizontally arranged leaves of Bruguiera gymnorrhiza tend to heat up more strongly and are therefore more subject to photodamage. Thus, B. parviflora dominates the canopy, whereas B. gymnorrhiza is less abundant at the top of the canopy.

7.5.4 Interacting Factors: Salinity, Irradiance, Elevated CO$_2$

Environmental factors can interact. Salinity and irradiance stress may be additive, e.g. between two sympatric mangrove species at saline sites Aegiceras corniculatum was found to be favoured where excess radiation was less frequent and Avicennia marina under conditions of persistent excess irradiance (Christian 2005). Very interesting findings on the interactions between salinity and irradiance were obtained in studies of seedling establishment and growth (Ball 2002). Mangrove seedlings need full sunlight and the formation of gaps in the mangrove forests is essential for regeneration. At full sunlight for most species there were no substantial differences in seedling survival after 12 months at low and high salinity except for 2 species Bruguiera parviflora and Ceriops australis. At 30% sunlight both species showed similarly high survival rates of seedlings at high and low salinity; however, at high irradiance they required high salinity in addition to the full sunlight. Obviously low salinity conditions induced sensitivity to high irradiance in these two mangrove species (Fig. 7.22).

Elevated atmospheric CO$_2$-concentration, $p_{CO_2}^a$, modulates water use and carbon gain and one might expect that it affects salt tolerance of mangrove trees. However, a comparative study of two mangrove species differing in salt tolerance, i.e. Rhizophora apiculata and Rhizophora stylosa, showed that when relative growth rates were limited by salinity, i.e. 350 mM as compared to 125 mM NaCl at the root level, $p_{CO_2}^a$ elevated from 340 to 700 ppm had little effect on the growth rates. However, elevated $p_{CO_2}^a$ stimulated growth when it was limited by air humidity.
i.e. at 43% as compared to 86% relative air humidity. Thus, elevated $p_{\text{CO}_2}^a$ in the future could modify competitive potentials of different mangrove trees along salinity × aridity gradients, but it is unlikely that it will allow mangroves to expand into areas with salinities much more extreme than currently tolerated (Ball et al. 1997).

**7.6 Nutrition**

Mineral nutrition of mangroves is much determined by decomposition of litter (Mfilinge et al. 2002; Ochieng and Erftemeijer 2002) and the activity of microbial mats (Sect. 7.7.2). Mangroves may occasionally suffer phosphorus and nitrogen limitation especially in dwarf mangrove formations further inland of zonations (Cheeseman and Lovelock 2004; Parida and Das 2004; Lovelock et al. 2006a, b). Phosphorus deficiency inhibits water transport and hampers water relations of man-
groves (Lovelock et al. 2006b, c). High salinity inhibits uptake and reduction of nitrate (Pariada and Das 2004), and nitrogen fertilization may stimulate growth (Kao et al. 2001; Yates et al. 2002). However, other stress factors are dominating so that mineral supply is not very likely to become the limiting factor (Yates et al. 2002; Alongi et al. 2003). An interesting ion is $K^+$ because under salinity stress when $Na^+$ is accumulated $K^+$ levels are normally reduced and this can lead to ion imbalances with adverse effects also in mangroves (Naidoo et al. 2002). However, since seawater has a $K^+$-concentration of 10 mM this may not be a particular problem of stress in mangroves (Cram et al. 2002).

### 7.7 Aquatic Communities

#### 7.7.1 Macroalgae in Mangroves

Macroalgae in mangroves grow between the roots but mainly epiphytically on the pneumatophores and trunks of trees (Post 1963). Species diversity is mainly given by red algae of the genera *Bostrychia*, *Caloglossa* and *Stictosiphonia*, although brown algae may also occur, e.g. mats of *Hormosira banksii* in SE-Australia (Karsten 1995). About 15–20% of the total biomass of mangrove communities is represented by these macroalgae (Karsten 1995).

The macroalgae are subject to the same stress conditions and even more so than the woody mangrove plants, e.g. changing salinity and desiccation at low tide. They show a broad salinity tolerance between 1/5- and 2/1-strength sea water (Karsten and West 1993). Some mangrove algae are also desiccation tolerant (Biebl 1962; see Sect. 11.4), e.g. *Stictosiphonia arbuscula* can lose up to 95% of its tissue water and recover within several hours when rewetted (Karsten 1995). Accumulation of compatible solutes (Sect. 7.4) plays a large role in the red algae in response to salinity and shows a rather high chemical diversity including floridoside, digenasiside, D-sorbitol, D-dulcitol, D-mannitol and isethionic acid (Box 7.1) (Karsten 1995, 1996; Karsten et al. 1995a, b, 1997a, b). Different compatible solute spectra have been found in *Bostrychia tenuissima* from different geographic provenance in Australia, i.e. sorbitol plus dulcitol and sorbitol plus digenasiside, respectively, and this was controlled genetically (Karsten et al. 1995b). In the mangrove fern *Acrostichum aureum* the gametophyte uses D-pinitol and the sporophyte D-1-O-methyl-muco-inositol (Sun et al. 1999).

Low irradiance is an important factor limiting the growth of macroalgae in mangrove forests. While the canopy of the trees may receive photosynthetic photon flux densities (PPFD) up to 2,500 $\mu$mol m$^{-2}$s$^{-1}$, the algae may not obtain more than 60–100 $\mu$mol m$^{-2}$s$^{-1}$. This is not only due to shading by the trees but also to turbid water with organic materials and debris (Karsten 1995). *Bostrychia simpliciuscula* and species of *Caloglossa* may still show positive relative growth rates at the very low PPFD of 2.5 $\mu$mol m$^{-2}$s$^{-1}$ (Karsten and West 1993; Karsten et al. 1994).
7.7.2 Microbial Mats

Microbial mats are an essential aspect of mangrove ecosystems. The surface muds are zones of net heterotrophy. Light limitation beneath mangrove forests might mean that photosynthesis by benthic microalgae only makes a minor contribution to primary productivity (Alongi 1994), but Karsten (1995) arrives at the estimate that microbial mats account for 5–20% of the total mangrove productivity. They are largely composed of diatoms, cyanobacteria, sulphur bacteria, purple sulphur bacteria and sulphate reducing bacteria (Table 7.4). Their thickness as given in Table 7.4 is 10–12 mm but can also be as much as 80–120 mm (Hussain and Khoja 1993). Root associations of mangroves with halotolerant \textbf{N}_2\text{-fixing bacteria} have been shown to improve N-supply and to contribute to the high productivity of mangrove ecosystems (Zuberer and Silver 1978, 1979; Sengupta and Chaudhuri 1991).

The main stress factors, as for the other mangrove communities are large varying amplitudes of salinity, irradiance and desiccation. Cyanobacteria use glycosylglycerol as compatible solute (Karsten 1996) and form scytonemin, pterins and mycosporine-like amino acid compounds as ultraviolet light protectives (Karsten et al. 1998; see Sect. 11.2.1.2).

Table 7.4 Layers in microbial mats of mangroves (after Karsten 1995)

<table>
<thead>
<tr>
<th>Thickness from top (mm)</th>
<th>Organisms</th>
</tr>
</thead>
<tbody>
<tr>
<td>0–2</td>
<td>Fine sand plus diatoms</td>
</tr>
<tr>
<td>2–4</td>
<td>Cyanobacteria</td>
</tr>
<tr>
<td>4–6</td>
<td>Sulphur bacteria</td>
</tr>
<tr>
<td>6–8</td>
<td>Purple sulphur bacteria</td>
</tr>
<tr>
<td>8–11</td>
<td>Sulphate reducing bacteria</td>
</tr>
<tr>
<td>&gt; 11</td>
<td>Sand</td>
</tr>
</tbody>
</table>

7.8 Mangroves as Endangered Ecosystems with Numerous Benefits for Man and the Need for their Conservation

Mangroves are among the most endangered ecosystems on earth (Springer 2002). They have been frequently considered to be useless and are disappearing rapidly. However, they are very unique, and with their characteristic physiognomic beauty they are among the outstanding natural heritages we have. Moreover, they have numerous direct benefits for us (Oo 2002). They are pioneer communities at the interface between sea and land and \textbf{stabilize coastlines}. Some mangrove trees provide useful \textbf{wood} for fuel and the production of charcoal and particularly \textbf{resistant timber} for construction purposes. They provide \textbf{fodder} and \textbf{medicine}. They serve as \textbf{nursery grounds} for breeding of marine life, for fish and crabs of coral reefs, and
sustain the economical basis of coastal fisheries (Ellison 2002). They are also used for establishing ponds for the culture of fish and prawns.

Mangroves are among the most productive ecosystems of the world. If we take the productivity of macroalgae as 15 – 20% and that of microbial mats as 5 – 20%, the productivity of trees would be 80 – 60%. This underlines the diversity of the mangrove communities.

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Chapter 8
Ecosystems of Coastal Sand Plains

8.1 Restingas

8.1.1 Geological History and Vegetation Physiognomy

The Atlantic rain forest of Brazil is one of the 25 biodiversity hotspots in the world. In the south eastern state of Rio de Janeiro it is surrounded by various marginal plant communities, one of which is the restinga (Scarano 2002; Scarano et al. 2005a). It stands on quaternary terrains, i.e. sandy coastal plains between the rain forest and the sea (Martin et al. 1993; Scarano et al. 1997). The vegetation has its origins mostly associated to the rain forest and there are hardly any endemic plant species (Rizzini 1979; Araujo 2000). Migration from the Atlantic forest to the restingas was successful for ecologically plastic species, which were able to adjust to the more extreme and seasonal conditions imposed to the restinga habitats (Scarano 2002). Approximately 80% of the plant species occurring in the restingas of the state of Rio de Janeiro are also found in montane rainforests (Araujo 2000). Along the coastline of Rio de Janeiro the quaternary sandy deposits and dunes date mostly from the Holocene, having been established and re-established from 5000 to 3000 years BP, but further north under the influence of the Paraiba do Sul river in some areas marine sandy deposits date from the Pleistocene (120,000 years BP) and remained acquiring their final shape after a series of invasions and regressions of the sea during the Holocene (Martin et al. 1993).

The restingas comprise a mosaic of plant communities ranging from open, patchy formations to forests (Fig. 8.1A,B). Across a transect from the sea inland, successive sand dune ridges, vegetation islands on the sand plain and dune forests, and where the ground water table is high, open fresh water lagoons and swamp forests contribute to the physiognomy of the landscape (Reinert et al. 1997; Duarte et al. 2005). The very diverse plant communities found in the restingas are subjected to conditions as extreme as seasonal drought and oligotrophy on the one hand, and permanent flooding on the other (Henriques et al. 1986). Thus, the flora of a given restinga plant community often is very different from the flora of closely adjacent communities (Araujo et al. 1998).
8.1.2 The Nurse Plant Syndrome
and Dynamics of Vegetation Islands

The nurse plant syndrome is effective when plant species shelter seedlings, young and/or adult individuals of other species through their ontogeny (Dias and Scarano 2007). In the restingas nurse plants are pioneers on the bare sand, and they comprise some small palms (e.g. *Allagoptera arenaria*; Fig. 8.2A) and bromeliads (e.g. *Aechmea nudicaulis*; Fig. 8.2B) but most importantly the shrubs of *Clusia* species, especially *C. hilariana* which is the dominant plant in the restingas of Rio de Janeiro (Sampaio et al. 2005). Therefore, restingas have also been called *Clusia* scrubs (Ule 1901). Characteristically nurse plants of the restingas are often terrestrial forms
of typical epiphytes of the neighbouring Atlantic rain forest possibly pre-adapted to stress related to missing or limited supplies of water and nutrients from a pe dadosphere (Scarano 2002). Many of them perform crassulacean acid metabolism (CAM), which is a biochemical adaptation of photosynthesis to stress due to high insolation and partially problematic supply of water (Sect. 5.2.2.2), i.e. bromeliads and Clusias including C. hilariana (Reinert et al. 1997; Scarano 2002; Lüttge 2007a,b).

Underneath the canopy of C. hilariana a higher species richness was found than under any other woody species (Zaluar 1997; Sampaio et al. 2005; Dias et al. 2005, 2007). The higher density and richness under scrubs of C. hilariana is mainly due to effects on seed dispersers and activation of dispersal (Dias et al. 2007). Aechmea

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Fig. 8.2A, B Establishment of new vegetation islands by nurse plants? A Allagoptera arenaria, the wind drawing circles on the sand by moving the leaves around (dry restinga of Massambaba, see Fig. 8.1). B Aechmea nudicaulis (foreground centre), Allagoptera arenaria (foreground left), dune forest (background) (intermediate restinga of Jurubatiba Park, see Fig. 8.1)
A. nudicaulis does not germinate and grow seedlings on the open sand, among other reasons probably due to the high temperatures reached on the bare sand. It only germinates within vegetation islands. Via directional growth of rhizomes and ramets, however, it then acquires space and selects its own habitats (Fig. 8.2B; Sampaio et al. 2004, 2005; Dias et al. 2005). Conversely, however, it is not only C. hilariana scrub that nurses A. nudicaulis. The Clusia may germinate inside the tanks of the bromeliad and is nursed itself (Dias and Scarano 2007). These reciprocal interactions between different nurse plants generating vegetation islands underline the non-linear dynamics of the spatiotemporal patchiness (see also Sects. 3.3.1, 3.3.3 and 8.2.2) of the restinga ecosystem.

8.1.3 Ecophysiology of Photosynthesis of Restinga Plants

The performance of the special mode of photosynthesis CAM is quite frequent among the plants of the restingas with many species of bromeliads, orchids, cacti and Clusia. Comparative ecophysiological studies have been performed of various shrubs which are much determining the physiognomy of the restingas (Figs. 8.1A, 8.2B) such as the Clusiaceae Rheedia brasiliensis, Calophyllum brasiliense, Clusia hilariana and Clusia fluminensis, the Myrsinaceae Myrsine parviflora and the Fabaceae Andira legalis (Duarte et al. 2005; Geßler et al. 2005; Scarano et al. 2005b). Restingas where these plants were investigated show a moisture gradient dependent on annual rainfall, the ground water table and the degree of groundwater salinity. Table 8.1 summarizes some relations of maximum apparent rates of photosynthesis (ETR\textsubscript{max}) deduced from measurements of instant light response curves (Sect. 4.1.7) to such moisture gradients, where intrinsic photosynthetic capacity given by ETR\textsubscript{max} increases in three of the species shown at the drier sites and shows a decrease or no response in a fourth species (A. legalis).

Table 8.1 Maximum apparent rates of photosynthetic electron transport ETR\textsubscript{max} (µ mol m\textsuperscript{-2} s\textsuperscript{-1}) obtained from light curve measurements of four restinga shrubs along a moisture gradient. Within vertical columns different letters at the numbers indicate statistically significant differences. (Data from Duarte et al. 2005; Geßler et al. 2005; Scarano et al. 2005b)

<table>
<thead>
<tr>
<th>Vegetation type</th>
<th>Myrsine parviflora</th>
<th>Rheedia brasiliensis</th>
<th>Clusia fluminensis</th>
<th>Andira legalis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Swamp forest at an intermediate restinga</td>
<td>63\textsuperscript{a}</td>
<td>136\textsuperscript{a}</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wet restinga</td>
<td></td>
<td></td>
<td>198\textsuperscript{a}</td>
<td>288\textsuperscript{a}</td>
</tr>
<tr>
<td>Intermediate restinga</td>
<td>90\textsuperscript{b}</td>
<td></td>
<td>113\textsuperscript{b}</td>
<td></td>
</tr>
<tr>
<td>Dry restinga</td>
<td>176\textsuperscript{c}</td>
<td>198\textsuperscript{b}</td>
<td>172\textsuperscript{a}</td>
<td>159\textsuperscript{b}</td>
</tr>
</tbody>
</table>
8.2 Salinas

8.2.1 Formation of Coastal Salt Marshes and Vegetation Physiognomy

Coastal salt marshes at the northern coast of South-America are formed in bays, where the sand-laden waves returning from the beach to the sea are driven back towards the shore by the North-Eastern trade winds. First a sandbar is formed leading
to a sandbank and to separation of a lagoon. Subsequently, this lagoon fills in with sand, drying out and becoming a salt marsh. Both fixed and mobile sand dunes may also form at the coast behind the salt marsh (Fig. 8.3). A typical example are the inland salt-marshes near the northern Caribbean coast of Venezuela first described briefly by Walter (Walter and Breckle 1984) and later studied ecophysiologically in some detail (Lüttge et al. 1989a,b; Medina et al. 1989; Smith et al. 1989). These salt marshes are much more extreme habitats than the restingas (Sect. 8.1) with a very strong seasonality. The most salt-resistant plants found first in such sites are mangroves, which begin to surround the lagoon (Fig. 8.3), an example being *Avicennia germinans* at the lagoon and salt marshes near Chichiriviche on the Caribbean coast of Venezuela.

The flat alluvial sand plain covering areas previously occupied by the lagoon is subject to marked seasonality because there is a pronounced rainy season in October to December and a strong dry season during the rest of the year interrupted only by a small and short wet period in April (Fig. 8.4). During the rainy season the sand plain may be covered by several decimeters of fresh water, whereas during the dry season the surface is dry and a considerable salt crust may form (Fig. 8.5). The very salty groundwater, with an NaCl-concentration several times that of seawater (Fig. 8.6), percolates upwards to the surface where the water evaporates and leaves behind the dissolved salt. The vegetation of the sand plain can be described by distinguishing five units (Fig. 8.7):

a) the vegetation-free sand and salt flats (Fig. 8.7A),

b) a halophyte zone with *Batis maritima* and *Sesuvium portulacastrum* as the dominating species (Fig. 8.7B),

c) a grass-land zone with *Sporobolus virginicus* and *Oxycarpha suaedifolia* as the characteristic plants (Fig. 8.7D),

d) vegetation islands with the mangrove associate *Conocarpus erectus* and the cactus *Subpilosocereus ottonis* as the physiognomically determinant species (Fig. 8.7A, C), [enumeration continuing on page 274]

![Fig. 8.4](https://example.com/fig84.png)

**Fig. 8.4** Average monthly values of rainfall, evaporation and temperature near the northern Caribbean coast of Venezuela close to Chichiriviche for a 22-year period. (Medina et al. 1989)
Fig. 8.5A, B Alluvial sand plain with vegetation islands near the northern Carribbean coast of Venezuela at Chichiriviche. A In the rainy season (November 1985) covered with fresh water. B In the dry season (February 1983) covered with a thick salt crust (background). (See Medina et al. 1989)
Fig. 8.6 A Ionic composition of the ground water from pits excavated in the dry season on the sand plain at some distance from (I and II) and close to the open lagoon (III) respectively, of Chichiriviche, Venezuela, as compared to seawater. B Example of a soil pit dug to examine the ground water (Medina et al. 1989). (For the position of the three soil pits see also the transect of Fig. 8.8)
Fig. 8.7A–D Vegetation units of the alluvial plain at Chichiriviche, Venezuela. A Vegetation island on the sand plain. B Halophyte zone with *Sesuvium portulacastrum* (front) and *Batis maritima* (middle ground) around a vegetation island with *Conocarpus erectus* in the background. C Vegetation island with bushes of *Conocarpus erectus* and *Subpilosocereus ottonis*. D Grassland with deciduous forest in the background.
a deciduous forest characterized by species of Capparis, Caesalpinia coriaria, Prosopis juliflora, Jacquinia revoluta, Maytenus karstenii, Erythroxylon cumanense, Croton sp. and Pereskia guamacho (Fig. 8.7D).

A transect presenting finer details is shown in Fig. 8.8. In addition to the seasonal differences in the water table the figure also gives an indication of the seasonal

Fig. 8.8 Transect of a part of the alluvial plain of Chichiriviche, Venezuela, showing topographical variations with the major vegetation units (centre), the water tables (centre) and top soil chloride concentrations in the rainy season and the dry season respectively (bottom) and the distribution of the most frequent plant species (top). (After Medina et al. 1989)
8.2 Salinas

changes in salt content of the upper 10 cm of top-soil. Overall salt concentrations in the soil as well as seasonal fluctuations tend to be highest in the bare areas and decrease with the sequence of vegetation units as follows: halophyte zone – grassland zone – vegetation islands – deciduous forest.

8.2.2 Dynamics of Vegetation Islands

The most conspicuous feature of these salinas are the small vegetation islands with a diameter of 3 – 10 m and a soil surface 10 – 40 cm higher than the sand plain. Observers have been tempted to consider these islands as a particular stage in a progressive succession, which starts from the bare sand plain, then leads to the halophyte vegetation, followed by island vegetation and finally on to grassland and deciduous forest (Walter 1973).

However, a closer examination extending over several years has shown that there is no such one-way progressive succession towards a stable climax community at the end. There are oscillations between the various vegetation units in time which may be determined by medium-term climatic fluctuations; e.g. the years between 1966 and 1975 appeared to be wetter, and the years between 1976 and 1986 were drier than the long term average (Fig. 8.9). The whole ecosystem is highly dynamic and provides an excellent example of an oscillating mosaic, as opposed to a stable climax equilibrium (see Sect. 3.3.3). By following the development of a given island, we see that islands not only grow into savannas and forest but also die, being eroded and eventually disappearing into the bare sand plain (Fig. 8.10). Thus, these islands appear to be metastable states between the more stable states of the forest and the sand plain, respectively.

Fig. 8.9 Variations of total annual rainfall near the northern Caribbean coast of Venezuela close to Chichiriviche for the years 1964 – 1986. (Medina et al. 1989)
8.2.3 Strategies of Adaptation of Plants in the Different Vegetation Units

8.2.3.1 Small Perennial Halophytes: Salt Inclusion and Stress Tolerance

The zone of small perennial halophytes surrounding the edges of vegetation islands and bordering the vegetation free salt flats is dominated by three species, namely *Portulaca rubricaulis*, *Sesuvium portulacastrum* and *Batis maritima* (Fig. 8.11). The creeping fruticose stems of the first two species contrast with *B. maritima*, which has a more upright growth habit. The three species are also primary colonizers of
the sand plain. They occupy the most extreme habitats in the sand plain, which range from being flooded with fresh water in the rainy season to dry, salt-encrusted soil in the dry season when the water table may drop to 1 m below ground (Lüttge et al. 1989b; Figs. 8.5 and 8.8).

All of the three halophytes are salt includers and accumulate NaCl in their highly succulent leaves. However, *P. rubricaulis* combines this strategy of stress tolerance with that of stress avoidance in that it is deciduous and sheds its leaves during the dry season. Among the three species, it has the lowest salt concentrations in its leaf sap, viz. 230 mM Cl$^-$ and 60 mM Na$^+$, while the other two species have much higher salt levels in their leaves, i.e. 260 – 1,080 mM Cl$^-$ and 370 – 720 mM Na$^+$ in the wet season, and 540 – 1,410 mM Cl$^-$ and 920 – 1,590 mM Na$^+$ in the dry sea-
son, respectively. However, *P. rubricaulis* is a C₄-plant while the other two species are C₃-plants. Thus *P. rubricaulis* may use the higher instantaneous productivity of C₄-photosynthesis (see Box 10.2) for production of enough perennial shoots to compete in the habitat effectively.

*B. maritima* also accumulated sulphate, with a twofold increase of leaf-sap concentrations in the dry season. In *S. portulacastrum*, Na⁺ accumulation exceeded Cl⁻ accumulation by far and synthesis of the organic acid anion oxalate is found to serve in maintaining charge balance. Increased salt accumulation in the leaves of *B. maritima* and *S. portulacastrum* in the dry season is accompanied by a 1.5- to 2-fold increase in leaf succulence (see also Sect. 7.4). *S. portulacastrum* was also shown to use compatible solutes (see Sect. 7.4 and Box 7.1) such as proline and pinitol which augments the tolerance of salt inclusion (Fig. 8.12).

In leaves of the erect stems of *B. maritima* photosynthetic gas exchange, measured as net CO₂ uptake and transpirational loss of water vapour, shows little response to the transitions between the rainy and the dry season (Fig. 8.13). In contrast, photosynthesis in the leaves of the prostrate stems of *S. portulacastrum* is severely impaired in the dry season, showing a pronounced midday depression of gas-exchange (see Sects. 5.2.2.1 and 10.1.2.3) and about 40% inhibition of light saturated rates of photosynthesis (Fig. 8.13). Thus, *S. portulacastrum* clearly suffers more under the stress of the dry season but it is also more of a pioneer coloniser of the sand plain as it occupies the outermost edges of the vegetation islands and larger areas of the flat plain (Figs. 8.7B and 8.11C).

In summary, the three species of halophytes, which are subject to very similar challenges by extreme environmental conditions, have different strategies of adaptation to stress. Notwithstanding the similarities in life-forms, with small fruticose stems and succulent leaves, the differences in ecophysiological comportment reflect ecological diversity, and once again prove to be a basis for species diversity (see Sect. 3.3.2).

![Fig. 8.12 Concentrations of the compatible solutes proline and pinitol in the leaf sap of Sesuvium portulacastrum in the wet season (W) and the dry season (D). (Lüttge et al. 1989b)](image-url)
8.2.3.2 Terrestrial CAM Plants: Salt Exclusion and Stress Avoidance

There are two different life forms of terrestrial CAM plants on the sand plain, which are stem succulent cacti and tank forming bromeliads. They are salt excluders. In this way they avoid the physiological stress of salinity, and their use of the flexibility of the CAM cycle (see Sect. 5.2.2.2 and Box 5.1) is important in this strategy in the salinas (Lüttge 1993).

8.2.3.2.1 Columnar Ceroid Cacti

The dominating cactus of the salinas at the North coast of Venezuela is the columnar cactus *Subpilosocereus ottonis* with strongly branching individuals more than 6 m tall (Fig. 8.14A). Small seedlings are frequently found at the rim of vegetation islands (Fig. 8.14B) as well as among other vegetation and within the tanks...
Fig. 8.14A–F Large plants (A), small seedling (B) and seedling rerooted after injury in the field (C) of *Subpilosocereus ottonis* in the alluvial plain of Chichiriviche, Venezuela. Experimental seedlings of *Cereus validus* (D), one rotting during an extended salt treatment (E), and another one dried out at the bottom and totally insulated from the substratum (F)
of bromeliads. A similar type of cactus occurs in the subtropical salinas, Salinas Grandes in Argentina, namely *Cereus validus*. Experiments with 10 cm tall seedlings of *C. validus* (Fig. 8.14D) and analyses of *S. ottonis* in the field show that these cacti are strong salt excluders (Fig. 8.15). When subject to salinity the roots rapidly accumulate large amounts of NaCl. However, there is no salt export from the roots to the shoots, so that the peripheral green stem chlorenchyma and the central water storage parenchyma of the stems receive very little additional salt during a salinity treatment of up to 14 days and 600 mM NaCl in the root medium (Fig. 8.15).

It is quite obvious that the fine absorptive roots of the cacti die under the stress of salinity and the rest of the cactus becomes quite isolated from the substratum. When the salinity treatment is extended for several months, in some cases salt solution may diffuse upwards killing the stem tissue so that eventually the whole cactus seedling rots away and dies (Fig. 8.14E). In other cases, however, the base of the shoot dries out and then finally becomes insulated very effectively from the ground (Fig. 8.14F). The major part of the green stem survives. But by what means and for how long?

Certainly, the cacti cannot survive indefinitely without water and nutrient supply from the substratum. In the strongly seasonal salinas, of course, they only need

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**Fig. 8.15A,B** Effects of NaCl solutions supplied to the roots of small seedlings of *Cereus validus* (see Fig. 6.14D–F) in pot culture with sand on Na$^+$ and Cl$^-$ levels in the roots, the water storage stem parenchyma and the peripheral green chlorenchyma. **A** NaCl concentrations in the watering solution were increased by daily increments of 50 mM up to 600 mM (*upper abscissa*), and the plants were analyzed as soon as the respective concentrations were reached at the times indicated (*lower abscissa*). **B** NaCl concentrations in the watering solution were increased by daily increments of 50 mM. At any given concentration indicated on the abscissa, plants were kept for 14 days after this concentration was reached and then analyzed. (Nobel et al. 1984)
Fig. 8.16A,B Root system of *Subpilosocereus ottonis* as shown on a seedling (A) and a tall fallen cactus (B) with extended horizontal root system and vertical tap roots.
To overcome the dry season when salinity-stress is present, particularly if they are able to form functional roots again in the wet season. Indeed, cacti are known to be capable of rapid **adventitious root regeneration** (Fig. 8.14C). *S. ottonis* also develops a large horizontal root system from which strong vertical tap roots protrude into the soil, and from which fine absorptive roots have a seasonal turnover related to substratum salinity (Fig. 8.16).

To overcome an extended dry season, the insulated stems of the cacti use the possibility of nocturnal **recycling of respiratory CO₂** provided by the CAM-mechanism (see Sect. 5.2.2.2 and Box 5.1). The experimental seedlings of *C. validus* under salt stress reduced photosynthetic gas exchange (Fig. 8.17), and the contribution of nocturnal CO₂-recycling to total night-time malate accumulation increased from 20% in the controls to 50% in the NaCl-treated plants. In the extreme case of total insulation, stomata may close permanently during both day and night, reducing gas exchange to an absolute minimum. In this way the plants do not gain carbon, but they minimize loss. Carbon from respiratory CO₂ is recycled into malate during the night and, after decarboxylation of malate, in photosynthetic CO₂-fixation and carbohydrate synthesis through the Calvin cycle during the day. Thus, metabolism

![Fig. 8.17](image_url)

**Fig. 8.17** Effect of NaCl on photosynthetic gas exchange of small seedlings of *Cereus validus*. The control plants were irrigated with water; the NaCl-treated plants received NaCl solutions of daily increments of 50 mM until 400 mM NaCl was reached and were then kept for 16 days at this NaCl level. The **horizontal black bar** indicates the dark period. (Nobel et al. 1984)
Fig. 8.18 Loss of fresh weight, i.e. loss of water, by small plants of *Subpilosocereus ottonis* (about 0.3 m tall) derooted and placed in full sun exposure in the dry season starting on day 0. Errors are SD, *n* was 6 to 18. (Lüttge et al. 1989a)

is maintained by respiratory and photosynthetic energy turnover, and the only input under these conditions is light energy, which keeps them alive.

