Aquarium Plants

Christel Kasselmann

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Preface

Dedicated to my parents in gratitude

Today, aquarium plants enjoy a surprising degree of popularity. On the one hand, the numerous new imports and cultivars have, over the last couple of years, expanded the range of plants available; on the other hand, the varied choice of technical and growth-enhancing accessories have increased the desire for beautifully arranged aquariums. A significant number of aquarium plants serve not only decorative purposes, but hobbyists have placed a special emphasis on the maintenance and propagation of species which are rare or threatened by the destruction of their native habitats. One expression of this trend is the special associations and clubs formed by plant enthusiasts, in both Germany and abroad. In Germany, the *VDA Working Group on Aquatic Plants* (*Arbeitskreis Wasserpflanzen im VDA*) is an important contributor to the dissemination of information about aquarium plants through their publication *Aqua-Planta*. To many aquarists the cultivation of aquatic and marsh plants also serves the purpose for research in biological and ecological contexts, which is why the maintenance of aquarium plants can also be seen as being part of the protection of species, nature and the environment in general.

In this book I want to try to offer a wide-ranging scope of information. The general section will cover the native habitats of aquatic and marsh plants in detail, a topic which has previously been neglected by other publications. Ecological data obtained on location are discussed in the context of contradictory assertions made by other authors, and will also provide clues regarding the optimum conditions for cultivation. The book's segment on plants delivers a comprehensive and complete overview of those species, cultivars and growth forms which are currently in culture. Along with familiar plants, species that are rare and difficult to maintain are included as well, this being an important aspect for those plant enthusiasts who tend to specialize in certain areas.

The plant descriptions, catalogued in alphabetical order for easy reference, contain all essential characteristics which are necessary to enable a definite plant identification and avoid any confusion. Furthermore, detailed information is provided about successful plant cultivation and propagation. I wish to emphasize at this point that, with very few exceptions, all species listed have been kept in home aquariums or have been researched in their natural environment. Data on the plants' ecology—listed for every plant catalogued—provides important information on the requirements of individual species. Much of this data is based on my own studies of biotopes, which were conducted in the course of 25 trips to tropical regions and countries. Important references for further reading conclude some of the individual plant descriptions and should, along with the comprehensive bibliography at the end of the book, refer interested hobbyists to more detailed publications. Also an extensive glossary of terms explains specialist terminology.

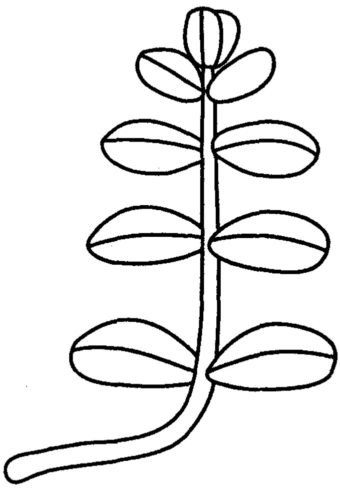
The importance of ecological factors for the growth of aquatic and marsh plants in their native habitats, as well as within the aquarium, forms the core of this book. Over the last 15 years, my main interest has been in the research of the natural environment of aquarium plants in order to expand the limited knowledge about their ecological needs, as well as to study their respective status within the natural community of living beings, thereby obtaining a sound basis for optimum cultivation. Studies in biotopes have so far only been completed for a comparatively small number of aquatic and marsh plants, and information on the ecology of individual species is very limited, even in specialist botanical literature. The efforts undertaken by travelling aquarists to collect and publish such data are considered especially valuable because they provide the plant enthusiast with a first indication on species-specific cultivation. Previous publications covering the ecology of aquarium plants have been primarily concerned with research on *Cryptocoryne* and *Aponogeton* habitats. Each one of these descriptions can only be evaluated as a "snapshot" of conditions prevailing at that particular time; nevertheless they permit a basic insight into the ecology and sociology of those plants. Even though the chemical composition of the water in native habitats is always subject to certain fluctuations, the fundamental underlying condition of the waterways will remain surprisingly stable over the entire year. Biotope studies are necessary and instrumental for our awareness and understanding of plant life in the aquarium, and its requirements. It was, therefore, my aim to include in this book all the informative ecological data available so far in the most comprehensive way possible. Also just as important are detailed observations made in aquariums, which will contribute in equal importance to the expansion of knowledge about aquatic plant ecology.

This book is aimed especially at those aquarists and hobby botanists who enjoy and are interested in aquarium plants. In compiling the manuscript it has not always been easy to find a linguistic basis and level of information which meet the eeds of both beginners and those aquarists with a prior knowledge of botany. The book's concept, and also the broad range of illustrations, enable a multifaceted use. The color atlas can assist the lay person with the identification of plants, and also with cultivation and maintenance, because the text offers a wide spectrum of information on selection, cultivation and propagation of aquarium plants. Specialized and more interested plant enthusiasts will find extensive information on the differentiation between species, as well as detailed bibliographical references in the individual plant listings, thereby enabling a closer focus on certain aspects. Furthermore, the book is also relevant to the scientific researcher due to its—probably unique—catalogue of ecological data and valuable information provided in it. Finally, many rare plants are portrayed in photographs for the first time.

During the preparation of this book, which took many years, I was extensively supported by several good friends. A special thank you goes to Mr. Josef Bogner (Botanical Gardens, Munich, Germany), whom I consulted with on many botanical and biological aspects. During a friendship lasting nearly 20 years, marked by a readiness to help, extensive discussion and a never ending application to the topic, he provided countless ideas and suggestions for my own plant research. Thanks also to Mr. Harry W.E. van Bruggen (Heemskerk, Netherlands) for the friendly cooperation over many years, as well as the careful scrutiny of and critical comments on my manuscript. Valuable ideas and support through information provided about the *Cryptocoryne*

genus was also received from Mr. Jan Bastmeijer (Emmen, Netherlands), Hans Ehrenberg (Berlin, Germany), Prof. Dr. Niels Jacobsen (Copenhagen, Denmark), as well as my unforgotten, late friend, Friedrich Möhlmann. My special thanks also go to Mr. Julius Hoechstetter (Trostberg, Germany) and Mr. Hartmut Loose (Botanical Gardens, Berlin, Germany) for their stimulating contributions and their supply of plant material. I was also supported over many years with the supply of live plants by the aquatic plant nurseries Dennerle (Vinningen, Germany), Hoechstetter (Trostberg, Germany) and Tropica (Denmark). Only with their assistance could my book be published in the present format. I also thank the publishers Eugen Ulmer Verlag and their associates for the friendly care and supervision as well as the generous design and make-up of the book.

Christel Kasselmann
Berlin, summer of 1999



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Aquatic and Marsh Plants in Their Natural Habitats

Compared to previous times, today there exists an ever increasing interest in the natural habitats of aquatic plants. The science covering the interrelationships of organisms and their surrounding environment is called ecology. The function of ecology is to analyze and comprehend all operative, active factors and their respective functions and tasks within natural biotopes and living environments.

Although the native habitats of local aquatic and marsh plants have previously often been the subject of research and have been studied exhaustively, our knowledge of the association (sociology) as well as the natural living environment of tropical aquatic and marsh plants is surprisingly fragmentary. Detailed ecological data on habitats of each and every aquarium plant, based, for instance, on the analysis of water, substrate, flow speed of the water current, as well as light conditions, is also extremely rare or completely unavailable. Furthermore, the little data listed in aquaristic literature often contains entirely misleading interpretations and generalizations which, in turn, convey a

Sagittaria guayanensis **is a genuine aquatic plant not cultivated in aquariums (native habitat in Mexico).**

Intlorescence of *Eichhornia azurea* in its natural habitat in Venezuela.

totally false picture of the ecology of tropical aquatic and marsh plants. Even the mere purpose of biotope studies is occasionally put into question and criticized as being irrelevant, the reason being that conclusions supposedly cannot be drawn from such studies which would be applicable to aquarium plant cultivation, and that, on the other hand, plants are, in any case, adaptable in their behavior. Such points of view are, of course, absolutely nonsensical and cause damage to aquaristics that are oriented towards the future and that stipulate the research of living organisms maintained in aquariums as the most important objective.

An in-depth study with the living environment of tropical aquatic and marsh plants will quickly show that their specific ecology is exceptionally multifaceted and their overall context of interrelationships is very complex. It also has to be remembered that only a small number of existing marsh and aquatic plants have previously been cultivated within an aquarium; the overwhelming majority have not been kept at all, or if so, only briefly. It also seems obvious that the causes for failures in cultivation are mostly found in the ignorance of the plants' basic requirements. It was never the objective of biotope research to carbon-copy the habitats, but only the desire to expand the level of knowledge about the way of life and the requirements of different plant species, with the specific aim of avoiding mistakes in cultivation. In order to comprehend their ecology, both general as well as specific descriptions of ecological systems which permit a differentiating consideration of the requirements of every individual species are extremely important. A lot can be learned from the research conducted in natural biotopes, and every analysis constitutes an important building block in the detailed knowledge of the living requirements of each and every plant. The objective must be to assemble all these building blocks to form a complete mosaic!

Environmental Factors

TEMPERATURE

Temperature not only has a decisive influence on plant metabolism but also on many other biological processes, for example, flower formation, fruit ripening, germination, etc. Plant photosynthesis is highly dependent on the surrounding temperature because every individual plant requires a specific temperature range for its growth. The lower limit of this temperature range constitutes the minimum; the upper limit constitutes the maximum conditions in which the plant can maintain its growth. Below or above these cardinal points, the plant will cease to grow. Within the minimum-maximum range, growth speed will not increase in a linear way with a rise in temperature but will instead drop off again after having reached a certain peak which is specific and unique for every plant species. This temperature point or value at which the plant displays its maximum growth intensity constitutes the optimum temperature.

It can be concluded from these observations on general growth behavior that aquatic and marsh plants will not prosper optimally in their native habitats over the entire spectrum of seasons. Accordingly, research data obtained from habitats has to be evaluated within this context. Some species react to extreme temperatures with a change in appearance, for example, through the formation of smaller leaves or shorter internodes.

Plants originating from warmer areas make heavier demands on temperature requirements, compared to those from areas displaying distinct seasonal variations. Studies of terrestrial plants have shown that the optimum temperature of tropical or subtropical plants ranges between 30–40 °C, and between 15–30 °C for all other species (Larcher 1984). It was also found that plants in their natural environment have adapted to a temperature change between night and day.

For successful cultivation of aquatic and marsh plants, it is essential to find both the tolerance limits as well as the optimum temperature for every individual species. A series of carefully planned and executed experiments is necessary to establish precise and optimal growth curves or projections, which have, until now, not been determined for aquarium plants. Important hints regarding growth limitations and approximate optimum temperature values for individual species can also come from everyday data and experience extracted from the daily practice of cultivation in hothouses and aquariums, as well as research conducted within natural living environments. Whereas some species (e.g., *Vallisneria*) display a big temperature tolerance range, others display very moderate growth limits (refer also to Appendix 1).

The following account illustrates the complex effects that the temperature factor has on the behavior of aquatic and marsh plants within an area displaying a distinct seasonality:

In July 1993 the author studied numerous habitats of aquatic and marsh plants in northeastern Argentina. This region has a distinct seasonal climate. The month of July is in the midst of the cold time of year. Median temperatures for the city of Corrientes measure 15.7 °C, with 47 mm of rainfall recorded. Both values constitute almost the minimum over the entire year and monthly average readings say little about the absolute temperature levels which can be considerably higher or lower. During the 2-week stay in July, nightly temperatures hovered around the frost limit. During this period daytime air temperatures reached a maximum of only 15 °C over an entire week. Daytime water temperatures measured 6 to 15 °C. The effects of these extremely low water and air temperatures on the plants was clearly visible everywhere. Large contingents of floating plants, including *Eichhornia azurea* and *Pistia stratiotes*, displayed frozen and dried foliage. Oxygen deficiency was evident in many waterways, caused by the large amount of dead foliage; this, in turn, led to massive fish mortality (refer to p. 56 for more information on oxygen content). It could also be observed that the low water temperatures often had no negative influence on plant growth under water. Unusually strong submersed specimens of *Eichhornia azurea*, thick contingents of *Cabomba caroliniana* var. *caroliniana* and var. *flavida*, *Egeria najas*, *Myriophyllum aquaticum* and *Hydrocleys nymphoides* could be found everywhere. Some of the aquatic and marsh plants flowered lushly during the short-days within this cold period, the low temperatures in several cases being an important triggering factor for flower formation (for example, *Echinodorus uruguayensis*).

LIGHT

Because it is an essential provider of energy for photosynthesis, light is important for many growth and developmental processes of plants. Furthermore, it has an important influence on the morphology and anatomy of plants, as well as on photoperiodic occurrences.

Measuring light intensity in natural habitats of tropical and subtropical aquatic and marsh plants is extremely important for the expansion of knowledge about the requirements of the different aquarium plants, and also to be able to sustain optimum maintenance conditions in line with their requirements. In order to better understand questions and problems relating to this, several basic aspects of the general importance of light as an environmental factor will be explored in more detail. The intensity and duration of light radiation within nature is not as continuous as it is in the aquarium; it not only changes in the course of a day but also over the whole year in accordance with geographic latitude.

Light radiation is reduced to a larger degree within water than is the case within air.

Detailed close-up of a Dutch aquarium.

Long-wave heat rays entering water are already absorbed in the top few millimeters, the bulk of infrared radiation being absorbed in the first couple of centimeters. Even in a depth of about 1 m, only half of the radiation will still be present. The range that can be utilized by aquatic plants for photosynthetic purposes lies between 380 and 780 nm and will be selectively absorbed with increasing depth, whereby red light will be absorbed first in clear water, followed by the yellow and green spectral range, and finally blue light, which thus manages to reach larger depths of water.

Furthermore, light absorption as well as the color spectrum are persistently influenced by coloring and clouding matter (humic substances, plankton, algae, floating matter resulting from wash off) contained in the water. In a yellow- or brown-colored waterway, for example, there will not only be strong light absorption because of humic matter, but the coloring of the water will simultaneously cause a modification of the spectral composition, which means that the yellow spectral range, and not the blue light, will penetrate deepest into the water.

Due to reflection on the water surface, the radiation supply in waterways depends to a large extent on the angle of incidence. With the sun high in the sky, reflection will be negligible so that light can enter the water almost unbroken. When the sun is low in the sky, reflection will increase to such a degree that a large amount of light is unable to penetrate the water. This intense reflection on the water surface during a low-positioned sun has the effect that the day will be shorter for plants existing under water and below a specific depth, compared to other species living on land.