Naturally, some loss of water vapour occurs via cuticular transpiration and leads to a gradual reduction of the water reserves in the water-storage parenchyma of the cactus stems (Fig. 8.18) and a decline of vitality. It has been shown that cacti survive when up to 54% of tissue water content is lost, although any subsequent loss is lethal (Holthe and Szarek 1985). Thus, the chance of a small cactus to survive the salinity stress of the dry season is much smaller than that of a large cactus. A certain minimal biomass, with a sufficiently large water reserve in the water-storage parenchyma, is required. Of course, survival also depends on the length of the dry and wet season, respectively. If the wet season is longer and the dry season relatively short, newly established seedlings have a better chance of survival. Thus, as shown for cacti and agaves in the deserts of North America (Jordan and Nobel 1979, 1982) seedlings do not survive every year, and one observes age classes of larger plants, which indicates the wetter periods when seedlings were able to become established.

For the larger cacti growing on the vegetation islands, salinity stress in the top soil is reduced even in the dry season. The major tap roots of 6 – 7 m tall plants of *S.*
ottonis are no longer than 50 cm, and even during the dry season they do not extend below the point where salinity becomes 150 meq Cl$^{-}$ kg$^{-1}$ air-dried soil (Fig. 8.19). In conclusion, the major problem for the cacti in the salinas really is to survive the vulnerable seedling stage.

8.2.3.2.2 Tank-Forming Bromeliads

Some tank-forming terrestrial bromeliads occur on the salinas. At the northern coast of Venezuela by far the most frequent is *Bromelia humilis*, with the type II or tank-root life form (see Sect. 6.4 and Fig. 6.15B). Since it does not necessarily need to form soil roots, the leaf rosettes may simply lie on the ground, and thus, *B. humilis* is effectively also a salt excluder and stress avoider.

Within tanks and through tank roots *B. humilis* can collect and utilize water. Therefore, in contrast to the columnar cacti (Sect. 8.2.3.2.1), *B. humilis* can replenish water reserves even from very small spells of rain during the dry season. There is a marked peripheral water-storage parenchyma of thin-walled, non-green and highly vacuolated cells, with little cytoplasm at the adaxial surface of the leaves (see Fig. 6.22C). The leaf tissue loses water during the dry season, and the leaves become less succulent and have increased dry weight : fresh weight ratios (Fig. 8.20). Overall, the CAM plant *B. humilis* demonstrates water storage at three different time scales:

- short term storage based on the osmotic effects of nocturnal malate accumulation in the leaf cells (see Sect. 6.6.2.2),
- medium term storage in the tanks,
- long term storage in the water parenchyma.

Fig. 8.20 The degree of succulence (fresh weight : area) and dry weight : fresh weight (DW/FW) ratios in leaves of shaded and exposed plants of *Bromelia humilis* in the wet season (W) and in the dry season (D) in the sand plain of Chichiriviche, Venezuela. (Lee et al. 1989)
*B. humilis* occurs in different vegetation units on the sand plain and expresses three different **phenotypes** of growth form and pigmentation (see Sect. 4.1.2), namely the dark green phenotype shaded under shrubs and trees of the deciduous forest, the yellow phenotype exposed on bare soil islands or in the grassland of the sand plain, and a light-green intermediate phenotype, which also grows in relatively exposed conditions (Fig. 4.3). The differential characteristics of shade and sun plants (Sect. 4.1.2) are fully expressed in these phenotypes. In the dry season net CO\textsubscript{2} exchange was reduced with 7.2 mmol m\textsuperscript{-2} day\textsuperscript{-1} in the yellow and 22.2 mmol m\textsuperscript{-2} day\textsuperscript{-1} in the green and shaded plants (Fig. 8.21), while an average rate obtained for all phenotypes in the rainy season was 33.0 mmol m\textsuperscript{-2} day\textsuperscript{-1}.

In the dry season the plants operated with increasing internal CO\textsubscript{2}-recycling which corresponded to 56% in the green and 87% in the yellow phenotype (Fig. 8.21).
8.21), while recycling for all phenotypes in the wet season was only 21%. Clearly, the yellow exposed plants are under the most severe stress of

- high irradiance,
- drought,
- low nutrient supply.

The latter applies because the exposed plants also lack-supplies from decomposing litter falling between the plants and into the tanks of the shaded plants in the deciduous forest. This is reflected in their productivity. It is seen that losses and gains are more or less balanced and net productivity is close to zero in the yellow exposed plants, as compared to the green shaded plants which have a distinct primary net productivity (Table 8.2).

8.2.3.3 Epiphytic CAM Plants: Avoidance of Salinity Stress

On the large cacti and the shrubs of the vegetation islands one frequently finds epiphytic CAM plants, especially the bromeliad *Tillandsia flexuosa* and the orchid *Schomburgkia humboldtiana* (see Fig. 6.39). Although there may be some salt spray driven inland by stronger winds, in their epiphytic habitat these plants largely avoid salinity stress. CAM serves adaptation to drought stress (Sect. 5.2.2.2). Additionally both species are myrmecophilous (Sect. 6.6.3). CO2-acquisition in *S. humboldtiana* is greatly reduced in the dry season. In contrast, rates of CO2-uptake are constantly low in *T. flexuosa* over both rainy and dry seasons (Fig. 8.22). Internal CO2-
recycling is similar in both plants at 65 – 76% and independent of season. *T. flexuosa* is more frequent and so, despite lower potential maximum productivity, the physiological characteristics maintain carbon acquisition continuously over the seasons.

### 8.2.3.4 Mangroves and Associates

The shrubby vegetation of the islands is dominated by the mangrove associate *Conocarpus erectus*. The true mangrove *Avicennia germinans* also plays a limited role, particularly on vegetation islands closer to the lagoon with more permanent salt stress. *A. germinans* appears to be much more salt tolerant than *C. erectus*. The more detailed ecophysiological comportment of the two species is discussed in Sect. 7.5.1.

### References


References

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9.1 Physiognomy and Terminology

Savannas are open habitats typically dominated by grasses and often strongly affected by seasonal changes of rainfall. The term savanna, *sabana* in Spanish and *savana* (or *campo*) in Portuguese, is a West Indian expression of uncertain Caribbean origin (Huber 1987). A classical example of a savanna is the Llanos north of the Orinoco in Venezuela (Fig. 9.1). Alexander von Humboldt vividly described the seasonal contrasts in this large Venezuelan savanna-area:

“When under the vertical rays of the sun, never covered by clouds the combusted layer of grass has fallen into dust, the hardened soil cracks as if it were shaken by mighty earthquakes.”

“The uniform vision of these steppes has some greatness but also some tristesse and depression in it. It is as if the whole nature would be frozen; scarcely every now and then the shade of a small cloud, which hurries across the zenith and announces the near rainy season, falls over the savanna. One hardly can get used to the vision of the Llanos, which offer a picture like the surface of the sea…”

“... as a saying goes here: ‘The large ocean of greenery’ (‘los Llanos son como un mar de yerbas’)”

“When after a long drought the beneficial rainy season sets in, the scene in the steppe suddenly changes. When the surface of the earth is just wetted the fragrant steppe covers itself with *Kyllingia* with highly panicled *Paspalum* and with a diversity of grasses. Stimulated

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1 “Wenn unter dem senkrechten Strahl der niebewölkten Sonne die verkohlte Grasdecke in Staub zerfallen ist, klafft der erhärtete Boden auf, als wäre er von mächtigen Erdstößen erschüttert…”

2 “Der einförmige Anblick dieser Steppen hat etwas Großartiges, aber auch etwas Trauriges und Niederschlagendes. Es ist, als ob die ganze Natur erstarrt wäre, kaum daß hin und wieder der Schatten einer kleinen Wolke, die durch den Zenith eilend die nahe Regenzeit verkündet, auf die Savanne fällt. Nur schwer gewöhnt man sich an den Anblick der Llanos, die… ein Bild der Meeresflächen bieten.”

Fig. 9.1A–C The Llanos, Venezuela (A, B) and a savanna in Costa Rica, protected within the borders of the Santa Rosa Park (C)
Fig. 9.2 Physiognomy of savannas with examples from all over the world. Transects of Vareschi (Vareschi 1980, with kind permission of R. Ulmer)
by the light, herbaceous mimosas open their folded dormant leaves and greet the rising sun like the early song of the birds.\(^3\)

In order to give an impression of the vegetation, Fig. 9.1 shows a picture of the Llanos in Venezuela and a savanna in Central America, and the drawings of transects in Fig. 9.2 present various types of savannas from all over the world. H. Walter (Walter and Breckle 1984) distinguished between savanna and park-land as follows:

- **Savanna:** homogeneous plant communities with scattered woody plants (trees, shrubs and bushes) in a grass layer closed in a greater or less degree over the soil and with a few herbs in between.
- **Park-land:** a mosaic of forest islands in an open grassland with few woody plants where the forest is associated with biotopes (e.g. river banks, valley bottoms, hills), which are ecologically different from the grassland.

In contrast, the geographer C. Troll (see Walter and Breckle 1984) considered various types of landscapes as savannas which constitute a macro-mosaic of grassland with different tree-formations (Fig. 9.3). Some of them are illustrated in the accompanying photographs:

- the gallery forest along rivers (Fig. 9.4),
- the forest of gullies,
- the termite savanna (Fig. 9.5),
- the “morichales” (Fig. 9.6).

Fig. 9.4A, B Gallery forests. A Rio Parupa, Gran Sabana, Venezuela. B In the cerrados near Brasília (Fazenda Agua Limpa), Brazil
Fig. 9.5A, B Termite savannas. A After a fire, Queensland, Australia. The termite nests scattered over the field are well visible after the vegetation has been burnt. B Acacia wooded savanna, Great Rift Valley, Ethiopia
Fig. 9.6 Savanna with dense stands of the moriche palm, *Mauritia flexuosa*. Such morichales are restricted to wet marshy parts of savannas. (Gran Sabana, Venezuela.) Alexander von Humboldt has described the morichales as follows: The palm *Mauritia flexuosa* “at moist places forms magnificent groups of fresh and shiny greenery, which recalls the green of our alder bushes. With their shade these trees maintain the moisture in the soil . . .”

“Sie bildet an feuchten Orten herrliche Gruppen von frischem glänzendem Grün, das an das Grün unserer Ellergebüsche erinnert. Durch ihren Schatten erhalten die Bäume die Nässe des Bodens . . .”


This already illustrates the problems inherent in the use of the term savanna, which has been applied to a wide range of habitats.

Attempts to delineate the term more precisely have been made repeatedly (Huber 1982, 1987, 1990). Clearly, in the open habitats of the savannas, the herbaceous ground-layer is the ecologically decisive stratum. There may be shrubs and trees, scattered or in small groups, but they never form a closed canopy. Thus, the major contribution to the input of energy into the whole ecosystem (by capture of solar radiation and primary biomass production) comes from the herbaceous ground-stratum. The herbaceous layer itself may be dominated by grasses and sedges or by broad leaved herbs so that one can distinguish between:

- **grass savannas** (Fig. 9.1), i.e. the savannas *sensu strictu*, and
- **herb savannas** (Fig. 9.7), which as “yerbazal” in Spanish, may not be considered as savannas in a strict sense but then would require use of a rather awkward term in English, e.g. “broad-leaved meadows”.

Typical tropical grass savannas are restricted to low and medium elevations not exceeding 1,000 – 1,200 m, while herb savannas may occur at higher elevations. In
Fig. 9.7 Yerbazal (herb savanna), Sierrania Parú (04°25′N, 65°32′W, 1,250 m a.s.l.), dominated by Stegolepis hitchcockii (broad flat leaves), Brocchinia hechtiiodes (slender tank-forming bromeliad) and Bonnetia crassa (small shrub)
either case it is essential that we are dealing with tropical or subtropical ecosystems (Fig. 1.3A), where in contrast to the tropical forests with a closed canopy of trees (Chap. 3) **the ground stratum of grasses and/or herbs dominates energy turnover** (Huber 1982, 1987, 1990). This may also occur in ecosystems outside the tropics, which then are distinguished as prairies, pampas or steppes. This strict distinction was not then familiar to Alexander von Humboldt who used “savanna” and “steppe” synonymously. On the other hand, the term savanna has also been used for physiognomic characterization of vegetation outside the tropics (Eiten 1986).

Even in the neighbouring countries of South America, Venezuela and Brazil, classification of savanna-like vegetation has led to different terminologies (Sarmiento 1984; Eiten 1972, respectively). For the vegetation in Brazil the **cerrado-concept** was developed, which is somewhat narrower than the more general **savanna-concept**. In Brazil, 20% of the area of the whole country and 40% of the non-Amazonian part are covered by cerrados (Eiten 1972; Gottsberger and Silberbauer-Gottsberger 2006a,b). They are geographically and ecologically intermediate between tropical rainforest and tropical/subtropical desert. The annual precipitation averages between 1200 and 1,600 mm ranging from 800 to 2,000 mm in the driest and wettest parts, respectively. There is strong seasonality with more than 90% of the rain falling in 7 months (October – April). The cerrado soil is very infertile and can vary from less than 5% to over 95% sand, the rest is clay and a little silt (Eiten 1972, 1986).

Table 9.1 attempts a systematic comparison of the terms used to describe Venezuelan and Brazilian savannas and cerrados (see also Figs. 9.1 and 9.8). The density

<table>
<thead>
<tr>
<th>Description</th>
<th>Venezuela</th>
<th>Brazil</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Savannas without woody species taller than the herbaceous stratum</td>
<td>Grass savanna</td>
<td>Campo limpo</td>
</tr>
<tr>
<td>2. Savannas with low woody species (&lt; 8 m) forming a more or less open stratum</td>
<td></td>
<td></td>
</tr>
<tr>
<td>a) Shrubs and trees isolated or in small groups, &lt; 2% of total surface</td>
<td>Tree and shrub savanna</td>
<td>Campo sujo</td>
</tr>
<tr>
<td>b) Shrubs and trees 2 – 15% of total surface</td>
<td>Woodland or bush savanna</td>
<td>Campo cerrado</td>
</tr>
<tr>
<td>c) Trees &gt; 15% of total surface</td>
<td>Woodland</td>
<td>Cerrado (sensu strictu)</td>
</tr>
<tr>
<td>3. Savannas with tall trees (&gt; 8 m)</td>
<td>Tall tree savanna</td>
<td></td>
</tr>
<tr>
<td>a) Isolated trees, &lt; 2% of total surface</td>
<td>Tall tree savanna</td>
<td></td>
</tr>
<tr>
<td>b) Trees 2 – 15% of total surface</td>
<td>Tall tree savanna</td>
<td></td>
</tr>
<tr>
<td>c) Trees 15 – 30% of total surface</td>
<td>Tall tree wooded grassland</td>
<td></td>
</tr>
<tr>
<td>d) Trees &gt; 30% of total surface</td>
<td>Tall woodland</td>
<td>Cerradão</td>
</tr>
<tr>
<td>4. Savannas with large trees in small groups</td>
<td>Park savanna</td>
<td>Campo coperto</td>
</tr>
<tr>
<td>5. Mosaic of units of savannas and forests</td>
<td>Park</td>
<td></td>
</tr>
</tbody>
</table>
Fig. 9.8A–D Aspects of the cerrado (A,B) and the cerradão (C,D) near Brasília (Fazenda Agua Limpa), Brazil
and size of woody plants, i.e. shrubs and trees is an important feature of this system. In Africa one also encounters the distinction between “wooded savanna”, where the trees stand more or less isolated, and “woodland savanna,” where the canopies of individual trees touch each other (Fig. 9.9).

Fig. 9.9A,B Wooded savanna (A) and woodland savanna (B), Great Rift Valley, Ethiopia
9.2 Seasonality

Water and nutrient availability distinguish different types of savannas (Baruch 2005). In his climatic-hydrological classification Sarmiento (1984) separates mainly four types of savannas based on water status and seasonality (Fig. 9.10):

- a **semi-seasonal savanna** with a long rainy period but without excess of water (i.e. flooding) and a short period with a water deficit,
- a **seasonal savanna** with changes between periods with sufficient water and periods of drought,
- a **hyperseasonal savanna**, where periods of excess of water and of drought provide strong seasonal contrast (see quotations of A. von Humboldt in Sect. 9.1),
- a **marsh savanna**, where long periods of water excess are interrupted by drier periods, when water, however, still is in sufficient supply.

The latter merges into wetland ecosystems of which there is a large variety of types which are difficult to separate and define (Esteves 1998). Many of them are river floodplains in wet tropical forests (Sect. 3.2.3) and also associated with ponds and lakes.

![Fig. 9.10 Scheme of the water budgets of savannas in the climatic-hydrological classification of Sarmiento (1984). Following the annual cycle described by the circumference of each circle shows the extensions of annual cycles dominated by water excess (hatched area), normal water availability (white area) and water deficit (dotted area) (Reprinted by permission of Harvard University Press)]
9.3 The Savanna Problem: Why Do Savannas Exist?

A more fundamental problem is why there are savannas at all. Why is closed forest not growing all over these sites in the tropics? Are savannas natural plant communities or only products of human activities? There is no generally accepted hypothesis, and a number of possibilities are listed by Huber (1982) as follows:

- **The climatic hypothesis.** This must be rejected for several reasons, but most simply because of the co-occurrence of forest with closed canopies of trees and open savanna under the same climatic conditions.
- **The edaphic hypothesis,** especially including the importance of the nutrient limitation.
- **The fluvial hypothesis,** i.e. colonization of ancient riverbeds by savanna.
- **The hydrological hypothesis,** i.e. the important influence of the water regime including limitations due to insufficient or excessive drainage.
- **The relict or refuge hypothesis,** where savannas are considered as relics of a formerly more widespread dry vegetation type.
- **The anthropogenic hypothesis,** implying the role of man in establishing, maintaining and extending savannas especially by forest clearing and burning.

A steady state model of grass/tree coexistence based on separated rooting niches, where trees have sole access to water in deeper soil horizons and grasses have preferential access to and are superior competitors for water in the surface soil (Sect. 10.1), is criticized by Higgins et al. (2000). Instead they propose a non-equilibrium non-linear model which is a very detailed model essentially based on a “storage” function considering tree seedling establishment and recruitment. Variations in rainfall (Sect. 10.1.2), where establishment of tree seedlings requires several humid years in sequence (Baruch et al. 1996) and fire (Sect. 10.3) on a background of low levels of adult tree mortality allow the storage effect. The grass/tree coexistence is then supported by the limited opportunities for tree seedlings to escape both drought and the flame zone during fires into the adult stage. This prevents forest formation but stores those individuals that have escaped.

In any event, savannas are not only man made. The cerrado of central Brazil also is a natural, original vegetation and not derived from tropical mesophytic forest by man’s destruction. Cerrados and natural savannas in the tropics are highly valuable biotopes both floristically and ecologically. It is mostly overlooked, that they are under enormous economic pressure and just as much threatened by the current destruction as tropical forests (Skole et al. 1994; Ribeiro et al. 2005). The cerrados of Brazil belong to the 25 biodiversity hotspots of the world’s vegetation (Myers et al. 2000; Oliveira and Marquis 2002; Gottsberger and Silberbauer-Gottsberger 2006a). They originally covered 1,783,200 km² and are now already reduced to 20% of their original area (356,630 km², 22,000 km² or 6.2% of which are protected) and they have 10,000 plant species, 4400 of which are endemic (Myers et al. 2000). In the 20 years from 1975 to 1996 the cerrado area covered by the crops soybean, maize, rice and beans increased from $4.20 \times 10^6$ (15%) to $9.17 \times 10^6$ (28%) ha, where the numbers in brackets give the cerrado area in per cent of the total area which
is covered in Brazil by these crops, and it is seen that the whole increment between 1975 and 1996 was due to cerrado cultivation (Resck et al. 2000; Gottsberger and Silberbauer-Gottsberger 2006a). There may even arise some kind of unsavoury contest in that destruction will increasingly turn towards savannas and cerrados as forests are protected.

9.4 Ecotones

9.4.1 Savanna-Forest Ecotone Dynamics

Savannas and forests are separated by water and nutrient relations. A comparison between two types of savannas and a rainforest in Table 9.2 suggests that the main differences between the savannas and the forest are the very high free evaporation and the deep infiltration, respectively. Comparing tree species in a savanna-forest tension-zone (ecotone) where both savanna and forest trees had a high light demand showed that the forest trees invested more in tall growth at the expense of root system development, while conversely the savanna trees developed more extended root systems and grew less tall (Hoffmann and Franco 2003). If nutrient supply is taken as a second dimension in addition to water supply, the two-dimensional separation of various types of tropical forests and savannas emerges as shown in Fig. 9.11. The forests require high nutrient supply, or at least high availability of water when nutrient supply is small, as in sclerophyll forest and in low-productivity rainforest. Conversely, savannas occupy areas with medium to low supply of the two resources.

Generally it is seen that the savanna-forest ecotone is moving towards the forest and that especially due to anthropogenic influences forest is destroyed and replaced by secondary savanna (Sect. 10.1.1.2). However, the opposite may also occur as shown for a site in the Western Ghâts, India, where Mariotti and Peterschmitt (1994) have performed historical studies of the dynamics of savanna-forest interfaces based on the different carbon isotope ratios ($\delta^{13}$C) in C$_3$- and C$_4$-plants (see Sect. 2.5). Sa-

<table>
<thead>
<tr>
<th>Table 9.2 Water relations of two types of savannas compared to a tropical rainforest. (Sarmiento 1984)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Precipitation (mm p.a.)</td>
</tr>
<tr>
<td>-------------------------</td>
</tr>
<tr>
<td><em>Trachypogon</em> savanna (Calabozo, Venezuela)</td>
</tr>
<tr>
<td><em>Leptocoryphium</em> savanna (Barinas, Venezuela)</td>
</tr>
<tr>
<td>Rainforest (Ivory Coast)</td>
</tr>
</tbody>
</table>

*Infiltration deeper than 2.3 m: > 600 mm p.a. (in savannas = 0)
vannas are dominated by C₄-grasses (Sect. 10.1.1.2). Thus, the soil-organic matter beneath, fed by the decomposing litter of savanna plants, should be much less negative than the soil under forest, where C₃-trees dominate. On this basis horizontal and vertical δ¹³C-analyses in soils have allowed to unravel historical savanna-forest ecotone dynamics. Figure 9.12 shows that at the study site deeper soil layers at 80 cm and below had more negative δ¹³C values indicating that the whole area once

![Fig. 9.11](image)

**Fig. 9.11** Separation of various types of savannas and tropical forests based on nutrient and water availability. (Medina 1987)

![Fig. 9.12](image)

**Fig. 9.12** Vertical and horizontal profiles of δ¹³C values in the soil organic matter along a savanna-forest topological gradient in Kattinkar, Western Ghâts (13°57′ N, 77°44′ E), India. (After Mariotti and Peterschmitt 1994)
was dominated by forest. The soil directly under the present savanna shows the less negative $\delta^{13}C$ values expected from the predominant C$_4$-photosynthesis by the vegetation and that under the present forest corroborates prevailing C$_3$-photosynthesis by the forest trees. However, in the zone between forest and savanna, less negative $\delta^{13}C$ values extend deep under the present forest, indicating that the savanna must have had a larger extension in the past, and that the forest must be currently expanding.

9.4.2 Savanna-Desert Ecotone Dynamics: The Sahel Problem as a Case Story

In Sect. 9.4.1 we have considered the savanna ecotone to the wetter side, i.e. the forest. There is another important interface, to the drier side, namely that between savanna and desert. The large deserts of the world lie mainly outside the tropics, and thus, it is not within the scope of this book to treat the ecophysiology of desert plants. It is interesting, however, to consider briefly the ecotone between savanna and desert in addition to that between savanna and forest.

To do this, desertification in the Sahel region of Africa offers itself as an appropriate case story as it has caused much public concern due to the dramatic economic and social implications. The Arab word “sahel” in fact means coast or shore, referring to the southern delineation of the sand-ocean of the Sahara, a pertinent way to portray the ecotone. The region is characterized by summer rain with an 8–10 months long drought period. According to the annual precipitation a north-south zonation is given as follows:

- saharo-sahelian transition zone 100 – 200 mm,
- sahelian zone 200 – 400 mm,
- sudano-sahelian transition zone 400 – 600 mm

(Fig. 9.13; Walter and Breckle 1984). The latitudinal position of the saharo-sahelian transition zone, the savanna-desert ecotone, may vary due to climatic oscillations. The case of the sahel is particularly interesting because very strong climatic oscillations have been documented both for the extended period of the last 30,000 years and for much shorter intervals in the last century. Figure 9.14 illustrates the large changes of the area occupied by the Sahara over the ages. During the last ice age (18,000–12,000 years B.C.) the Sahara had enlarged considerably and then, in the post-glacial period (9,500–4,500 years B.C.) contracted again. At that time the river Niger near Timbuctu had a large inland delta with a flooding plain of 20,000 km$^2$. At present the Sahara again occupies a large area similar to that in the last ice age (Petit-Maire 1984). The stochastic appearance of drought periods interchanging with wetter intervals or the movement of the saharo-sahelian transition zone more to the south and more to the north respectively, during the last century is shown in Fig. 9.15. Remote-sensing of the vegetation density (Sect. 2.3) resolves differences for individual years. The long wet period between 1942 and 1966 led to the
extension of savannas and was followed by an increase of the human population and the herds of the nomads. However, this prepared the ground for the catastrophes of the years after 1966. During the increasingly frequent and extended drought periods the land could not sustain the population growth any longer. The example is both tragic and illustrative. It shows that it is impossible to make long term prognoses on the basis of few singular events during periods of short or medium duration.
9.5 Productivity

Productivity of savannas is largely determined by nutrients. Generally, conditions required for intensive and productive agriculture in the tropics can be listed after Eiten (1972):

i) **above rocks**, which lead to soils rich in minerals, e.g. limestone and volcanic rocks,

ii) **in flood-plains** with periodically rising water-tables, leading to repeated renewal of the mineral content of the soils, e.g. in the Amazonas, the Nile, the Ganges,
iii) strong organic fertilization,
iv) use of chemical fertilizers.

Limitations to the third and fourth possibilities are the economic costs, and with only small areas available for organic fertilization. Table 9.3 gives some data for productivity of seasonal and hyperseasonal savannas.

| Table 9.3 Productivity of savannas, biomass in g m$^{-2}$ (Sarmiento 1984) |
|-----------------|-----------------|-----------------|
| Savannas     | Above ground   | Below ground | Total          |
| Seasonal     | 800 – 1300     | 600 – 800      | 1400 – 2100    |
| Hyperseasonal| 800 – 1400     | 900 – 1100     | 1700 – 2500    |

References

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Chapter 10
Savannas. II. The Environmental Factors Water, Mineral Nutrients and Fire

Very important anthropogenic factors determining the existence of savannas are herbivory by cattle (see anthropogenic hypothesis in Sect. 9.3) and fire. The major natural environmental factors are:

- water (hydrological hypothesis, Sect. 9.3),
- mineral nutrients (edaphic hypothesis, Sect. 9.3),
- fires caused by natural events

(Högberg 1986a). These are discussed in this chapter.

10.1 The Water Factor

A model of the water budget of savannas explaining the various inputs and losses is shown in Box 10.1. The key elements, of course, are precipitation for the input and evapotranspiration by the vegetation plus free evaporation for the losses. The strong seasonality often encountered in savannas is mainly determined by the water factor (Fig. 9.10). Woody plants and grasses in savannas have different requirements from the annual precipitation, dependent on the distribution of rainfall, soil availability of water over the year and the water-capacity of the soil (Table 10.1). As a result the phenological behaviour of savanna trees and grasses is also different (Sects. 10.1.1.1 and 10.1.2.1). This strongly affects overall fluxes of carbon, water and energy in the seasons as documented by an important comprehensive investigation in a Brazilian cerrado (Miranda et al. 1997) some comparisons of which are depicted in Fig. 10.1. The leaf area index (see Sect. 3.4.1) was 1.0 and 0.4 in the wet and dry season, respectively, and during the light periods of the days loss of \( \text{H}_2\text{O} \)-vapour (transpiration rate), downward fluxes of \( \text{CO}_2 \) and ecosystem surface conductance were much higher in the wet season than at the end of the dry season. With the different hydraulic requirements of grasses and trees it is appropriate to consider them separately in the following two sections.
Fig. 10.1 Canopy fluxes of water vapour ($J_{H_2O}$) (A), carbon ($J_{CO_2}$) (B) and surface conductance (C) over a Brazilian cerrado towards the end of the wet season (April 1993, solid lines) and at the end of the dry season (September 1993, dotted lines). Negative values of $J_{CO_2}$ and $J_{H_2O}$ give the downward fluxes from the atmosphere to the canopy.

(Drawn after data of Miranda et al. 1997; with kind permission of Blackwell Science, Oxford, UK)

Table 10.1 Different requirements of grasses and woody plants in savannas with respect to the water factor. (After Walter and Breckle 1984)

<table>
<thead>
<tr>
<th></th>
<th>Grasses</th>
<th>Woody plants</th>
</tr>
</thead>
<tbody>
<tr>
<td>(i)</td>
<td>Amount of precipitation</td>
<td></td>
</tr>
<tr>
<td>Lower</td>
<td>amounts of annual precipitation</td>
<td>Larger amounts of annual precipitation</td>
</tr>
<tr>
<td>(ii)</td>
<td>Annual distribution of precipitation</td>
<td></td>
</tr>
<tr>
<td>Precipitation</td>
<td>must occur during the growth period</td>
<td>Precipitation may occur during the rest period</td>
</tr>
<tr>
<td>(iii)</td>
<td>Annual distribution of water uptake</td>
<td></td>
</tr>
<tr>
<td>During the rest period no water is taken up from the soil</td>
<td>The soil must provide enough water for a minimal water-uptake also in the dry season</td>
<td></td>
</tr>
<tr>
<td>(iv)</td>
<td>Soil-water capacity</td>
<td></td>
</tr>
<tr>
<td>The water capacity of the soil must be high: the plants do not limit their transpiration as long as the soil provides enough water, and then the leaves dry rapidly</td>
<td>The water capacity of the soil does not need to be high: the crumb size of the soil may be large, the soil may be stony and rocky; the root system develops far in both horizontal and vertical direction</td>
<td></td>
</tr>
</tbody>
</table>

Box 10.1

Model of the water budget of savannas with a continuous vegetation-soil compartment separated from the atmosphere. Rom. = losses, ital. = input. (Sarmiento 1984; reprinted by permission of Harvard University Press).
10.1.1 Grasses

10.1.1.1 Phenology

Due to the mostly only superficial rooting of grasses phenological differentiations are highly important for adaptations of grasses relating to the water factor (Table 10.1). The following phenological groups are observed among savanna grasses:

- perennial with a seasonal semi-dormant-period,
- annual, ephemeral with a short cycle,
- annual with a long cycle,
- perennial with a seasonal dormant period,
- continuous growth and flowering.
The first group is most frequent. It is represented, for example, by *Trachypogon plumosus* and *Leptocoryphium lanatum* (Fig. 10.2). The phenological diagrams for the two species, in contrast to the tree *Curatella americana*, Dilleniaceae (see Sect. 10.1.2.1), show flowering and new shoot production during the rainy season, but closer to the end of the rainy season in *T. plumosus* than at the beginning as

![Fig. 10.2A–C Semiquantitative phenograms (relative units on the ordinates) of two tropical grasses with C₄-photosynthesis (A, B) and a tropical savanna tree (C). (Sarmiento 1984; reprinted by permission of Harvard University Press)](image-url)
for *L. lanatum* (Fig. 10.2). The phenological diagram of *L. lanatum* also shows the stimulation by fire of shoot production at the end of the dry season (see Sect. 10.3.3 for more details). Such phenological diagrams, as discussed by Solbrig (1993; for many phenological diagrams of cerrado plants see Gottsberger and Silberbauer-Gottsberger 2006) allow the separation of functional groups of savanna grasses. Thus, there are grasses that grow early and reproduce quickly in the rainy season (more like *L. lanatum* in Fig. 10.2) as opposed to grasses that grow gradually and develop shoots slowly and reproduce in the middle or towards the end of the rainy season (more like *T. plumosus* in Fig. 10.2). In general terms, the former (i.e. early growers and reproducers):

- are more drought resistant,
- have higher turgor pressures during the dry season,
- have higher water use efficiencies (WUE),
- partition more of their photosynthetic products to roots and below-ground organs,
- are more competitive under dry conditions and have increased importance along wet to dry gradients.

Grasses need less water than savanna trees, but the water must be available during the growth period.

### 10.1.1.2 Metabolic Adaptation: C₄-Photosynthesis

A major ecophysiological aspect of savanna grasses is the dominance of C₄-photosynthesis (Box 10.2). C₄-photosynthesis is occurring among a few shrubs and woody plants but it is absent in real trees. Although it is frequent in some dicotyledonous families, such as the Chenopodiaceae, C₄-photosynthesis is a typical biochemical trait of sub-tropical and tropical grasses. Somewhat similar to CAM (see Sect. 5.2.2.2 and Box 5.1), during C₄-photosynthesis CO₂ is first cycled through malate, before it is assimilated in the Calvin cycle. However, during C₄-photosynthesis there is simultaneously CO₂-fixation via PEP-carboxylase (PEPC), together with CO₂-remobilisation, refixation via RuBISCO and reduction via the Calvin cycle. The PEPC- and RuBISCO-functions are localized in different cell types and hence separated spatially, in contrast to CAM, where they occur in the same cells but are separated in time. Leaves of most C₄-plants have two distinct photosynthetic tissues, first the outer spongy mesophyll where CO₂ is fixed to produce malate and in many cases also aspartate via oxaloacetate, and second, the inner bundle sheath where malate or aspartate are decarboxylated and the CO₂ is refixed. Depending on the enzymic mechanism of decarboxylation, three different types of C₄-photosynthesis can be distinguished (Box 10.2). Because the affinity of PEPC for CO₂ is about 60 times higher than that of RuBISCO, fixation of atmospheric CO₂ in the mesophyll, which tightly surrounds the bundle sheath, is highly effective. The malate and aspartate so produced are transported symplastically to the bundle sheath, via plasmodesmata connecting the two tissues. Frequently, there is suberization of the cell walls between the two tissues to prevent leakage to the
Box 10.2  Biochemical pathways of C₄ plants
Primary CO₂ fixation via phosphoenolpyruvate carboxylase (PEPC) and refixation of CO₂ via ribulose-bis-phosphate carboxylase (RuBISCO) occur simultaneously in time and are separated in space.

The biochemical reactions in the mesophyll are basically similar in all types of C₄ plants. The first CO₂ fixation product is the C₄ acid anion oxaloacetate, which is subsequently transformed to malate and/or aspartate. Three types of C₄ plants are distinguished by the mode of decarboxylation of these C₄ acids after their transport to the bundle-sheath cells:

- the NADP-malic enzyme type [reaction (3)],
- the NAD-malic enzyme type [reaction (8)],
- the PEP-carboxykinase type [reaction (10)].

**Enzymatic reactions**

1. PEP-carboxylase (PEPC),
2. NADP-dependent malate dehydrogenase,
3. NADP-dependent malic enzyme,
4. Pyruvate, P₃ dkinase,
5. 3-PGA kinase, NADP-dependent glyceraldehyde-3-P dehydrogenase and triose-P isomerase,
6. Aspartate aminotransferase,
7. NAD-dependent malate dehydrogenase,
8. NAD-dependent malic enzyme,
9. Alanine aminotransferase,
10. PEP-carboxykinase,
11. Mitochondrial NADH oxidation systems.

**Metabolites and cofactors**

AMP, ADP, ATP: adenosine mono-, di- and tri-phosphate;
DHAP: dihydroxyacetone phosphate;
NAD: nicotine-adenine-dinucleotide;
NADP: nicotine-adenine-dinucleotide phosphate;
OAA: oxaloacetic acid;
P: phosphate;
PCR: photosynthetic carbon reduction;
P₃: inorganic phosphate;
PP₃: inorganic pyrophosphate;
PEP: phosphoenolpyruvate;
PGA: phosphoglyceric acid;
RubP: ribulose-bis-phosphate.

(Hatch and Osmond 1976; Hatch 1987)
apoplast, and decarboxylation in the bundle sheath leads to a 6- to 10-fold increase of CO₂-concentration as compared to atmospheric CO₂. This has several ecophysiological advantages which are important for savanna grasses in dry open habitats with high irradiation:

- Under water stress the high CO₂-affinity of the first step of CO₂-fixation (PEPC) draws down CO₂-concentration inside the leaf, providing a steeper gradient for inward diffusion of CO₂, and allows operation of photosynthesis with partially closed stomata, which reduces transpiratory loss of H₂O. Hence, the water use efficiency of C₄-plants is much higher than that of C₃-plants, although still lower than that of nocturnal CO₂-fixation in CAM plants (Box 10.3).

- The high CO₂-affinity of PEPC, together with the simultaneous use of light in refixation of CO₂ via RuBISCO, also allows high maximum rates of photosynthesis and high productivity, which in C₄-plants are the highest of the three modes of photosynthesis (Box 10.3).

- The high CO₂-concentration in the bundle sheath cells reduces photorespiration and the plants are less susceptible to the danger of photoinhibition and photodamage.

**Box 10.3**

Some major ecophysiological characteristics of the three major modes of photosynthesis in terrestrial plants, viz. CAM (D dark; L light period), C₄- and C₃-photosynthesis. (Black 1973)

<table>
<thead>
<tr>
<th></th>
<th>CAM</th>
<th>C₄</th>
<th>C₃</th>
</tr>
</thead>
<tbody>
<tr>
<td>Water-use efficiency (WUE)</td>
<td>(6 – 30) × 10⁻³ (D)</td>
<td>(1.7 – 2.4) × 10⁻³ (L)</td>
<td>(0.6 – 1.3) × 10⁻³</td>
</tr>
<tr>
<td>(mol [CH₂O]: mol H₂O)</td>
<td>(1 – 4) × 10⁻³ (L)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Maximum net CO₂ uptake (µmol m⁻² s⁻¹)</td>
<td>0.5 – 2.5 (D)</td>
<td>25 – 50</td>
<td>10 – 25</td>
</tr>
<tr>
<td>Maximum productivity (g DW m⁻² day⁻¹)</td>
<td>7 – 8 (L)</td>
<td>1.5 – 1.8</td>
<td>400 – 500</td>
</tr>
</tbody>
</table>

Therefore, it is not surprising that C₄-grasses dominate in tropical savannas and C₃-grasses are more scarce. The most frequent tribes and genera are listed in Table 10.2. Table 10.3 gives a comparison of average daily fluxes of carbon over the canopy of a C₄-pasture and a forest in SW-Amazonia, Brazil, and Table 10.4 lists representative rates of photosynthesis with the highest maximum rates obtained in the C₄-grasses. In addition to pastures some tropical C₄-grasses have been developed into major agricultural crops of mankind, e.g. sorghum, millet, maize and sugar cane; the Ethiopian tef is also a C₄-grass, *Agrostis tef*.

Although evolution of C₄-photosynthesis dates back to much earlier periods of lowered atmospheric CO₂ levels in the Mesozoic, at the geological times when savannas and cerrados began to develop in the neotropics in the late Oligocene 30
to $25 \times 10^6$ years ago they were dominated by C$_3$-grasses. In the Miocene the first C$_4$-grasses began to appear $10 \times 10^6$ years ago. C$_4$-grasses became dominant over C$_3$-grasses $7.6 \times 10^6$ years ago and reached absolute dominance in the Pliocene $3.7 \times 10^6$ years ago (Cerling et al. 1997, 1998; Jacobs et al. 1999; Fig. 12 in Gottsberger and Silberbauer-Gottsberger 2006). African C$_4$-grasses are also being introduced anthropogenically in the neotropics and are invading savannas displacing the native herbaceous vegetation. In relation to the advantages of C$_4$-photosynthesis listed above the competitive superiority of the African grasses is due to:

- higher net-photosynthesis rates,
- more efficient use of soil nutrients,
- higher proportion of assimilates allocated to new leaves,
- higher tolerance to defoliation.

Many grasses in the Llanos of Venezuela are also C$_4$-grasses. In the Llanos, the native grass *Trachypogon plumosus* and the successful invader *Hyparrhenia rufa*, both C$_4$-plants, are distinguished as follows:

- *H. rufa*, has higher transpiration and stomatal conductance for water vapour, using water opportunistically when available; it shows earlier leaf-senescence during the dry season, i.e. drought avoidance; however, it needs relatively deep soils;
- *T. plumosus*, uses water conservatively; it is more drought tolerant and can withstand poorer nutrient and water status on shallower soils (Baruch and Fernandez 1993).

### Table 10.2
Genera of neotropical savanna grasses according to their photosynthetic pathway. (Reference to Venezuelan tribes, Montaldo 1977; Medina 1982)

<table>
<thead>
<tr>
<th>Tribe</th>
<th>Genera</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eragrostae</td>
<td><em>Eragrostis</em>, <em>Leptochloa</em></td>
</tr>
<tr>
<td>Chlorideae</td>
<td><em>Microchloa</em>, <em>Bouteloua</em>, <em>Chloris</em>, <em>Gymnopogon</em></td>
</tr>
<tr>
<td>Sporoboleae</td>
<td><em>Sporobolus</em></td>
</tr>
<tr>
<td>Paniceae</td>
<td><em>Digitaria</em>, <em>Eriochloa</em>, <em>Paspalum</em>, <em>Echinochloa</em>, <em>Axonopus</em></td>
</tr>
<tr>
<td>Andropogoneae</td>
<td><em>Imperata</em>, <em>Andropogon</em>, <em>Trachypogon</em>, <em>Dietcomis</em></td>
</tr>
<tr>
<td>Aristideae</td>
<td><em>Aristida</em></td>
</tr>
<tr>
<td>Arundinelleae</td>
<td><em>Tristachya</em></td>
</tr>
<tr>
<td>Paniceae</td>
<td><em>Lasiacis</em>, <em>Oplismenus</em></td>
</tr>
</tbody>
</table>

### Table 10.3
Assessments of average daily fluxes of carbon (mol m$^{-2}$ day$^{-1}$) over the canopy of a C$_4$-pasture of the dominant introduced C$_4$-grass *Brachiaria brizantha* and a forest in comparison. (Grace et al. 1998)

<table>
<thead>
<tr>
<th></th>
<th>Photosynthesis</th>
<th>Respiration</th>
<th>Net</th>
</tr>
</thead>
<tbody>
<tr>
<td>C$_4$-pasture</td>
<td>0.67</td>
<td>0.51</td>
<td>0.16</td>
</tr>
<tr>
<td>Forest</td>
<td>0.57</td>
<td>0.55</td>
<td>0.02</td>
</tr>
</tbody>
</table>
### Table 10.4

Representative rates of photosynthesis (µ mol CO₂ m⁻² s⁻¹) of savanna grasses with C₃- and C₄-photosynthesis. (Medina 1986)

<table>
<thead>
<tr>
<th></th>
<th>South American grasses</th>
<th>African grasses</th>
</tr>
</thead>
<tbody>
<tr>
<td>C₃-grasses:</td>
<td>11.1 – 13.2</td>
<td>–</td>
</tr>
<tr>
<td>C₄-grasses:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Field data</td>
<td>3.2 – 16.4</td>
<td>2.2 – 7.9</td>
</tr>
<tr>
<td>Laboratory data</td>
<td>28.1</td>
<td>14.7 – 43.9</td>
</tr>
</tbody>
</table>

In the tropics also **altitude determines the relative abundance of C₄- and C₃-grasses**. The former only dominate at lower altitudes and C₃ grasses strongly prevail at higher altitudes (Fig. 10.3). The essential factors are:

- temperature,
- water availability,
- irradiance, and
- to a more limited extent nutrient availability.

Although irradiance increases with altitude, temperatures are lower, water availability is larger, and the altitudinal distribution of C₄- and C₃-grasses in Kenya has been related to the soil-moisture index (Table 10.5). Moreover, cold nights in tropical high altitude sites play an important role (Chap. 12). A study in Papua New Guinea has shown that C₄-grasses at altitudes of 1550 and 2,600 m a.s.l. were chilling sensitive, while C₃-grasses at 3280, 3580 and 4,350 m a.s.l. were chilling resistant (Earnshaw et al. 1990).

CAM plants are rare in typical savannas. Stem succulent CAM species, i.e. Cactaceae in America and Euphorbiaceae in Africa, are important in dry thornbush-

![Fig. 10.3](image-url)
Table 10.5 Altitudinal distribution of C_4- and C_3-grasses in Kenya. The soil moisture index is in arbitrary units increasing approximately linearly with altitude (10 at 600 m; 100 at > 3,500 m). (Tieszen et al. 1979)

<table>
<thead>
<tr>
<th>Altitude (m)</th>
<th>Soil moisture index</th>
<th>C_4- vs C_3-photosynthesis</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt; 2000</td>
<td>50</td>
<td>C_4-grasses dominate</td>
</tr>
<tr>
<td></td>
<td></td>
<td>C_3-grasses only in the shade</td>
</tr>
<tr>
<td>2,000 – 3,000</td>
<td>60 – 70</td>
<td>Transition zone</td>
</tr>
<tr>
<td>&gt; 3000</td>
<td>80</td>
<td>C_3-grasses dominate</td>
</tr>
</tbody>
</table>

Towards the wet side of the spectrum of savanna types (Fig. 9.10), i.e. in wetland ecosystems, C_4-photosynthesis has also proved to be highly successful. For example in fertile flood plains of nutrient rich rivers and lakes (white waters) of the Amazon region in South America (Sect. 3.2.3) the perennial C_4-grass *Echinochloa polystachya* may form monotypic stands over 5,000 km² and displays extraordinarily high rates of net-CO_2 uptake in photosynthesis of 30 – 40 µmol m⁻² s⁻¹ (compare Table 10.4) with fast growth and high productivity during the wet season of 108 tonnes ha⁻¹ year⁻¹ (comparable to the productivity of sugar cane plantations) when the flood plains are submerged. During the shorter dry period CO_2-uptake rates are 17 µmol m⁻² s⁻¹ and photosynthesis shows a midday depression (Piedade et al. 1992, 1994; Esteves 1998).

10.1.2 Trees

10.1.2.1 Phenology

The trees can develop large root systems reaching far into the soil in both vertical and horizontal directions. Nevertheless, due to the strong seasonality of water supply in most savannas, appropriate phenological behaviour remains important (Table 10.1). Trees need larger amounts of precipitation than grasses. The requisite rain can also fall during dormant periods, and so a small amount of water uptake into the trunk and branches must be possible even during drought periods.

One of the most striking phenological aspects is the flowering of savanna trees which is most attractive when it occurs in the leaf less period of deciduous trees (Fig. 10.4). An intriguing physiological question is how these flowers are supplied with water in the absence of leaf transpiration and substantial xylem water flow. In some species – although not in all of them – flowers can be supplied with water via the phloem. This requires a sink for phloem flow, which could be nectar secretion (Chapotin et al. 2003). In Africa and Australia a few trees are evergreen and most are drought-deciduous, whereas in South America evergreen trees prevail (Medina...
Fig. 10.4 See next page for details
Fig. 10.4 Flowering savanna trees of the Llanos in Venezuela: *Tabebuia chrysantha* (A), *Tabebuia orinocensis* (B), *Yacaranda filicifolia* (C), *Pseudobombax* sp. (D), *Palicourea rigida* (E), *Byrsonima crassifolia* (F)
Curatella americana (Fig. 10.5), a dominant tree of the Venezuelan Llanos, is evergreen with seasonal growth. Production of flowers and fruits, new leaves and shoots begins in the middle to the last third of the dry season, so that the plants are “ready” when the rainy season comes, as shown in the phenological diagram of Fig. 10.2C.

Among the deciduous trees the length of the leafless periods may be different:

- trees with a short leafless period afford low (highly negative) water potentials and high respiration rates, e.g. *Bursera simaruba* (Burseraceae), *Spondias lutea* (Anacardiaceae), *Pereskia guamacho* (Cactaceae);
- trees with a long leafless period have high (less negative) water potentials and low respiration rates, e.g. *Tabebuia chrysanthha* (Bignoniaceae).

The precise phenological behaviour of plants in the tropical savannas (see also grasses, Sect. 10.1.1.1) is a reliable indicator of season. For example, using up the last water reserves for formation of reproductive and vegetative biomass in the last third of the dry season, as shown for the savanna tree *Curatella americana* (Fig. 10.5) in the phenogram of Fig. 10.2C, would be dangerous if the rainy season were not close. This raises the question which signals are sensed in phenological timing. It has been observed that several phenological phenomena, including water budget, leaf abscission and flowering are related to *phytochrome equilibria* (see Box 4.7) (Reich and Borchert 1984). Several suggestions have been made to explain phenological timing on a hormonal basis. It was also proposed that water stress itself is involved. However, accurate phenological timing is also observed in water storing stem succulent savanna tress (Sect. 10.1.2.2), and moreover, with variations of only 10 to 15 days year after year, its precision is much better than it would be given by the stronger inter annual variations of rain fall (Borchert and Rivera 2001; Rivera and Borchert 2001; Rivera et al. 2002). Directly at and very near to the equator endogenous regulation of annual rhythmicity must play a role (Wright
However, even at very low latitudes away from the equator, photoperiod is the decisive signal.

The proposal that the decisive external signal is photoperiod has long been rejected *a priori*, because near the equator the differences between the longest and the shortest days are rather small (Reich and Borchert 1984). However, empirical facts demonstrate very precise photoperiod sensing of plants. In the forest tree *Hildegardia barteri* in Nigeria at 7° N where photoperiod changes by 53 min a similar decrease of photoperiod inhibits seedling leaf production (Njoku 1963; Wright 1996). An experiment with *Hyptis suaveolens* (Lamiaceae), although an annual species and not a tree, showed, that in principle plants can even sense differences in photoperiod close to 20 min (Fig. 10.6; Medina 1982). Seeds were germinated at the beginning of

![Diagram](image)

**Fig. 10.6A, B** Experiments with the annual tropical short-day plant *Hyptis suaveolens* showing that plants can sense very small differences of photoperiod (daylength). Note that, by definition, short-day plants require daylengths below a certain species-specific threshold for induction of flowering. **A** The daylengths from May to September at the site of the experiment. **B** The columns give the number of days passed after sowing and the height of the plants attained after sowing by the end of September. Independent of both time passed after sowing and height attained, all plants flower at the end of September, i.e. the photoperiod of 12 h 24 min in August was still too long (above the threshold) but the only 18 min shorter photoperiod of 12 h 06 min in September was short enough to induce flowering in *H. suaveolens* at the tropical site. (After Medina 1982)
each month at a location north of the equator starting in May and ending in September. At the end of September, all plants were flowering irrespective of the age and biomass they had attained during growth, such that the 180 cm tall, ∼150 day old plants, germinated in May flowered simultaneously with the 12 cm high, ∼30 day old plants, only germinated in early September. Thus, flowering was not related to age or biomass. The photoperiod, which did not lead to flowering (plants germinated in August with no flowering in August photoperiod 12 h 24 min), and that which elicited flowering in September (photoperiod ∼12 h 06 min) differed by only 18 min. Borchert and coworkers have compiled a large amount of data from field observations made at frequent intervals over several consecutive years and from herbarium collections which now provide strong evidence for photoperiod sensing with a precision of at least 30 minutes in phenological synchronizations year after year. Moreover, phenological phase shifts between the northern and the southern hemisphere are found to be six months (Borchert 2000; Borchert and Rivera 2001; Rivera and Borchert 2001; Rivera et al. 2002). Thus, clearly many of the phenological phenomena observed in savannas can be regulated by photoperiod.

10.1.2.2 Morphological and Anatomical Traits

For the trees the water capacity of the soil does not need to be high (Table 10.1). In the Brazilian cerrados the soil is always deep and well drained. The groundwater table therefore is low, i.e. from 3 to 6 m down to 30 – 50 m. Hence, the trees develop deep roots, which reach water even during the dry season, as shown by high transpiration rates. Woody cerrado plants have substantially higher root-to-shoot ratios than trees in nearby forests (Hoffmann et al. 2004). In the Llanos in central Venezuela there is frequently a hard pan – “arecife” – of lateritic iron-oxide (see Sect. 10.2.4.1) above the ground water-table (Fig. 10.7). The roots of savanna trees must penetrate this layer to reach the ground water, which also varies on a seasonal basis.

Leaf xeromorphy is another structural feature frequently observed among savanna trees. It is very important in Australia and South America, but less so in Africa (Medina 1993). It has already been noted in Sect. 3.4.4.3 that the formation of small and longlived leathery leaves may be considered as a strategy which gives the best return for investment of resources when nutrient supply is low. In addition such leaves also offer ways to economise on water use by some of the following traits:

- **dense venation,**
- **water storage tissues** (see also Fig. 6.22C),
- **thick and water tight cuticle,** which reduces water loss via cuticular transpiration,
- **dead hairs** on the surface,
- **sunken stomata,**
- prevailingly **hypostomatic** distribution of stomata, i.e. stomata only on the lower surface;
Fig. 10.7 Relations between the vegetation, the hard lateritic ferrous-oxide layer (“arecife”) and the seasonally shifted groundwater table in the Llanos of central Venezuela. (Walter and Breckle 1984, with kind permission of S.-W. Breckle and G. Fischer-Verlag)

(the latter three properties are generally assumed to reduce evapotranspiration by supporting the built up of unstirred layers although in detail leaf boundary-layer relations are very complex; Schuepp 1993);

- **thick cell walls**, 
- **lignification** of cell walls, 
- **formation of idioblasts and sclereids**, 

(these three properties help to stiffen the leaves, so that the trees are sclerophyllous and leaf-shape is maintained even when turgor pressure is low);

- production of **etheric oils**, which due to their hydrophobic nature may also assist in preventing water loss into the gas phase around the leaves.

Many cerrado trees were found to store water in their sapwood which may play a dominant role in the regulation of diurnal water deficits (Scholz et al. 2007). However, a particularly conspicuous peculiarity of some savanna trees is real **stem succulence**. With particularly thickened stems these trees really look very succulent, such as the Bombacaceae *Pseudobombax* in South America and *Adansonia*, the baobab (Fig. 10.8). The latter is a most spectacular plant. There is only one species on the African continent, *A. digitata*, which may be up to 9 m in diameter (Fig. 10.8D,E) and has a geographical distribution clearly correlated with the occurrence of savanna (Fig. 10.9). There are seven species of *Adansonia* in Madagascar and two in Australia. Woody stem succulent plants are abundant in seasonally dry tropical environments. A list of families and species is given in Table 10.6. They are all deciduous C₃-plants, in contrast to fleshy stem succulent plants which mostly perform CAM (Sects. 5.2.2.2 and 8.2.3.2.1). Stable isotope ratios of *Adansonia*
Table 10.6 Families and species of tropical woody stem-succulent plants. (Borchert and Rivera 2001, and personal observations)

<table>
<thead>
<tr>
<th>Family</th>
<th>Species</th>
<th>Occurrence</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anacardiaceae</td>
<td>Spondias purpurea</td>
<td>Costa Rica, Mexico</td>
</tr>
<tr>
<td>Apocynaceae</td>
<td>Plumeria rubra</td>
<td>Costa Rica, Mexico, Nigeria</td>
</tr>
<tr>
<td></td>
<td>Plumeria acuminata</td>
<td>Hawaii</td>
</tr>
<tr>
<td>Bombacaceae</td>
<td>Adansonia spp.</td>
<td>Africa, Madagascar</td>
</tr>
<tr>
<td></td>
<td>Bombax malabaricum</td>
<td>India, Ceylon, Singapore, Java</td>
</tr>
<tr>
<td></td>
<td>Bombacopsis quinta</td>
<td>Costa Rica</td>
</tr>
<tr>
<td></td>
<td>Chorisia insignis</td>
<td>Argentina</td>
</tr>
<tr>
<td>Burseraceae</td>
<td>Bursera simaruba</td>
<td>Costa Rica, Mexico, Venezuela</td>
</tr>
<tr>
<td></td>
<td>Commiphora spp.</td>
<td>Africa</td>
</tr>
<tr>
<td>Cochlospermaceae</td>
<td>Cochlospermum vitifolium</td>
<td>Costa Rica</td>
</tr>
<tr>
<td>Moringaceae</td>
<td>Moringa ovalifolia</td>
<td>Namibia, Africa</td>
</tr>
<tr>
<td>Vitaceae</td>
<td>Cyphostemma currori</td>
<td>Namibia, Africa</td>
</tr>
</tbody>
</table>

gregorii in Australia were found to be $\delta^{13}C = -29.06\%e$ and $\delta D = -90.10\%e$ (H. Ziegler, unpubl.).

These succulent stems are water-stores and below ground lignotubers or xylopodia (see Sect. 10.3.3) may also serve water storage. A vast quantity of wa-
ter is present in the succulent stems. This water is mainly stored in a proliferate parenchyma and water storage is highly correlated with wood density (Meinzer 2003; Meinzer et al. 2003), so that the wood density is low ($< 0.5 \text{ g cm}^{-3}$) and the stem water potential in the dry season may be high ($> -0.5 \text{ MPa}$) (Borchert and Rivera 2001). The water storing parenchyma is separated from the transpiration stream by a high-resistance pathway, which applies to both transport directions, i.e. filling and emptying. Thus, this water storage does not function as a buffer against
daily water deficits in the rainy season because refilling of stem water via the roots is slow (Goldstein et al. 1998) and rather is a long term commodity (Chapotin et al. 2006a). It is the most important resource for phenological leaf flushing before
the onset of the rainy season (Sect. 10.1.2.1). In baobab trees stem water content declined by up to 12% during this period and the water was almost exclusively used for leaf growth. Stomatal opening and transpiration only started with the rainy season after considerable rainfall and was associated with the onset of sap flow from the soil at the base of the trunks. High transpiratory water flow cannot be supported by the water stored in the tree trunk parenchyma but must come from uptake via the roots (Chapotin et al. 2006b).