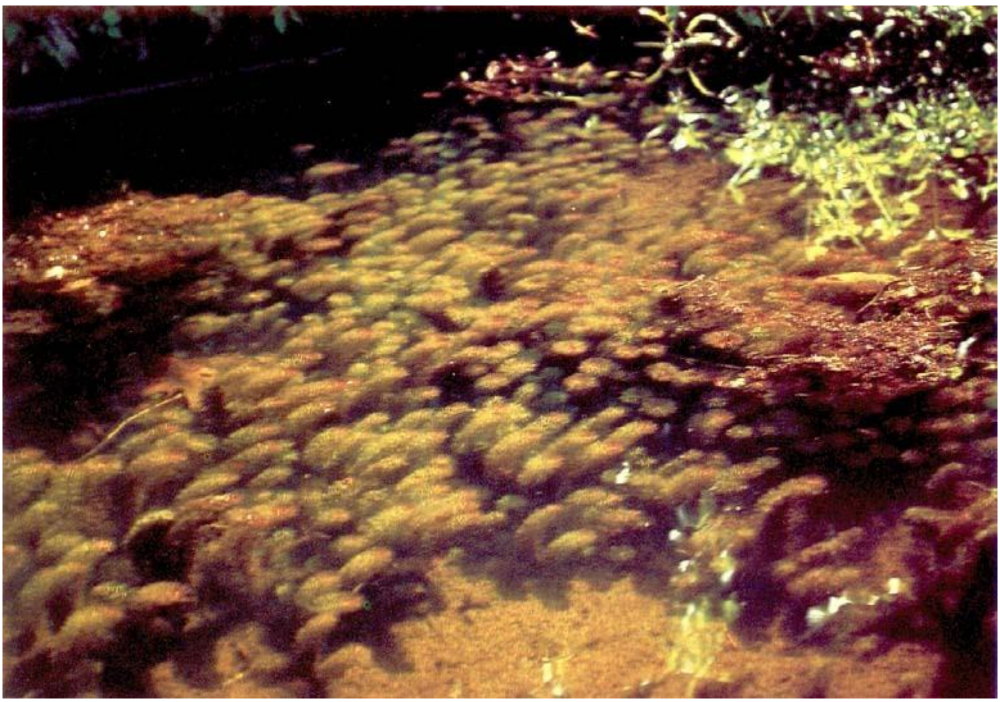
Generally, with regard to the overall bal-

Habitat of *Vallisneria americana* var. *americana* in Papua New Guinea. The plant displays a high temperature tolerance.

ance of radiation, the light climate in the tropics does not differ much from areas in medium latitudes. There are, however, fundamental differences. For one, the sun will rise and set much quicker in the tropics. Also, radiation intensity will be generally higher in the tropics and can reach readings over 150 klx during clear midday skies, whereas values in our areas will be only about 100–120 klx. Furthermore, the length of day in equatorial regions will vary only slightly over an entire year and will more or less measure a constant 12-hour period.

Light intensity is greatly influenced by the degree of clouding. Light intensity for species growing in water will additionally decrease through the reflection on the water surface already mentioned, as well as possibly through the shading effect of floating plants. Comparably few higher plants are able to reach depths of 3–10 m in clear freshwater. Beyond that, only limited societies of algae will exist in depths of 30 m. For those species growing in great depths, quantity and quality of light will change considerably. Most aquarium plants are found in their natural habitats either outside the waterways in the form of marsh plants, or within a depth range of up to 30 cm, and will only occasionally be found in deeper water during peak water. Furthermore, a large range of aquarium plants will populate unshaded and semi-sunny areas within their natural biotopes, and do not prefer shaded locations as is occasionally falsely indicated in aquaristic literature. Even though less light for photosynthesis is available to plants existing in water—compared to their terrestrial counterparts—due to light being absorbed by reflection on the water surface as well as a greater depth, levels of light intensity at the natural locations of aquarium plants are nevertheless generally

This biotope of *Limnophila indica* features crystal clear water.



considerably higher than in the aquarium (see also the recorded readings at the end of this chapter).

It is interesting to note in this context that the plants' photosynthetic production cannot be randomly increased through an increase in light intensity, but that (in line with the optimum temperature curves) a species-related optimum light curve can be established for every plant species through experimental research. During rising light intensity, this curve will show an increase in assimilatory activity only up to a specific range (optimum); thereafter it will not increase any further or will even decrease, which is possibly caused by a reciprocal relationship with other limiting factors of influence, for instance, temperature or CO_2 supply.

Corresponding to their differing capacities to utilize strong or weak light, one distinguishes between strong light or sun plants, and weak light or shade plants. Shade plants have the advantage of being able to better utilize low-light intensity compared to sun plants; they reach their highest assimilation during conditions of weak-light intensity. For this reason shade plants can still populate relatively dark locations in a forest and will prosper best under conditions of weak light. A typical feature is large wide leaf blades, as found, for example, in certain wide-leaved *Cryptocoryne* species and also *Barclaya motleyi.* Shade plants will die off under certain conditions if they are subjected to too high light radiation. Sun plants, in contrast, require intensive radiation and, compared to shade plants, will make better use of the latter through a superior photosynthetic performance. They require more light and will die off if they receive an insufficient amount of light.

Optimum light curves as well as assimilation curves for aquarium plants have so far been compiled for only a few individual plants, resulting in a limited definite classification of species into shade or sun plants.

Bacopa caroliniana **under intense sunlight at a locality in Mexico.**

Photosynthesis curves of *Anubias barteri* var. *nana* and *Bacopa caroliniana* were established at the University of Marburg, resulting in the classification of *A. barteri* var. *nana* as a typical shade plant and *B. caroliniana* as a sun plant (Sauer 1989).

Within these two major groups very different reaction formations occur, which are either genetically predetermined or modifiable through environmental conditions. Gessner (1955) conducted research on the assimilation performance of several aquatic plants and found that populations of *Aponogeton madagascariensis* and *Elodea canadensis* both belong to the category of shade plants, but, nevertheless, react differently from one another. During intensive lighting of 110 klx over a period of several hours, and under a constant temperature, *Elodea canadensis* displayed a constant rate of assimilation. In contrast, a drop in the assimilation performance was noticeable with *Aponogeton madagascariensis* after only an hour into the same experiment.

Most aquarium plants will probably be classified as sun plants if subjected to similar studies, with only very few species, for instance several *Cryptocoryne* and *Anubias* species, ending up in the category of shade plants. However, as long as there is no scientific data available on aquarium plants that enables a clear-cut classification into either sun or shade plants and their reaction formations, these assumptions will remain subjective and hypothetical. Experience in cultivation as well as research at native locations already teach us today that most aquarium plants will prosper better under conditions of intense lighting compared to less light. Damage to plants caused by too much light in the aquarium can thus hardly be expected to occur in the majority of cultivated species. In contrast, the danger of assimilation being downgraded through insufficient light intensity to such an extent that the point of compensation—at which CO_2 absorption (photosynthesis) and CO_2 release (respiration) are at the same level—is consistently undercut and far greater, resulting in the plant dying off eventually.

On the other hand, it must not be overlooked that plants, within certain limitations, have the capacity to adapt to different light intensities and light qualities within their natural habitats. Plants living in greater depths, for example, will generally display reduced respiration, compared to their counterparts living on the water surface. Furthermore, higher aquatic plants will react to different light conditions through the formation of differing anatomical and morphological features.

Aquarists are well aware of the behavior of *Salvinia*: if its shoots are cultivated under intensive lighting they will produce strong boot- and bag-shaped leaves, whereas the leaves of the shade form are much smaller and lie flat on the water. Gessner (1955) also reports on the formation of shade and sun forms in several species. For example, the shade form of *Lagarosiphon major* will display more limited branching compared to the sun form, a phenomenon also visible in other higher aquatic plants. *Lobelia dortmanna* reacts to decreasing light intensity with increasingly longer leaf blades. Lack of light suppressed the formation of utricles in *Utricularia intermedia*. Many fast-growing plants react to a lack of light with characteristic changes (etiolation), which, for example, become visible in the form of long internodes and petioles and often as smaller blades.

With the kind support of Mr. Karlheinz Sauer as well as the Osram company, the author had the opportunity to conduct lux readings using the measuring device Optronic, at natural habitats in Madagascar and Ecuador (see Table 1).

The results of light intensity tests show that aquatic and marsh plants, which grow in totally sunny locations above the water or in shallow depths, are subjected in the course of

Table 1: Light intensity readings.

Location	Date	Time	Cloud cover	Lux values
Madagascar				
Berenty	26/12/86	08:30	cloudless	114,000
		09:00	cloudless	121,000
Fort Dauphin	27/12/86	08:00	cloudless	64,000
		14:00	cloudless	114,700
		14:30	cloudy	67,000
		15:00	heavy clouds, sun hardly visible, shortly prior to rainfall	25,200
		16:45	Strong clouds, sun invisible, rainy	4,890
Fort Dauphin (surrounding region)	28/12/86	07.20	clear, very little clouds	51,700
		08:00	slightly cloudy	67,100
		09:40	cloudless	104,100
		10:30	cloudless	116,400
		13:30	cloudless	108,000
			shaded by trees	8,460 up to 25,000
	29/12/86	06:15	cloudless	20,000
		12:00	cloudless	127,800
		12:30	cloudless	128,500
		12:35	cloudy	67,000
		15:00	cloudless	95,200
		18:15	heavy, dark clouds	1,885
		18:40	slightly cloudy, sun visible	330
		18:45	as above	260
		18:50	light clouds, sunset	120
		18:55	as above	30
		19:05	as above	5
	30/12/86	05:30	cloudless	4,890
		07:30	cloudless	56,300
		07:45	cloudless	60,600
		08:45	cloudless	87,400
		11:00	cloudless	122,300
		11:30	cloudless	125,200
		11:50	cloudless	128,600
		12:00	cloudless	139,300
		12:30	slight clouds	127,000
		12:55	cloudless	130,200
		14:00	slight clouds	102,800
		14:05	cloudless	119,900
		14:25	cloudless	105,700

Table 1: Light intensity readings *continued.*

Location	Date	Time	Cloud cover	Lux values
Andasibé	31/12/86	12:00	cloudless	139,300
	10/01/87	09:00	very slight clouds	74,800
		09:05	slightly more clouds	53,400
		09:45	heavy clouds	24,000
		11:30	small, white clouds, sun unobscured	137,500
		11:35	sun behind clouds	80,000
		15:00	uniform, heavy clouds	1,350
Near Beforona	03/01/87	10:00	sun clearly visible, small white clouds	70,000
altitude 900m		10:10	sun clearly visible, almost cloudless	146,000
Ecuador				
Coca	07/02/90	08:35	all readings	58,300
		08:50	very light clouds,	63,700
		09:00	sun always unobscured	68,400
		09:30	by clouds	80,000
		10:00		91,200
		10:35		104,100
		10:50		106,000
		11:00		113,300
		11:35		127,500
		12:00	heavier clouds	77,300
		12:07	slightly cloudy	126,800
		13:30	slightly cloudy	119,200
		14:15	heavy clouds	33,600
		15:30	slightly cloudy	90,500
	08/02/90	07:30	white and black clouds	16,310
		08:10	white and black clouds	19,800
		12:45	cloudless	156,400
		13:00	sun obscured by dark clouds	34,600
		14:00	cloudless	127,700
		14:30	cloudless	108,600
		15:00	cloudless	90,100
		15:30	sun obscured by clouds	19,600
		15:30	under trees, cloudy	8,000 up to 13,000
		16:00	cloudless	62,200
		16:50	small white clouds	32,400
		17:30	small white clouds	13,070
		18:00	small white clouds	2,420
		18:30	sunset	280
	09/02/90	08:00	heavy rain	550

Table 1: Light intensity readings *continued.*

Location	Date	Time	Cloud cover	Lux values
Quito	10/12/90	06:00	dawn	—
altitude 3000		06:40	sunrise	1,433
m directly on		06:42	cloudless	2,070
the equator		06:45	cloudless	4,000
		06:50	cloudless	5,390
		06:55	cloudless	8,550
		07:00	cloudless	11,520
		07:15	cloudless	18,800
		07:30	cloudless	26,700
		07:45	cloudless	29,800
		08:00	cloudless	41,000
		08:15	cloudless	49,500
		08:30	cloudless	58,000

the day to a very strong—in comparison to aquariums—and highly varying radiation which is dependent on both the degree of clouding and time of day. Average readings will be considerably lower in half-shaded locations but will still lie well above values recorded in aquariums (refer also to data on lighting intensity on p. 49). Highly shaded biotopes, however, will display only a reduced lighting intensity of maximal 3000 lx on the water surface, even under cloudless skies, which will be reduced even further with increasing depth. Horst (1986), for example, in a highly shaded streamlet filled with *Cryptocoryne* in southern Thailand, recorded 1500 lx on the water surface during a bright sunny day at around 15:00 h, and further readings of 600 lx in a depth of 20 cm

Many *Eriocaulon* species—one of which is seen here in its habitat in Malawi—are purely aquatic plants, the cultivation of which in aquariums has so far been unsuccessful.

and only 120 lx in 40 cm. In a *Cryptocoryne cordata* biotope (*C. siamensis*-type) readings of 50 lx in complete shade and 40,000 lx in full bright sunlight were recorded in locations only a few hundred meters apart.

THE SUBSTRATE AS A SOURCE OF NUTRIENTS

Only a few of the cultivated aquarium plants constitute genuine aquatic plants in which nutrient absorption occurs both through the root system as well as through the entire surface area. The majority of aquarium plants are marsh plants which, in contrast to genuine aquatic plants, will in most cases develop a strong root system and extract most of their nutrients required for growth from the substrate. In doing so, not all plants behave the same; the absorbed amount of nutrients and its composition are, in fact, specific to the individual species and highly dependent on the substrate. A chemical analysis of the plant's dry matter, conducted in a laboratory, can show the content and distribution of individual nutritional elements within the plant. The analysis will provide information about the occurrence of plants in specific substrates (indicator plants) and also serve to determine fertilization requirements. If plants are cultivated in the laboratory with nutrient solutions, the composition of which are known, and subsequently analyzed with the aid of the dry matter analysis to determine their content of individual nutrient elements, conclusions can be drawn about the nutrient requirements of plants which, in turn, will enable focused fertilization in cases of deficiency symptoms.

The structure of the soil is essentially determined by the size of the grains. This, in turn, defines the pore volume which plays an important role in the aeration and water circulation within the soil. Coarse-grained soils will let air, water and roots penetrate it more easily than fine-grained soils. Sand, clay, loam (mixture of sand and clay), lime and

Iron precipitation on *Blyxa aubertii* in a biotope in Sri Lanka.

humus soils, among others, can be distinguished. Pure clay soils are rich in nutrients and extremely fine-grained, thus permitting hardly any air or water exchange.

Loam soils (clay and sand parts at 20–50% each) with a high humus portion are the most suitable for plant growth. A large pore volume guarantees good aeration which in turn is also supported by living organisms existing within the soil, for example, dog periwinkles in aquariums.

Laterite-containing soils (red soils) and pure laterite soils are typical for tropical areas. They are identifiable by their red coloring and hardening, to which the term laterite (later [lat.] = brick) refers. They are extremely poor in nutrient content and in most cases rich in iron and/or aluminum. Nevertheless, they usually contain sufficient nutrients for aquatic plants because, due to the rapid mineralization of the dead plant matter as well as the generally low conductivity of the water, the released nutrients can immediately be reabsorbed by the plants.

The acid or alkaline reaction of the soil (pH-value) has a big influence on the water's constitution and the nutrient supply of the plants. Most soils within the tropics have a pH-value within the acid to neutral range; lime soils with alkaline reaction are found only in areas with low precipitation (around 1000 mm). Different plants have varying demands on the pH-value of both soil and water. Most tropical and subtropical aquatic plants grow in acid to neutral soils. There are, however, species, e.g., *Vallisneria* as well as several *Potamogeton* species, which prefer both a calcium-rich base and water with a pH-value within the alkaline range. Typical aquatic living environments with high pH-values are, for example, the great African lakes, Lake Malawi and Lake Tanganyika. Several of the lime-preferring species, however, display a large tolerance range so that their cultivation in the aquarium remains satisfactory even in a weak acid or neutral environment. Lime-avoiding species, in contrast, which prosper in very acid conditions in their natural habitats, react in a less adaptive manner. It was impossible, for example, to keep several *Cryptocoryne* species originating from Borneo in an aquarium without an appropriate acid environment.