10.1.2.3 Hydraulic Architecture, Water Use and Photosynthesis

Some extraordinarily high maximum photosynthetic rates of the mature leaves of savanna trees have been reported, i.e. around 40 µmol CO₂ m⁻²s⁻¹ for dominant trees, Curatella americana (Fig. 10.5) and Byrsonima crassifolia, of the Llanos of Venezuela (Medina 1982). However, in trees of the cerrados of Brazil rates near light saturation ranged between 4 and 18 µmol CO₂ m⁻²s⁻¹ (Moraes and Prado 1998; Franco and Lüttge 2002) comparable to average rates of 10 – 25 µmol m⁻²s⁻¹ for C₃-photosynthesis (see Box 10.3). Savanna trees are always C₃-plants. Water use efficiency may vary considerably among tropical trees, e.g. between 1.6 mmol carbon mol⁻¹ H₂O in Tectona grandis and 4.0 mmol carbon mol⁻¹ H₂O in Platymiscium pinnatum which is not directly correlated with relative growth rate (Cernusak et al. 2006).

Water relations and a very high irradiance load are conspicuous stressors for photosynthesis in savannas. Life long acclimation to drought basically can involve three contrasting changes in the water transport capacity per unit leaf area for given plant size, namely a decrease or constancy or an increase (Maseda and Fernández 2006). It is interesting to note therefore, that savanna trees are isohydric with respect to their minimum leaf water potential which is highly regulated at similar levels between dry and wet seasons. It is also noted for the cerrados that in relation to the water factor diurnal limitations are more important than seasonal ones (Gottsberger and Silberbauer-Gottsberger 2006). Among other adaptations a reduction in total transpiring leaf surface area in the dry season is contributing to this, but a major physiological mechanism involved is strong stomatal control of evaporative water loss (Bucci et al. 2003, 2005). A midday depression (see Sect. 5.2.2.1) may assist in regulating the water economy on hot days both during the rainy and the dry season. It is expressed in:

- daily courses of root and leaf petiole hydraulic conductivity,
- photosynthetic gas exchange, and
- photoinhibition.

Often there is root limitation of water movement in the soil-leaf continuum, and in cerrado trees a linear correlation is given between stomatal conductance and loss of water conductivity of the roots in the afternoon (Domec et al. 2006). Daily courses of cavitation and embolism in the afternoon and refilling during the night were observed in both roots (Domec et al. 2006) and petioles of leaves of cerrado trees
Daily courses of specific hydraulic conductivity of leaf petioles of two cerrado trees, *Caryocar brasiliense* (circles) and *Schefflera macrocarpa* (triangles) in the wet season (January), in the dry season (August) and at the end of the dry season (September). (After data of Bucci et al. 2003)

Midday depressions of specific hydraulic conductivity, $k_s$, of petioles in the dry and wet seasons. The degree of embolism in petioles is a function of tension in the xylem water stream and the rate of refilling is determined by internal pressure imbalances, where effects of starch remobilization may be involved (Bucci et al. 2003). Nevertheless, transpiration during the night may also be high and can amount to 15 – 25% of total daily water loss (Bucci et al. 2005).

Midday depressions of net CO$_2$-exchange, $J_{CO_2}$, are frequently found in cerrado trees (Moraes and Prado 1998; de Mattos 1998; Franco and Lütte 2002; de Mattos et al. 2002) where $J_{CO_2}$ considerably drops at the times of highest irradiance (Fig. 10.11). In the examples of Fig. 10.11 there was no recovery of $J_{CO_2}$ in the afternoon. Figure 10.12 shows measurements revealing rapid responses to changing weather conditions in the rainy season. After a dry spell amidst the rainy season there was a pronounced midday depression of net CO$_2$ uptake, $J_{CO_2}$, and transpiration, $J_{H_2O}$, which was reversible in the afternoon, and immediately after a rainfall on the following day no midday depression was expressed any more (de Mattos et al. 2002).

The midday depression of gas exchange is a reflection of the strong stomatal control involved in the isohydric performance over the seasons as noted above (Franco and Lütte 2002), but also creates the danger of photoinhibition as discussed in Sects. 4.1.6 and 5.2.2.1 (Fig. 5.3). Protective mechanisms, such as photorespiration (Sect. 4.1.3) and harmless thermal energy dissipation via the xanthophyll cycle.
Fig. 10.11 Daily courses of net CO₂-exchange (\(J_{CO₂}\), closed circles) and photosynthetically active photon flux density (PPFD, open triangles) of three cerrado tree species. (From Franco and Lüttge 2002)

(Sect. 4.1.4), are expressed in the cerrado trees (de Mattos 1998; Franco and Lüttge 2002). Protective acute photoinhibition is reflected in a pronounced midday depression of potential quantum yield of photosystem II as indicated by \(F_v/F_m\)-values below 0.83 (see Sect. 4.1.7). Some species show a quite severe photoinhibition at midday with \(F_v/F_m\)-values well below 0.6 while other species are less strongly inhibited (Fig. 10.13). In many cases this is only acute photoinhibition reversible over night but in others (especially in the examples of Fig. 10.13B) \(F_v/F_m\) remains below 0.83 over night so that there is also chronic photoinhibition.

### 10.2 The Nutrient Factor

Savanna soils are mostly very poor and infertile. Mineral-nutrient relations of savannas are mainly determined by the physicochemical properties of the upper soil layers, such as:

- texture,
- pH,
Savannas. II. The Environmental Factors Water, Mineral Nutrients and Fire

Fig. 10.12 Daily courses of net CO$_2$-exchange, $J_{CO_2}$, and transpiration, $J_{H_2O}$, of the cerrado tree *Miconia albicans*, after a dry spell amidst the rainy season (open symbols) and on the subsequent day after a rain (closed symbols). (From de Mattos et al. 2002, with access at http://www.publish.csiro.au/nid/66/issue/501.htm; thanking the authors and CSIRO-PUBLISHING, Australia)

- cation exchange capacity,
- extractable bases ($K^+ + Ca^{2+} + Mg^{2+} + Na^+$),
- content of potentially mineralizeable N,
- availability of N and P

(Medina 1993). Nutrient categories of savannas depend on the nutrient levels in the soil and the recirculation rates (Table 10.7). Nutritional fertility of savannas may be estimated and ranked by the sum of extractable bases

$$\sum (K^+ + Ca^{2+} + Mg^{2+} + Na^+)[cmol(+)/kg(soil)] ,$$

where values lower 5 cmol (+) kg$^{-1}$ mark dystrophic and values higher than 20 cmol (+) kg$^{-1}$ eutrophic savannas, with mesotrophic savannas in between (Medina 1993). Generally, however, nitrogen and phosphorus are the most strongly limiting elements, although even potassium can become limiting in situations of rapid recirculation. A particular mineral stress factor in savannas is aluminium.
Nutrient availability in the various soil horizons of savannas is much lower than in tropical forests (Table 10.8). The height and density of the woody layer in the cerrados (see Table 9.2) depends on the fertility, depth and drainage of the soil and not on rainfall (Eiten 1972, 1986). The typical distribution of some mineral elements between the vegetation and the soil in tropical forests and savannas is schematically summarized in Table 10.9. In the savanna most of the K, N, Ca and Mg is in the soil,
**Table 10.7** Nutrient categories of savannas. (After Sarmiento 1984)

<table>
<thead>
<tr>
<th>Rate of recirculation</th>
<th>Amount in the soil</th>
</tr>
</thead>
<tbody>
<tr>
<td>Slow</td>
<td>Ca, Mg, Na</td>
</tr>
<tr>
<td>Large</td>
<td>Various elements</td>
</tr>
<tr>
<td>Slow</td>
<td>K can be limiting</td>
</tr>
<tr>
<td>Small</td>
<td>P most strongly limiting</td>
</tr>
</tbody>
</table>

**Table 10.8** Comparison of the nutrients in a forest and a savanna soil in Nicaragua, both profiles on the same piedmont deposit. (Data from Alexander 1973)

<table>
<thead>
<tr>
<th>Soil horizon</th>
<th>Organic C (%)</th>
<th>Total N (%)</th>
<th>Cation exchange capacity (meq/100 g)</th>
<th>Ca (meq/100 g)</th>
<th>Mg (meq/100 g)</th>
<th>K (meq/100 g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rainforest</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A11</td>
<td>5.3</td>
<td>0.53</td>
<td>36.7</td>
<td>4.29</td>
<td>3.53</td>
<td>0.68</td>
</tr>
<tr>
<td>A12</td>
<td>4.1</td>
<td>0.39</td>
<td>26.2</td>
<td>1.90</td>
<td>1.91</td>
<td>0.43</td>
</tr>
<tr>
<td>A3</td>
<td>2.7</td>
<td>0.26</td>
<td>19.1</td>
<td>0.26</td>
<td>0.79</td>
<td>0.15</td>
</tr>
<tr>
<td>B1</td>
<td>0.9</td>
<td>0.12</td>
<td>11.0</td>
<td>Trace</td>
<td>0.56</td>
<td>0.16</td>
</tr>
<tr>
<td>B21</td>
<td>0.5</td>
<td>0.08</td>
<td>14.0</td>
<td>0.05</td>
<td>1.07</td>
<td>0.07</td>
</tr>
<tr>
<td>B22</td>
<td>0.2</td>
<td>0.07</td>
<td>12.3</td>
<td>0.11</td>
<td>0.89</td>
<td>0.05</td>
</tr>
<tr>
<td>B23</td>
<td>0.2</td>
<td>0.06</td>
<td>17.9</td>
<td>0.11</td>
<td>1.06</td>
<td>0.05</td>
</tr>
<tr>
<td>Savanna</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A1</td>
<td>2.1</td>
<td>0.14</td>
<td>10.3</td>
<td>Trace</td>
<td>0.29</td>
<td>0.05</td>
</tr>
<tr>
<td>A2</td>
<td>1.0</td>
<td>0.07</td>
<td>6.2</td>
<td>Trace</td>
<td>0.23</td>
<td>0.04</td>
</tr>
<tr>
<td>B21</td>
<td>0.9</td>
<td>0.08</td>
<td>8.1</td>
<td>Trace</td>
<td>0.25</td>
<td>0.04</td>
</tr>
<tr>
<td>B22</td>
<td>0.5</td>
<td>0.05</td>
<td>9.3</td>
<td>Trace</td>
<td>0.29</td>
<td>0.03</td>
</tr>
<tr>
<td>B23</td>
<td>0.3</td>
<td>0.02</td>
<td>8.4</td>
<td>Trace</td>
<td>0.25</td>
<td>0.03</td>
</tr>
<tr>
<td>B24</td>
<td>0.1</td>
<td>0.01</td>
<td>8.1</td>
<td>Trace</td>
<td>0.29</td>
<td>0.04</td>
</tr>
</tbody>
</table>

**Table 10.9** Nutrient distribution between vegetation and soil in a tropical forest and a savanna. (After Sarmiento 1984)

<table>
<thead>
<tr>
<th>Relation of vegetation vs soil</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forest:</td>
</tr>
<tr>
<td>K</td>
</tr>
<tr>
<td>P</td>
</tr>
<tr>
<td>N</td>
</tr>
<tr>
<td>Ca, Mg</td>
</tr>
<tr>
<td>Savanna:</td>
</tr>
<tr>
<td>K</td>
</tr>
<tr>
<td>P</td>
</tr>
<tr>
<td>N</td>
</tr>
<tr>
<td>Ca, Mg</td>
</tr>
</tbody>
</table>

whereas in the forest most K and P is contained in the vegetation. For forests N is about equally distributed between vegetation and soil, similarly to P in savannas.
10.2.1 Nitrogen

10.2.1.1 Nitrogen Cycles

Nitrogen is one of the most critical elements for plant growth in savannas. The nitrogen cycle in general is determined by assimilatory processes in microorganisms and plants, and the use of this primary production by consumers and decomposition by microorganisms (Box 10.4).

Figure 10.14 gives a comparison of the annual nitrogen-cycles and the nitrogen levels in various compartments of the ecosystem of a non-tropical prairie and a seasonal tropical savanna (a similar presentation for N-cycles in tropical forests is presented in Fig. 3.33).

![Diagram of nitrogen cycles in prairie and savanna](image-url)

**Fig. 10.14A, B** Compartmentation and annual turnover of nitrogen in two grassland ecosystems. **A** Andropogon gerardi – Andropogon scoparius prairie in Missouri (USA). **B** Seasonal Axonopus purpusii-Leptocoryphium lanatum savanna in Barinas (Venezuela); strongly modified and simplified from Sarmiento (1984) (reprinted by permission of Harvard University Press). Sizes of N pools in the different compartments (boxes) and transfer rates between the compartments (arrows) were drawn to scale to allow direct comparisons of pools and rates both within and between the two ecosystems.
Box 10.4 Nitrogen cycles in ecosystems

Pools of N in various groups of organisms of the ecosystem and in various N-compounds (boxes) and transfer between the pools (arrows).
Box 10.4 (Continued)

-\( \text{NH}_2 \), \(-\text{N} \), organic N;
\( \text{NH}_4^+ \), ammonia;
\( \text{NO}_2^- \), nitrite;
\( \text{NO}_3^- \), nitrate;
\( \text{N}_2 \), atmospheric dinitrogen gas.

(After Lüttge et al. 2005)

The compartments distinguished are:

- soil, organic N,
- soil, mineralized N,
- roots,
- living epigeous biomass,
- dead litter,
- atmosphere.

The largest amount of N in either case is in the organic matter of the soil, and it is similar in the prairie and the savanna. The amount of mineral N in the soil is much smaller, and it is somewhat larger in the prairie as compared to the savanna. The amount of N in the roots and in the living epigeous biomass, as well as in the litter, is not very different in the two systems. The rates of N-transfer between the individual compartments, namely absorption of mineral N from the soil, root-shoot translocation, mortality, decomposition/humification and mineralization, as well as precipitation, throughfall and drainage are similar within the two systems.

It is noticeable that the rate of absorption of mineralized N from the soil is lower in the savanna and that the root/shoot recycling of N (translocation between roots and epigeous biomass) is higher than in the prairie. More important, however, is the presence of two additional transfer processes in the savanna as compared to the prairie, namely:

- volatilization,
- atmospheric N\(_2\)-fixation.

Volatilization is largely due to fire in the savannas (Sect. 10.3). However, it is also known that tropical soils are significant natural sources of gaseous N-compounds, e.g. in the savannas of the Venezuelan Llanos:

<table>
<thead>
<tr>
<th>Nitrogen Oxides</th>
<th>3 – 13 kg N ha(^{-1}) year(^{-1})</th>
</tr>
</thead>
<tbody>
<tr>
<td>NO-nitrogen</td>
<td>2.6 kg N ha(^{-1}) year(^{-1})</td>
</tr>
<tr>
<td>N(_2)O-nitrogen</td>
<td>0.65 kg N ha(^{-1}) year(^{-1})</td>
</tr>
<tr>
<td>Ammonia</td>
<td>11 kg N ha(^{-1}) during the reproductive period</td>
</tr>
</tbody>
</table>

(Garcia-Méndez et al. 1991; Medina 1993). Atmospheric N\(_2\)-fixation is an important activity of mats of cyanobacteria between the tussocks of savanna grasses and of free living soil bacteria and root nodule symbioses (Sect. 10.2.3.2).
In summary, it is surprising how small are the differences between the two grasslands, namely the mesic prairie and the tropical savanna. It should be recalled, however, that diagrams similar to Fig. 10.14 have been drawn for tropical forests (Fig. 3.33), giving a very different picture. Although the soil organic N is similar, amounts of N in the roots and in the epigeous living biomass are very much larger, and N in the dead litter is somewhat larger in the forests than in the grassland systems. Mineral N in the soil is smaller in the forest. With the exception of precipitation, throughfall and drainage, the rates of N-transfer between the individual compartments are considerably larger in the forests than in the grassland systems. This relates to absorption of mineral N from the soil, root-shoot translocation, mortality, decomposition/humification and mineralization, such that the cycling of N in the forest is much more rapid than in the prairie and the savanna.

10.2.1.2 Nitrogen-Use Efficiency

In Sect. 4.1.2 we have already discussed the nitrogen-use-efficiency (NUE) of photosynthesis in relation to the light climate in tropical forests. Again in savannas and cerrados, for both grasses (Fig. 10.15) and trees (Fig. 10.16A), we observe generally linear relationships between levels of N in biomass and rates of photosynthesis. As mentioned above, there are often differences between species (Sect. 4.1.2). In savannas, the slope of the line for the tropical C₄-grass is much steeper than for the two C₃-grasses of the temperate zone given for comparison (Fig. 10.15). For crops the ratio of photosynthetic CO₂-fixation to leaf-N also was found to be higher in the C₄-plant maize (1,056 µmol CO₂ m⁻² s⁻¹/mol N) than in the C₃-plant rice (640 µmol CO₂ m⁻² s⁻¹/mol N). On the other hand, C₄-plants do not necessarily have a competitive advantage over C₃-plants under conditions of low N-supply. Experiments with C₄- and C₃-grasses under natural conditions of a Central Euro-

---

**Fig. 10.15** Relations between rates of photosynthesis and nitrogen content in the biomass of a tropical C₄-grass (filled circles: Panicum maximum) and two C₃-grasses of the temperate zone (open triangles: Lolium perenne; filled squares: Festuca arundinacea). (Medina 1986)
pean summer have shown that the C₃-grasses tended to be more successful at low N-supply (Gebauer et al. 1987). The authors suggest that this could result from lower transpiration in the C₄-grasses because of the water-saving functions of C₄-photosynthesis (see Sect. 10.1.1.2). This would imply lower N input via the transpiration stream from the soil to the shoots. However, some of this effect may be offset by higher temperatures, and the situation may be very different in tropical savannas, and indeed, a higher NUE may be important for C₄-grasses which dominate in the nutrient-poor savannas.
There are even differences between C₄-groups of grasses forming malate and aspartate as the primary CO₂-fixation product. Those species which synthesise the amino-acid aspartate from the oxaloacetate (following CO₂-fixation via PEP-carboxylase) have a higher N-requirement than the malate-forming NADP-malic enzyme group (see Box 10.2). In S-Africa it was observed that NADP-malic enzyme C₄-plants with their lower N-requirement are characteristic of particularly nutrient-poor, moist savannas while the more N-demanding aspartate-formers (NAD-malic enzyme and PEP-carboxykinase groups) are more frequent in arid savannas.

### 10.2.2 Phosphorus

In addition to nitrogen, phosphorus is one of the most critical nutritional elements in savannas. Both elements are so important because they are the two mineral elements most abundantly and most directly involved in the metabolic machinery of cells. Like for N there is a linear relationship between leaf P levels and maximum rate of photosynthetic carbon gain on a leaf mass basis (and not a leaf area basis in contrast to the observations of Figs. 4.6 and 4.7) in cerrado trees (Fig. 10.16B), and P and N levels in the leaves of these trees are linearly related to each other (Fig. 10.17). Ratios of P/N have also been used to describe the state of P nutrition. In semi-arid grasslands of the Sahel region of Africa P/N-ratios (mol/mol) of $17 \times 10^{-3}$ to $68 \times 10^{-3}$ are considered to mark the range within which there is response to P-fertilization, with the lower value characterizing P-deficient and the higher one P-sufficient plants. A more detailed comparison is presented in Fig. 10.18. Within the “P-responsive” range N-nutrition alone only slightly lowers P/N-ratios, whereas P-nutrition highly stimulates P/N ratios, which are somewhat lower when N + P

![Fig. 10.17](image-url) Correlation between N and P levels in the leaves of various evergreen (closed triangles) and deciduous (open circles) cerrado trees in Brazil. (Franco et al. 2005)
10.2 The Nutrient Factor

Fig. 10.18 P/N-ratios in the above-ground biomass of different grasslands in the Llanos of Venezuela (cut or burned at the end of the dry season), Africa and Australia (C controls), and effects of fertilization with N, P or N + P. (After Medina 1993)

fertilization was applied. Special metabolic features may make some plant species very phosphorus-efficient which are much searched for agricultural applications in the tropics, such as the forage grass *Brachiaria* which covers $10 \times 10^6$ ha of pastures in Brazil (Nanamori et al. 2004).

10.2.3 Biotic Interactions

10.2.3.1 General Overview

Biotic interactions, when considered in relation to the nutrient “stress factor”, determine growth, development and productivity of plants in savannas. This includes:

- plant-plant interactions,
- fungi- or microorganism-plant interactions,
- animal-plant interactions.

Among the nutritional plant-plant interactions the grass-tree relations are of particular interest in savannas. With the extended root systems of trees, tree-biomass may concentrate nutrients from large soil volumes. Due to litter fall and decomposition,
the availability of K, Ca and Mg is often higher under tree canopies, and soil improvement due to litter may be even more important than by biological N₂-fixation (Campa et al. 2000; Sect. 10.2.3.2). The droppings of perching birds may also add to improved nutrient availability in the vicinity of trees (Medina 1993).

For the **animal-plant interactions** termite savannas (Sect. 9.1) are interesting because mound-building **termites** excavate and explore large volumes of soil reaching depths of 0.5 – 1 m. In this way they affect soil texture, but in addition they may also enrich nutrients like Ca, K and Mg and to some extent also P. Termites accelerate nutrient recycling and in termite dominated savannas (Sect. 9.1, Fig. 9.5) this may make a very considerable contribution to nutrient turnover. In Australia it was observed that termite-mediated mineralization of organic matter may amount to 250 kg ha⁻¹ year⁻¹ (Medina 1993). As described in Sect. 3.4.4.1, **leaf-cutter ants** (Fig. 3.34) concentrate nutrients in a similar way to mound-building termites. Leaves of grasses and trees are carried into complicated underground chamber systems, where the ants cultivate fungi and play a significant role in nutrient cycling, particularly for deep rooted trees. For the animal-plant interactions carnivory deserves a separate section (Sect. 10.2.3.3).

**Plant-fungi interactions** are of basic importance as **mycorrhiza** is a very widely expressed symbiosis of plants and fungi facilitating plant’s mineral nutrient acquisition. With respect to P-supply it was observed that genes which are active in P-deficiency are down-regulated independent of each other by internal phosphorus levels and mycorrhiza, where signalling involves inorganic phosphate transport from the root to the shoot and a transportable shoot factor signalling back to the root (Burleigh and Harrison 1999). Mycorrhiza is also important in interactions with atmospheric dinitrogen fixation and root nodule symbioses which are treated in a separate section (Sect. 10.2.3.2.2).

### 10.2.3.2 Fixation of Atmospheric Dinitrogen (N₂)

Fixation of N₂ is mediated by the enzyme-complex **nitrogenase**. It is restricted to procaryotic microorganisms, bacteria and cyanobacteria (“blue-green algae”), which however, can make important contributions to the N-supply of eucaryotic plants in **associations** and **symbioses**. The overall process is highly energy demanding, i.e.

\[
N_2 + 4[2H] + 16\text{ATP} \rightarrow 2\text{NH}_3 + \text{H}_2 + 16(\text{ADP} + \text{P}_i)
\]

Nitrogenase is very oxygen sensitive and requires hypoxia for its operation.

#### 10.2.3.2.1 Plant associations with Free Living Dinitrogen Fixing Microorganisms

Free living N₂-fixing bacteria are in the genera **Acetobacter, Azoarcus, Azospirillum, Azotobacter, Beijerinckia, Clostridium, Herbaspirillum** and **Paenibacillus** (Gottsberger and Silberbauer-Gottsberger 2006). All cyanobacteria (“blue-green algae”)
which have heterocytes are N$_2$-fixing. As the nitrogenase is O$_2$-sensitive it is located in special cells in the photosynthesizing filamentous cyanobacteria, i.e. the heterocytes, which have thick cell walls limiting O$_2$ diffusion into these cells, and lack photosystem II and hence photosynthetic O$_2$-evolution. From the possession of heterocytes, most of the cyanobacteria in the savannas are shown to be N$_2$-fixers (see also Sect. 11.2.1.2).

Associations of plants with N$_2$-fixing soil bacteria in the rhizosphere may be of mutualistic benefit, where exudates from the plant roots provide substrates and vitamins and other regulatory compounds to the microorganisms and plants receive N-compounds. The contribution of rhizosphere associations to total N-input to savanna soils may be quite significant (Table 10.10), and possibly in many cases their overall contribution may even be larger than that of root nodules. In fact, there have been considerable efforts to improve agricultural productivity of tropical grasslands with such associations (Baldani et al. 2002). Some of the N$_2$-fixing bacteria can even live endophytically in the host plants (Baldani et al. 2002). Attempts have also been made to use genetic engineering for the introduction of the nitrogenase-genes (nif$^+$-genes) into some rhizosphere bacteria, which occur more abundantly in the soil than natural N$_2$-fixing organisms (Hess 1992).

The contribution of cyanobacteria in the examples of Table 10.10 is shown to be rather modest. However, in places cyanobacteria are extraordinarily abundant in savannas, often forming dense, continuous mats between the tussocks of grasses (Fig. 10.19). In an example from savannas in Nigeria, where the ground coverage with cyanobacterial mats and crusts was 30%, a much higher value of cyanobacterial N$_2$ fixation is reported, namely 23 g ha$^{-1}$ day$^{-1}$ in the rainy season, and 60 g ha$^{-1}$ day$^{-1}$ have also been recorded in savannas corresponding to several kilograms per ha over the year (Medina 1993, Sect. 11.2.1.2).

A step between associations of plants with free living prokaryotes and N$_2$-fixing endosymbioses may be exosymbioses such as the endophytic bacteria mentioned above. Another example which has become important in tropical agriculture is the mutualism between the fern *Azolla* and the cyanobacterium *Anabaena*, which

<table>
<thead>
<tr>
<th>Table 10.10 Nitrogen balances in two humid tropical savannas in South America, Central Venezuela (<em>Trachypogon</em> savanna) and in Africa, Ivory Coast, and values of bacterial N$_2$ fixation associations in grasslands of Brazil and Zimbabwe. (Medina 1987, 1993)</th>
<th>Venezuela</th>
<th>Brazil (kg N ha$^{-1}$ year$^{-1}$)</th>
<th>Ivory Coast</th>
<th>Zimbabwe</th>
</tr>
</thead>
<tbody>
<tr>
<td>Input through rain</td>
<td>19</td>
<td>2.6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(inorganic 4.5)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Biological fixation</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Blue-green algae</td>
<td>1.4 – 2.5</td>
<td>0.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rhizosphere association</td>
<td>9 – 12</td>
<td>5 – 18</td>
<td>6.7</td>
<td>78</td>
</tr>
<tr>
<td>Losses through fire</td>
<td>17 – 23</td>
<td></td>
<td>8.5</td>
<td></td>
</tr>
<tr>
<td>Percolation and leaching</td>
<td>5.6</td>
<td></td>
<td>0.5</td>
<td></td>
</tr>
<tr>
<td>Balance</td>
<td>+4.9 to +6.8</td>
<td>+1.0</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Fig. 10.19A, B Mats of cyanobacteria between tussocks of grasses in the Llanos of Venezuela after a longer rainless period (A) (February 1989) and a few days after rain (B) (March 1991)

lives extracellularly in special intercellular air spaces of the fern fronds. *Azolla* grows equally well on fresh-water surfaces and on mud and is successfully used for mulching in tropical rice culture.
10.2.3.2.2 N₂-fixing Endosymbioses: Root and Stem Nodules

In the neotropics and palaeotropics there are 40 – 45 species of *Gunnera* which form a fascinating symbiosis with cyanobacteria of the genus *Nostoc*. Various *Gunnera* species range from small creeping stoloniferous herbs up to tall plants of a height reaching 6 m. They inhabit nutrient poor super-humid areas and bogs, leached soils with high rainfall and are also pioneers on bare lands. There is a preference of high altitudes in the genus, which also can inhabit sites with mesic climate. *Gunnera* is the only genus of angiosperms that forms an endosymbiosis with cyanobacteria. *Nostoc* is incorporated via peculiar stem glands secreting a mucilage. These glands are induced by nitrogen deprivation of the plants but independent of the cyanobacterial symbiont. Inside the host tissue *internal nodules* are formed which are invested with vascular tissue. Light does not penetrate the host organs towards the cyanobacterial symbionts which are photosynthetically inactive. Venation of the internal nodules is also necessary for the export of combined nitrogen. The N₂-fixing cyanobacterial symbionts provide ammonia to the host which has been shown to be sufficient for fulfilling the entire N-demand even of the larger plants of *Gunnera* species (Bergman et al. 1992; Osborne et al. 1992; Johansson and Bergman 1994; Stock and Silvester 1994; Silvester et al. 1996; Rai et al 2000; Parsons and Sunley 2001; Chiu et al. 2005).

Of a much more general importance are the *external root and stem nodules* of higher plants with N₂-fixing bacterial endosymbionts. Nodule eliciting bacterial endosymbionts are rhizobia of the genera *Azorhizobium*, *Bradyrhizobium*, *Rhizobium* and *Sinorhizobium*. Nodules (Fig. 10.20) are of a structurally high complexity providing the anatomical basis for various physiological requirements, especially for oxygen compartmentation and venation. *Oxygen compartmentation* is required to solve the *oxygen dilemma* of nodules, where on the one hand the oxygen sensitive nitrogenase needs a hypoxic environment and on the other hand the high energy demand of N₂-reduction as well as other essential metabolic activities in the nodules require high respiratory activity which needs oxygen. In addition to appropriate anatomical differentiations keeping these functions spatially separated leghemoglobin, which binds oxygen and diffuses between the different compartments of the nodules, effectively lowers and increases oxygen levels at the sites of nitrogenase and respiration, respectively (Werner 1992; Pimenta et al. 1998). *Venation* is essential for import of assimilates needed as substrate for respiratory energy supply as well as acceptors of reduced nitrogen (ammonia) and for export of organic nitrogen compounds to the nitrogen sinks of the plants. Here, an interesting detail of ecological biochemistry is the nature of the organic compounds functioning in nitrogen export from the nodules. These are often amides or nitrogen-rich ureide molecules. Amides are more water soluble than ureides and therefore their transport requires less water. Thus, among the Sahelian Acaciae, amide transporting plants may colonize more arid regions and ureide transporting plants inhabit areas of greater water availability (Campa et al. 2000).