Even though the substrate is of great importance as a source of nutrients, it has so far been largely neglected as an ecological factor within aquaristics. This is especially evident in the fact that, on the one hand, soil analyses of natural locations have hardly been conducted, resulting in only a very limited knowledge of it. On the other hand, daily aquaristic practice utilizes liquid fertilizers as a useful aid in the event of nutrient deficiency. They are added to the water, whereas special soil fertilizers are almost entirely absent from the retail market. By adding liquid fertilizers, however, an unwanted and difficult to control algae development is aided. The use of soil fertilizer, on the other hand, enables a focused fertilization of only those plants that display inhibited or bad growth.

For this reason the manufacturers of fertilizer products are called upon to supplement their liquid preparations with a soil fertilizer, for instance, in the form of small capsules, which, similar to preparations developed for the fertilization of potted plants, enables a targeted and effective fertilization of individual plants.

WATER

Water constitutes an important ecological factor for the life of aquatic and marsh plants. Water movement, currents, hardness, pH-value and nutrient composition especially influence the growth of plants and are very important.

Aquatic and marsh plants can be found in both stagnant and flowing waterways. The different character of these living environments is defined essentially by water movement as well as the currents to which the plants are subjected. The strength of the current, in turn, influences the soil quality.

The majority of aquarium plants exist in stagnant or weak current biotopes. A smaller number are found in fast-flowing waters, with only very few species being able to adapt to strong and ripping currents.

Water movement is of great importance for several physiological metabolic processes. It enables processes of exchange and accelerates the supply of nutrients as well as the removal of waste products.

Assimilation in different plants (*Ceratophyllum demersum*, *Myriophyllum spicatum*, *Elodea canadensis* and *Potamogeton perfoliatus*, among others) in both stagnant and flowing water was compared in a range of scientific studies (Gessner 1955). A distinctly slower growth could be observed in stagnating water, compared to moving water. This is due to the fact that in stagnant water a surrounding zone low in carbonic acid will form around the plant due to the plant's respiration and assimilation, leading to a slow-down in growth. The positive effect of water movement is found in its destruction of this zone, thereby aiding diffusion processes. The water movement only has to be strong enough to prevent the formation of such a zone low in carbonic acid around the plant. A further increase in water movement does not necessarily lead to an increase in the assimilation performance, but quite to the contrary, can again lead to an impediment to growth. Research on the strength of water movement and current conditions in the natural habitats of our aquarium plants is, therefore, extremely important and has to be considered and assessed individually for each separate species.

Although many aquatic plants exist in stag-

Living environment of *Jasarum steyermarkii* in the Gran Sabana in Venezuela. This rare aquatic plant is not being cultured in the aquarium.

nant waters within their native environment, there is nevertheless a slight water movement present, caused mainly by wind, which should not be underestimated in its effect. Switching off the filter in an aquarium, as is occasionally recommended, does in no way correspond to natural conditions but will instead lead to an impediment to the assimilation process due to the stagnating water and thus result in a worse growth performance of the plants.

In contrast to biotopes with stagnant water, the presence of aquatic plants in moving waterways is predominantly influenced by the speed of the current. The latter itself is subject to large variations, even within one and the same river section. For example, the current flow above the riverbed is considerably lower than within free-flowing water or on the water surface. Aquatic plants which prefer currents are often adapted to the ripping water movement to such a degree that they cannot exist without them anymore.

Some aquatic plants, for example, species from the Podostemaceae and Hydrostachyaceae families, which exist exclusively in rapids and waterfalls, have adapted in such an extreme way to the fast-flowing and ripping water of their environments that their cultivation in an aquarium is entirely impossible for this very reason alone. These plants display a variety of adaptations to such strong currents and the rocky soil riverbeds which even enable them to display generative reproduction within these rapids.

The native habitats of our aquarium plants are furthermore characterized by a specific water condition which, within certain limits, is subject to daily and annual variations. Most tropical and subtropical waters which accommodate aquatic plants display very salt-deficient, soft water with a pH-value within a weak acid to neutral range (around pH 6.0–7.0) due to their mineral-deficient substrate. Occasionally pH-value readings between 5.5 and 6.0 can be recorded. In such waters, though, the species count is already somewhat reduced. Only few aquatic plants are specially adapted to live in such an acid environment, an example of which is the black water of the Rio Negro in Brazil.

Waterways that contain medium to hard water with a more or less high alkaline pH-value are relatively rare in tropical and subtropical regions. Examples for such habitats are Lake Tanganyika and Lake Malawi in Africa, as well as several rivers and lakes in Mexico. In these environments, characterized by unusual water pH-values, the number of aquatic plant species is also noticeably more limited. This finding is based not only on water analyses in natural biotopes conducted by the author, but also corresponds to tests done by other authors. The results, however, are in distinct contrast to the many studies completed on native, genuine submersed aquatic plants (see Gessner 1959), the presence of which is almost exclusively limited to alkaline waters.

Essential for optimum plant growth in their natural habitats is a complete and constant nutrient supply within the water. Head springs often transport nutrient-rich water into the streams and thereby visibly promote plant growth.

The water analyses listed in Table 3 convey an idea of the chemical characteristics as well as the nutrient conditions in several tropical waterways, which are characterized by plant populations with varied species and individual plants. The studies done by Horst (1986) are recommended for additional reference.

BLACK WATER, CLEAR WATER, WHITE WATER

Numerous scientific studies conducted in the 1950s, mainly in the Amazon river system (Sioli 1950, Braun 1952, Gessner 1959, Sioli and Klinge 1961, among others), led to a rough classification into three types of water, based on physical (coloring and clouding) and chemical differences between a number of rivers. Based on their typical features black, clear and white water can be distinguished, with many intermediate forms existing, of course, resulting in not every waterway being able to be categorized within this model.

Typical white water rivers display loamy-yellow, turbid water and, in contrast to clear and black water rivers, contain a large amount of inorganic floating matter which deposits on the riverbanks and forms an especially fertile soil. Examples of white water rivers are the Rio Solimões, in the upper Amazon, as well as rivers mentioned on pp. 36 and 42, namely the Yanayacu in Peru and the Sepik in Papua New Guinea.

Clear water rivers, on the other hand, are poor in sediments and contain very clear, yellow green to dark olive green water with high visibility. White sandy beaches often form on the riverbanks. One such river described in detail is the Rio Guaporé in Brazil's southwest (see p. 29).

The third group is made up of black water rivers which are characterized by clear, transparent but dark brown-colored water. The typical deep brown color is a result of the regular flooding of the surrounding forests which leads to the inflow of humic matter. As a result black water is exceptionally acid and very poor in dissolved minerals. Due to its interesting fish fauna the Rio Negro (Brazil) is the most widely known black water river in aquaristics.

The main reasons for the formation of different types of waterways are the composition of the riverbed as well as climatic and geographic conditions.

Because of the large differences between these three categories of waterways with regard to their physical, chemical and biological constitution, the character of the water flora differs accordingly in the respective types.

Genuine black water rivers provide extremely inhospitable living conditions for

Utricularia foliosa **and** ***Azolla caroliniana*** **exist in the black water of the Rio Nanay (Peru).**

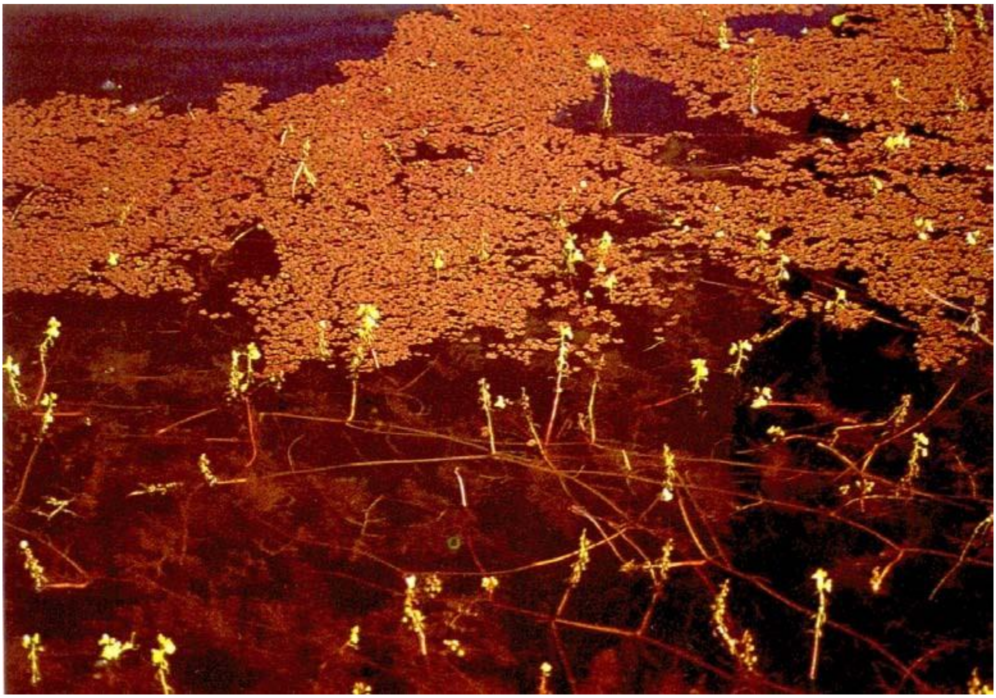


Table 2: Water values of selected black water, clear water, and white water biotopes.

		Biotope		
		Black water Rio Negro (Brazil)	**Black water** Rio Copal (Peru)	**Clear water** Rio Tapajoz (Brazil)
Date		—	June 1983	—
Water temperature	in °C	26–29.5	27.5	—
pH-value		3.7–4.3	6.0	4.6–6.65
Conductivity (at 20 °C)	in µS/cm	6–9	17	10–16
Carbonate hardness (KH)	in °dH	<0.1	0	0.15–0.4
Total hardness (GH)	in °dH	<0.1	0.12	0.13–0.82
Calcium hardness	in °dH	0.26	0.07	0.21
Magnesium hardness	in °dH	traces	0.05	0.03
Carbon dioxide (CO_2)	in mg/L	high	~1	0.71–3.5
Oxygen (O_2)	in %	—	—	86–117 (27 °C)
Sodium (Na)	in mg/L	0.75	1.9	1.26
Potassium (K)	in mg/L	0.35	1.1	0.50
Iron ($Fe^{2+/3+}$)	in mg/L	<0.24	—	0–0.3
Ammonium (NH_4^+)	in mg/L	—	—	0.07–0.18
Chloride (Cl^-)	in mg/L	1.20	<7	0.05–1.60
Sulfate (SO_4^{2-})	in mg/L	4.81	n.d.	0–2
Nitrate (NO_3^-)	in mg/L	—	1.6	0–0.08
Nitrite (NO_2^-)	in mg/L	—	<0.1	—
Phosphate (PO_4^{3-})	in mg/L	<0.157	—	0
Zinc (Zn)	in µg/L	—	5	—
Cadmium (Cd)	in µg/L	—	n.d.	—
Lead (Pb)	in µg/L	—	n.d.	—
Copper (Cu)	in µg/L	—	7	—
Humic acids		high	high	traces

n.d. = not detectable

plant growth. Apart from their strong coloration, they are defined by the very acid water of many Amazonian rivers with pH-values of 3.7 to 4.3 as well as the low content of hydrogen carbonates, leading to the plants' exclusive dependency on free carbon dioxide for their nutrition. These characteristics constitute important limiting factors and prevent growth of most aquatic plants within black water. Only a select few and highly specialized species have managed to adapt to this unusual living environment and are, in turn, unable to adapt to a change to different conditions.

Black water rivers are not only found in the Amazon region and in Guyana, but also in many other countries. The limited range of pH-values for this type of waterway as laid down by earlier authors in conjunction with studies in the Amazon river system, has to be expanded up to a pH range of about 5, based on further studies conducted in other black water rivers. Nevertheless it is a common feature of all black water rivers that they are always extremely poor as to plant populations. Typical aquatic plants in the black water of the Rio Negro are, for example, *Cabomba aquatica*, *Utricularia foliosa*, *Azolla*

Table 2: Water values of selected black water, clear water, and white water biotopes *continued.*

		Biotope		
		Clear water Rio Chinipo (Peru)	**White water** Amazon, Rio Solimões (Brazil)	**White water** Rio Ucayali (Peru)
Date		June 1983	—	June 1983
Water temperature	in °C	26	27–28	25
pH-value		7.2	6.5–7.5	7.1
Conductivity (at 20 °C)	in µS/cm	142	10–127	154
Carbonate hardness (KH)	in °dH	4.7	0.6–1.8	3.9
Total hardness (GH)	in °dH	4.9	0.64–1.27	2.9
Calcium hardness	in °dH	3.6	1.08–1.2	2.9
Magnesium hardness	in °dH	1.3	0.03–0.14	0
Carbon dioxide (CO_2)	in mg/L	10	3.95	10
Oxygen (O_2)	in %	—	<91	—
Sodium (Na)	in mg/L	3.9	2.60–3.35	9.0
Potassium (K)	in mg/L	0.5	0.90–1.10	1.8
Iron ($Fe^{2+/3+}$)	in mg/L	—	0.22	—
Ammonium (NH_4^+)	in mg/L	—	traces	—
Chloride (Cl^-)	in mg/L	<5	0–3.40	<5
Sulfate (SO_4^{2-})	in mg/L	n.d.	0–4.94	n.d.
Nitrate (NO_3^-)	in mg/L	0.8	0.16–0.28	0.8
Nitrite (NO_2^-)	in mg/L	—	—	—
Phosphate (PO_4^{3-})	in mg/L	<0.7	<0.145	0.7
Zinc (Zn)	in µg/L	11	—	7
Cadmium (Cd)	in µg/L	n.d.	—	n.d.
Lead (Pb)	in µg/L	n.d.	—	n.d.
Copper (Cu)	in µg/L	27	—	13
Humic acids		traces	0	0

n.d. = not detectable

caroliniana and several species of the Podostemaceae family. In the black water biotopes of Guyana, with pH-values between 3.9 and 4.2, one occasionally finds *Mayaca fluviatilis* and *Tonina fluviatilis*. But the living environments of several *Cryptocoryne* species in Asia, too, constitute typical black waters. An example, described in detail, is the channel system of Tasek Bera on the Malaysian Peninsula with *Cryptocoryne purpurea* (p. 212).

Clear water rivers, too, display an acid environment, pH-values between 4.6 and 6.6 as well as the transparency of the water providing a more advantageous light climate, thereby enabling many plants to adapt to such conditions. Clear water rivers are also characterized by an extreme deficiency in minerals and are accordingly poor in nutrients. But, as the water analysis of the Rio Guaporé, for example, shows, there nevertheless exists a comprehensive and consistent nutrient supply which enables multifaceted plant growth in these waters. Possibly the most limiting factor for aquatic plant populations is the considerably changing water level as it fluctuates with the seasons.

The clear water of the Rio Guaporé (Brazil) provides an optimum living environment for many plants.

Typical white water rivers are also very soft waters which, in contrast to black water, display a distinctly higher content of dissolved minerals which is reflected accordingly in higher conductivity. Also, white water has a pH-value within the weak acid to slightly alkaline range between 6.6 and 7.2. The richness in nutrients in this type of water essentially permits the survival of many species. Strong turbidity, reduced light penetration as well as varying seasonal water levels are, however, important growth limiting factors. Submersed plants are mostly absent from white waters and the vegetation is limited to the growth of floating plants, for example, *Azolla* and *Ceratopteris* species, *Eichhornia crassipes*, *Phyllanthus fluitans*, *Pistia stratiotes* and others.

The different water analyses of several Brazilian and Paraguayan rivers listed in Table 2 illustrate the differences between black water, clear water and white water as outlined above (Brazilian rivers according to Gessner 1959, Sioli and Klinge 1961 as well as data from the author, with the water samples of the Peruvian rivers having been collected by W. Staeck).

Seasonal Influences, Vegetation Rhythm, and Types of Waterways

Tropical and subtropical aquatic and marsh plants have conquered very different living environments in the course of evolution. Their natural biotopes are boggy flood areas, puddles, ponds, lakes, more or less fast-flowing streams and rivers as well as man-made living environments, such as rice paddies, pools and storage lakes. These ecosystems are subjected to the seasonality typical for the tropics, namely rain-intensive and rain-deficient seasons and associated variations in water levels,

Growth of floating plants in the white water of the Rio Yanayacu (Peru).

as well as seasonally changing light and climate conditions.

Waterways can be classified as constantly water-carrying (permanent) and periodically dry (temporary) biotopes. These in turn can have either stagnant or flowing water. Within these types of waters there are intermediate stages if the amount of rainfall or the length of the dry period changes decisively due to climatic change. A generally periodically drying waterway can thus carry water during the dry season due to extreme climatic conditions. Alternatively, a usually permanent biotope can dry out during prolonged periods of drought. Generally, though, biotopes can quite clearly be categorized into the above types of waterways. Even though plants are adaptable within limitations and are able to react in a flexible manner to changes in their environment, irreparable damage to these living communities, which have evolved over millennia, will occur in the event of major climatic change, and many species will be unable to survive in their present locations.

Populating a specific waterway is possible by only those plants which are able to adapt to the prevailing ecological realities. Temporary waters, for example, were permanently populated by only those species which had the capacity to survive dry periods with the aid of bulbs, tubers or drought-resistant seeds. The occurrence of individual plants in temporary waters is thus determined by the duration of the dry period which is, in turn, defined by the geological and climatic conditions of the regions. The length of the dry period is, therefore, partly responsible for the distribution of different species. Simultaneously, conclusions on life cycles can be drawn from the occurrence of plants in certain areas. The presence of certain species in temporary waters, however, does not exclude the possibility that they may also be found in permanent waters.

The giant pond lily (*Victoria amazonica*) inhabits the tranquil bays of the Amazon.

Temporary biotope on Mafia Island (Tanzania) with dense plant growth during the wet season. The same biotope during the dry season, completely dried out.

In contrast to plants in temporary biotopes, species in permanent waters (mostly rivers, lakes or very large swamp areas) lead a different existence. The difference between high and low water, which is dependent on the seasonal alternation of dry and wet periods, is essentially responsible for the populating of such waterways. Only a few aquatic and marsh plants are able to adapt to an increased water level of more than 1.5 m during the wet season and the corresponding reduction in light, and to survive for several months in a greater depth. Furthermore, there is the strong current often prevalent in permanent waters in which only a few aquatic plants (for example, Podostemaceen) can survive. For this very reason this ecological niche was conquered by only a few species.

Permanent waters usually display plant growth in only the shallow bank area or on the water surface. It is mostly absent in greater depth. Accordingly, only very few aquatic or marsh plants anchored to the soil bed are found in rivers with great variations in water levels measuring several meters, but only species which float on or below the water surface and which prefer calm enclaves. An exception is *Victoria amazonica* which can take root even in turbid white water of calm tributaries of the Amazon, in 8–10 m of depth.

Climate Rhythmics

Light and temperature variations which, on the one hand, occur during the course of the day and, on the other hand, are dependent on the periodic seasonal change, have an essential influence on the conditions under which tropical and subtropical aquatic and marsh plants prosper. In the tropics the length of both day and night vary only a little in the course of a year, so that there generally occurs a daytime warming-up phase as well as a cooling-down period during the night, lasting 12 hours each. The consistently moist equatorial zone is characterized by high precipitation, more or less evenly distributed over the year, as well as balanced temperatures, average annual temperature readings ranging between 25 and 27 °C, with those recorded during the coldest month not falling below 18 °C on average. Therefore—in contrast to subtropical or temperate zones—there are no distinct seasons, the plants' growth instead being essentially influenced by the daily temperature variations between day and night (daytime climate).

With increasing latitude, the ratio between length of day and length of night over a year will shift increasingly. Accordingly, depending on these seasonal variations, the temperature, too, changes, so that one finds clearly defined seasons in subtropical regions to which the vegetation has adapted. The cold season, with its short days, generally constitutes the time of year with the least light availability.

Not only the length of day and night, but also the difference between day and night temperatures, influences growth processes (see vegetation rhythms), flowering behavior and germination. For example, it is known from the cultivation of some *Echinodorus* species that they display genetically determined photoperiodical behavior and form inflorescences only at a specific length of day, thereby clearly indicating an adaptation to the geographical distribution (see also introduction to the genus *Echinodorus* on p. 229).

Plants from subtropical regions are especially in a position to endure extreme temperature variations. For example, in subtropical areas of the Southern Hemisphere (South Brazil to North Argentina), areas populated by numerous aquarium plants, night temperatures can occasionally drop to the frost levels during winter. On the other hand, air temperatures can reach values above 35 °C during the day. These extreme temperature differences in native locations, however, do not in any way always have a positive impact on plant growth. Studies of terrestrial plants (Larcher 1984) have shown that for species from temperate zones, differences between day and night temperatures of 5–10 °C, in the case of tropical plants of about 3 °C, have an optimum effect on growth. These research results can certainly allow limited conclusions on the growth behavior of tropical and subtropical aquatic and marsh plants. The author is not familiar, however, with any comparative studies of individual species. A consistent difference in temperature between day and night corresponds to a natural rhythm. It is necessary to differentiate, though, between those species which populate small and stagnant waters, and which are consequently subjected to larger daily fluctuations in temperature in accordance with their geographic distribution, and those species which are found in expansive, stagnant or flowing waters. Within the latter, daily temperature variations in the tropics are only small; temperatures in waters outside the equatorial zone, however, can be subject to considerable variations over the seasons.

Some aquarium plants which are subject to the periodic change of wet and dry seasons in their natural habitats are identified in scientific literature as being annual. In contrast to perennial species, the life-span of these annual plants is limited. In most cases, though, this short life-span is imposed upon the plants categorized as annual by their disadvantageous environmental conditions (summer and winter, wet and dry seasons) within their natural locations. As is often found during cultivation, this annual characteristic is rarely genetically predetermined.

Of the numerous aquarium plants, only very few are really annual or rather have a short life-span: among these are *Hydrothrix gardneri*, *Blyxa aubertii*, races of *Echinodorus major* which die off after the flowering stage in emersed cultivation, as well as the individually less known and less kept *Eriocaulon* species. Several other aquarium plants, however, *Barclaya longifolia* and *Aponogeton* species among others, display a regular change between rest and vegetation periods.

Adaptation Characteristics of Aquatic and Marsh Plants

Typical for many tropical and subtropical marsh plants living in temporary waters or in flood areas of stagnant or flowing waters, are their symptoms of adaptation to the periodic change of rain-intensive and rain-deficient seasons. During the dry season, the plants grow more or less on the edges of waterways, either completely emersed or in only a few centimeters of water. In case of the waterway drying up, this can also lead to the plant completely dying off after some time. During high-water levels, plants lead a partial or entire existence under water. Plants found in such locations are obviously in a position to adapt to an emersed and submersed existence over the course of annual seasons. They display a changing life cycle and have to have blossomed and borne fruit within a certain period of time, i.e., from the start of the rainy season up to their possible withering stage at the end of the dry period, in order to ensure their reproduction.

At the onset of the wet season many aquatic and marsh plants will initially form typical juvenile forms. From the vegetation organs which have remained in the soil from the dry period (rhizome, tuber, bulb), some mostly delicate juvenile leaves will emerge which are often narrow, strap-shaped, soft and pellucid. In the course of plants developing from seeds, these typical juvenile leaves will also form, following the formation of one or two cotyledons. Only with increasing age and progressing plant growth will those submersed and floating leaves develop which are typical for every individual species. These leaves, through their anatomical structure which is characterized by more or less absent stomata, thin outer epidermis as well as wide air ducts, display a special adaptive quality to water as a medium. The aquatic leaves are thus able to absorb oxygen, carbon dioxide and nutrients directly from the water. The leaves will shrivel rapidly and wither in dry air due to the lack of support tissue and transpiration protection. If the water level begins to slowly drop again, amphibious growing plants will change over to their emersed stage, i.e., they will cease to form submersed leaves but will increasingly form air leaves above the water surface and will then proceed to mature to their full size. These leaves growing above the water surface will assume a totally different appearance in many species compared to their submersed state (heterophylly = having different leaves). Whereas the underwater leaves are often delicate, thin, transparent and ribbon-like or dissected in order to achieve a larger surface, entire, hard, leathery and often hairy leaf blades are typical features of air leaves. The formation of differently structured leaves in different mediums can be observed especially well in *Hygrophila difformis*, as well as *Limnophila* and *Myriophyllum* species. During sinking water levels during dry periods, flower and seed formation will commence. If the locations are beginning to dry out, the plants will develop an increasingly squat appearance until the foliage will often entirely dry up in line with the reduced moisture within the soil. Whereas in some species only the survival organ will survive in the dry soil, other species will die off entirely, and only their seeds will remain in a state of suspense until the onset of the next wet season, when advantageous environmental conditions will initiate germination. Once they reach the water surface, many genuine aquatic plants will form floating leaves

Hygrophila corymbosa **with submersed and emersed shoots in a river on Sulawesi.**

which lie flat on the surface and which also display typical features of adaptation in their anatomical structure. They are especially rich in intercellulars which aid photosynthesis. At the same time, the floating leaves of some plants, for example, water lilies, display countless hydropotes ("water drinkers," gland-like cells of the epidermis) on the leaf's underside which assist in the absorption of water and mineral nutrients. Such hydropotes can also be found on the leaves of many aquatic plants.

Using their roots and rhizomes, some aquatic plants, such as *Nymphaea* and *Nuphar* species, are in a position to grow in badly aerated and oxygen-deficient soils. As a form of morphological adaptation to this environment, they have formed a system of cavities through which oxygen from the floating leaves can be transported to those plant segments existing within the soil. These cavities are so large that it is possible to actually blow air through the petiole of a water lily.

In especially thick soils, roots growing above the surface, bulbous roots on shoots, and, as an extreme adaptation to this environment, pneumatophores can be found occasionally on plants in tropical waters. The presence of such pneumatophores in several *Ludwigia* species is well-known. Pneumatophores generally develop in a very oxygen-deficient environment and can be distinguished from normal roots by their white, spongy and bloated tissue, incorporating large intercellular cavities (aerenchyma) which serve aeration and air storage purposes. These pneumatophores grow vertically into the air, probably absorb oxygen from the atmosphere and transport it to the submersed shoots via the aerating tissue.

Floating plants, too, display adaptive morphological and anatomical features. In the *Salvinia* species, for example, the two floating leaves are equipped with numerous intercellular spaces, whereas the submersed leaf hanging in the water is divided into many

Flowering *Nymphaea lotus* in temporary waters in Senegal.

filiform pubescent lobes and has adopted the functions of the absent roots. The bloated, spongy petioles, which display a comprehensive aerating tissue and thus enable the plants to float on the surface, are conspicuous in *Ceratopteris pteridoides*, *Eichhornia crassipes* and *Trapa natans*. The underside of the leaf in *Limnobium* is conspicuously bloated and thickened, which also enhances the floatability of the plant.

Specifically worth mentioning is the often distinct moisture protection found in floating plants. This protection serves to keep the transpiring upper leaf sections above the water surface dry from rain or dew. The fact that it is impossible to moisten the leaf of *Nelumbo nucifera*, which is covered with papilla, is well-known. But in the *Salvinia* species, too, the floating leaves are effectively protected from moisture by papilla arranged in rows and on which hairs are located. At the same time, the boat-shaped floating leaves enable a quick run-off of rainwater. Moisture protection in other species (e.g., *Pistia stratiotes*) is achieved through a strong pubescence. The bulging in floating leaves in some aquatic plants (e.g., *Phyllanthus fluitans*) is also notable. It also has the purpose of ensuring a rapid flow-off of rainwater from the surface.

The occurrence of strap-shaped and especially smooth, undulate or bullate leaves, for example, in some *Aponogeton*, *Cryptocoryne* and *Vallisneria* species, is a conspicuous feature in some aquatic plants. Such leaf shapes and structures can be explained both as measures of adaptation as well as protection, since the leaves, due to their shape or surface structure, offer the least possible resistance to any water current. Narrow or ribbon-like leaves are especially formed by those species that exist in flowing waterways. They are also

Ceratopteris pteridoides **forms spongy, thickened petioles which increase the plant's floatability (photographed on the Rio Yanayacu, Peru).**

typical of rheophytes, plants that are found between high and low water zones and are often subjected to short-time flooding. Their leaves are firm, leathery or coarse, and have at least a length to width ratio of 4:1.

Other features of adaptation to the surrounding environment can be observed in several other aquatic plants originating from Lake Malawi and Lake Tanganyika. These two East African lakes are well-known to aquarists because of their rich content of fish fauna. In the transitional zone between gravel and sand, and within the reed zone, there exist some aquatic plants which have created living conditions for themselves with the help of special adaptive features geared to the special living environment within these waters. *Vallisneria spiralis* var. *denseserrulata*, for example, features conspicuously short and very hard leaves through which the plants can better resist any wave movement. *Ceratophyllum demersum* and *Myriophyllum spicatum*, too, display a variation in appearance totally different from other habitats by having short internodes as well as hard leaf and stem structures, which can also be interpreted as a protective and adaptive measure against wave movement. Furthermore, the shoots in *C. demersum* are of such compact growth that they do not move freely in the water as is common in other populations, but, due to their greater density, will drop to the bottom where they are subjected to a lesser wave movement compared to that found on the water surface.

The giant water lily, *Victoria amazonica*, too, has developed an optimum adaptive and protective characteristic to the natural living environment. The plant produces imposing floating leaves up to 2.5 m in diameter, on the surface of which the necessary stoma, which are important for respiration and assimilation, can be found. These floating leaves feature a strongly ribbed leaf venation as well as an up to 10-cm high curved margin, thereby setting a strong resistance against the water's wave movement and preventing the leaf's destruction.