The symbiotic formation of root nodules with N₂-fixing bacteria is best documented in the Leguminosae. With N-supply limiting so much the productivity of sa-
vannas, one might expect that plants capable of fixing atmospheric dinitrogen would be particularly frequent. An important leguminous savanna tree in South America is *Bowdichia* and in Africa various species of *Acacia* (Figs. 1.8A and 9.9) play an equivalent role. Open woodlands tend to contain more nodulated trees than adjacent forests. There is a progressive increase in the proportion of nodulated trees along a gradient from humid to arid areas, which is negatively correlated with the N-content of the soils (Högberg 1986b) and N\(_2\)-fixation carried out by N\(_2\)-fixing trees is more important in woodland than in rainforest (Högberg and Alexander 1995). Such a negative correlation is expected. N\(_2\)-fixation requires much input of energy, of carbon skeletons for binding of reduced N, and also special morphological differentiation (nodules), and in view of these costs N\(_2\)-fixation should not give a competitive advantage when sufficient N is available in the soil. Alternatively, the symbiotic association may be more susceptible to drought stress although nodulated Leguminosae such as *Prosopis* and *Acacia* are phreatophytes (see Fig. 10.7).

In Africa Fabaceae/Leguminosae trees are important and often dominant elements of savannas (Fig. 9.9). In the Etosha National Park in Namibia there are often sharp separations between *Acacia nebrownii* and *Colophospermum mopane* dominated savannas, which are determined edaphically and where the former appears to be somewhat more salinity-tolerant (Fig. 10.21; Berry and Loutit 2000). It has been noted by Ethiopian scientists that in agro-forestry systems it should be sufficient
to keep about 40 Acacia trees per ha to have sufficient N-fertilization. However, although in Africa numerous tree species contribute significantly to the N-budget of savanna-woodland ecosystems through their N$_2$-fixation (Högberg 1986b), it is often observed elsewhere that Leguminosae comprise a surprisingly low proportion of biomass in other savanna grasslands. In the Llanos of Venezuela, legumes rarely make up more than 1% of the biomass (Medina 1993). This limitation does not necessarily hold for the number of species of Leguminosae in such savannas. In one case among 127 species 109 were found to be nodulated. The frequency of leguminous species in Venezuela is related to low levels of exchangeable aluminium in the soil (see Sect. 10.2.4) and high levels of exchangeable calcium, i.e. two factors which are inversely related to each other. Overall root-nodule symbioses appear to contribute little to the productivity of this particular savanna system (Medina 1993).
Other factors limit the growth of legume species, and in particular the balance between the supply of nitrogen and other elements must be crucial. Nodulation itself is nutrient limited (Souza Moreira et al. 1992), and the most important limiting nutrient factor in savannas frequently is phosphorus (Högberg 1986a; Sect. 10.2.2). The particular demand of phosphorus for root nodules is a well known general phenomenon (Almeida et al. 2000). In soybean plants the total response of symbiotic N2-fixation to altered P-supply is a function of both indirect effects on growth of the host plant and more direct effects on the metabolic functions of the nodules (Israel 1993). In Africa, the low availability of phosphorus was found to be a severe restriction for nitrogen-fixing species in moist savannas, and this can explain their low abundance in such ecosystems. The increase in the number of nodulated trees towards drier sites already mentioned above is correlated with a decline in soil-N and an increase in available soil-P so that in African, and perhaps also in Australian savannas, one may distinguish between:

- moist/dystrophic and
- arid/eutrophic savannas

(Högberg 1986a).

Phosphorus limitations of nodulation can at least be partially alleviated when the leguminous plants develop a second symbiosis in addition to root nodules, namely mycorrhiza. The fungal hyphae of mycorrhiza enhance nutrient acquisition and may have positive effects, particularly due to increased supply of P to the host plants (Högberg and Alexander 1995). In the experiments presented in Table 10.11, nodulation was much more effective when mycorrhiza was present than if production of mycorrhiza was prevented. However, mycorrhiza could be readily replaced by phosphate supply in these experiments. The higher nodulation in plants with mycorrhiza or additional P-nutrition was accompanied by a considerably larger production of total fresh weight and a reduced root/shoot ratio, showing a lower investment in nutrient allocating roots foraging for nutrients and hence larger resource allocation to photosynthezising shoots. In another experiment, where nodulated soybean plants and maize plants were connected by a common mycorrhizal mycelium, it was even observed that the source-sink relations led to P- and N-flows in opposite directions.

<table>
<thead>
<tr>
<th>Genus</th>
<th>Total FW g</th>
<th>Root/shoot ratio</th>
<th>Nodules (1–5)</th>
<th>Mycorrhizal infection %</th>
<th>P and N content (mg/g)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Centrosema</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mycorrhiza</td>
<td>3.88</td>
<td>0.86</td>
<td>5</td>
<td>86</td>
<td>2.0</td>
</tr>
<tr>
<td>Non-mycorrhizal</td>
<td>1.67</td>
<td>1.70</td>
<td>1</td>
<td>0</td>
<td>0.5</td>
</tr>
<tr>
<td>+ phosphate</td>
<td>4.95</td>
<td>0.68</td>
<td>5</td>
<td>0</td>
<td>2.2</td>
</tr>
<tr>
<td>Stylosanthes</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mycorrhiza</td>
<td>1.63</td>
<td>0.54</td>
<td>5</td>
<td>74</td>
<td>4.4</td>
</tr>
<tr>
<td>Non-mycorrhizal</td>
<td>0.47</td>
<td>1.12</td>
<td>0</td>
<td>0</td>
<td>2.0</td>
</tr>
<tr>
<td>+ phosphate</td>
<td>0.91</td>
<td>0.34</td>
<td>5</td>
<td>0</td>
<td>5.8</td>
</tr>
</tbody>
</table>

Table 10.11 Effect of mycorrhiza and additional phosphorus supply on growth and nodulation of legumes. (Crush 1974)
There was a P-flow from maize to soybean, while soybean could provide maize with N (Bethlenfalvay et al. 1991).

Although tropical wetlands and floodplains are not only characteristic of some savanna types (Fig. 9.10) but also typical elements of tropical forests (Sect. 3.2.3) it may be the best place here to mention N₂-fixing nodule symbioses in these habitats, some of which are heavily leached, and where under flooded conditions mineralization of organic matter is slow so that they are nutrient poor and biological N₂-fixation is of great importance. Many nodulated Leguminosae also grow on floating mats of vegetation in the flooded areas. Flooding and especially cycles of fluctuating water levels highly amplify the dilemma of the oxygen metabolism of nodules. Oxygen levels are low in inundated and flooded soils (see also in mangroves, Sect. 7.3.1). This may appear beneficial for the oxygen sensitive nitrogenase but on the other hand it hampers the required respiratory activity. Hence, adaptations are important which include nodule formation on more superficial adventitious roots and even on stems to overcome the oxygen constraints by the submerged main root system, structural facilitation of oxygen diffusion pathways from stems via particularly developed lenticels (see Sects. 3.2.3 and 7.3.1) and aerenchymas to the root and the root nodules, and special structural features of the root nodules themselves (Loureiro et al. 1998). However, these adaptations facilitating oxygen supply of nodules under flooded conditions prove disastrous when nodules are exposed to the air in flooding and emergence cycles and emergent nodules deteriorate due to rapidly increasing oxygen levels (Loureiro et al. 1998; James et al. 2001). Stem nodules primarily may have evolved in response to flooding. Stem nodule forming species are in the genera of Aeschimone, Discolobium, Sesbania and Vigna (Loureiro et al. 1998). Nitrogen accumulation by stem-nodulated Leguminosae can be very high, ranging from 41 to 532 kg N ha⁻¹ in 1.5 – 2 months (Loureiro et al. 1998). These plants can also be used successfully in green-manuring to improve tropical agriculture. Sesbania rostrata fixing up to 200 kg N ha⁻¹ season⁻¹ contributes 50 – 150 kg N ha⁻¹ year⁻¹ to the soil nitrogen. In this way rice production can be increased two- to threefold (Clarkson et al. 1986).

10.2.3.3 Carnivory

Carnivory has already been mentioned in relation to lianas and epiphytes, as a potential strategy for nutrient acquisition (Sect. 6.6.3). In the temperate climate, carnivorous plants are particularly frequent in moist and acidic sites and especially in peat bogs, which are very poor in nutrients. Similarly, in the tropics, carnivorous plants of the genus Drosera are frequently found in great numbers in the wet and often peaty soils of upland herbaceous vegetation types with savanna-like meadows at 1,000 – 2,800 m a.s.l. (Fig. 10.22; see Huber 1988 for site description). The carnivorous genus Heliamphora (Sarraceniaceae) is endemic to the Tepuis, the characteristic table mountains of the Guayana highlands in tropical South America.

Drosera attracts its prey by the numerous brilliant droplets of mucilage (“sun dew”) secreted via special glands on the surface of colourful, often reddish, tentacles
Fig. 10.22A, B *Drosera roraimae*. A Gran Sabana, Venezuela. B Sierra Maigualida, Venezuela, with droplets of mucilage on the leaf tentacles.

(Fig. 10.23). The sticky mucilage usually prevents the escape of small insects once they have touched it. The tentacles move in response to mechanical and chemical stimuli caused by the captured animals making thigmotropic and chemotropic as well as thigmo- and chemo-nastic movements. The prey is thus enveloped and then digested by proteases secreted from the tentacle glands. Mineral elements like N, S,
P, Mg$^{2+}$, K$^+$ from the prey then stimulate growth and productivity of the *Drosera* plants (Lüttge 1983).

*Heliamphora* is a genus of pitcher plants with several species (*H. nutans*, *H. heterodoxa*, *H. minor*, *H. ionasii*, *H. tatei*). The pitchers are formed of single leaves. They are morphogenetically derived from peltate leaves, so that the interior of the pitcher wall corresponds to the upper leaf surface and the exterior to the lower leaf surface. In the middle of the pitchers there is a small opening, which allows water to flow out and thus prevents over-filling in the high rainfall habitats of *Heliamphora*. Animals are attracted by coloration and nectar secretion at the pitcher orifice. Escape is hindered by hairs and trichomes directed downwards to the bottom. Most of the criteria of true carnivory are fulfilled by all *Heliamphora* species, such as:

- attraction of prey through special visual and chemical signals,
- trapping and killing of prey,
- presence of wax scales and other structures preventing escape of prey,
- absorption of nutrients.

Most of the *Heliamphora* species, however, lack one important trait of true carnivory, i.e. digestive glands and enzyme secretion. In these cases digestion of prey is mediated by bacterial commensals (Schmucker and Linnemann 1959). There is one noticeable exception though, which is *H. tatei*. In this species there is enzymatic activity in closed pitchers just as they maturate and open. Since microbes have no
access to the closed pitchers, this proves to be genuine enzyme secretion by the pitcher tissue. Capture of small animals is very effective in *Heliamphora* species in their natural habitat. The carnivorous traits are lost, however, in low light conditions, which indicates that nutrient supply is limiting only under conditions of higher growth rates, and in terms of cost-benefit optimization the sophisticated carnivorous traits are not affordable under limited light (Jaffe et al. 1992). The occurrence of enzyme secretion in only one of the species of *Heliamphora* also suggests evolutionary trends in carnivory within the genus, with enzyme secretion being the most advanced trait in carnivory.

The expression of true carnivory is more dubious in the tanks formed by the leaf rosettes of bromeliads. Jolivet and Vasconcellos-Neto (1993) note that in general, in contrast to dicotyledonous carnivorous plants, among the monocotyledons there is only “protocarnivory” (see Sect. 6.6.3). Examples include *Catopsis berteroniana*, *Brocchinia reducta* and *Brocchinia hechtioides* among bromeliads or *Paepalanthus bromelioides* (Eriocaulaceae) of upland plateaus in northern Brazil. In moist upland savannas of Venezuela the terrestrial bromeliad *Brocchinia reducta* shows such extensive developments in some areas, that one may speak of a “*Brocchinia*-savanna”. It catches many animals and has a waxy inner surface to prevent escape (Fig. 10.24). There is breakdown of the bodies of small animals and absorption of solutes via the bromeliad scales. The outer walls of the scale cells have an unusual structure. They have a labyrinthine-like appearance and particularly large pores (6.6 nm) allowing the passage of rather large molecules, which possibly is followed by cellular uptake via endocytosis-vesicles (Owen and Thomson 1991). The species has been considered as a true carnivorous plant (Givnish et al. 1984), although glands and enzyme secretion are totally absent.

### 10.2.4 The Aluminium Problem

High levels of aluminium in soils are a particular problem in the tropics (Sect. 10.2.4.1) but also globally develop severe adverse effects in agriculture and forestry. Therefore the literature on aluminium/plant interactions is immense. To develop a background here for the aluminium relations of plants in the tropics key points were extracted from ca. 300 references to illustrate potential damage (Sect. 10.2.4.2) and responses of defence (Sect. 10.2.4.3). (These references cannot be cited here; a few reviews are the following: Lüttge and Clarkson 1992; Delhaize and Ryan 1995; Kochian 1995; Rengel 1996; Ma 2000; Čiamporová 2002.)

Fig. 10.24A–D *Brocchinia reducta* in a wet marshy savanna (A), with the typical bromeliad inflorescence (B), with the wax on the adaxial leaf surface that should prevent the escape of animals fallen into the bromeliad tank (C), and a tank cut open to show the putrefying mass of animals at the bottom (D). (Gran Sabana, Venezuela; February 1989)
10.2.4.1 The Aluminium Load in Tropical Soils

Clay minerals typical for savanna soils are:

- kaolinite, $\text{Al}_2\text{O}_3 \cdot \text{SiO}_2 \cdot 2\text{H}_2\text{O}$,
- gibbsite, $\text{Al}_2\text{O}_3 \cdot 3\text{H}_2\text{O}$,
- goethite, $\text{FeO(OH)}$.

They have low cation-exchange capacity (CEC) and low water storage capacity. Ferralization is a frequent process where bases and silicious acid are leached, leaving aluminium and iron oxides ($\text{Al}_2\text{O}_3$, $\text{Fe}_2\text{O}_3$). Thus, ferralitic soils always have very high concentrations of $\text{Al}^{3+}$. A special formation is the “arecife” in the Llanos of Venezuela (see Sect. 10.1.2.2 and Fig. 10.7). Iron oxide is precipitated at high groundwater table level in the young alluvial sediments forming these soils, such that gravel, sand and clay are solidified to a hard crust of a thickness of 1 – 3 m. It generally lies at a depth of 30 – 80 cm but may also be lower or closer to the surface (Fig. 10.7). Soils of the Brazilian cerrados contain between 75 and 360 ppm $\text{Al}^{3+}$ (Eiten 1972).

By comparison, high Al-load in acidifying soils has also been observed in the temperate zone. It is thought to be one of the possible reasons for forest decline, and here, the equilibrium soil solution contains up to 20 – 40 ppm Al.

10.2.4.2 Potential Damage to Plants by Aluminium

Damage of plants by high aluminium levels in the substratum occurs at multiple levels and is due to both extracellular effects on the surface of roots and cells and intracellular effects after uptake and translocation of aluminium in the plants. The major interactions can be listed as follows.

- **Ionic interactions:**
  - Phosphate. Al precipitates phosphate at surfaces in the apoplast in the form of the hardly soluble $\text{Al}_2(\text{PO}_4)_3$ salt and thus reduces P-availability.
  - Iron. High Al levels in the medium are associated with high acidity, which at the same time leads to increased mobility of iron and thus may induce Fe-stress. Conversely Al may also induce Fe deficiency and chlorosis because it inhibits the biosynthesis of phytosiderophores, Fe-complexing agents functioning in iron uptake of plants.
  - Divalent cations, $\text{Ca}^{2+}$, $\text{Mg}^{2+}$, $\text{Mn}^{2+}$, $\text{Zn}^{2+}$. Al occupies important cation-exchange sites in the apoplast and thus prevents access of essential divalent cations to these sites, which adversely reduces their availability to the plants.
  - Various other nutrients. Al may inhibit nitrate uptake and induce boron deficiency.

- **Cell wall interactions:**
  - Al modifies cell wall components making the cell wall thick and rigid, thus inhibiting growth.
10.2 The Nutrient Factor

- **Al binds to pectins** (depending on the degree of methylation of the pectins) occupying ion exchange sites.

**Membrane interactions:**
- Al binds to proteins and phospholipids of membranes. Thus, Al affects **structure and fluidity** of membranes increasing their rigidity and reducing permeability and it occupies cation exchange sites.
- Al blocks **K⁺- and Ca²⁺-channels** in membranes.
- Al inhibits **proton-pumping ATPases** of membranes (plasma membrane and tonoplast) and thereby reduces electric membrane polarization.

**Metabolism interactions:**
- Al generally affects metabolism. It **binds to ATP** making it metabolically unavailable.
- Al elicits **oxidative stress** indirectly via enhancement of Fe-mediated peroxidation which affects membrane structure and can cause DNA-damage.

**Cytoskeleton interactions:**
- Non-hydrolysable Al³⁺-ADP and Al³⁺-ATP complexes bind to actin/myosin and prevent cytoskeleton function.

**Interactions with intracellular messenger networks:**
- Al-induced callose formation blocks apoplastic and symplastic transport routes, and thus, **inhibits basipetal transport of the phytohormone indole acetic acid** (IAA).
- Al may become involved in **Ca²⁺/calmodulin interactions**, which are important in intracellular regulatory processes and signalling at the molecular level.
- Binding to phosphorylated proteins associated with DNA Al may interfere with **transcription**.

**10.2.4.3 Protective Plant Responses**

There are multicomponent tolerance and resistance mechanisms, a summarising listing of which is as follows.

**Aluminium exclusion:**
- **Alkalization of the rhizosphere.**
- **Secretion of Al-chelators**, such as organic acids (malate, citrate, oxalate) and flavonoid-type phenolics (catechin), supports Al-exclusion from the cells.
- **Excretion of phosphate** diminishes Al-mobility.
- Al-elicited formation of reactive oxygen species (e.g. H₂O₂) may result in kind of a **hypersensitive reaction** killing small areas of tissue and excluding Al from the remaining tissue.
Aluminium inclusion:
- Organic acid complexes (malate, citrate, oxalate) of Al are not toxic and serve as transport forms for sequestration, especially in the central cell sap vacuoles, and thus, provide internal tolerance.
- Complexes with inorganic phosphate bind Al, but the disadvantage is that this locks up significant amounts of phosphate.
- Al-silicon complexes can form in the shoot tissue.

Gene regulation is involved in protective plant responses, which affects various metabolic functions involved in organic acid secretion. We have seen above that the organic acid anions malate, citrate and oxalate are involved in both exclusion and inclusion and internal tolerance mechanisms of aluminium. Aluminium signalling elicits upregulation of de novo synthesis of organic acids and transport mechanisms and activation of anion channels and the proton transporting ATPase in the plasmamembrane.

10.2.4.4 Al-relations of Tropical Plants

Aluminium has different consequences for tropical forests as compared to savannas. In the forests, even when Al-concentrations in the soil are high the effect on plants is smaller, because the nutrient cycle is tightly coupled between the decomposing litter and the vegetation and tends not to involve the mineral soil very much. In savannas, however, plants take up minerals from the soil solution, which is in equilibrium with an Al-enriched exchange complex. Since most forest-tree species are more sensitive to aluminium than savanna plants, the Al-load of soils can in part explain the competition between forest, cerrados and savannas (Eiten 1972) and this may be one important determinant of the complex ecological regulation leading to the co-occurrence of forest and savanna in the tropics (Medina 1982). Under certain circumstances Al may even stimulate growth, e.g. by alleviating H⁺-toxicity at low pH and by attenuation of excess phosphorus toxicity (Watanabe et al. 2006). For Miconia albicans (Melastomataceae) from the cerrados of Brazil, conditions which lead to a degree of aluminium accumulation, such as non-calcareous acid soils, are even favourable for growth (Haridasan 1988). In another tropical Melastomataceae, Melastoma malabathricum, growing on acid sulphate soils, Al is a nearly essential mineral reducing toxic iron accumulation in roots and shoots (Watanabe et al. 2006).

Among trees in a cloud forest of Northern Venezuela there are Al-accumulators and Al-excluders, reflected in the xylem sap concentration in Al. In the Al-accumulator Richeria grandis (Euphorbiaceae), Al-levels in the leaves increased with age to levels of about 15,000 ppm (Cuenca et al. 1990, 1991). The gallery-forest tree Vochysia venezolensis (Vochysiaceae) in South America also accumulates up to 25,000 ppm Al related to dry matter (Eiten 1972; Sarmiento 1984). In a savanna in Trinidad, Al-levels in the grass Panicum stenoides were on average 910 ppm with maximum levels over 4,000 ppm, and the herbaceous Melastomataceae Acisan-
thera uniflora contained over 20,000 ppm (Sarmiento 1984). Haridasan (1982) lists Al-levels between 4000 and 14,000 ppm for various Al-accumulating cerrado species of central Brazil, but the highest levels of Al in plants quoted from the literature are 66,100 ppm for the Melastomataceae *Miconia acinodendron* and 72,300 ppm for the Symplocaceae *Symplocos spicata*. For comparison, in areas of forest decline in the temperate zone, Al-levels in the root dry mass range from 20 to 14,000 ppm depending on sites and soil depths (Lüttege and Clarkson 1992).

10.3 The Fire Factor

10.3.1 The Causes of Fire: Anthropogenic and Natural

Fires play an important role in tropical biota (Goldammer 1990; Fig. 10.25). Dynamical global vegetation models (Bond et al. 2005) impressively illustrate the role of fires (Fig. 10.26). There would be more forest and less savanna coverage without fire (compare the South-American and the African continents with the actual tree cover in Fig. 10.26A, the tree cover simulated with fire on in Fig. 10.26B and the simulated tree cover with fire off in Fig. 10.26C). Fires can originate naturally (see below) but currently the major cause of fires is man. Alexander von Humboldt (1808/1982) (Humboldt 1982) recognized this in his “Journey to South America” and mentions benefits and even the pleasure of fires, but also suggests the drawbacks.
“The pastoral people burn the grassland to obtain fresher and finer grass by new growth . . . Thus, if one relaxes on a magnificent tropical evening at the shore of the lake\textsuperscript{1} and enjoys the delightful coolness, one observes with pleasure the picture of the fires along the horizon, reflected in the waves beating the shore. . . . The savanna is frequently burnt to improve the pasture ever since the Llanos were inhabited. Together with the grasses by chance the scattered groups of trees are also destroyed. No doubt, these plains in the 15th century were not as bare as now. Nevertheless, even the first conquerors coming from Coro describe the savannas, in which one sees nothing but sky and grass, widely tree-less and difficult to pass because of the heat reflected by the ground.\textsuperscript{2}

Fires ignited by man have not only been used in slash-and-burn agriculture (Sects. 1.3 and 3.3.3) or in the management of pastures (Sect. 10.3.3) but also by very early hunter/gatherer societies to drivegame out of forest thickets (Kern 1994). However, fires in savannas, as well as in other tropical and non-tropical ecosystems, may also be caused naturally (Overbeck and Pfadenhauer 2007). In certain dry savannas of Africa during storms there is often lightning with little rain or before the rain sets in. In Australia, fire has been long considered as a natural environmental stress factor (Walter and Breckle 1984). Palaeontological findings show that fires destroying vegetation must have occurred since the Devonian (376 × 10\textsuperscript{6} years ago). The prerequisites for ignition of such fires are:

- a certain minimal atmospheric concentration of oxygen,
- the presence of combustible material.

The minimal O\textsubscript{2}-concentration required was shown experimentally to be 13\%, i.e. slightly less than two-thirds of the present level. Since it is assumed that atmospheric oxygen has resulted from photosynthetic O\textsubscript{2}-evolution, we may conclude that 13\% must have been reached by the time of the Devonian. Terrestrial vegetation had also developed to a stage that the second of the above criteria was fulfilled. As the possible causes we may list:

- lightning,
- sparks formed during rockfalls,
- vulcanism, and
- self-ignition of fermenting material

(Walter and Breckle 1984; Jones and Chaloner 1991). Thus, plants have been exposed to fire for long enough to allow evolution of special adaptations with stress avoidance and resistance in an ecophysiologicaly defined group of plants called pyrophytes.

\textsuperscript{1} Lake of Valencia, Venezuela.
\textsuperscript{2} Südamerikanische Reise “... brennt das Landvolk die Weiden ab, um ein frischeres, feineres Gras als Nachwuchs zu bekommen... Wenn man so an einem herrlichen tropischen Abend am Seeufer\textsuperscript{1} ausruht und die angenehme Kühle genießt, betrachtet man mit Lust in den Wellen, die an das Gestade schlagen, das Bild des roten Feuerrings am Horizont... Seit die Llanos bewohnt... sind, zündet man häufig die Savanne an, um die Weide zu verbessern. Mit den Gräsern werden dabei zufällig auch die zerstreuten Baumgruppen zerstört. Die Ebenen waren ohne Zweifel im 15. Jahrhundert nicht so kahl wie gegenwärtig; indessen schon die ersten Eroberer, die von Coro herkamen, beschrieben die Savannen, in denen man nichts sieht als Himmel und Rasen, im allgemeinen baumlos und beschwerlich zu durchziehen wegen der Wärmestrahlung des Bodens.”
Fig. 10.26A–C Tree cover in the South-American and African continents as actually observed (A) and simulated by Bond et al. (2005) with fire on (B) and fire off (C). The graphs have been redrawn and strongly simplified from Fig. 6 in Bond et al. (2005)
10.3.2 Pyrophytes

Discussing adaptations of plants to fire as an important natural ecological factor it is useful to distinguish between:

- **pyrophilous plants**, which obtain an advantage in the competition with other plants, and
- **true pyrophytes**, which essentially need fire at least at some stage in their life cycle.

Smaller plants may survive fires since the temperature at the soil surface may reach values of $\sim 75^\circ C$ only for a few minutes, and 1–5 cm below the surface temperatures may already be much lower (Walter and Breckle 1984). Thus the terminal buds in the center of tussock grasses are well enough protected, and regeneration can also occur from below-ground plant organs. Taller fire resistant plants, apart from specialized savanna trees with thick bark and dormant buds (see Sect. 10.3.3), are often tree ferns or monocotyledonous plants (like palms, *Yucca* or *Xanthorrhoea*, Fig. 10.27). These plants do not have a cambium at the periphery of their stems, as found in dicotyledonous shrubs and trees. In some *Eucalyptus* species in Australia, survival is guaranteed by formation of below-ground stem-thickenings (“lignotubers”), and reproduction by seeds is facilitated by removal of dry litter during fires and by killing the predators of young seedlings (Walter and Breckle 1984).

The genuine pyrophytes are literally dependent on fire. In the Cyperaceae *Bulbostylis spadicea* in the Brazilian cerrados flowering is stimulated by fire (Gottsberger and Silberbauer-Gottsberger 2006). A member of the Australian Liliaceae (or Xanthorrhoeaceae), *Xanthorrhoea*, only flowers after a fire. Among the woody plants of the cerrados in Brazil, Coutinho (1976) (see also Gottsberger and Silberbauer-Gottsberger 2006) distinguished the following responses of flowering to fires:

- species which quantitatively and qualitatively depend on fire and where fire elicits flowering at any time during the seasons,
- species where fire elicits flowering only during the dry season or in combination with short days,
- species which do not react to fire and flower during the dry season or after induction by short days,
- species which are damaged by fire and normally flower during the rainy season or after induction by long days.

Among the Australian Proteaceae there are many species where the fruits can only open and disperse seeds after a fire, e.g. *Banksia ornata*, *Hakea platysperma* and *Xylomelum pyriforme*, as well as the conifer *Actinostrobus*.

The evolution of such fire resistant and fire demanding plants also implies that fire is necessary to stabilize the ecological equilibria in ecosystems which have always been regularly subject to fire. In fact, it has been noted in some conservation areas and national parks that total prevention of fires has had adverse effects (Walter and Breckle 1984).
10.3 The Fire Factor

10.3.3 Burning by Man: Losses and Gains

During severe drought periods in savannas the decomposition of above-ground dead organic matter by microorganisms is very much reduced. This cover prevents new growth. Perennial grasses die back and seedling mortality under such a dense layer of dead plant material is high. Eventually the whole grass layer may die, as shown in a long-term experiment over 20 years, where specific areas were protected from fire and grazing at the biological field station at Calabozo in the Venezuelan Llanos (Medina and Silva 1990).