Other features of adaptation to life in the water are the animal traps in *Aldrovanda vesiculosa* and the utricles in *Utricularia* species with which the plants catch, digest and exploit smaller animals as an additional source of nitrogen. The formation of hibernacles (winter buds, turions) in numerous aquatic plants is to be seen as an adaptation to disadvantageous periods of vegetation. Many endemic aquatic plants develop such hibernaculums which drop to the bottom during autumn where they survive the cold season. During the following spring they will again rise to the surface and develop new shoots.

Interesting in this context is the behavior of some Lemnaceae. During late summer they develop modified small limbs with greatly retarded intercellulars and increased firmness which leads to an increase in their specific weight. The plants consequently lose their ability to float and drop to the bottom. In spring the limbs will recommence growth and again rise to the surface.

Apart from the typical features of adaptation of life within water mentioned here, the numerous pollination mechanisms of aquatic plants have to be mentioned (see also "Flower Biology") but will not be dealt with at this stage.

Description of Selected Natural Habitats

THE RIO GUAPORÉ (BRAZIL)

Biotope No. 1

The Rio Guaporé has its source in the Brazilian state of Mato Grosso, near the border with Bolivia. Its riverbanks are the only place where primary forests are still found. The starting point for the excursion in August 1987 was the little town of Vila Bela on the upper course of the Guaporé (about 60°W, 15°S), where the river features a wide range of species and dense plant populations in its flood areas and tributaries.

Ecological Data of the Upper Rio Guaporé

In its upper course the Rio Guaporé is a clear water river. In this area the wet season extends from mid September to the end of April. The high-water period accordingly falls into our European 6-month-long winter; the low-water period coincides with our summer. The highest temperatures are reached during the wet season. For the city of San Luiz de Cáceres, 250 km away, the average daily maximum in the warmest month (March) measures 32.8 °C, and the average daily minimum during the coldest month (July) measures only 14.6 °C (absolute minimum 3.8 °C). The data helps to explain the surprisingly low water temperature of the Rio Guaporé of 20 °C recorded in August. It can be concluded from the water analysis (Table 3, Biotope No. 1) that the Guaporé is a very soft, nutrient-deficient (oligotrophic) waterway in which aquatic plants are nevertheless able to find a sufficient nutrient supply to sustain growth.

At many locations on the riverbed, the soil base is washed out and consists of fine white sand. Emersed plants of the riverbank and flood areas, however, grow mainly on muddy loamy soil. Dense plant populations are found mainly on open and shallow parts of the riverbank where intense solar radiation is also possible.

During low tides, the water level of the Rio Guaporé drops during the dry period by a maximum of 1.5 m. Plant species located on the banks of the waterway, for example, the large-growing *Echinodorus* species *E. paniculatus* and *E. grandiflorus* subsp. *grandiflorus*, are found emersed only a few centimeters underwater. During high water, these species will temporarily grow in a depth of 1–1.5 m and are partially able to adapt to the raised water level and the associated reduction in light by developing longer petioles. It is assumed that plants growing several meters away from the riverbank, for example, the smaller *Echinodorus* species *E. tenellus*, *E. bolivianus* and *E. grisebachii*, are found in relatively shallow water during high water periods where they develop submersed leaves. These light-requiring and small-remaining sword plants grow in those locations in nature where they will still continue to receive sufficient light to support adequate growth even during high-water periods, i.e., in an area which is only just reached by the river during maximum high tides. These small to medium-sized species thus occupy a different ecological niche compared, for example, to the larger *Echinodorus* species.

Plant Societies and Species Diversity

The diversity of aquatic and marsh plants in the vicinity of this river is exceptionally high. Alongside 5 *Echinodorus* species, 3 of which belong to the smaller to medium-sized species and 2 to the larger species, 15 other species from other genera were located: 11 in the river and 4 in the nearby flood areas.

Under closer scrutiny, the river displays a number of different living environments in which certain species tend to be found more often, e.g., species which have adapted to the prevailing ecological conditions to a specific degree. In the following, these living environments will be portrayed in order to convey an insight into the ecology and sociology of several aquatic and marsh plants which are of interest to aquaristics. The sedge belt, often several meters wide, found at many places in the Rio Guaporé and its flood areas, is not included.

The zone accommodating the amphibious growing species constitutes an important living environment. On the Guaporé, the five *Echinodorus* species already mentioned are among these, as well as *Limnophila indica* (introduced) which, on the one hand, can be found in up to 50 cm of depth during low water, and at the same time produces emersed flowering populations.

Adjacent to this zone is a plant community made up of submersed plants which flower above the water surface. Among these are *Cabomba furcata* which is often found in association with *Limnophila indica*. *Cabomba furcata* grows in the placid sunny border areas of the river in depths of more than 50 cm. Larger populations are found mainly in subsidiary branches and quiet coves with slow-moving water. A species which is found quite often in the Guaporé is *Ottelia brasiliensis*, which also only grows submersed and only sends its flowers to the water surface. During low water it can be located in both very shallow water, for example on sunny sand banks, as well as in depths of almost 2 m. It can be assumed that these plants will stand in more than 3 m of water during high-water periods. According to the author's observations, *Ottelia brasiliensis* occupies a similar ecological niche to *Limnophila indica* and *Cabomba furcata*; *Ottelia brasiliensis* seems to prefer locations with strong currents and far deeper water, whereas *Limnophila* and *Cabomba* are more likely to be found in more placid zones of shallow water. This does not preclude all three species occasionally occurring next to each other at the same location under appropriate conditions. Common to all these species obviously is their preference to populate spots that are fully sunlit. The overall picture of the river landscape on the Guaporé is essentially defined by a belt of *Eichhornia*, consisting of

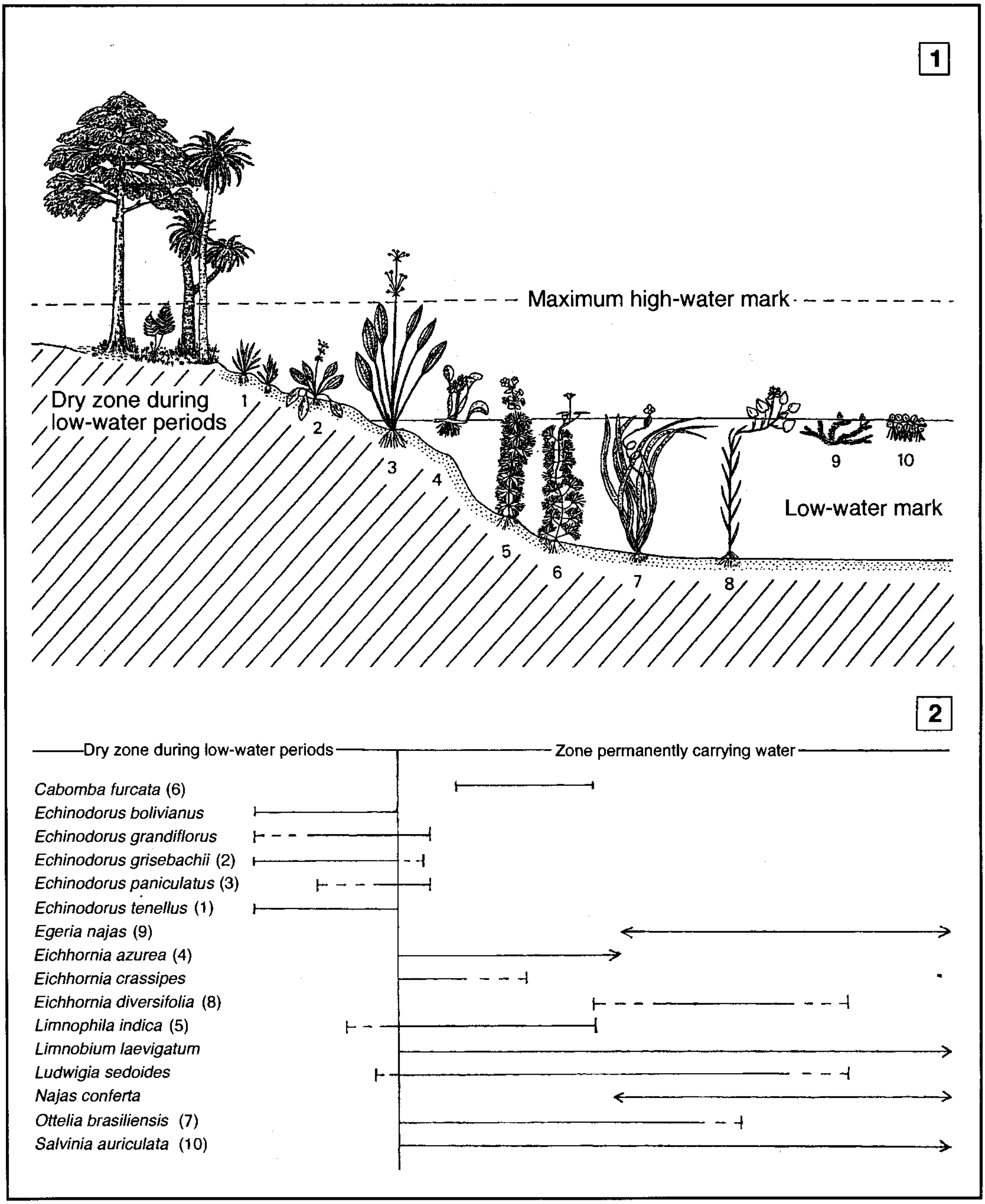
***Eichhornia azurea*, *Echinodorus paniculatus* and *Echinodorus grandiflorus* grow on this riverbank on the Rio Guaporé (Brazil).**

Impressive dense populations of *Eichhornia diversifolia* in a floating plant zone on the Rio Guaporé.

Diagram 1 Schematic representation of the distribution of plant populations in different living environments in the Rio Guaporé at low-water levels (excluding the marsh zone). The following species were selected to represent the different living environments and their respective plant populations: *Echinodorus tenellus* (1), *E. grisebachii* (2) and *E. paniculatus* (3) are typical of the riverbank zone; *Eichhornia azurea* (4) is common in the *Eichhornia* belt; *Limnophila indica* (5) represents amphibious species; *Cabomba furcata* (6) and *Ottelia brasiliensis* (7) represent those submersed plants flowering on the water surface; *Eichhornia diversifolia* (8) typifies the floating plant belt; *Egeria najas* (9) is characteristic of those submersed plants floating freely in the water; and *Salvinia auriculata* (10) is an example of those species inhabiting the floating plant zone.

Diagram 2 Simplified graphic representation of the living environments of aquatic and marsh plants in the Rio Guaporé at low-water levels (excluding species inhabiting the marsh zone). In reference to Diagram 1 the continuous lines represent the most important area or zone of presence of the respective species, which is dependent on the river's water levels and the degree of moisture in the substrate, thereby limiting it accordingly.

The arrows indicate presence also in adjoining living environments. The broken lines point to a rare, limited occurrence in the respective environment. The vertical dividing line marks the border between the dry zone during low-water levels and the permanent water zone.


1
Maximum high-water mark
Dry zone during low-water periods
1
2
3
4
5
6
7
8
9
10
Low-water mark
2
Dry zone during low-water periods
Zone permanently carrying water
Cabomba furcata (6)
Echinodorus bolivianus
Echinodorus grandiflorus
Echinodorus grisebachii (2)
Echinodorus paniculatus (3)
Echinodorus tenellus (1)
Egeria najas (9)
Eichhornia azurea (4)
Eichhornia crassipes
Eichhornia diversifolia (8)
Limnophila indica (5)
Limnobium laevigatum
Ludwigia sedoides
Najas conferta
Ottelia brasiliensis (7)
Salvinia auriculata (10)

Eichhornia azurea and *Eichhornia crassipes* and which stretches along the embankment zones of the waterway. The prevailing ecological conditions, however, don't seem to be optimal for *E. crassipes* since the plants were unusually frail for tropical conditions and found to exist only in small groups. The *Eichhornia azurea* specimens, in contrast, displayed a surprisingly strong habit. The meter-long, tangled shoots were anchored to the bank and stretched from there into the river. In areas with a strong current, the populations are smaller compared to the waterways' quieter fringe zones. The belt of *Eichhornia* often borders on the belt of floating leaf plants or the area of floating plants.

The belt of floating leaf plants in the Guaporé can be found primarily in the numerous shallow and quiet fringe waters as well as in the current-deficient coves on the banks. Next to the real-floating leaf plants it can, however, also be interspersed with genuine aquatic plants, for example, *Egeria najas* and *Najas conferta*. In the Guaporé's belt of floating leaf plants *Eichhornia diversifolia* and *Ludwigia sedoides* species can be found, species which shaped this habitat during the Brazilian winter with their floating leaf shoots carrying numerous flowers. In contrast to *Eichhornia diversifolia*, *Ludwigia sedoides* populates the free-water zone as well as those areas of the riverbank having no currents. It is also able to produce emersed leaves.

The free-water zone with submersed, free-floating plants in the water is made up mainly of *Egeria najas* and *Najas conferta*. Whereas the strong current areas in the center of the Guaporé are free of any plant growth, one can often find mass groups of both these species in tranquil subsidiary arms or current-deficient bays which have the characteristics of stagnant waterways. The tender shoots of *Egeria najas* and *Najaş conferta* float in dense groups underwater in locations fully exposed to the sun.

Besides the *Eichhornia* populations on the riverbanks, the author found only two floating plant species in the actual riverbed of the Guaporé: *Limnobium laevigatum* and *Salvinia auriculata*. Both floating plants are rare in the Guaporé and will occur only occasionally, so the ecological conditions for both species are obviously not optimal.

Plants of the Marsh Zone

Even though marsh areas are directly exchanging water with the Guaporé for at least some of the time, they nevertheless form a separate individual living environment since they contain stagnant water, in contrast to the river's flowing water. Whereas, for example, *Echinodorus paniculatus* and *Ludwigia sedoides* are also found in the marsh zone, species that prefer currents are completely absent from it. Instead, several other aquatic plants can be found there which obviously seem to prefer stagnant water and therefore avoid the riverbed. Among these are *Hydrocleys nymphoides* as well as *Utricularia breviscapa* and *U. hydrocarpa*. The mentioned species exist in association in marshy locations in the most confined areas possible. The soil in these habitats is boggy and shaded by surrounding trees.

FLOODING AREA OF THE RIO SIPAO (VENEZUELA)

Biotope No. 2

The Rio Sipao is a north-flowing confluent of the middle Orinoco in Venezuela. Studies were conducted in a large flooded area of this river, located a few kilometers away from the town of Maripa in the direction of Caicara. The waterway was fast-flowing, loamy, and clouded in its middle sections. In many places, however, little calm bays have formed in which dense populations of *Eichhornia diversifolia*, *Bacopa* sp. and *Tonina fluviatilis* could be found growing in knee-deep water. The populated locations were usually in the sun and were hardly shaded by any trees. The soil was sandy but mostly covered by a thick level of dead plant matter.

The fish fauna consisted of cichlids (*Apistogramma*, *Aequidens*, *Papiliochromis*) and salmon (*Aphyocharax*, *Pyrrhulina*).

MARSH AREAS IN THE RIO ARO (VENEZUELA) RIVER SYSTEM

Biotope No. 3

This biotope is located in Venezuela, about 80 km from the city of Bolivar, on the road to Maripa. It is a marsh area in the river system of the Rio Aro, a north-flowing confluent to the middle Orinoco. Dense populations of many marsh and aquatic plants, e.g., *Cabomba furcata*, *Ludwigia inclinata* featuring verticillate leaves, *Bacopa reflexa* as well as *Sagittaria* sp., grew in stagnant water about 30–50 cm deep. The soil consisted of brown loam. The marsh area was surrounded by palm trees, with the palms being partially shaded, partially in the sun. The only fish caught were small *Copella*. The water at this location was acid, soft, and displayed—as a unique feature—symptoms of a creeping over-fertilization (ammonium, phosphate, and a lot of carbon dioxide) which was likely to have been caused by cows grazing the surrounding meadows.

LAKE IN THE RIO PARANÁ (ARGENTINA) CATCHMENT AREA

Biotope No. 4

Between the towns of Resistencia and Ramada Paso (Argentina), about 30 km before the latter, there is a large lake within the catchment area of the Rio Paraná into which a small stream enters. In July 1993, this stream formed a 1-m long, knee-deep ditch with very slow-moving, brown-colored, clear water. The edge of the lake as well as this little ditch were thickly populated with *Limnobium laevigatum*, *Hydrocotyle ranunculoides*, *Myriophyllum aquaticum* and flowering *Cabomba caroliniana* var. *flavida*. The uppermost layer of the substrate was boggy, with sand located under it. Most of the plants grew in sunny places, only some sections being shaded by isolated trees. Conspicuous in the test results, which were recorded during the cold season, was the low temperature of the very soft water relatively rich in oxygen. The local fish fauna consisted of cichlids (*Cichlasoma*, *Crenicichla*, and *Apistogramma*), catfish (*Corydoras* and *Hoplosternum*) and tetras (*Copella*, among others).

RIVER IN THE RIO URUGUAY (ARGENTINA) CATCHMENT AREA

Biotope No. 5

Studies were done on plant populations in a smaller river about 30 km past the city of Santo Tomé in the direction of La Cruz (Argentina). This waterway, as well as the adjacent flood area, featured thick populations of aquatic and marsh plants as well as an unusually large diversity of species within a small space. *Eichhornia azurea* and *Hygrophila guianensis*, among others, were found in the quick-flowing water in a depth of 1–2 m with *Nymphoides* sp. also present in water about 3 m deep. On the edge of the river, in a slightly weaker current, *Egeria najas*, *Myriophyllum aquaticum*, *Eleocharis* sp. and flowering *Cabomba caroliniana* var. *caroliniana* could be found in water with a maximum depth of 1 m. Emersed shoots from *Myriophyllum aquaticum*, *Hygrophila guianensis* and *Ludwigia* grew on the water surface. On the river's edge the soil was loamy. All plants at the researched locations were subjected to intensive sunlight because the biotope was not shaded by any surrounding vegetation on the riverbank.

Apistogramma and tetras (*Hyphessobrycon*, *Copella*) were also found.

RIO YANAYACU (PERU)

Biotope No. 6

The Rio Yanayacu is a confluent to the Uyacali. The biotope from which the water sample was taken in July 1990 consists of a quiet cove. A thick layer of floating plants, such as *Ceratopteris pteridoides*, *Ceratophyllum demersum*, *C. submersum*, *Eichhornia crassipes*, *Limnobium laevigatum*, *Ludwigia helminthorrhiza*, *Phyllanthus fluitans*, *Pistia stratiotes*, *Ricciocarpus natans*, *Salvinia auriculata* and *Utricularia foliosa*, was found on the banks in slow-moving water. Due to the too small sample taken, it was not possible to determine the phosphate content. For the same reason, data on iron and manganese concentrations are also absent. Worth noting is the extremely low content of heavy metals.

The local fish fauna consisted of cichlids (*Apistogramma*, *Crenicara*, *Pterophyllum*) and a variety of tetras.

A dense layer of floating plants (*Limnobium laevigatum*, *Pistia stratiotes* and *Salvinia auriculata*) has formed on a riverbank and edge of the Rio Yanayacu (Peru) where there is hardly any current.

THE EAST AFRICAN RIFT VALLEY LAKES: LAKE MALAWI AND LAKE TANGANYIKA

Biotope No. 7

With their numerous colorful cichlids, the two East African lakes, Lake Malawi and Lake Tanganyika, form a fish paradise for aquarists. The following description and listing of aquatic plants collected from both lakes by the author shows that—contrary to popular opinion—the plant populations are not rare at all. The overall number of species present, though, is low despite the size of the lakes.

Ecological Data on Lake Malawi and Lake Tanganyika

Lake Tanganyika and Lake Malawi are located within the East African Rift Valley. Their banks are characterized by tremendously steep coastlines as well as rocks and pebbles, reed banks and sand zones. In the course of evolution, different societies of life forms have developed in these ecologically different areas. For lovers of cichlids specific to both Lake Malawi and Lake Tanganyika, the most interesting biotopes are found in the rock and pebble littoral. Because the soil there is unsuitable for higher aquatic plants, and free-floating aquatic plants, too, cannot resist the strong wave movement which is occasionally comparable to the surf on ocean coastlines, no aquatic plants are found in these interesting fish biotopes. Biotopes with plant growth are located in the transitional zone between boulder or pebble and sand zone, in the reed banks and in the sand littoral or, in other words, everywhere water movement is not as strong, for instance in quiet coves where plants can obtain a hold in the soil.

Due to the special ecological conditions, i.e., water readings which are rather extreme for tropical conditions (see Table 3, biotope

No. 7), as well as the strong current and wave movement and the great water depth, an effective process of selection took place in the lakes. Only species that were highly specialized or very adaptable and resistant were able to survive.

The water sample from Lake Tanganyika was taken by W. Staeck near Kalemie on the central west coast.

Plant Societies

The only floating plant in the Rift Valley lakes is the well-known *Pistia stratiotes*. However, it seems to grow only in locations that are protected to a certain degree by coves or islands. But even there it doesn't find ideal living conditions and thus cannot reproduce in large numbers, as is known to occur in marsh areas, due to the surf. All other aquatic plants in both Lake Malawi and Lake Tanganyika grow exclusively submersed and are either rooted in the soil or float freely above the water bed.

Populations of *Valisneria spiralis* var. *denseserrulata* can be found most often in both lakes. The living environment of the *Vallisneria* species is the sand zone, as well as the transitional zone between pebble and rock zone. The plants grow in a depth of 0.5–4 m (rarely up to 6 m) and are firmly rooted in the sand soil. They are found growing protected by stones and also in open sand coves, the beaches of which are often covered with torn off *Vallerisneria* leaves after a storm. Compared to *Vallisneria spiralis*, which are cultivated in aquariums, these plants have very hard leaves which is probably due to the extreme water chemistry prevalent in both lakes. Recovered samples developed similarly soft

The sand zones in Lake Tanganyika are typical living environments for aquatic plants.

leaves as the ones known to aquaristics, which clearly shows that *V. spiralis* reacts very changeably in its habit to different environmental factors and that it is a very adaptable and robust species.

Two other species often found in both lakes are *Ceratophyllum demersum* and *Myriophyllum spicatum.* Of all species evident in the lakes, the former will penetrate to the greatest depth: populations of this species will still grow in 10 m of depth whereas *Myriophyllum* is only found in a depth of about 3 m. Both species are often found growing close together in one location, obviously without obstructing each other's growth. Especially conspicuous in both species were their short internodes as well as the already mentioned leaf structure in *Vallisneria spiralis,* whereby a totally different appearance is formed compared to the cultivated plants. The shoots of *Ceratophyllum demersum* display a very compact growth within their natural habitat. Since their density is obviously larger than that of the cultivated specimens, they will not drift freely in the water or on the surface where they would be subjected to strong wave movement and would soon succumb, but on the substrate bed instead where the water movement is weaker. The fact that the unusual appearance of the plants was a consequence of their adaptation to the special conditions of their living environment became evident when the recovered shoots behaved just like the known cultivated specimens after a very short time and floated on the water surface in the aquarium.

Also among the plants often found in both Lake Malawi and Lake Tanganyika are *Potamogeton pectinatus* and *Potamogeton schweinfurthii.* Both often exist in association, or they form large submersed meadows with the already mentioned species. They often populate nearly the same ecological niche. Preferred habitats are protected sand coves or the transitional zone from the pebble to the sand zone. On the open coastline, however, the plants seem to be entirely absent due to their lack of resistance towards the powerful surf. Both species exist in a depth of about 0.5–4 m. The leaves of *P. pectinatus* are only 1 m wide and very hard, obviously again an adaptation to the strong water movement. *Potamogeton schweinfurthii,* with stems of up to 3.5 m in length, is the largest plant in the lakes. In this species, too, the hard and coarse leaf blades are worth noting. Especially conspicuous in both *Potamogeton pectinatus* and *P. schweinfurthii* were lime deposits on the leaves which can be attributed to the extreme water values in the lakes.

Of special interest, too, was the find of *Hydrilla verticillata* at Ndole Bay in the southern part of Lake Tanganyika. There the plant formed large, herbaceous populations in the sand zone which were rooted into the substrate by up to 1 m and stretched almost as far as the water surface. *Hydrilla verticillata* is well-known in aquaristics; the habitus of plants in Lake Tanganyika, however, varies distinctly from the appearance of cultured plants known by the same name (see also description on pp. 302–303). In Ndole Bay, the author also found *Najas horrida* in association with *Hydrilla verticillata,* a very conspicuous plant because of its habitus. A site together with populations of *Najas marina* subsp. *armata* in a reed zone in the vicinity of Monkey Bay in Lake Malawi was also found. Even though *Hydrilla verticillata, Najas horrida* and *Najas marina* subsp. *armata* are comparatively rare in both lakes, they seemed to be widely prevalent in that area.

The hard leaf and stem structure is worth noting in all aquatic plants found in the two lakes, an observation which can be clearly interpreted as an adaptation to the prevalent ecological conditions.

In contrast to the numerous endemic cichlid species, there are no endemic aquatic plants in either lake, but only exclusively those species that have a large distribution because of their adaptability.

LAKE ON MAFIA (TANZANIA)

Biotope No. 8

The small island of Mafia lies about 20 km off the Tanzanian mainland. In the north there are two lakes, the larger of which was researched. It featured rich plant populations which, because of the low water level, were not limited to the banks but were spread over the entire lake. Most of the lake was unshaded. Thick groups of *Ceratophyllum demersum*, *Utricularia inflexa* and *U. stellaris* grew in stagnant water and floated freely. Rooted into the substrate were numerous flowering samples of *Nymphaea lotus* and, on the banks, *Ceratopteris cornuta*. *Pistia stratiotes* and dense populations of *Salvinia* floated on the water surface. The strong alkaline pH-value of this lake as well as its very high conductivity (base rich in calcium) were conspicuous.

RIVER BIOTOPE WITH *APONOGETON MADAGASCARIENSIS* (MADAGASCAR)

Biotope No. 9

Aponogeton madagascariensis has without doubt been the most popular aquarium plant for many years. Because its continuous cultivation in the aquarium succeeds only rarely and the depth of variation of this species is exceptionally large, detailed ecological data can contribute answers to many open questions regarding a separation of different varieties or subspecies within this species. The most important known information on the ecology of *Aponogeton madagascariensis* has been summarized on pp. 132–133. A detailed analysis of the water of biotope No. 2 was undertaken. This habitat is located about 1 km

Aponogeton madagascariensis **in its native habitat on Madagascar (biotope No. 9).**

Table 3: Water values from several selected native habitats.

		Biotope No.					
		1 Rio Guaporé Brazil	2 Rio Sipao Venezuela	3 Rio Aro Venezuela	4 Rio Paraná Argentina	5 Rio Uruguay Argentina	6 Rio Yanayacu Peru
Date		July 1987	14/08/89	13/08/89	12/07/93	15/07/93	01/08/90
Water temperature	in °C	20	27	28	13	10.6	25
Air temperature	in °C	—	29.5	30.5	15	13	—
Time		—	—	12:00	12–14:00	12:00	—
pH-value		6.38	5.99	6.06	7.02	6.78	7.5
Conductivity (at 20 °C)	in µS/cm	22	12.2	22.6	35	18	205
Carbonate hardness (KH)	in °dH	0.69	<0.5	1.0	0.76	0.33	5.50
Total hardness (GH)	in °dH	0.41	<1.0	<1.0	0.51	0.31	5.11
Calcium hardness	in °dH	0.41	0.13	0.51	0.51	0.31	5.11
Magnesium hardness	in °dH	0	0.10	0.07	0	0	0.77
Carbon dioxide (CO_2)	in mg/L	10	19.3	32.4	2.5	1.9	5.9
Oxygen (O_2)	in %	—	—	—	70	90–99	—
Sodium (Na)	in mg/L	1.69	0.83	1.26	1.0	1.1	3.9
Potassium (K)	in mg/L	0.35	0.50	1.54	3.4	0.2	2.2
Iron ($Fe^{2+/3+}$)	in mg/L	0.21	—	—	—	—	—
Ammonium (NH_4^+)	in mg/L	—	0.07	0.32	traces	0.1	0.14
Chloride (Cl^-)	in mg/L	—	1.0	0.7	0.9	0.4	4.3
Sulfate (SO_4^{2-})	in mg/L	—	n.d.	0.2	1.2	0	4.4
Nitrate (NO_3^-)	in mg/L	<3	n.d.	n.d.	0	0.6	0
Nitrite (NO_2^-)	in mg/L	—	<0.16	<0.16	0	0	0
Phosphate (PO_4^{3-})	in mg/L	0	n.d.	0.12	0.1	0	—
Zinc (Zn)	in µg/L	—	7.1	21.6	24	27	7.0
Cadmium (Cd)	in µg/L	—	n.d.	n.d.	n.d.	n.d.	n.d.
Lead (Pb)	in µg/L	—	2.6	6.2	3	1	n.d.
Copper (Cu)	in µg/L	—	1.9	4.0	10	10	0.1

n.d. = not detectable

Table 3: Water values from several selected native habitats *continued*.