Rapid mineralization by fire removes the dead biomass and also has nutritional effects. Burning decreases soil acidity, and promotes mineralization of nitrogen. After an episode of fire, rates of nitrification increase for several years, followed by a decline of nitrification and increase in ammonium availability (Stewart et al. 1993). However, fire not only enriches the soil with minerals, it may also lead to losses especially of N and S in the form of volatile oxides (Table 10.12). Most of these losses are from vegetation rather than soil (Stewart et al. 1993). For N the range of such losses is:

- $4.5 - 5.6$ kg ha$^{-1}$ year$^{-1}$ in Australia,
- $8 - 10$ kg ha$^{-1}$ year$^{-1}$ in Africa, and
- $8$ kg ha$^{-1}$ year$^{-1}$ in Venezuela

Fig. 10.27A, B Pyrophilous plants of Australia. A *Xanthorrhoea* (Liliaceae). B *Cycas media* (Cycadaceae)
Table 10.12 N- and S-input and losses and biomass production in a *Trachypogon* savanna in central Venezuela. (Medina 1982)

<table>
<thead>
<tr>
<th>Biomass production (t ha(^{-1}))</th>
<th>Losses as volatile gases N (kg ha(^{-1}) year(^{-1}))</th>
<th>Losses as volatile gases S (kg ha(^{-1}) year(^{-1}))</th>
<th>Input by rain N (kg ha(^{-1}) year(^{-1}))</th>
<th>Input by rain S (kg ha(^{-1}) year(^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Minimum</td>
<td>2.9</td>
<td>9.3</td>
<td>2.6</td>
<td>1.3</td>
</tr>
<tr>
<td>Maximum</td>
<td>10.0</td>
<td>32.0</td>
<td>9.0</td>
<td>4.7</td>
</tr>
</tbody>
</table>

(Medina 1993). It may much exceed the import via rain (Tables 10.10 and 10.12).

The global role of fires has been surveyed by Fontan (1993). Table 10.13 shows the annual turnover of biomass in forests and savannas in the tropical regions of the world. The contribution of savanna fires to the total biomass burnt per year is seen to be high in America but particularly so in Africa. Fires not only cause losses of minerals but also make a significant contribution to atmospheric loading of infrared-active gases which cause the greenhouse effect (CO\(_2\), CO, CH\(_4\), O\(_3\)) and with straightforward pollutants (like CO, N-oxides, O\(_3\)) (Table 10.14).

Frequent man-made fires also open the soil surface to solar radiation, which leads to oxidation and burning of humus (Eiten 1972) and leaching following rainfall. Therefore **in dry savannas fire is always detrimental.**

Moreover, of course, fire always damages the **forests** unless it is wet gallery forest with permanently inundated soil (Fig. 10.28). The fires intrude from the edges

---

**Fig. 10.28** Savanna in the Llanos of Venezuela near Puerto Ayacucho with scattered islands of semi-evergreen forest and wet gallery forest (*background to the right*)
Table 10.13  Burnt biomass in the tropical regions of the world from tropical forests, savannas and other sources (firewood plus agricultural waste) in Tg dry matter per year. (After Fontan 1993)

<table>
<thead>
<tr>
<th>Tropical region</th>
<th>Forests</th>
<th>Savannas</th>
<th>Other sources</th>
</tr>
</thead>
<tbody>
<tr>
<td>America</td>
<td>590 (34%)</td>
<td>770 (44%)</td>
<td>370 (22%)</td>
</tr>
<tr>
<td>Africa</td>
<td>390 (12%)</td>
<td>2430 (76%)</td>
<td>400 (12%)</td>
</tr>
<tr>
<td>Asia</td>
<td>280 (13%)</td>
<td>70 (3%)</td>
<td>1840 (84%)</td>
</tr>
<tr>
<td>Oceania</td>
<td>– (0%)</td>
<td>420 (94%)</td>
<td>25 (6%)</td>
</tr>
<tr>
<td>Total</td>
<td>1260 (17%)</td>
<td>3690 (49%)</td>
<td>2635 (34%)</td>
</tr>
</tbody>
</table>

Table 10.14  Global gas emissions form bushfires in Tg year⁻¹ and in % of total global emissions. (Fontan 1993)

<table>
<thead>
<tr>
<th>Compound</th>
<th>Emissions from bush fires</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carbon dioxide (CO₂)</td>
<td>3500</td>
</tr>
<tr>
<td>Carbon monoxide (CO)</td>
<td>350</td>
</tr>
<tr>
<td>Methane (CH₄)</td>
<td>38</td>
</tr>
<tr>
<td>Hydrocarbons other than methane</td>
<td>24</td>
</tr>
<tr>
<td>N-oxides</td>
<td>9.3</td>
</tr>
<tr>
<td>Ammonia (NH₃)</td>
<td>5.3</td>
</tr>
<tr>
<td>Chloromethane (CH₃Cl)</td>
<td>0.5</td>
</tr>
<tr>
<td>Hydrogen gas (H₂)</td>
<td>19</td>
</tr>
<tr>
<td>Ozone (O₃)</td>
<td>420</td>
</tr>
</tbody>
</table>

into the forests, and where the trees are not fire-resistant, year by year savanna gradually encroaches into the area previously occupied by forests (Fig. 10.29).

Savanna trees are particularly fire resistant (Figs. 10.30 and 10.31), being predominantly evergreen, with a thick corky bark and dormant buds, and sprout after fires before the beginning of the rainy season (see Sect. 10.1.2.1). It is estimated that only trees with a bark less than 5 mm thick can be killed by fires in the cerrado (Miranda et al. 1993; Gottsberger and Silberbauer-Gottsberger 2006). Some trees, in areas where regular burning occurs, may restrict formation of their woody stems to below the ground surface in the form of lignotubers or xylopodia, where dormant buds are protected and can readily produce new growth after a fire (Fig. 10.31B). Xylopodia may also serve storage of water and minerals, and the plants forming such organs can be considered to represent the typical life form of xylohemicryptophytes (Gottsberger and Silberbauer-Gottsberger 2006; for definitions of life forms see Sects. 3.3.4 and 11.3.1, Table 11.2). Deciduous trees, with phenological cycles related to the seasonality of rainfall, are more sensitive to fire, and they are excluded from regularly burned savannas (Medina and Silva 1990). In the experiment at Calabozo mentioned above, during 20 years of protection, total tree density increased considerably, both of fire-resistant savanna trees and fire-sensitive species from the surrounding semideciduous forest (Table 10.15), and Table 10.16 shows similar findings for a Brazilian cerrado. In dry savannas of Namibia where fires are disastrous and burning is now strictly avoided one can observe Acacia mellifera ssp. detinens spreading out and occupying vast areas, which has become a curse for cattle farmers.
Fig. 10.29 A Remains of montane forest near Akanzobe in Madagascar. B In the centre is shown a zone of common brake fern (*Pteridium aquilinum*) between the grassland and the forest, which burns very readily and gradually progresses towards the forest. (Photographs courtesy M. Kluge)
In wet savannas fire can be beneficial, but only when the timing is correct. If a fire occurs before the start of the rainy season, the trees are protected (see above) and safe sprouting of grasses is obtained. The centers of tussocks of grasses supporting the meristems for regrowth are protected from the heat of the fire by an insulat-
ing layer of old leaves. If burning occurs too early in the dry season, subsequent new growth uses up water reserves and dies before the rainy season sets in, and the whole plant may dry out totally. If burning is done too late in the dry season, new
Table 10.16 Comparison of adjacent hectares of low-tree and scrub cerrado of central Brazil periodically burned each 2 – 3 years and not burned for over 20 years, respectively. (Density of stems is larger than density of individuals since some individuals produce more than one stem.) (G. Eiten and R. H. R. Sambuichi, pers. comm.)

<table>
<thead>
<tr>
<th></th>
<th>Not burned</th>
<th>Burned</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stems (number ha$^{-1}$)</td>
<td>6677</td>
<td>1765</td>
</tr>
<tr>
<td>Individuals (number ha$^{-1}$)</td>
<td>5788</td>
<td>1663</td>
</tr>
<tr>
<td>Species</td>
<td>92</td>
<td>57</td>
</tr>
</tbody>
</table>

Fig. 10.32 Variations in the epigeous biomass ($T$ total; $G$ green; $D$ dry) of a savanna at Calabozo, Venezuela, after it was burned and until it reached a steady state (dotted line) in five years. (Sarmiento 1984; reprinted by permission of Harvard University Press)

growth is induced when the water reserves are already exhausted and growth is very limited. If burning occurs in the middle of the dry season, green biomass is produced, which is maintained until the beginning of the rainy season (Medina 1982; Medina and Silva 1990). The experiments at Calabozo have shown that maximum above-ground biomass in a protected savanna increased during four years after the last fire (Table 10.17) and then stabilized at a certain level (Fig. 10.32). Fire later at the beginning of the rainy season led to lower biomass production than fire before the middle of the dry season (Table 10.18). The seasonal development of the grass *Trachypogon plumosus* shows that the green biomass after a fire is somewhat increased as compared with the control (Fig. 10.33) and new dry biomass and total above-ground biomass increase rapidly over the year after most of the old biomass was destroyed by the fire.

Table 10.17 Maximum epigeous biomass in a fire-protected *Trachypogon* savanna at Calabozo, Venezuela. (Sarmiento 1984)

<table>
<thead>
<tr>
<th>Time since last fire (years)</th>
<th>Maximum epigeous biomass (g m$^{-2}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>230 – 730</td>
</tr>
<tr>
<td>2</td>
<td>520 – 850</td>
</tr>
<tr>
<td>3</td>
<td>980</td>
</tr>
<tr>
<td>4</td>
<td>1200</td>
</tr>
<tr>
<td>5</td>
<td>1200</td>
</tr>
</tbody>
</table>
Fig. 10.33 Variations in the epigeous biomass of a savanna at Calabozo, Venezuela, during the first year after a fire (F) and in a non-burnt control plot (C). (Sarmiento 1984; reprinted by permission of Harvard University Press)

Table 10.18 The effect of fire given at different times during the year on daily biomass production in a savanna at Calabozo, Venezuela. (Medina 1982)

<table>
<thead>
<tr>
<th>Time of Fire</th>
<th>Biomass Production (g m⁻² day⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Three to four years protected from fire</td>
<td>2.5 – 2.6</td>
</tr>
<tr>
<td>Fire before the middle of the dry period</td>
<td>2.9 – 3.7</td>
</tr>
<tr>
<td>Fire at the beginning of the wet period</td>
<td>1.8 – 2.1</td>
</tr>
</tbody>
</table>

References


References


Chapotin SM, Razanajaharizaka JH, Holbrook NM (2006b) Baobab trees (Adansonia) in Madagascar use stored water to flush new leaves but not to support stomatal opening before the rainy season. New Phytol 169:549–559


Piedade MTF, Long SP, Junk WJ (1994) Leaf and canopy photosynthetic CO$_2$-uptake of a stand of Echinochloa polystachya on the Central Amazon floodplain. Are the high potential rates associated with the C$_4$-syndrome realized under the near-optimal conditions provided by this exceptional natural habitat? Oecologia 97:193–201


Chapter 11
Inselbergs

11.1 Physiognomy

Inselbergs\(^1\) are isolated rock outcrops in the palaeotropics and the neotropics coming up out of different vegetation of savannas or cerrados (Fig. 11.1A) or rainforests (Fig. 11.1B). In savannas with a certain savanna affinity of their flora they also have been described as “rock savanna”. They consist of monolithic blocks, mostly of granite or gneiss, of a considerable geological age, i.e. \(10 \times 10^6\) years at least and \(40 – 50 \times 10^6\) years on average. More rarely inselbergs may also consist of sandstone. They range from several tens or hundreds of meters high, the highest one found in French Guiana being 740 m high (Schnell 1987). “Shield-type” inselbergs may have extensions of several square kilometers. In arid regions and deserts they may have been eroded to heaps of rather small rocks (Fig. 11.1D). Inselbergs evolve by deep and intensive weathering (Fig. 11.2A). Thus, inselbergs are really islands separated from the surrounding savanna or forest vegetation (Figs. 11.1A, B and 11.2B; Barthlott et al. 1993; Porembski and Barthlott 2000a). They provide very different ecological conditions.

In the analysis of inselberg vegetation, one tries to determine whether the occupation of these isolated habitats is deterministic or stochastic, and whether there are climax states or dynamic oscillations and if there is a coexistence of equilibrium and non-equilibrium communities (Barthlott et al. 1993; Porembski et al. 2000b). In fact, the inselbergs themselves are again fragmented in a number of sub-islands and smaller ecological units (Porembski et al. 2000a; Fig. 11.3), and therefore their \(\beta\)-diversity (see Sect. 3.3.1) is high. Besides a large spectrum of higher plant life forms, cryptogamic life forms are particularly important. The rock itself is rarely free of life, usually being covered by dense cryptogamic crusts of cyanobacteria, lichens and mosses. Interestingly, depending on the respective dominance of lichens or cyanobacteria, one may distinguish lichen and cyanobacteria inselbergs. The former are more abundant in Africa, the latter in South America (Barthlott et al. 1993).

\(^1\) The term *inselberg* from the German *Insel* = island and *Berg* = mountain, coined by Bornhardt (1900), is somewhat more specific than “rock outcrop” and has been widely adopted in scientific writing.
Sub-islands on the rock are formed by individual plants or small groups of plants growing in humus in cracks, gaps and hollows (Fig. 11.3). Xerophilic plants, such as succulents and epiphytes, grow saxicolously. Patches of shrubbery originate from the vegetation islands (Fig. 11.4A,B) and small forests often form on top of the inselbergs (Fig. 11.4C). In South America these forests comprise the only deciduous vegetation units occurring in the area around the Guayana shield, with trees like *Pseudobombax chrysati*, *Tabebuia orinocensis* and *Yacaranda filicifolia* (Fig. 10.4), and also palms (*Syagrus orinocensis*, Fig. 11.4C). While most sites on inselbergs are extremely dry and hot in the dry season (see Sects. 11.2 and 11.3), there are also wetter sections (Fig. 11.5) and even rock pools (Porembski et al. 2000a), which seasonally keep small ponds of water and harbour aquatic plants. **Floristic diversity** of inselbergs in various regions of the world is documented in detail in Porembski
and Barthlott (2000a). It is very high and inselbergs are extraordinarily rich in endemic species. Huber (1980) listed the natural habitats of the inselbergs along the Orinoco in Venezuela as belonging to the “flower paradises and botanical gardens of the earth”.

Phytogeography, plant sociology and vegetation analysis are advancing to ask the pertinent questions for providing a deeper understanding of these exciting sites (see Barthlott et al. 1993). Ecophysiology of this fascinating vegetation is still less developed. One exception are studies of desiccation tolerance in inselberg plants (Sect. 11.4). Where there is strong seasonality, pools will dry out in the dry season. The rock surface during midday may easily heat up to temperatures around 60 °C (Fig. 11.6). Not only cryptogams but also many angiosperms of the inselbergs have been shown to be able to overcome such dry periods by ecophysiological adaptations, particularly by desiccation tolerance (Sect. 11.4).
11.2 Cryptogams

11.2.1 Cyanobacteria

11.2.1.1 Ubiquity

A conspicuous feature of the inselberg rocks is their superficial appearance of dark coloration. This was first noted in Venezuela by Alexander von Humboldt (Humboldt von 1849) who described the black surface of the rocks in the riverbed of the Orinoco and also of the rock outcrops further away:

“In the Orinoco, especially in the cataracts of Maypures and Atures, all granite blocks and even white pieces of quartz to the extent they are touched by the water of the Orinoco
Fig. 11.3 Isolated plants and sub islands on inselbergs:
The bromeliad *Pitcairnia pruinosa* on the inselberg at Galipero near Puerto Ayacucho, Venezuela (A), the bromeliad *Tillandsia araujei* (B) and the orchid *Maxillaria* sp. (C) on the inselberg Pedra Grande at Atibaia, S.P., Brazil, and the Velloziaceae *Pleurostima gounelleana* (D) on rock outcrops at Itatiaia, R.J., Brazil

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develop a greyish-black cover which does not penetrate more than 0.01 line\(^2\) into the interior of the rocks. One might think to see basalt or fossils stained by granite. In fact the sheath appears to contain manganese oxide and carbon.\(^3\)

\(^2\) 1 line = 2.0 to 2.5 mm; Fig. 11.7.

\(^3\) “Im Orinoco, besonders in den Cataracten von Maypures und Atures, ... nehmen alle Granitblöcke, ja selbst weiße Quarzstücke, so weit sie das Orinoco-Wasser berührt, einen graulich-schwarzen Überzug an, der nicht 0,01 Linie ins Innere des Gesteins eindringt. Man glaubt Basalt oder mit Granit gefärbte Fossilien zu sehen. Auch scheint die Rinde in der That braunstein- und kohlenstoffhaltig zu sein.”
Regarding the dark colour of the rock outcrops at a greater distance from the current river bed of the Orinoco he assumed that the river had extended much further in earlier times:

“This assumption is supported by several observations. One sees black caves 150 to 180 feet above the present water level. Their existence teaches . . . that the streams, whose size presently excites our admiration, are only humble remains of the enormous amounts of water in archaic times . . . These simple observations even did not escape the rough natives. Everywhere they drew our attention to the old waterlevel.”

The finding of prehistoric petroglyphs in the rocks of the inselbergs (Fig. 11.8A) also played a role in Humboldt’s discussion, since he asked how the Indians might have found access to the steep walls of rock for carving them:

“Between Encaramada and Caycara on the banks of the Orinoco one frequently finds . . . hieroglyphic pictures in considerable height on the rock faces, which now would only be accessible by means of extraordinarily high scaffolding. If one asks the natives how these pictures could have been carved, they reply with a smile, as if they were telling a story which

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“Selbst den rohen Eingeborenen . . . sind diese einfachen Bemerkungen nicht entgangen. Überall machten uns die Indianer auf die Spuren des alten Wasserstandes aufmerksam.”
Fig. 11.4 Shrubs (A, B) with *Clusia criuva* (B) on the inselberg Pedra Grande at Atibaia, S.P., Brazil and deciduous forest (C) with the palm *Syagrus orinocensis* on top of the inselberg at Galipero near Puerto Ayacucho, Venezuela
Fig. 11.5 Wetter sections and pools on the inselberg Galipero near Puerto Ayacucho, Venezuela, where seasonally water is flowing and small ponds with water are formed in hollows.

Fig. 11.6 Temperature of the air above the inselberg at Galipero (○) and the rock surface (●) during two consecutive days (15 – 16 March 1991) (Pto. Ayacucho, Venezuela)

only the white man may not know: that in the days of the extended waters their forefathers were boating in canoes in such a height. This is a geological dream for the solution of the problem of a long vanished civilization.”

Furthermore, regarding the extensive distribution of the petroglyphs, HUMBOLDT alludes to his correspondence with Sir ROBERT SCHOMBURGK:

“I may be permitted to include a remark, which I take from a letter of the distinguished traveller Sir Robert Schomburgk: ‘The hieroglyphic pictures have a much wider distribution than you might have assumed’ . . . the symbolic figures, which ROBERT SCHOMBURGK found engraved in the river valley of the Essequibo at the rapids of Waraputa according to his observation resemble the truly Caribbean ones on one of the small Virgin Islands (St. John)⁶, however, notwithstanding the wide expansion of the invasions of Caribbean tribes and the ancient power of this beautiful human race, I cannot believe that this whole immense belt of carved rocks which cuts across a large part of South America from west to east is the work of the Caribs. They are rather traces of an ancient civilization, which possibly belongs to an epoch, when the tribes which we distinguish nowadays were still unknown by name and relationship. Even the reverence, which everywhere is deferred to these rough sculptures of the forefathers, proves that the present Indians have no idea of the creation of such works.”⁷

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⁶ See Fig. 11.8B,C.
However, there are also already some slight reservations in HUMBOLDT’s writings regarding the inorganic nature of the black sheets on the rocks. He stressed that it appears to be manganese oxide and carbon:

“I say, it appears; because the phenomenon has not been investigated diligently enough. At the Orinoco these leadlike coloured rocks if wetted emit harmful emanations. One believes their proximity to be a cause of fevers.”8

A biological cause is suggested by the observation that the black coloration is associated with only the organically rich white-water rivers and not the more sterile black-water rivers:

“It is also noteworthy that the rivers with black water, aguas negras, the coffee-brown or wine-yellow waters, in South America do not stain the granite rocks black.”9

Indeed, an elemental analysis of the black cover of the inselbergs along the Orinoco using X-ray fluorescence spectroscopy shows that there are traces of manganese only (Table 11.1). There is only one exception, and these are the rocks directly in the riverbed of the Orinoco (Table 11.1), where the analysis actually indicates the dominant presence of manganese oxide. The high levels of Al and Si in all cases, of course, are due to the bed rock. The dominance of elements like S, K and Ca is consistent with the occurrence of life in these crusts. Indeed, lichens and small mosses are often readily discerned on the rock surfaces (Sect. 11.2.2). However, microscopic inspection shows that even the smooth black covers of these rocks result from living organisms. They are mainly composed of epilithic and endolithic cyanobacteria, predominantly of the genera Gloeocapsa, Stigonema and Scytonema (Figs. 11.9 and 11.10). Similar coverings of cyanobacteria are found on rocks throughout the tropics and the diversity of species is quite large (Büdel 1999). The phenomenon has also been described for sandstone rocks, e.g. near Cumana in eastern Venezuela (Golubic 1967), and examples are given in Fig. 11.11 of the granite rocks of Sierra Maigualida and sandstone rocks of Tepuis (Sierrania Parú) in the Guayana highlands of Venezuela. They resemble the “Tintenstrich” (“ink strip”) formation frequently found in the European Alps, particularly on calcareous rocks (Jaag 1945).

In the tropics almost every free surface on rocks is covered by cyanobacterial mats and crusts. Based on the large extension of supporting rocks these cyanobacteria overall must constitute an enormous biomass in the tropics.
Fig. 11.9A, B Closeup photographs of rocks covered with cyanobacteria on the inselberg at Galipero (A) and on the granite in the Sierra Maigualida, Guayana Highlands (05° 30' N, 65° 15' W, 2,040 m a.s.l.) Venezuela (B)

Fig. 11.10A–C Cyanobacteria composing the black crusts of the inselbergs along the Orinoco, Venezuela. A Stigonema ocellatum. B Scytonema crassum. C Gloeocapsa sanguinea. (Courtesy B. Büdel, Kaiserslautern; see Büdel et al. 1994)
11.2 Cryptogams

A

B

C
Fig. 11.11A–C Black granite rocks of the Sierra Maigualida (at 05° 30′ N, 65° 15′ W, 2,040 m a.s.l.; A and B, in B shortly after a rain storm) and sandstone rock of the Serrania Parú (at 04° 25′ N, 64° 32′ W, 1,200 m a.s.l.; C), Guayana Highlands Venezuela, with cyanobacteria
Table 11.1 Elemental analysis (elements of order-number 11 – 80) by X-ray fluorescence spectroscopy of samples from sandstone rocks of the Serriana Parú (04° 25′ N, 65° 32′ W, 1,200 m a.s.l.), inselbergs along the Orinoco and the riverbed of the Orinoco near Puerto Ayacucho. (See Büdel et al. 1994)

<table>
<thead>
<tr>
<th>Element</th>
<th>Serrania Parú</th>
<th>Inselbergs Orinoco</th>
<th>Riverbed Orinoco</th>
</tr>
</thead>
<tbody>
<tr>
<td>Al</td>
<td>37.9 ± 9.5</td>
<td>16.8 ± 1.3</td>
<td>7.8 ± 0.1</td>
</tr>
<tr>
<td>Si</td>
<td>46.0 ± 10.0</td>
<td>55.1 ± 4.2</td>
<td>18.9 ± 3.1</td>
</tr>
<tr>
<td>S</td>
<td>3.2 ± 2.4</td>
<td>1.1 ± 0.4</td>
<td>0</td>
</tr>
<tr>
<td>K</td>
<td>4.3 ± 0.7</td>
<td>7.5 ± 1.2</td>
<td>1.9 ± 0.3</td>
</tr>
<tr>
<td>Ca</td>
<td>1.1 ± 0.7</td>
<td>2.7 ± 1.0</td>
<td>2.8 ± 0.2</td>
</tr>
<tr>
<td>Mn</td>
<td>0.2 ± 0.1</td>
<td>0.5 ± 0.1</td>
<td>49.7 ± 4.0</td>
</tr>
<tr>
<td>Fe</td>
<td>0.5 ± 0.3</td>
<td>6.3 ± 1.3</td>
<td>15.5 ± 0.9</td>
</tr>
<tr>
<td>Others</td>
<td>6.8 ± 0.5</td>
<td>10.0 ± 2.4</td>
<td>3.4 ± 0.3</td>
</tr>
</tbody>
</table>

a Serrania Parú 3 samples, 1 – 2 analyses each.
b Inselbergs Orinoco 8 samples, 4 – 13 analyses each.
c Riverbed Orinoco 1 sample, 10 analyses.

Values are ± SE for the averages of the individual analyses of the three and eight samples in a and b respectively, and for the ten analyses of the sample in c. One sample of b had 82% Os.

11.2.1.2 Success on Bare Substratum

The role of cyanobacteria in cryptogamic soil crusts of deserts and other dry habitats has recently received much attention (Lange et al. 1992; Evans and Ehlehringer 1993; Jeffries et al. 1993a,b; Belnap and Lange 2001). Very little is known, however, about the ecophysiology of cyanobacteria on rocks in the tropics, and in view of the enormous distribution of terrestrial cyanobacteria, which cover almost any surface not occupied by other vegetation, this is quite astonishing. The major reasons for the success of cyanobacteria on the bare substratum of rocks appear to be:

- a potential to adapt to high light intensities,
- the ability to fix atmospheric dinitrogen, and
- desiccation tolerance.

High light intensities bring about considerable heating up of the rock surfaces with cyanobacterial crusts. In response various heat shock proteins (hsp) are synthesised in the cyanobacteria (Adhikary 2003). Survival of high light intensities in the extremely sun exposed habitat of the inselbergs is also sustained by the production of effective sunblocking pigments, such as the indol-alkaloid scytonemin (Garcia-Pichel and Castenholz 1991), which occurs in cyanobacteria in light-exposed environments (Büdel et al. 1997b; Büdel 1999). In exposed epilithic cyanobacteria of Venezuela and French Guiana, scytonemin, with its absorption maximum at 380 nm, is found in such high concentrations that irradiance up to 500 nm is reduced inside the cells. Furthermore, intracellular carotenoids such as zeaxanthin (Demmig-Adams et al. 1990) and canthaxanthin (Albrecht et al. 2001; Lakatos et al. 2001) may prevent photodamage. The formation of these pigments is slow and takes place over days adapting the cyanobacterial cells to high irradiance.
Thus, the responses of photosynthesis of cyanobacteria to high light intensities depend greatly on the irradiance experienced during growth. Cells grown at 50 $\mu$mol photons m$^{-2}$ s$^{-1}$ (at $\lambda = 400 - 700$ nm) or below are already photoinhibited at 250 $\mu$mol m$^{-2}$ s$^{-1}$ and strongly affected at still higher light intensities (Samuelsson et al. 1985; Lüttge et al. 1995). However, inselberg rocks usually receive full sunlight unless clouds and rain quench exposure. Figure 11.12 shows that in an inselberg sample from Ivory Coast, a transfer from 480 to 1,200 $\mu$mol photons m$^{-2}$ s$^{-1}$ did not affect fluorescence yield and photochemical fluorescence quenching, indicating unimpaired photochemical and carbon-assimilatory activity.

**Fig. 11.12** Optimal quantum yield of photosystem II ($F_v/F_m$), effective quantum yield ($\Delta F/F_m'$) and photochemical quenching ($q_p$) of cyanobacterial crusts of an inselberg near Seguèla, Ivory Coast ($07^\circ 42' N, 06^\circ 43' W$) in drying (arrow drying above the graphs) and rewetting (arrow $H_2O$ above the graphs) cycles and during transfers between lower and higher light intensities (arrows with numbers above the graphs giving light intensities at $\lambda = 400 - 700$ nm in $\mu$mol photons m$^{-2}$ s$^{-1}$). Dark and white bars above the graphs indicate dark and light periods respectively (Lüttge et al. 1995)
while a transfer from 240 to 1,280 µmol photons m$^{-2}$s$^{-1}$ resulted in a slight and rapidly reversible inhibition. (The drying and wetting cycles shown in Fig. 11.12 will be discussed in Sect. 11.4.) As in higher plants (Schreiber and Bilger 1993), potential quantum yield of photosystem II after dark adaptation ($F_v/F_m$), effective quantum yield ($\Delta F/F_m'$), and photochemical fluorescence quenching ($q_p$) (see Sect. 4.1.7, Box 4.6) decrease with increasing light intensity in cyanobacterial crusts (Fig. 11.13). (In higher plants $F_v/F_m$ is close to 0.8 in non-photo inhibited samples (Sect. 4.1.7) and we note that in comparison in the cyanobacteria in Figs. 11.12 and 11.13 $F_v/F_m$ is rather low even in the early morning. This is an intrinsic property

![Figure 11.13](image)
of the prokaryotic cells due to the particular structure of their photosynthetic membranes (Lüttge 1997) and does not imply that these cyanobacteria were under very severe chronic photoinhibition.) The multiplication of \( \Delta F/F'_m \) by photosynthetic photon fluence density (PPFD) gives relative photosynthetic electron transport rates, which saturated at the high intensities of 1,000 \( \mu \text{mol photons m}^{-2}\text{s}^{-1} \) or above in the inselberg sample from Madagascar and the rock outcrop sample from Ethiopia measured in the experiments of Fig. 11.13. Thus, although even cyanobacteria crusts grown under full sun exposure may be subject to partial photoinhibition, it is quite clear, that cyanobacteria can adapt very well to very high irradiance (Lüttge et al. 1995).