		Biotope number					
		7 **Lake Tanganyika (Kalemie)** Zaire	**8** **Lake (Mafia)** Tanzania	**9** **River** Madagascar	**10** **Sepik River** Papua New Guinea	**11** **River** Papua New Guinea	**12** **Tasek Bera** Malay Peninsula
Date		July 1982	January 1981	03/01/87	06/07/88	22/07/88	—
Water temperature	in °C	27	30	23.2	—	27	23–31
Air temperature	in °C	—	32	27.5	—	30	—
Time		—	14:00	10:00	—	12:30	—
pH-value		9.5	7.8	6.45	6.50	6.70	5.33
Conductivity (at 20 °C)	in μS/cm	593	1054	30	84	82	14.2
Carbonate hardness (KH)	in °dH	18.4	31	0.75	2.5	2.4	0.17
Total hardness (GH)	in °dH	11.03	>30	0.53	2.5	2.4	—
Calcium hardness	in °dH	—	—	—	1.8	1.1	0.05
Magnesium hardness	in °dH	—	—	—	0.7	1.3	0.06
Carbon dioxide (CO_2)	in mg/L	<2	10	10	—	—	14.9 (07:00 hrs)
Oxygen (O_2)	in %	50.8*	—	—	—	—	26
Sodium (Na)	in mg/L	61	5.56	3.3	4.3	4.7	0.86
Potassium (K)	in mg/L	31	0.44	0.6	0.7	1.3	0.56
Iron ($Fe^{2+/3+}$)	in mg/L	n.d.	0.05	0.05	0.02	0.02	0.64
Ammonium (NH_4^+)	in mg/L	0	0.1	0.1	0.10	0.10	0.304
Chloride (Cl^-)	in mg/L	31	6.9	—	traces	traces	1.93
Sulfate (SO_4^{2-})	in mg/L	traces	1.20	—	traces	traces	3.19
Nitrate (NO_3^-)	in mg/L	0	—	5	5	7	0.107
Nitrite (NO_2^-)	in mg/L	—	—	0.05	<0.05	<0.05	0.0074
Phosphate (PO_4^{3-})	in mg/L	0.09	—	0.3	<0.05	<0.05	0.624
Zinc (Zn)	in μg/L	n.d.	—	7	365	6	—
Cadmium (Cd)	in μg/L	n.d.	—	n.d.	—	—	—
Lead (Pb)	in μg/L	n.d.	—	8	5	n.d.	—
Copper (Cu)	in μg/L	n.d.	—	12	18	12	—

n.d. = not detectable. *Laboratory data: all water samples (except biotopes 8 and 12) were analyzed in the laboratories of the Tetra company.

away from the township of Beforona on the identically named river at an altitude of 900 m. Narrow-leaved plants of *Aponogeton madagascariensis* var. *madagascariensis* grew in knee-deep, slightly turbid water in a strong current, with the leaves hardly touching the water surface. The substrate consisted of sand rich in loam and mixed with gravel, larger stones and boulders. *Aponogeton madagascariensis* was found under a bridge as well as unshaded in loosely associated groups. Readings with a luxmeter (tolerance 1%) on 3 January 1987 at 10:00 h produced the following data: under slightly cloudy open skies (sun clearly visible, small white clouds) 70,000 lx, and 15,000 lx under the bridge in the shade; several minutes later, under a near cloudless sky and intensive sun radiation, the luxmeter showed a reading of 146,000 lx. The brown coloring of the leaves points to the plants growing under stronger light in their natural location, compared to cultivation, because the retrieved samples developed olive green leaves only at a later stage in the aquarium. It can be assumed that the water level at this location drops during the dry period to such an extent that the species' leaves flood to the water surface. This studied biotope, however, almost certainly does not completely dry up. Samples probably also grew in deeper water but were not visible due to the loamy, cloudy and murky water.

SEPIK RIVER NEAR ANGORAM (PAPUA NEW GUINEA)

Biotope No. 10

The Sepik River in Papua New Guinea is a river several hundred meters wide. Possibly because of its murky and clouded water as well as its quick current, only floating plants were found in this river, occurring increasingly in coves with hardly any current. During a boat trip which lasted 2 days and led from Ambunti downstream to Angoram, the following species were found, more or less always in large population groupings: *Salvinia molesta* (with sporocarps), *Pistia stratiotes* and *Azolla pinnata*, which flooded the water surface, as well as individual samples of *Ceratopteris thalictroides* and *Hydrocharis dubia*, which was often rooted on the riverbank. The water analysis of this biotope shows that the plants live in a very soft water, deficient in electrolytes and nutrients, and with a low conductivity. Whereas the content of the major plant nutrients, nitrogen and phosphorus, is very low, the high content of zinc is conspicuous.

RIVER BIOTOPE WITH *APONOGETON LORIAE* (PAPUA NEW GUINEA)

Biotope No. 11

Aponogeton loriae is a very rare aquatic plant which is endemic in Papua New Guinea. The studied biotope is located on the road from Port Moresby in the direction of the Vaimauri Plateau, 61 km from the airport of the Papua New Guinea capital. There *A. loriae* grows in dense populations in a small river that is about 2–4 m wide. The clear water flows slowly at a speed of about 25 cm/s. Whereas the water was knee-deep at the river's edge (without a distinct shallow water zone), it reached a depth of up to 1 m in the center. The plants were anchored in muddy, loose soil which was interspersed with a bit of gravel and a few stones, and could easily be plucked from the substrate soil. The location was unshaded. Conspicuous in the water analysis was the relatively high content of magnesium and potassium.

The fish fauna consisted of *Melanotaenia papuae* and *M. goldiei*.

TASEK BERA

Biotope No. 12

Tasek Bera is a 60 km^2 low-lying marsh area on the Malay Peninsula in the southwestern part of the State of Pahang. It is crisscrossed by many channel-like waterways and forms an important environment for aquatic and marsh plants. Furtado and Mori (1982) studied numerous ecological aspects of this biotope and summarized their 4 years of research in a comprehensive publication. Even though the author is not personally familiar with Tasek Bera, some essential research results should be summarized because this ecological data is of interest to aquarists. It is there that the largest populations of *Cryptocoryne purpurea* are found.

The marsh area, densely covered in parts by *Lepironia articulata* and *Pandanus helicopus*, and containing several lake-like areas of open water, is crisscrossed by numerous waterways as well as a main channel which has a weak current with a speed of 0.25 m/s. The dark brown water, which the authors compare to the black water of the Amazon region, is very clear and has a visibility between 1 and 2.5 m, depending on the time of year. Its surface temperature varies between 23 and 31 °C; readings on the bottom measured 23.0–26.6 °C. The water is very acidic and mineral-deficient, pH-testing revealed an average value of 5.33. The minimum read 4.5, and the maximum, depending on the testing method, read 5.2 and 6.8, respectively. With an average value of 2.09 mg/L the content of dissolved oxygen is rather low. The bottom is sandy but covered, however, with a thick layer of peat which is mixed with non-decayed plant material, wood and mud. Under the influence of heavy monsoon, rainwater levels will vary considerably by up to 5 m.

The following known marsh and aquatic plants were found in the studied area: *Blyxa aubertii* var. *echinosperma*, *Cryptocoryne purpurea*, *Eleocharis ochrostachys*, *Hydrilla verticillata*, *Ludwigia prostrata*, *Nymphoides indica*, *Potamogeton wrightii*, *Scirpus confervoides* and *Utricularia aurea*. Jacobsen (1986) also mentions the presence of *Barclaya motleyi*. The predominant aquatic plant in Tasek Bera is *Cryptocoryne purpurea* which is found in dense populations in the channels and in open water up to a depth of more than 1 m. They are more lush in semishaded areas compared to exposure to full sunlight. Water values listed in Table 3 represent average values resulting from numerous tests.

The Importance of Ecological Factors in the Cultivation of Aquarium Plants

The chapter on natural habitats of aquatic and marsh plants dealth with environmental factors which exert an essential influence on the plants' photosynthesis and growth. It can be concluded from the observations made that nature, as our teacher, can in many respects adopt a certain model function for the culture of aquarium plants. For aquarists this results in the challenging task of drawing the right conclusions not only from research of natural habitats, but also from the results of scientific experiments in laboratories and open areas. The goal to be achieved is the optimum cultivation of the plants in an aquarium.

In the following chapter, the importance of ecological factors for the maintenance of aquarium plants will be discussed. Attempts have been made to give general recommendations and suggestions in cases where it seems useful and appropriate.

Aquarium Temperature

Temperature in an aquarium is often underestimated in its importance as an ecological factor. As explained in detail on pp. 3–4 it has an important influence on the plants' metabolism. If some aquarium plants don't really want to grow and develop, the cause is often looked for in the lighting set up, in the water values or in the supply of nutrients, but it is common that an unsuitable temperature level is responsible for such bad and slow growth. *Cabomba caroliniana*, for example, can be kept at temperatures between 20 and 25 °C without any problems. At consistently higher temperatures, however, the shoots will soon perish. The bad growth of the plant in high temperatures is, therefore, not surprising because the species occurs in areas with a distinct seasonal climate. There, *Cabomba caroliniana* populates waters that display relatively low temperatures for most of the year. The question of optimum temperatures in an aquarium cannot be answered in general terms because each plant prefers a very specific and unique temperature range. Even though most aquarium plants can be maintained between 24 and 26 °C, this range does not always constitute the optimum environment. To facilitate the selection of the correct water temperature for the specific species kept in the aquarium, the temperature tolerances of the most important aquarium plants have been compiled in a table. The minimum, optimum and maximum temperatures can be read in Appendix 1. Data on the minimum and optimum temperatures constitutes reliable values derived from day-to-day operations and gathered on the basis of longstanding experience with the cultivation of aquarium plants in hothouses as well as aquariums. Maximum temperatures are based on, among others, numerous tests conducted in natural habitats. The maximum values of many species are possibly even higher than is currently assumed.

According to the current state of knowledge about the natural habitats of aquatic and marsh plants, it can basically be assumed that a moderate difference in temperature between day and night is conducive to plant growth. At the same time, considering the multitude of maintained aquarium plants from subtropical and temperate zones, it is recommended that the aquarium temperature be reduced by a few degrees during winter, which can be vital and essential for the continuous upkeep of the *Aponogeton* species. When translating these suggestions into everyday practice, the living requirements of those fish kept in the aquarium must, of course, also be taken into consideration. For fish, daily and seasonal variations in temperature are generally conducive and, in many cases, stimulating for their spawning behavior.

Light in the Aquarium

The fundamental importance of light for many growth processes in plants is discussed extensively on pp. 4–13. In their natural habitats the species have, over the course of evolution, adapted to the daily and seasonal changes in sunlight in order to make optimum use of the available light for photosynthesis. In contrast, plants in the aquarium rely on artificial light sources which, in addition, radiate continuously all day in an unnatural way. Most of the aquarium plants kept, though, are defined by the ability to adapt to this highly modified environment. It should be remembered that there are also aquatic plants that have not previously been successfully cultivated in the aquarium. One reason for this failure could be their lack of adaptability to static artificial lighting.

In early aquaristics, aquariums were often located close to a window where plants were exclusively subjected to daylight. Whereas growth was excellent during summer and many floating plants especially prospered lushly, many plants succumbed to conditions of very weak light intensity and very short lighting periods during winter. The uneconomical use of lighting with incandescent bulbs, too, is no longer up-to-date. Today, there is a large range of lamp types available to the aquarist from which he or she has to make the right choice to suit individual requirements.

For aquarists interested in solid plant growth, the choice of lamp type is made mainly according to two criteria: one, they have to feature a color spectrum suitable for the plants' photosynthesis; on the other hand, plants and fish are supposed to be displayed in lighting comfortable to human vision. What are the differences?

For a better understanding of this problem a few fundamental explanations of light are provided as follows.

Visible "white" light contains all spectral colors (from violet to blue, green, yellow, orange to red) which are each characterized by a specific wave length. This light is located in the range of 380 to 780 nm (nanometers). Over one hundred years ago, it was discovered that different light colors had different effects on plants. It was also found, however, that the spectral colors were received differently by the human eye compared to the plants. The latter require the entire light spectrum for the purposes of photosynthesis, preferably the red (around 700 nm) and, to a lesser extent, the blue (around 450 nm) spectrum range. In contrast, the maximum sensitivity of the human eye lies in the green-yellow spectral zone at 555 nm. Photosynthesis, however, displays a marked decline within this range. For plant growth, light utilization (efficiency) of the lamps alone is not the only relevant factor. The color spectrum ranges of the lamps are also important. Special plant lamps, for example, Sylvania Gro-Lux or Osram L-Fluora, were designed in such a way that they achieve maximum values in both red and blue spectrum ranges. This "red" light, however, is often perceived by humans as unnatural and is, therefore, only acceptable to most users in conjunction with other lamp types.

Remarkably, plants, within certain limitations, are able, because of their assimilatory pigmentation, to adapt to light colors (chromatic adaptation) as was shown in numerous scientific experiments using different colored light (see Gessner 1955). However, plants first have to adapt to a change in light quality, a process for which they probably need a couple of weeks. Some Cryptocorynes quite often react in an extreme way to a change in light color and intensity, displaying total decomposition of their leaves. Even when many plants display a proven and certain adaptability to light changes, one should not draw the conclusion that any arbitrarily chosen lamp will have the same enhancing effect on plant growth, and that the respective light spectrum is irrelevant. Such an opinion would totally contradict all previous knowledge about plant photosynthesis gathered from numerous scientific experiments. The importance and relevance of "plant-friendly" lamps because of their positive effect both on growth, as well as development of the pigmentation system (e.g., enhancement of the brown and red coloring agents carotenoids), remains highly controversial. For this reason the emphasis, when choosing lamp types, should always be laid on light quality, and aesthetic aspects should only be of secondary importance.

CHOICE OF LAMP TYPES AND LIGHT COLORS

There are a number of lamp types available to the aquarist for the purpose of illuminating plants and fish. For the hobbyists interested in solid plant growth, there is the initial basic question whether to use fluorescent tubes or high-pressure lamps (incandescent lamps, halogen incandescent lamps and mixed light appliances will not be dealt with here because of their negligible relevance and poor light utilization). The next consideration—as pre-

Dense and diversely planted aquariums are beautiful to observe.

viously explained—concerns the choice of light color that features a light spectrum with a high proportion of red focused on the plants' photosynthesis but, at the same time, also has a high degree of light exploitation as well as good quality color reproduction.

FLUORESCENT LAMPS

The advantages of fluorescent lamps are especially high light exploitation (higher degree of efficiency than high-pressure lamps), long durability, good color reproduction, good value for money and low energy consumption (high efficiency). The choice of light colors in fluorescent lamps is greater than that in high-pressure lamps.

Typical for fluorescent lamps is the fact that they provide balanced lighting of the entire aquarium in contrast to discharge lamps. A conclusion as to under which light plants and fish achieve a better effect, however, is purely subjective. The utilization of fluorescent lamps is around 7500 hours. A too high surrounding temperature, which can easily arise in lamps enclosed in hoods or reflectors, has to be avoided. The maximum light radiation lies around 20–25 °C. Surrounding temperatures deviating greatly from these figures will rapidly reduce light utilization and efficiency. Bad reflectors, too, considerably reduce light intensity. Self-adhesive aluminum foil has good reflectory qualities and is very inexpensive and of good value.

The new generation of three-banded spectrum (tri-phosphor T8) lamps with a diameter of 26 mm features a higher light exploitation compared to the "older" lamps with a diameter of 38 mm. Further development and expanded application in aquaristics of the modern compact fluorescent lamps is both trendsetting and desirable. These lamps are distinguishable by their compact design, very high light exploitation and long life-span. For the purposes of aquarium plant cultivation, warm-tone lamps produced by several manufacturers as well as special "plant bulbs" featuring a high content of red light are especially recommended. Obtaining individual special light colors is, however, not always easy.

Recommended warm-tone lamps (color temperature between 2700 and 4000 Kelvin) are the light colors with the international indications 827, 830, 930 and 940, as well as the corresponding compact lamps Dulux 830 and 827. If required, these can be combined with neutral white fluorescent lamps (e.g., 840, 940 or 184).

The specially developed plant bulbs Osram 77 L-Fluora, Sylvania Gro-Lux and Philips Aquatelle 89, have a lower efficiency than many other L-lamps, and today are also used to a lesser degree than previously because of the availability of other good light sources. However, their positive effect on plants due to their high red and blue content cannot be discounted.