Cyanobacterial communities show conspicuous zonations and niche occupation across furrows running down the rocks of inselbergs (Fig. 11.14). On an inselberg at Les Nouragues in French Guiana a community in the centre of such furrows was found to be dominated by compact growth forms, like the unicellular, colony-building *Gloeocapsa sanguinea* (Fig. 11.10C) and the short branching species *Stigonema mamillosum*. The growth form appears important because during and after rainfall the cyanobacterial mats are covered by water up to a few centimetres in depth, occasionally with strong current. The lateral slopes of the furrows are covered by a different community dominated by a thick layer of *Stigonema ocellatum* (Fig. 11.10A). A third community dominated by *Scytonema myochrous* was found at some distance (normally > 50 cm) from the furrows in the more or less horizontal rock areas covering more than 80% of the whole rock surface (Rascher

![Fig. 11.14 Drainage furrow running down from a small vegetation island on the inselberg Pedra Grande at Atibaia, SP, Brazil](image-url)
et al. 2003). After rainfall before drying again the mats in the centre of the furrows and at the lateral slopes are covered for longer times by water and films of water than the mats on the horizontal rocks, and therefore, their photosynthesis is more pronouncedly limited by diffusion of CO₂ and HCO₃⁻ in the liquid phase. To counterbalance the liquid diffusion limited carbon supply cyanobacteria have evolved an inorganic carbon concentrating mechanism or a CO₂/HCO₃⁻ pump, where transport mechanisms and carbonic anhydrase catalyzing the CO₂/HCO₃⁻ equilibrium are involved (Sklerýk et al. 1997; Sültemeyer et al. 1997). Diffusion limitation is reflected in the stable isotope ratios δ¹³C of the cyanobacteria. They are performing C₃-photosynthesis and the enzyme of primary CO₂-fixation ribulose-bis-phosphate carboxylase/oxygenase (RuBISCO) has a ¹³C-discrimination of +27‰. The δ¹³C-values of cyanobacteria of inselbergs, however, are much less negative than −27‰.

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**Fig. 11.15A, B** Carbon isotope ratios (δ¹³C, ‰) of cyanobacteria in a transect across a seepage furrow of the inselberg at Galipero (A) and distribution of δ¹³C-values among 17 samples of cyanobacterial crusts and mats from the area around Caicara – Puerto Ayacucho along the Orinoco river, Venezuela (B). (Lütte 1997; Ziegler and Lütte 1998)
which would be obtained if RuBISCO were mainly determining $^{13}$C-discrimination during photosynthesis (Ziegler and Lüttge 1998; Fig. 11.15). This is due to the lower $^{13}$C-discrimination of dissolution of CO$_2$ ($-0.9\%$) and diffusion of CO$_2$ and HCO$_3^-$ in water ($0.0\%$) determining CO$_2$ delivery to RuBISCO, and as expected then, there is also a gradient from less negative to more negative $\delta^{13}$C values from the centre via the lateral slopes to the open rock surfaces of the inselbergs (Fig. 11.15). The mats in the centre of the furrows also have a somewhat lower effective quantum use efficiency ($\Delta F/F_m'$) and apparent electron transport rate (ETR) of photosynthesis than the mats at the slope and outside the furrows (Fig. 11.16).

The second important trait of cyanobacterial rock crusts as highlighted above is N$_2$-fixation. By the possession of heterocytes they are characterized as N$_2$-fixing organisms, because heterocytes are special cells in the coenobial colonies

![Figure 11.16A, B](image)

**Fig. 11.16A, B** Apparent effective quantum yield ($\Delta F/F_m'$) (A) and apparent rates of electron transport (ETR) (B) recorded over several days while the cyanobacteria communities across furrows of the inselberg at Les Nouragues, French Guiana, were wetted after rainfall. Lines indicate linear regressions (A) or fitted exponential growth to maximum (B). Filled circles and continuous lines, cyanobacterial community in the centre of the furrows, open squares and broken lines with long dashes, cyanobacterial community at the sides of the furrows, open triangles and broken lines with short dashes, cyanobacterial community on the vertical rocks beside the furrows. (Rascher et al. 2003)
or filaments bearing the enzymatic machinery for the reduction of atmospheric N\textsubscript{2} (Sects. 10.2.3.2.1 and 10.2.3.2.2). Evidently N\textsubscript{2}-fixation of the cyanobacteria is important primarily for their own nutrition and growth. However, by leachates cyanobacterial crusts and mats on the rock habitat probably provide an essential starting point for succession and possibly also contribute considerably to the N-input into the ecosystems of the inselbergs themselves and via run-off into the surrounding savannas or forests. In fact the nitrogen content of the soil 10 m from the base
of inselbergs in savannas was three times (1.40 g N/kg soil) that measured more than 30 m from the base (0.45 g N/kg soil) (E. Medina in Büdel et al. 1997a,b). On the basis of a map of the inselbergs along the upper Orinoco river (Fig. 11.17) presented by Grüger (1995) one can estimate the total savanna area with inselbergs as ca. 3,425 km$^2$ ($342.5 \times 10^3$ ha) and the area of the inselbergs as ca. 480 km$^2$ ($48 \times 10^3$ ha) or 14%. The N$_2$-fixation of cyanobacterial mats in tropical savannas was estimated as 60 g N/ha per day (Medina 1993) so that with assuming 300 good days per year as Grüger (1995) gives the number of dry months in the area at only one to three and a total coverage of the inselbergs with cyanobacteria, the fixation of the inselbergs would be ca. 18 kg N/ha per year. This appears small in comparison to N-fertilisation in high-technology agriculture (several 10s to 200 kg N/ha; see Lüttge 1997) but is substantial for the nutrient poor savanna ecosystem.

The third of the traits highlighted above which allow cyanobacteria survival on bare rocks, i.e. desiccation tolerance, appears to be the most important one and is discussed in Sect. 11.4.

### 11.2.2 Lichens and Mosses

Lichens (Büdel et al. 2000, Fig. 11.18) and bryophytes (Frahm 2000, Fig. 11.19) are important elements of the inselberg vegetation. Their photosynthesis like that of the cyanobacterial crusts (Sect. 11.2.1.2) is also much determined by the frequent

![Fig. 11.18 Lichens (Peltula tortuosa) on the rock surface of the granite inselberg at Galipero, Venezuela](image)
wetting and drying cycles on the inselberg rocks. Diffusion limitation of inorganic carbon supply for photosynthesis is modulated by the growth form of the lichens and mosses determining the extent and duration of the build up of water films in the thalli after precipitation (Tuba et al. 1996a; Büdel et al. 2000; Lüttge et al. 2007), and this may effect niche occupation of different inselberg mosses (Lüttge et al. 2007). Different moss species may perform characteristic belts around small vegetation islands on inselbergs (Fig. 11.19) but apparently do not differ in their basic photosynthetic capacity (Lüttge et al. 2007). A major adaptive trait of these cryptogams for life on inselberg rocks is their desiccation tolerance (Sect. 11.4).

11.3 Vascular Plants

11.3.1 Diversity and Life Forms

The floristic diversity of cryptogamic and phanerogamic vascular plants of inselbergs is large (Sect. 11.1). The diversity of life forms occurring on rock outcrops is also quite noticeable. It varies at different locations (Table 11.2). The dominance of different life forms is governed by the size of the inselbergs (Table 11.3) and the richness of vascular species increases with inselberg size (Fig. 11.20).

11.3.2 Physiological Ecology

Although at least some inselbergs are readily accessible even with heavy equipment (Fig. 11.21) only very little ecophysiological work has been performed on site. From the frequency and intense development of species of Agavaceae, Bromeli-
aceae, Cactaceae, Crassulaceae, Euphorbiaceae and Orchidaceae on inselbergs in the palaeotropics and the neotropics (Kluge and Brulfert 2000) we may conclude that **crassulacean acid metabolism (CAM)** is an important mode of photosynthesis on these rock habitats. On the inselbergs along the Orinoco both CAM-bromeliads (e.g. *Ananas ananassoides*, *Bromelia goeldiana*, and the epiphytic *Tillandsia flexuosa*) and **C$_3$/CAM-intermediate Clusiaceae** (various species of *Clusia* and *Oedematopus*...
### Table 11.3 Life-form specific size classification of inselbergs in relation to the number of therophytes in the Ivory Coast (Porembski et al. 2000b)

<table>
<thead>
<tr>
<th>Inselberg type</th>
<th>Therophytes (%)</th>
<th>Minimal size of inselberg (m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lichen inselberg</td>
<td>–</td>
<td>ca. 1</td>
</tr>
<tr>
<td>Therophyte inselberg</td>
<td>&gt; 80</td>
<td>ca. 50</td>
</tr>
<tr>
<td>Perennial herb inselberg</td>
<td>ca. 60</td>
<td>ca. 10,000</td>
</tr>
<tr>
<td>Phanerophyte inselberg</td>
<td>ca. 45</td>
<td>ca. 50,000</td>
</tr>
</tbody>
</table>

**Fig. 11.21** Negotiation of the inselberg at Galipero, Venezuela, with heavy equipment

{oovatus, see Sect. 6.6.2.3} are found on South-American inselbergs. Bromeliads, like *Ananas ananassoides* and *Bromelia goeldiana*, develop the contrasting phenotypes of yellow-reddish fully exposed plants and dark-green shaded plants under the canopy of shrubbery and small forests respectively, as already described for *Bromelia humilis* (Sect. 4.1.2). On an inselberg in Madagascar, the distribution of three *Kalanchoë* species with different expression of CAM was found to be related to micro-habitat characteristics: *K. campanulata* with a very weak CAM capacity in the shade of deep humid gaps performed largely C₃ photosynthesis; *K. miniata* in open bush formations showed pronounced CAM performance; *K. synsepala* spreading by stolons on the bare rocks showed the strongest expression of CAM (Kluge and Brulfert 2000). On the other hand, **C₃-photosynthesis** is also dominant among vascular plants of inselbergs.

Desiccation tolerance as for cryptogams is a most important adaptation of vascular plants on inselbergs (Sect. 11.4).
11.4 Desiccation Tolerance

Desiccation tolerance appears to be the most outstanding particular ecophysiological adaptation among the plants of tropical inselbergs. Drought tolerance allows plants to overcome shorter periods of stress, such as the duration of dry seasons. In contrast, desiccation tolerant plants can survive equilibration with ambient air humidity below 50% and down to 0%, and withstand the loss of more than 90% of their normal water content for many years (Gaff 1977, 1987). We call desiccation tolerant plants poikilohydrous in contrast to the homoiohydrous non-desiccation tolerant plants. Because of their recovery from dryness they are also called resurrection plants. Poikilohydrous plants may degrade or retain their chlorophyll during drying and are then called poikilo-chlorophyllous and homoio-chlorophyllous, respectively. Poikilohydry is well known of lower cryptogams, such as terrestrial cyanobacteria, lichens and bryophytes. However, it is also found among vascular plants and these are especially species adapted to the life on inselbergs in the tropics.

11.4.1 Cyanobacteria

As it is illustrated by the loss and reappearance of chlorophyll-fluorescence signals in drying and rewetting cycles performed in the laboratory on a rock sample with cyanobacterial crusts from an inselberg in Ivory Coast (with the cyanobacteria Stigonema mamillorum, Scytonema lyngbioides and Gloeocapsa sanguinea, and traces of Stigonema ocellatum) desiccation and recovery can occur very rapidly (Fig. 11.12). Triggered by sensing the loss of a small amount of water a rapid deactivation of photosynthetic activities is essential to avoid oxidative stress during desiccation (Hirai et al. 2004). Recovery from desiccation may occur within a few minutes up to several hours after rewetting and recovery of photosystem I activity is faster than that of photosystem II (Jones 1977; Coxson and Kershaw 1983; Lüttge et al. 1995; Satoh et al. 2002; Rascher et al. 2003). It depends on the duration of the dormant state of desiccation, and frequent drying and wetting cycles maintain stability (Scherer and Zhong 1991). The sequence of events during recovery is firstly, reappearance of respiration, followed by photosynthesis and finally N₂-fixation (Scherer et al. 1984). Rapid recovery is associated with rapid repair mechanisms, e.g. of the D1-protein (see Sect. 4.1.5) of photosystem II (Harel et al. 2004).

11.4.2 Lichens and Bryophytes

Wetting and drying cycles have been studied in much detail for lichens in arid habitats. Photosynthesis of lichens is related in a complex and delicate way to the
transient water conditions of the thallus (Fig. 11.22). At very low water content, i.e. below 20% of dry weight, the lichens are metabolically dormant showing neither photosynthesis nor respiration. Between 20% and 50% water content, photosynthetic net CO₂-uptake increases sharply and then reaches a plateau as optimal water content is attained. However, when the water content increases further and thalli are fully saturated with water, CO₂-assimilation is depressed. This is due to increased limitation of photosynthesis by CO₂ diffusion when the capillary system of the lichen thallus is infiltrated. Thus, upon drying the assimilation rates may first increase again and then decline as the thalli desiccate (Lange 1988).

Both protection and repair mechanisms are essential during desiccation as well as rehydration. Reactive oxygen species can be formed during desiccation and rehydration, especially when the use of excitation energy of the photosynthetic apparatus by photochemical work is reduced. Protection mechanisms such as by the redox state of glutathione are effective in both lichens and mosses (Kranner 2002; Mayaba et al. 2002). However, we must assume that in the desiccated state water structures required for enzymatic reactions including photochemical work of CO₂-reduction and photorespiration as well as epoxidases and de-epoxidases of the xanthophyll cycle (Sect. 4.1.4, Box 4.4) are not intact, and therefore, these excitation-energy using processes are negligible in dry homiochlorophyllous material.

Thus, by the excitation of chlorophyll in homiochlorophyllous plants in the dry state high irradiance causes photo-oxidative stress. An interesting feature of

![Net CO₂ exchange vs Water content](image)

**Fig. 11.22** Net CO₂ uptake in the light (○) and net CO₂-release in the dark (●) of the lichen Ramalina maciformis at varied thallus water content related to dry weight. (Lange 1988, with kind permission of the author and Journal of Ecology)
homoiochlorophyllous desiccation tolerant lichens and bryophytes is the **loss of ground fluorescence of chlorophyll a**, $F$ (see Sect. 4.1.7) in the desiccated state in great contrast to desiccation tolerant vascular plants. While $F$ decreases during desiccation and increases again during rewetting in mosses and lichens, the opposite dynamics are found in vascular plants (Lange et al. 1989; Calatayud et al. 1997; Eickmeier et al. 1993; Heber et al. 2000, 2001).

High irradiance causes **photodamage** in dried vascular plant leaves but not in dried mosses (Heber et al. 2000). This shows that the reduction of $F$ to very low levels in the latter can be considered as a protection mechanism against photodamage under full sunlight on exposed rock surfaces of inselbergs in the dehydrated stage. Effective mechanisms of chlorophyll fluorescence quenching mediate the conversion of excitation energy into heat when metabolism can no longer control it. Two

Fig. 11.23A–D Development of basic fluorescence, $F$, of light adapted dry cushions of *Campylopus savannarum* (A), *Racocarpus fontinaloides* (B) and *Ptychomitrium vaginatum* upon rewetting (C,D) (Lüttge et al. 2007)
processes are involved in this, namely zeaxanthin-dependent energy dissipation in the antenna of photosystem II (see Sect. 4.1.4) and desiccation induced thermal energy dissipation in the reaction centres (RCs) of photosystem II (Deltoro et al. 1998; Heber et al. 2000, 2006a,b; Bukhov et al. 2001). The latter is essential in desiccated lichens and mosses because zeaxanthin does not protect RCs directly from photodestruction and in the absence of photosynthetic electron transport dynamics in the dry state dissipation must be extremely fast given the half-lives of first and second singlet excited states of chlorophyll of $10^{-11}$ to $10^{-9}$ and $10^{-15}$ to $10^{-13}$, respectively (Box 4.3).

Homoiochlorophylly is an important prerequisite of rapid recovery upon rewetting (Tuba et al. 1996b; Csintalan et al. 1999). Kinetics of recovery can vary considerably among mosses (Csintalan et al. 1999; Proctor 2000; Proctor and Smirnoff 2000). In the example of Fig. 11.23 the recovery of $F$ has a very fast initial phase with a drastic increase within less than 1 min followed by a more gradual increase lasting much longer. Protein synthesis is not required during the fast initial phase (Proctor and Smirnoff 2000), but the gradual increase following the first rapid phase suggests that in addition to an immediate reactivation slower repair mechanisms involving protein synthesis, such as that of the D1 protein may be involved (Proctor and Smirnoff 2000).

### 11.4.3 Vascular Plants

#### 11.4.3.1 Evolution and Diversity of Poikilohydrous Vascular Plants

Inselbergs are the diversity centres of poikilohydrous vascular plants (Meirelles et al. 1997; Biedinger et al. 2000; Porembski and Barthlott 2000a,b; Proctor and Tuba 2002). Desiccation tolerant vascular plants, especially phanerogamic species, were initially known especially from inselbergs of Africa (Gaff 1977) and then also from South America, Australia and India (Gaff 1987; Meirelles et al. 1997). Although dormant dried developmental stages, such as spores, pollen grains and seeds, are known from the life cycles of all vascular plants, desiccation tolerance of the vegetative plant bodies is rare and there are only 200 (Kappen and Valladares 1999) to 350 (Proctor and Tuba 2002) desiccation tolerant species among vascular taxa. It has been proposed to consider desiccation tolerant cryptogams such as cyanobacteria, algae, lichens and bryophytes as constitutively poikilohydrous as they are exohydric and cannot actively control their water relations as compared to the vascular plants which are constitutively homoiohydrous with their complex regulation of water relations. In the former desiccation tolerance is a primary trait during evolution, in the latter it is a special late development in highly advanced taxa (Kappen and Valladares 1999; Proctor and Tuba 2002). Indeed, although among cryptogamic vascular plants desiccation tolerance occurs in a high proportion of taxa (e.g. in the class Lycopodiopsida, order Selaginellales; in the class Pteridopsida orders Schizales and Pteridales), tolerance appears to be less pronounced than observed in angiosperms. Among the phanerogams desiccation tolerant species mostly are mono-
cotyledons and there are fewer desiccation tolerant dicotyledons (Gaff 1977), with the latter apparently absent from South America (Gaff 1987). Evolution of poikilohydry in the angiosperms was polyphyletic and occurred at least eight times (Proctor and Tuba 2002). The poikilohydrous vascular plants of the more basic taxa and of the dicotyledons generally are homoiochlorophyllous and retain their photosynthetic apparatus in a recoverable form. Poikilochlorophyllly is only found among the desiccation tolerant monocotyledons (Kappen and Valladares 1999; Proctor and Tuba 2002) and appears as an advanced trait in evolution where plants lose all of their chlorophyll and 70–80% of their carotenoids (xanthophylls and β-carotene) and the internal structure of their chloroplasts (thylakoids) only retaining the outer envelope. While homoiochlorophyllly has the advantage of rapid resumption of photosynthetic metabolism during rehydration, poikilochlorophyllly provides much better protection from oxidative stress in the dehydrated stage which appears to outweigh the disadvantage of much slower recovery.

11.4.3.2 Dynamics of the Performance in Dehydration/Rehydration Cycles

The dynamics of dehydration/rehydration cycles are best documented considering capacity of photosynthesis.

In homoiochlorophyllous species recovery upon rehydration is generally much faster than in poikilochrophyllous plants. A unique example of a homoiochlorophyllous angiosperm is the aquatic species Chamaegigas intrepidus (Scrophulariaceae) living in rock pools of granite outcrops in Namibia (Hartung et al. 1998). Effects of dehydration on photosynthetic quantum yield are maximal between 10 to 15 h and photosynthetic quantum yield rises again rapidly to high values within a few hours of rehydration and reaching maximum values after 10 h (Fig. 11.24).

For poikilochlorophyllous species desiccation and recovery has been studied in much detail in the Velloziaceae Xerophyta scabrida growing in the Uluguru Mountains in Tanzania at 650 m a.s.l. (about 05° 30’ S, 35° 30’ E), where they form a semi-desert like bush vegetation on cliffs.

![Fig. 11.24 Quantum yield (circles) during a dehydration/rehydration cycle of a single plant of Chamaegigas intrepidus and development of abscisic acid levels during dehydration (Hartung et al. 1998)]
During desiccation net photosynthesis declined to the compensation point within 8 h, while respiration continued beyond the 24th hour at water potentials much lower than $-3.2$ MPa. An active respiration, which lasts until the end of the desiccation period, is responsible for the metabolic degradation of chlorophylls and other components of thylakoids (Tuba et al. 1996b).

Water uptake and rehydration after rewetting initially must occur predominantly via the surface of the leaves, because functional roots are lost during desiccation. As in other desiccation tolerant plants (Gaff 1977), water uptake subsequently occurs via the roots when new adventitious roots are developed (Tuba et al. 1993a). Times required for recovery vary considerably between species and up to several days may be needed (Kappen and Valladares 1999). The events occurring in *X. scabrida* upon rehydration are summarized in Fig. 11.25 after the work of Tuba et al. (1993a,b, 1994). The sequence in time is turgor $\rightarrow$ maximum leaf water content $\rightarrow$ respiration $\rightarrow$ resynthesis of carotenoids and $\rightarrow$ chlorophylls accompanied by thylakoid development $\rightarrow$ chlorophyll fluorescence yield $\rightarrow$ net $\text{CO}_2$-fixation. Turgor reappears after 2 h, maximum leaf water content is reached after 10 h. Among the biochemical activities respiration generally recovers early

![Fig. 11.25 Recovery of the poikilochlorophyllous desiccation tolerant Velloziaceae *Xerophyta scabrida* upon rehydration. The graphs in the lower three panels indicate the relative increases of the structures and functions described in the left column. Compiled after data in Tuba et al. (1993a, b, 1994)](image-url)
Mitochondrial membranes are better preserved during desiccation than the thylakoids of chloroplasts. In *X. seabraida* respiration is increased above the normal rates after 12 h. This so-called rehydration respiration must be related to repair mechanisms and ceases after 30 h, when normal rates are attained again. In contrast to chromoplasts and gerontoplasts of senescing leaves, which cannot regreen, the chloroplasts of desiccation tolerant plants, which lose their entire photosynthetic apparatus, i.e. thylakoid membranes and pigments during desiccation, are totally rebuilt after rehydration. Tuba et al. (1993b) have named these plastids *desiccoplasts*. Some of the carotenoids, i.e. 22–28%, are preserved during desiccation, and they may play an essential role in reorganization. Reaccumulation of carotenoids and chlorophyll $a + b$ starts after 12 h when thylakoid development also begins to appear, as indicated by the thylakoid frequency, thylakoid stacking and the ratio appressed/exposed membranes. We recall that appressed thylakoid regions and the membranes stacked in the grana are the sites of photosystem II (see Box 4.2). Chlorophyll fluorescence reappears at about the same time, while it takes considerably longer, i.e. about 24 h for the onset of net CO$_2$-uptake. Recovery of photosystem I usually is faster than that of photosystem II (Kappen and Valladas 1999). After 72 h all functions have reached their normal levels again.

### 11.4.3.3 Structure Function Relations

**Whole leaves** shrink, curl, roll and fold during desiccation and the epidermis of leaves is much wrinkling (Hartung et al. 1998; Proctor and Tuba 2002; Vicré et al. 2004). This is a consequence of water loss, but it also contributes to a much reduced light absorption and irradiance stress in the dry state. In addition resurrection plants may develop accumulation of anthocyanin a sun-blocking pigment (Farrant et al. 2003). During the reduction of the volume of leaf cells and the associated extensive folding of cell walls a tight connection remains established between the plasma membrane and the cell wall, a phenomenon called *cytorrhysis*, which is important for recovery during rehydration (Hartung et al. 1998; Vicré et al. 1999). The **cell wall** is subject to considerable mechanical stress in this process. Resurrection plants develop cell walls with particular tensile strength. Arabinan polymers and arabinogalactan proteins, xyloglucans, homogalacturonan, rhamnogalacturonan and unesterified pectins are important macromolecules building up the special cell wall structure with the high mobility and water absorbing capacity required in dehydration/rehydration cycles and cross linking Ca$^{2+}$ ions may also be involved (Vicré et al. 1999, 2004; Moore et al. 2006).

**Hydraulic architecture** is especially important during rehydration. Conductive elements of the xylem suffer embolism during desiccation. Lipids lining the water conducting elements of the xylem may be involved in preventing complete loss of water in the dry state (Schneider et al. 2000, 2003; Wagner et al. 2000; but see also Tyree 2001). In the initial stages of moistening before xylem emboli are repaired and especially in the poikilochlorophyllous *Vellozias*, which lose their absorptive roots in the desiccated state (Sect. 11.4.3.2) external capillary water movement is
important. In the Vellociaceae species this can occur quite effectively in the external space of the pseudostems built up of the retained leaf bases of dead leaves (Proctor and Tuba 2002; Fig. 11.26). In the xylem in addition to capillary water movement root pressure is essential for overcoming embolis and for refilling the conductive elements with water (Kappen and Valladares 1999; Proctor and Tuba 2002; Schneider et al. 2000, 2003; Wagner et al. 2000). This may be the reason why desiccation tolerant angiosperms do not reach larger sizes than up to 3 – 4 m tall (Gaff 1977; Kappen and Valladares 1999; Proctor and Tuba 2002), e.g. monocotyledonous pseudo shrubs such as Vellozia (Fig. 11.26). The homoiohydrous resurrection plant Craterostigma plantagineum (Scrophulariaceae) has desiccation tolerant roots which die two weeks after rehydration (Norwood et al. 2003).

Fig. 11.26A–C Vellozia gigantea (A) and detailed views of its pseudo stem (B, C). Serra do Cipó, MG, Brazil
11.4.3.4 Cell Physiology

At the cell physiological level during desiccation and rehydration the three most important functions are the dynamics (i) of compatible solutes for the protection of cellular components and (ii) of lipids for the maintenance of membrane structures and (iii) the control of reactive oxygen species.

(i) Compatible solutes. Compatible solutes stabilize proteins and membranes (Sect. 7.4, Box 7.1). In resurrection plants mainly sugars function as compatible solutes, predominantly sucrose but also glucose, fructose and unusual sugars, such as trehalose, glucopyranosyl-β-glycerol and arbutin (Hartung et al. 1998; Vicré et al. 2004). Increase in hexokinase activity is associated with the acquisition of desiccation tolerance (Whittaker et al. 2001). Unusual sugars, such as stachyose (Norwood et al. 2003) and in C. plantagineum the C8-sugar 2-octulose are converted to sucrose (Norwood et al. 2000; Bartels and Salamini 2001; Ramanjulu and Bartels 2002). Hydrophilic protective proteins are also important (Rodrigo et al. 2004) and are for example accumulated in plastids (Bartels and Salamini 2001). An interesting cytological consequence of the accumulation of sugars with a higher degree of polymerization such as raffinose, stachyose and other galactosyl-sucrose-oligosaccharides in addition to sucrose is the suppression of crystallisation of protoplastic constituents and the promotion of glass formation or vitrification controlling metabolism in the desiccated state at low water content (Hartung et al. 1998; Proctor and Tuba 2002; Vicré et al. 2004).

(ii) Lipids. Membranes of resurrection plants appear to be well protected (Hartung et al. 1998). Dynamics of the chemical composition of membrane lipids are important to maintain the structure of membranes including the plasma membrane and chloroplast membranes during desiccation/rehydration cycles, where the unsaturation level of phospholipids and the level of total lipids decrease during desiccation (Navari-Izzo et al. 2000; Quartacci et al. 2002; Ramanjulu and Bartels 2002).

(iii) Reactive oxygen species (ROS). The formation of ROS is a particular problem during desiccation/rehydration cycles especially in homoioclorophyllous resurrection plants (Sect. 11.4.3.1). Antioxidative defence systems such as the ascorbate/glutathione cycle and superoxide dismutases play an important role in protection to keep functional sulphydryl groups in the reduced state (Smirnoff 1993; Hartung et al. 1998; Kappen and Valdares 1999; Proctor and Tuba 2002; Vicré et al. 2004). Angiosperms with internal carbon concentrating mechanisms such as C4-plants (Sect. 10.1.1.2) and CAM-plants (Sect. 5.2.2.2) where oxidative stress is at least partially controlled by high internal CO2 concentrations appear to be rare among resurrection plants. A curiosity is the small desiccation tolerant cactus with CAM Blossfeldia liliputana (Barthlott and Porembski 1996; Hartung et al. 1998).

11.4.3.5 Gene Regulation

The protection of the genome against desiccation and rehydration induced damage and the down regulation and up regulation of genes follow longer time constants
than metabolic processes (Cooper and Farrant 2002). As many as 800 to 3000 genes may be involved in desiccation tolerance of plants (Hartung et al. 1998). Screening and transcriptomics techniques show differential expression, up regulation and down regulation, of a large number of genes (Ingram and Bartels 1996; Bockel et al. 1998; Velasco et al. 1998; Garwe et al. 2003; Collett et al. 2004; Neale et al. 2000). This underlines the high complexity of molecular responses in desiccation tolerance. Many of these genes can be related to special functions, but the roles of very many others are not understood. Some of these genes are specific in desiccation tolerance many others are seen to be involved in general in various stress responses. Gene regulation cascades and networks in desiccation tolerance (see Ramanjulu and Bartels 2002) are modulated by various phytohormones (Ghasempour et al. 2001; Vicré et al. 2004). The most central messenger, however, is abscisic acid (ABA) (Ingram and Bartels 1996; Hartung et al. 1998; Kappen and Valladares 1999; Bartels and Salamini 2001; Proctor and Tuba 2002; Bernacchia and Furini 2004; Vicré et al. 2004). Its levels, for example, increase rapidly in desiccating Chamaegigas intrepidus (Fig. 11.24). Gene expression dynamics in relation to the various cell physiological functions discussed in Sect. 11.4.3.4 have been revealed, namely carbohydrate metabolism for compatible solutes (Kleines et al. 1999; Bernacchia and Furini 2004), lipid metabolism (Bartels and Salamini 2001), photosynthesis (Phillips et al. 2002; Collett et al. 2003), and aquaporins, channel proteins facilitating water exchange across membranes (Hartung et al. 1998; Ramanjulu and Bartels 2002). Differential gene expression also addresses protective hydrophilic proteins such as the late embryogenesis abundant proteins (LEA) first discovered due to their involvement in cellular protections in dehydrating seeds, dehydrins and small heat shock proteins (Hartung et al. 1998; Bartels and Salamini 2001; Ditzer et al. 2001; Bernacchia and Furini 2004).

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12.1 Summer Every Day, Winter Every Night

The cold tropics (Sect. 1.2) comprise the “regions within the tropics occurring between the upper limit of continuous, closed-canopy forest (often around 3,500–3,900 m) and the upper limit of plant life (often around 4,600–4,900 m)”. In this way Rundel et al. (1994a) define “tropical alpine environments”. They use “alpine” as a more general term in an attempt to avoid regional terms like páramo and jalca for the moist Andes and puna for the drier Andes in South America and Afro-alpine and moorland in Africa. However, “alpine” is also a regional term applying to environments outside the tropics. On the other hand, since the conditions and the physiognomy of vegetation are similar on tropical mountains in different continents, especially in Africa and South America, we might as well choose the term páramo. Increasingly, this is used as the general term to describe vegetation in the cold tropics extending from somewhat above 3,000 m to nearly 5,000 m above sea level (Fig. 12.1).

The high altitude tropical environments were succinctly described by Hedberg’s (Hedberg 1964a) aphorism “summer every day and winter every night”. The most important feature of the tropical alpine zone is the “Frostwechselklima”¹ (Troll 1943) with an extraordinarily high amplitude of day/night fluctuations of humidity and especially of temperature (Fig. 12.2). Clearly, general characteristics of tropics are strongly accentuated in these high altitudes, such that daily oscillations of temperature are much more pronounced than the seasonal ones. Thus, nocturnal frosts followed by high day-time temperatures represent the most conspicuous stress to which plants are exposed in these environments. Additional, often very important stressors, are limited water supply and mineral nutrition.

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¹ Day-night freezing climate.
Fig. 12.1A–C Profiles of high tropical mountains in South America (A Chimborazo and Cotopaxi of the Andes) and Africa (B Mount Kenya; C Mt. Kilimanjaro) with the altitudinal vegetation zones indicated, and in C also the approximate annual precipitation. (Walter and Breckle 1984, with kind permission of S.-W. Breckle and G. Fischer-Verlag)
Fig. 12.2A,B Thermohygrograms obtained in September 1981 at the Shira Plateau on Mt. Kilimanjaro at about 3,950 m (A) and in March 1985 on Mt. Kenya at 4,200 m altitude (B). Upper part of each graph temperature °C; lower part relative humidity %. (Courtesy E. Beck)
12.2 The Stress Factor Frost

With temperatures below 0 °C every night, frost is the permanently dominating environmental stress factor (“stressor”) in the tropical alpine habitat. Some relations between cold stress and cold resistance are presented in Fig. 12.3 according to the stress concept (see Sect. 3.3.2; Box 3.1).

First of all we need to distinguish between low-temperature stress at temperatures above the freezing point (0 to +6 °C) and stress caused by sub-freezing temperatures. Low-temperature stress may lead to a loss of fluidity of membrane lipids or to an increase in membrane rigidity with many consequences for membrane permeability and intracellular compartmentation. It also slows down many metabolic reactions. It may cause injury, elastic and plastic strain, and it requires chilling resistance. It is largely presented by the upper panel in Fig. 12.3 but will not be discussed here further, since we are dealing with sub-freezing temperatures.

![Fig. 12.3](image-url) Cold stress (left part) and cold resistance (right part) with low temperatures above the freezing point (upper panel) and subfreezing temperatures (lower panels) as stress factors. The terminology presented in this scheme according to the stress concept (see Box 3.1) is used in the present chapter to discuss adaptations of páramo plants.
in the páramo habitat. Sub-freezing temperatures sooner or later may lead to ice formation, i.e. the crystallization of cellular water. For stress resistance, the location of ice crystal formation in the cells is critical. If it is on the outer face of the cell walls, i.e. apoplastic, ice formation is tolerable and thus frost resistance may be achieved through freezing tolerance. However, if ice crystals are formed in the cell interior, i.e. intracellularly, this always leads to cell death, and frost resistance can only be achieved by freezing avoidance. These two cases are represented by the lower two panels in Fig. 12.3. They constitute options with different advantages and disadvantages, and it is interesting to note that Afro-alpine species commonly tolerate extracellular freezing while Andean species apparently rely on the freezing avoidance mechanism, as will be shown below in Sects. 12.4.1 and 12.4.2 respectively.

12.3 Life Forms of Páramo Plants

The five major life forms of páramos are:

- giant-rosette plants,
- tussocks of grasses or sedges,
- acaulescent rosette plants,
- cushion plants, and
- sclerophyllous shrubs

(Hedberg 1964a; Beck et al. 1983) (Fig. 12.4), and, in South America:

- cacti

may also be included.

12.3.1 Giant-Rosette Plants

The most typical life form of alpine tropical regions are the giant-rosette plants of the genera Lobelia (Lobeliaceae) and Senecio (Asteraceae) in Africa, Espeletia (Asteraceae) in South America and Argyroxiphium (Asteraceae) in Hawai’i (Fig. 12.5). They may reach heights of several meters and have developed a number of morphological and anatomical features adapting them to the diurnal type of climate in their habitat.

The tallest plant of Senecio johnstonii ssp. cottonii actually measured by Beck et al. (1983) was 9.60 m, but an even taller one was also encountered at another location. The plants bear giant rosettes of living leaves at the end of their branches. Dead leaves usually cover the entire shoot in a dense layer. The dead leaves are kept for decades and perhaps even centuries, since the larger giant-rosette plants may be of considerable age. Estimations for Senecio keniodendron suggest that about 50
new leaves are formed annually, the stem growth rates are approximately 2.5–3 cm per year giving an age of 35 years per meter of unbranched stem (Beck et al. 1980). A 10 m tall giant-rosette plant then might have an age of 350 years.

These dead leaves provide heat insulation of the stem. However, the morphology of the living leaf rosette, together with some physiological reactions, enables most important acclimatory strategies (Fig. 12.6).

The conical leaf bud in the center of the rosette is protected by nyctinastic movements of the adult leaves. Thus, a “night-bud” is formed in these plants, which of course grow during the whole year and have no dormant periods, as plants in the temperate zone have in the form of winter buds. In Espeletia schultzii the new leaves, which had just developed from the central bud, wilted and died when the formation of the night-bud (by nocturnal closure of the rosette) was experimentally prevented (Smith 1974).

In African giant-rosette plants the leaf water may freeze apoplastically during the night (see Sect. 12.4.1). The closing mechanism of the inward movement of the adult leaves in these plants is based on water loss from the cell interior and the associated decrease of pressure in the whole tissue as turgor of the individual cells declines due to cellular loss of water. The opening of the night-bud is due to instantaneous resorption of the water and restoration of turgor after melting of the apoplastic ice in the morning.

The dense packing of the developing leaves in the central bud gives this organ a massive structure with a considerable inherent heat-storage capacity. In addition,
Fig. 12.5A–D Tropical alpine giant-rosette plants. *Espeletia timotensis* (A) and *E. schultzii* (B), Aguila Pass, Venezuela, 3,600 – 4,000 m a.s.l.; *Lobelia keniensis* (C) and *Senecio keniodendon* (D), Teleki valley, Mt. Kenya, at 4,100 m and 4,300 m a.s.l. respectively. (C, D courtesy E. Beck)
excreted fluid and mucilage may also contribute to the heat-storage capacity. The bases of the adult leaves form tanks or cisternae where mucilaginous fluid is collected during the day. In *Lobelia keniensis*, for example, this may amount to several liters per rosette. During the nyctinastic leaf movements this fluid, which warms up during the day, is pressed upwards to cover the meristematic part of the night-bud in the evening (Beck et al. 1982).

Moreover, the leaves are very pubescent and have large intercellular air spaces which add to the insulating effect (Fig. 12.7). The consequences of leaf pubescence are not straightforward. There are complex interactions between several factors...
implying non-linear behaviour of the system. The role of pubescence has been examined in more detail in *Espeletia timotensis* in relation to temperature, wind speed and high solar radiation in the páramo habitat (Meinzer and Goldstein 1985; Schuepp 1993). Pubescence is more effective at high wind speeds. Increased boundary layer thickness due to a coat of hairs hinders exchange between leaf surface and ambient wind, and its primary effect in cool air would be an increase in surface temperature. This may be about 7 °C in the case studied, which is associated with a small increase in transpiration (≈ 17%) due to the effects of leaf temperature on leaf/air water vapour pressure difference. In numerical simulations it was shown however, that in contrast an increase of surface temperature of about 7 °C would result in a doubling of the transpiration rate of non-pubescent leaves. Increased transpiration will have a feed-back on leaf temperature because of the effect of transpirational cooling, which adds to the complexity of the system.
Fig. 12.8 Exponential heat decay curves and time constants, $t_e$, for inflorescences of *Puya hamata* (controls and denuded, respectively), *P. clava-herculis* and *P. aequatorialis*. $t_e$ is the time when the heat decay curve crosses the line of $\frac{1}{e}(T_1 - T_2) + T_2$ and is independent of the magnitude of the $T_1 - T_2$ temperature difference. Thus, $t_e$ gives the time it takes for a 63% decrease in the total temperature difference between the plant organ ($T_1$) and the atmosphere ($T_2$). (After Jones 1992; Miller 1994)

In any event, pubescence will slow down the establishment of thermal equilibrium of plant organs with air temperature. For the pubescent inflorescences of *Puya* (Bromeliaceae) in the equatorial páramo zone of the Ecuadorian Andes this has been quantified using time constants ($t_e$) derived from the exponential heat decay curves (Fig. 12.8). Clearly, in the non-pubescent species *P. aequatorialis*, which grows on rocky outcrops between 1900 and 2,100 m a.s.l., $t_e$ is much lower (15 s) than in the pubescent species *P. hamata* (135 s) and *P. clava-herculis* (126 s), and in *P. hamata* it drops to 30 s when inflorescences are denuded (Jones 1992; Miller 1994).

All of the features discussed above in this section are mechanisms to delay cooling and provide freezing avoidance in the buds. Indeed, measurements in Kenya showed that only the temperature of adult leaves closely follows air temperature and is for many hours every night below the freezing point. However, nocturnal bud temperatures in *Lobelia* and *Senecio* are significantly higher and may even remain positive. In *Senecio brassica* for example, at air temperatures around $-8^\circ$C, bud temperature remains $+1^\circ$C (Fig. 12.9). We shall see below (Sect. 12.4.2) that for Andean giant-rosette plants the mechanisms of freezing avoidance based on insulation, heat storage and delay of cooling, together with some supercooling effects, may suffice for the frost-resistance of the adult leaves. However, in Afro-alpine giant-rosette plants they are insufficient and freezing tolerance is needed (Sect. 12.4.1).
12.3.2 Other Life Forms: Tussocks, Cushions, Acaulescent Rosettes, Sclerophylls

In general, it appears that smaller plants are less threatened by frost than taller ones, as suggested by Fig. 12.10, which relates average plant height of cushions and small rosettes, shrubs and perennial herbs, giant rosettes and small trees to temperature causing injury.

In tussock and cushion plants the regenerating buds are insulated by adult leaves and dead material. Extensive studies on alpine plants in Europe have shown that the internal microclimate, temperature and air humidity, within such plant bod-
Fig. 12.10 Injury temperature of tropical alpine plants related to average plant height of cushions and small rosettes, shrubs and perennial herbs, giant rosettes and small trees. (Squeo et al. 1991)

ies and mats can be much different and highly protected from the outside (Reischigl and Keller 1987). The acaulescent rosettes (Fig. 12.11) closely adopt the soil temperature. In the Andes, Squeo et al. (1991) found that all ground-level plants (cushions and acaulescent rosettes) were freezing tolerant. Day-night temperature changes are somewhat buffered by the heat-storage capacity of the soil and stress may be less extreme than from air temperature alone (Fig. 12.12A). Moreover, for taller plants, a specific problem of the day-night freezing climate is not only the freezing during the night but also the process of thawing at the beginning of the day. If ice formed in leaves thaws more rapidly than ice in the stems, transpiration sets in, while water transport in the shoot is still blocked. Thus, thawing every morning after regular nocturnal freezing leads to cavitation in the conductive elements of the xylem and the serious problems of embolism (Ball et al. 2006).

This is avoided in acaulescent rosettes, where the whole plant body thaws at the same time. An example is given in Fig. 12.13 showing leaf temperatures and corresponding maximum photosynthetic electron transport rates at light saturation (ETR-max) in Haplocarpha rueppellii (Fig. 12.11A) during a clear day at 4,100 m a.s.l. in the Simien Mountains in Ethiopia. As irradiance (PPFD in Fig. 12.13) increased after sunrise, the rosettes thawed and leaf temperatures increased to the average value of 20 °C when a PPFD of 400 µmol m⁻² s⁻¹ was reached. Above 400 µmol m⁻² s⁻¹ leaf temperature was independent of irradiance which clearly indicates dissipation of heat via the soil. Maximum rates of photosynthetic electron transport obtained from measurements of chlorophyll fluorescence (Box 4.6) at light saturation were linearly related to leaf temperature between ~5 and ~20 °C indicating limitation of photosynthesis by temperature dependence of electron transport in the thylakoids and/or biochemical reactions of CO₂-assimilation.

Some acaulescent rosette plants follow the CAM mode of photosynthesis, e.g. Echeveria columbiana (Crassulaceae) in the Andes (Fig. 12.11B) (Medina and Delgado 1976). These plants thus must be able to maintain the intensive metabolism during the night as it is required for dark CO₂-fixation. They may possibly achieve this in a state of supercooling or non-ideal equilibrium freezing (see Sect. 12.4).
Fig. 12.11 Small acaulescent rosettes of *Haplocarpha rueppellii*, Simien Mountains, Ethiopia, 4,100 m a.s.l. (A) and *Echeveria columbiana*, Aguila Pass, Venezuela, 3,600 m a.s.l. (B) and a cushion of *Helichrysum newii*, Shira Plateau, Mt. Kilimanjaro, Tanzania (C). (C Courtesy E. Beck)
Fig. 12.12A, B Air temperature and soil temperature (A) and subepidermal temperatures (B) of the hairy and the hairless variety of *Tephrocactus floccosus* growing at the same site. (Keeley and Keeley 1989)

Fig. 12.13 Relationships between leaf temperature and ambient irradiance (PPFD; dotted line) and maximum photosynthetic electron transport rate at light saturation (ETR$_{\text{max}}$; solid line) in acaulescent rosettes of *Haplocarpha rueppellii* (see Fig. 12.11A). (Unpubl. results of the author)

In the sclerophyllous shrubs transpiration is reduced and water economy is sustained by leaf-xeromorphy with reduced leaf surfaces, folded leaves and other morphological/anatomical adaptations.
Rundel et al. (1994b) invoke two different reasons for the diversity of life forms found in páramo ecosystems, namely:

- the complexity of environmental stresses, i.e. the diurnal freezing cycles and water and nutrient deficiencies, and
- the occurrence of microhabitat mosaics.

However, additional research is required to determine the correlations between life forms, habitat conditions, and physiological characteristics.

### 12.3.3 Cacti

The expression of CAM (see Box 5.1) in Andean plants has been studied in some detail in the cacti *Oroya peruviana* and *Tephrocactus floccosus* in central Peru at 4,000–4,700 m a.s.l. (Keeley and Keeley 1989). There was nocturnal malate accumulation even at air temperatures of $-8^\circ C$ and subepidermal temperatures of $-3^\circ C$.

The occurrence of hairy and hairless varieties in *T. floccosus* offered the opportunity to demonstrate the effects of a cover by hairs for insulation (see also Sect. 12.3.1). During the night the hairy form had subepidermal temperatures that were several degrees higher than in the hairless form (Fig. 12.12). A disadvantage of the hairs, however, is light scattering and therefore shading of the photosynthetically active stem tissue. Hence, the cacti have a problem of optimizing the two options to allow maximal CAM activity. It is interesting to note that at sites where one of the two forms predominated consistently the dominant form showed the higher nocturnal malate accumulation ($\Delta mal$). Thus, where the hairless type was rare, the hairy morph had the higher $\Delta mal$, and where the glabrous type was frequent, the hairy type had the lower $\Delta mal$.

### 12.4 Frost Resistance in Giant-Rosette Plants

#### 12.4.1 Afro-Alpine Plants: Freezing Tolerance

As already noted above (Sect. 12.2), formation of ice crystals in the cytoplasm is always disastrous. This is predominantly due to effects of ice competing with the ordered superficial water film of membranes. In addition ice crystals may puncture membranes and organelles. Thus, freezing tolerance is only possible with extracellular ice formation. For the Afro-alpine giant-rosette plants the phenomenon has been studied in detail by E. Beck and collaborators (Beck 1983).

For the formation of extracellular ice, the basic laws of cell water relations (see Box 6.1) apply as follows:

$$
\psi_{cell} = P - \pi
$$

(12.1)
where $\psi_{\text{cell}}$ is the water potential of the cell, $P$ and $\pi$ are turgor and osmotic pressure respectively. During freezing the cell looses water, and ice forms outside the plasmalemma in the intercellular spaces. Thus, the protoplast shrinks and turgor becomes zero ($P = 0$). Therefore

$$\psi_{\text{cell}} = -\pi,$$

and at equilibrium of the protoplasts with the extracellular ice

$$\psi_{\text{ice}} = \psi_{\text{cell}} = -\pi,$$

a situation called “equilibrium freezing” (Fig. 12.14). Essentially, ice forms gradually as water moves out of the symplast, and not abruptly as occurs after supercooling (see Sect. 12.4.3). Therefore, the occurrence of nucleating agents in the apoplast, which may include mucilage (Goldstein and Nobel 1994), are important in eliciting ice-crystal formation and avoiding supercooling (Krog et al. 1979).

According to (12.3), the concentrations of solutes in the protoplasm, which determine $\pi$, are therefore given by the water potential of the ice, which is linearly dependent on the subfreezing temperature. The increased cytoplasmic concentrations of solutes may damage or protect membranes and proteins. Often special cryoprotective solutes decrease the injurious effects of high ion concentrations on the membranes. In Afro-alpine plants, sucrose is most likely to fulfil such a role (Beck 1994a). Cryoprotectants are similar to compatible solutes discussed above in relation to osmotic stress (Sect. 7.4 and Box 7.1). In fact extracellular ice formation is nothing more than a dramatic osmotic stress, however, at low temperatures.

In this way, for example in *Lobelia keniensis* at $-6^\circ C$, 85% of the tissue water is frozen. When the ice thaws in the morning, the water is immediately taken up

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**Fig. 12.14** Equilibrium freezing: water potentials of frozen leaves ($\psi_{\text{cell}} = \bullet$) of *S. keniodendron* and *L. keniensis* and frozen expressed cellular sap ($-\pi = \circ$) of *S. keniodendron* compared to ice at subfreezing temperatures (lines: $\psi_{\text{ice}}$ calculated by two different methods A and B; see (12.3)) give the same relationships. (Beck et al. 1984)
Table 12.1 Frost tolerance of leaf segments of four species of Afro-alpine megaphytes. (Beck et al. 1982)

<table>
<thead>
<tr>
<th>Species</th>
<th>Frost tolerance (°C)</th>
<th>50% damage (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Senecio keniodendron</td>
<td>−8</td>
<td>−10</td>
</tr>
<tr>
<td>Senecio brassica</td>
<td>−10</td>
<td>−15</td>
</tr>
<tr>
<td>Lobelia keniensis</td>
<td>Lower than −20</td>
<td>Lower than −20</td>
</tr>
<tr>
<td>Lobelia telekii</td>
<td>Lower than −20</td>
<td>Lower than −20</td>
</tr>
</tbody>
</table>

osmotically into the cells again, and full competence of photosynthesis is regained rapidly. Using this mechanism, the Afro-alpine giant-rosette plants achieve frost resistance at temperatures of $-8$ °C down to $-20$ °C (Table 12.1).

There may also be deviations from the ideal behaviour given by (12.3) due to the osmotic contribution of extracellular solutes, which allow lower external water potentials (non-ideal equilibrium freezing) (Goldstein and Nobel 1991; Zhu and Beck 1991). At water losses > 50% a matrix potential is also generated which prevents intrusion of air between the cell wall and the plasmalemma, and in this way the wall may get under tension (negative turgor).

12.4.2 Andean Plants: Freezing Avoidance

In contrast to the behaviour of Afro-alpine plants, Andean *Espeletia* are injured by freezing of the cell water. Obviously ice formation is occurring intracellularly in these plants. They need to avoid freezing of cellular water and survive the nights in a super-cooled state. As depicted in Fig. 12.15 for all the different organs and tissues of *Espeletia spicata* and *E. timotensis* in the Andes, the supercooling points, at which ice formation would happen, are always much lower than the lowest temperatures actually found in these organs and tissues. Ambient temperature is modulated in the tissues by the various strategies discussed in Sect. 12.3.1. Supercooling and freezing avoidance for the Andean giant-rosette plants therefore must be considered as an appropriate mode of achieving sufficient frost resistance.

12.4.3 Comparison of the Strategies of Freezing Tolerance and Avoidance

If freezing tolerance and freezing avoidance are such successful adaptations of giant-rosette plants to the Frostwechsel climate in the African and South-American tropical high mountains, the question arises why the plants in the two continents evolved two such different modes of frost resistance. As compared to freezing and its tolerance, freezing avoidance by supercooling has one important advantage and one important disadvantage:
the advantage is that the cells always remain metabolically competent,
the disadvantage is the very high risk inherent in the supercooling strategy, since
supercooling is a thermodynamically labile state; at the lowest supercooling
point the water freezes instantaneously, there is no time for water-export into
the apoplast, and cell death becomes unavoidable.

Continuous metabolic competence should allow higher productivity. In the Andean
páramos, where night temperatures go down to 0 °C and rarely below −5 °C, the risk
of reaching the crystallization point of water is small (Fig. 12.15) as compared to
the benefit of higher productivity. Conversely, in the Afro-alpine zone temperatures
are frequently below −10 °C and the risk inherent in supercooling becomes too high
to be a reasonable choice.

Table 12.2 Productivity of an African and two Andean giant-rosette plants. (After Rada et al.
1985)

<table>
<thead>
<tr>
<th>Species</th>
<th>Productivity (g DW m⁻² leaf surface year⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Africa</strong></td>
<td></td>
</tr>
<tr>
<td>Senecio keniodendron</td>
<td>166</td>
</tr>
<tr>
<td>South America</td>
<td></td>
</tr>
<tr>
<td><em>Espeletia spicata</em></td>
<td>671</td>
</tr>
<tr>
<td><em>Espeletia timotensis</em></td>
<td>370</td>
</tr>
</tbody>
</table>
Hence, it appears fairly straightforward that the different nocturnal temperature regimes in the two regions led to evolution of the two different strategies, one taking the risk and obtaining more productivity and the other one avoiding the risk on account of the loss of some productivity. Indeed Table 12.2 suggests that the African Senecio keniodendron has a much lower annual productivity than the Andean Espeletias (Rada et al. 1985).

Interestingly, Lipp et al. (1994) note that in species growing at high elevations in Hawai‘i features of both adaptive strategies are combined and a complete suite of

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**Fig. 12.16A–C** Plants of high altitudes on Haleakala volcano, Maui island, Hawai‘i. *Styphelia tameiameiae* (A), *Dubautia menziesii* (B), *Argyroxyphiun sandwicense* (C)
characteristics with either strict tolerance or avoidance of extracellular ice formation is not expressed. Five species were studied, namely Argyroxiphium sandwicense and Dubautia menziesii (both Asteraceae), Sophora chrysophylla (Fabaceae), Vaccinium reticulatum (Ericaceae) and Styphelia tameiameiae (Epacridaceae) (Fig. 12.16). Typical freezing tolerance is not fully expressed possibly due to a more recent evolutionary status of these taxa. A combination of the two possible adaptive strategies is given in that a period of supercooling occurs prior to ice nucleation. Four of the five species could tolerate extracellular ice formation to a certain degree. For example, in S. tameiameiae in the laboratory there was considerable supercooling prior to ice formation at \(-9.4\) °C, and the latter did not cause tissue injury.

12.5 Other Stress Factors

12.5.1 Water Availability

Precipitation decreases with increasing altitude in the cold tropics (Lauer 1975; Rundel 1994). Although patterns of precipitation in páramo regions are very complex and do not give as clear a picture as the temperature patterns, it is evident that diurnal drought problems are associated with the tropical Frostwechsel climate. Massive structures which contribute to heat-storage capacity (Sect. 12.3.1) may also provide water-storage capacity. Thus, the pith storage capacity of Espeletias in the Andes is thought to be involved in diurnal drought avoidance mechanisms. This may also explain the apparent paradox that the height of giant rosette species increases with higher altitudes as this implies an increase of stem water-storage capacity (Meinzer et al. 1994). Water retaining gels have also been thought to contribute to water storage, e.g. in Argyroxiphium sandwicense (Carlquist 1994). Although water relations in high elevation tropical plants have been studied to some extent (Meinzer et al. 1994), ecophysiological studies of drought tolerance are less advanced than for the frost stressor.

12.5.2 Mineral Nutrition and Carbon

Nutrient relations of tropical high elevation plants have been little investigated (Rehder 1994).

An interesting case story is presented by Beck (1994b). Dead leaves kept on the stems of Senecios for heat insulation (Sect. 12.3.1) obviously are withheld from mineralization in the soil and the soil-plant nutrient cycle. However, in Senecio keniodendron leaves may gradually decay in situ on the stems, and where moisture is retained, adventitious roots emerge from the stems and produce a network in the sheath of decaying leaf bases not unlike the tank roots of bromeliads (Sect. 6.4, Fig. 6.15B). Mineralised nutrients are reabsorbed by living plant tissues and the nutrient cycle is closed within the plant.
Another intriguing case of mineral nutrition is inorganic carbon acquisition from the pedosphere by terrestrial páramo species of *Isoëtes* (Lycopodiopsida, Isoëtaceae). *Isoëtes andicola* is a terrestrial species which has no stomata on the short leaves of its rosettes and gains the bulk of its carbon from the peat sediment near lakes and lagoons in the high Andes. Most of the C-uptake occurs during the day with C-reduction via the Calvin cycle; however, there is also some CAM-type C-acquisition during the night. The significance of this pedosphere-based carbon nutrition is not clear. Sediment-based carbon acquisition is well known of aquatic *Isoëtes* species, which also may perform CAM. Among other hypotheses, in terrestrial *Isoëtes* species adaptation to seasonal droughts may be an explanation, as sealing off the leaves from the atmosphere may provide an advantage under drought-stress conditions. Other stomata-less terrestrial species with similar modes of carbon nutrition are *I. andina* and *I. novo-grandensis* in the Andes and possibly *I. hopei* in New Guinea. Aquatic *Isoëtes* species are nearly ubiquitous in páramo regions of South America providing a possible ancestral pool for the terrestrial forms with their unique strategy (Keeley et al. 1994).

**12.5.3 Irradiance and Heat**

Leaf hairs and scales represent an effective barrier against high-light stress, photoinhibition and damage of the photosynthetic apparatus (see also Sect. 5.2.2.1) and UV-radiation (Lang and Schindler 1994), as well as overheating (Melcher et al. 1994). Naturally the same insulating effect which reduces cooling during the night delays heating during the day under the *Frostwechsel* climate. Melcher et al. (1994) showed that in *Argyroxcphium sandwicense* on the Haleakala volcano on Maui island, Hawai‘i, temperature of expanded leaves was similar to, or even lower than, air temperature at full solar radiation. Conversely, the apical bud in the center of the rosette was usually 25 °C warmer than air at noon. This may facilitate physiological processes required for the maintenance of growth of new leaves in the apical bud. However, this must also be the reason which limits *A. sandwicense* to altitudes of ≥ 1,900 m a.s.l. below which apical bud-temperatures might reach lethal levels.

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Research in tropical forestry is confronted with the task of finding strategies to alleviate pressure on remaining forests and techniques to enhance forest regeneration and restore abandoned lands, using productive alternatives that can be attractive to local human populations. In addition, sustainable forestry in tropical countries must be supported by adequate policies to promote and maintain specific activities at local and regional scales.

Here, a multi-disciplinary approach is presented to better the understanding of tropical forest ecology, as a necessary step in developing adequate strategies for conservation and management. The authors have long experience in both academic and practical matters related to tropical forest ecology and management.