DISCHARGE LAMPS

Mercury vapor high-pressure lamps and halogen metal-vapor (metal halide) lamps have been increasingly used in aquaristics over the last couple of years. For most aquarists using this type of lamp, two aspects are usually decisive: aquariums opening on top (limited accessability also by free-hanging fluorescent lamps) permit unusual effects; however, the selective spotlighting of the aquarium creates an appealing play of light and shade. A necessity also often arises to adequately illuminate especially deep aquariums. In these considerations the question of suitability of the light colors for plant growth are not sufficiently taken into account.

The disadvantages of discharge lamps are especially their high purchase costs, a comparatively small light exploitation compared with fluorescent lamps, the very limited choice of light colors and a disadvantageous compatibility with other lamp types or light colors. Also, the undesirable high-water evaporation in "open" aquariums and the consequently high humidity in the room should not be underestimated. The "dazzling" light of high-pressure lamps is also often considered to be irritating and interfering.

MERCURY VAPOR HIGH-PRESSURE LAMPS

Mercury vapor high-pressure lamps have a low light exploitation and a relatively bad color reproduction. An advantage of this lamp type, however, is the high life-span of around 9000 hours. For the lighting of plant aquariums, warm-tone lamps with a high content of red light are primarily considered. The most suitable is the light color Osram HQL Super de Luxe, only after which others such as the warm white-light colors Osram HQL de Luxe, Philips HPL Comfort, Radium HRL de Luxe and Sylvania HSL Comfort should be considered for use.

HALOGEN METAL-VAPOR LAMPS

In comparison to mercury vapor high-pressure lamps, light exploitation and color reproduction in metal halide lamps have been improved considerably. A disadvantage of the latter, however, is the comparatively low exploitation period of about 6000 hours. It is especially important for the user to know that halogen metal-vapor lamps emit UV radiation of around 2–5%. For this reason, the lamp may not be used uncovered but has to be fitted with a cover glass or discs which filter and absorb damaging UV radiation. During very high light intensity, a special UV filter has to be used. Negative experience with this type of lamp is possibly based on the absence of a cover glass. The destruction of pigmentation in the plants can occur as a consequence of excessive UV radiation.

In halogen metal-vapor lamps, too, the choice of light colors is, so far, very limited and the spectral range necessary for the

Most aquarium plants love light and require a high light intensity for optimum growth.

plants' photosynthesis is not sufficiently considered. Recommended primarily are warm-tone lamps from several manufacturers with the light colors Osram WDL, Philips HPI, Radium WDL and Sylvania WDL.

REQUIRED AMOUNT OF LIGHT

In order to adequately address this question, the author conducted numerous tests in natural habitats using a luxmeter (see Table 1). The results of these tests are also reflected in Appendix 2. Such test data is, of course, not exactly transferable to the aquarium environment, which obviously cannot be expected. For one, daylight features a different and changing spectrum compared to artificial light sources; also, the spectral range relevant for the plants' photosynthesis cannot be captured using a luxmeter which is tuned to the sensitivity of the human eye. Such test results, though, can still permit various conclusions as to the light requirements of plants in the aquarium and can, therefore, be useful and important in daily aquarium practice.

According to the studies undertaken by Sauer (1989), the light intensity on the water surface of an aquarium generally ranges between 10,000 and 30,000 lx. Already in a depth of 40 cm in a newly installed aquarium, a loss of light of 69% was registered. Tests conducted by the author resulted mostly in even lower readings. In aquariums that have operated for some time, light intensity is considerably reduced and changed negatively by the increase in coloring and clouding matter in the water. For this reason alone a regular water exchange is useful. Furthermore, it must also be considered that red light is absorbed first by the water, which is why, in very deep aquariums, this photosynthetic effective range only reaches the substrate in minimal quantities. Only very few plants, especially those that grow in deep water in their natural habitats, are optimally adapted to these conditions. The choice of suitable species for aquariums with a height of over 60 cm is thus drastically reduced. For an aquarist interested in solid plant growth, the first rule should be not to use very deep aquariums in order to create an advantageous light climate for the plants right from the outset.

If the test data of the natural habitats (Table 1) is compared to data obtained from aquariums, it can be clearly concluded that sun plants—and these constitute the majority of plants kept in aquariums (compare Appendix 2)—receive a considerably higher average light intensity in the natural biotope than in the aquarium. Furthermore, if the fact is taken into consideration that the majority of plants in their natural habitats are found in a maximum water depth of 30 cm, or above water in moist ground, these species can hardly be damaged by too intensive artificial lighting within the aquarium, as is often stated. It is hardly ever possible to subject the aquarium's light-resilient plants to too much light. However, considering the variety of species that are found in an aquarium within very limited confines, one has to clearly differentiate between plants with low light requirements (weak light or shade plants) and those with high light requirements (strong light or sun plants), and the aquarist has to try to accommodate both types. As clearly outlined on p. 8, shade plants achieve their highest assimilation at a low light intensity and can be damaged and die off due to too high light radiation. The requirements of shade plants thus have to be considered in the overall lighting of an aquarium. These needs can easily be met by choosing a shaded location in the aquarium, e.g., near side and rear panels.

The degree of light intensity cannot optimally meet the light requirements of both shade and sun plants simultaneously. Each aquarist has to select the degree of light intensity on an individual basis. As a rule, a "golden middle course" will have to be taken which has to meet and satisfy the needs of a variety of species. This, however, generally implies that extremely light-appreciating plants cannot optimally develop. The plant aquarist should, therefore, always select a higher luminosity and allocate shade-loving plants to a less bright spot in the aquarium.

Many aquarists have the understandable desire to be provided with guiding values for the necessary light intensity of their aquarium. The often employed parameter of watts per liter, however, is an inaccurate value, even when considering different aquarium dimensions, with which one can quite easily do entirely without. Also, the author has often asked herself how the installation of fluorescent lamps can take place on the basis of figures of one watt per liter of water. The number of lamps resulting from this calculation can usually not be accommodated in the lighting compartment! A better solution than the watt/liter data is the testing of the light intensity using a luxmeter or, alternatively, an exposure meter in consideration of light colors used. This solution, too, is generally impractical for the aquarist, is too expensive, and, furthermore, is unsatisfactory because the resulting values have hardly any meaning or relevance.

The most important pointer to optimum growth and correct lighting is provided by the plants themselves. They react, for example, to a favorable or unfavorable light environment with typical changes in their appearance. Check for yourself if the shoots display a strongly elongated growth with extended internodes (etiolation), if the stems lose their lower leaves, if the plants remain much smaller than indicated in the species descriptions given in this book, if they develop less luxuriantly than seen in the photos, if red coloring is unsatisfactorily pronounced, and if no red stem tips have developed which are typical for many well-illuminated plants. If you basically have to answer these questions in the affirmative then you should definitely increase your aquarium's light intensity.

It was stressed that special care has to be

Close-up of a Dutch aquarium displaying lush plant growth.

taken of shaded plants because they could be damaged under certain circumstances through excessive luminosity. Practice, however, shows that this danger is rarely prevalent because the usual aquarium lighting is designed as too weak in any case.

Things look different, however, in the typical Dutch aquariums which became famous for their excellent plant growth. The secret of these aquariums lies in a very high light intensity which is achieved through a maximum number of mountable fluorescent lamps. Under close scrutiny the preferred use of demanding and light-requiring plants becomes evident. These intensely illuminated aquariums can be considered as a yardstick for optimum plant maintenance. If you are interested in a similar and quick plant growth you should follow this path and not save on light intensity. Such aquariums, however, are not only very demanding with regard to care and maintenance, because the rapid plant growth necessitates continuous trimming and replanting, but also have a high energy demand. An entirely practicable alternative, as proven by practice, involving a far lower energy consumption, consists of selecting only aquarium plants that are satisfied with low-to-medium light intensities. This way an aquarium of Dutch standards can be realized.

In conclusion, it should be stressed that satisfactory plant growth can only be established if the interrelation of all growth factors like temperature, substrate and nutrient conditions are taken into account.

DAILY LIGHTING PERIODS

The question about the daily lighting period can best be answered if one visualizes the conditions to which aquarium plants are subjected within their natural habitats. Almost all cultivated aquatic and marsh plants exist in the tropics and subtropics between the equatorial zone and a geographical latitude of 30°. In the vicinity of the equator the daily lighting period measures a constant 12 hours. In a geographical latitude of 10° the length of day will vary according to the season between 11:30 and 12:40 hours, at 20° between 11:00 and 13:20 hours, and at a 30° geographical latitude between 10:12 and 14:05 hours. In this area plants under an open sky will thus be subjected to a daily lighting period of about 10 to 14 hours. In the course of evolution plants have, to a large degree, adapted to this day-night rhythm. For species existing in deeper water the length of day will be shorter than on land because of the light reflection on the water surface during a lower positioning of the sun.

It has previously been concluded from this assumption that the lighting period in the aquarium has to last only 8–10 hours. This conclusion, however, has to be strenuously contradicted since its implementation can lead to a considerable loss of plants! The above data has to be considered in a far more differentiated way: for one, it has to be taken into account that the shortest lighting period of 10 hours at a latitude of 30° does not continuously last over the entire year, but only during a short span lasting a couple of weeks during "winter" and thereafter again slowly increases to 14 hours. On the other hand only a relatively limited number of aquarium plants permanently exist in greater water depths where reflection, in fact, does considerably shorten the underwater day. For all other species, however, i.e., most aquarium plants, the reflections on the water surface have no essential effect on the lighting period.

As is the case with many other factors one would have to differentiate between different species with regard to the question of the optimum lighting period. Since this is impossible due to the, in many cases, insufficient knowledge about natural habitats, a middle course, which satisfies just about all plants, is suggested. This compromise consists of a minimum lighting period of 12 hours. The maximum lighting period is less critical and can be around 15 hours. Assimilation performance, however, cannot be increased beyond a certain lighting period which is why its extension will not have any positive influence. Furthermore, it also has to be considered that a very low light intensity can be balanced through extending the lighting period.

To accommodate as many plants as possible in the aquarium the recommended daily lighting period lies between 12 and 13 hours. A reduction to as low as 10 hours daily can be handled temporarily by many plants, but studies conducted by the author also showed that several species collapsed entirely after several weeks under such conditions.

The seemingly curious and alien plant-damaging call for a "rain day," in other words the switching off of the aquarium lighting for one day per week, also must be strenuously contradicted. Even if it should rain uninterrupted in the tropics for an entire day, which is very rare, light intensity is thereby not reduced to 0.

The Aquarium Substrate

Most cultivated aquarium plants are marsh plants which draw their nutrient requirements to a large extent from the substrate through an extensive root system and only to a limited degree from the surface of the plant. Only in genuine aquatic plants are the roots reduced to such an extent that their function mainly lies in the plant's anchoring and only to a lesser extent in the absorption of nutrients. These plants exist almost exclusively on ions freely available in the water, where, however, they occur in much smaller quantities than in the substrate.

Even though a lot has been said in the past about the quality of the substrate it can not be disputed that the substrate has an important function for the nutrition of aquarium plants. If optimum plant growth is the set goal, the choice of substrate material containing sufficient nutrients has to be considered in setting up an aquarium. Liquid fertilizers, added to the aquarium water, only serve as an additive and are no substitute for a nutrient-rich substrate.

The following factors have to be considered when choosing a substrate:

- The substrate should contain little or no substances which could rot (e.g., humus).
- The pore volume has to be sufficiently large so as not to impede aeration and water movement within the soil but also enable the roots to easily penetrate. Only then is an optimum exchange of substances by the plants guaranteed.
- A nutrient-rich substrate should be used.
- The substrate should feature an acid to neutral reaction (check with minimum 6% hydrochloric acid; in case of strong foaming the substrate contains excessive lime). Only few aquarium plants (e.g., *Cryptocoryne affinis*, *C. crispatula* or *Vallisneria* species) react to a substrate's alkaline pH-value with improved growth compared to an acid milieu.

In the chapter on the substrate as a source of nutrients (pp. 13–14) it was pointed out that, in the natural habitat, loam soils (mixture of sand and clay) with a high content of humus have the most favorable effect on plant growth. Soil analyses (see Horst 1986) also show that the nutrient depot in the soils of natural waters is generally higher than in aquarium substrates. However, conditions in natural locations can be transferred only in a limited way to the aquarium because, in contrast to the natural habitat, there are far fewer soil organisms in the aquarium providing good aeration, and, furthermore, the substrate also lacks a sufficient current. The ratio of water to substrate, too, is considerably smaller in the aquarium compared to the natural environment where rotting processes have a different effect than in an artificial biotope.

In fact some aquatic plants are able to adapt to their natural living conditions in such a way that they can even exist quite well in muddy, badly aerated and oxygen-deficient anaerobic soils, possibly even preferring this sort of milieu. The number of aquatic plants found in such soils is, however, limited to very few species, for example, some water lily plants and *Ludwigia* which, due to numerous morphologic adaptations (large cavity system, rich aeration tissue and respiratory roots), nevertheless allow root respiration. It has to be emphatically stressed that most aquatic plants cannot prosper in such an extreme milieu. Even though some soils in which many aquarium plants grow in their natural habitats often hold a content of humus substances, it can be shown from soil profiles that sufficient aeration and oxygen supply are provided because it is usually a mixture of different soil components.

Because the soil in natural locations often contains humus, this realization in the past occasionally led to the portentous conclusion that organic material in large quantities had to be added to the substrate to obtain good plant growth in the aquarium. Experience in cultivation, and also some experiments conducted by the author, however, have repeatedly shown that the use of a lot of organic material as substrate in the aquarium can lead to excellent growth results in the initial months, with plant populations subsequently collapsing due to the substrate becoming strongly compressed, as well as lack of aeration. In the same way, the exclusive use of loam, clay, laterite or similar soil substrates in the aquar-

Due to morphological adaptation, *Nymphaea micrantha* is able to prosper in soils low in oxygen content (native habitat in Senegal).

ium is to be fundamentally rejected because an inescapable dying off of the roots within a couple of months will be the consequence for the reasons mentioned.

As a consequence of the interrelationships outlined above, rough, coarse, unwashed lime-deficient sand is recommended as the main component of the substrate. This can be covered with quartz gravel with a maximum grain size of 1–3 mm. Depending on the plants' nutrient requirements a small quantity of loam or clay or commercially available laterites (usually with added trace elements) can be added to the sand (don't use all three) in order to boost the substrate's nutrient depot for the plants. When using such additives there is always the danger that, over time, they will compress and condense the substrate too much. There are several ways to counteract such compression and hardening in the long term:

- Using a substrate heating system or the installation of timers on the fluorescent lamps under the aquarium floor is recommended. The achieved heating of the substrate effects a slight increase in water movement and thereby aeration of the substrate. The same effect can be achieved if the aquarium is positioned (with a gap of a few centimeters) above a central heating element.
- Keeping dog periwinkles (*Melanoides tubercularia*) is useful. The reproduction of the snails, however, can be explosive if provided with a good substrate climate, necessitating their regular removal. This is possible, for example, by using a piece of apple connected to a piece of string, positioned on the aquarium floor, around which the snails will gather after a while.
- Occasional and partial loosening of the substrate, for instance during cleaning or planting, also has a very growth-enhancing effect.

These measures, however, will not prevent the substrate's depletion, over the course of time, in nutrient content. Unfortunately aquarium dealers do not offer any comparable fertilizer preparations for the substrate, similar to ones that have been available for years for pot plants. Fertilizer rods or granulate fertilizers for potted plants should only be used in aquariums with extreme care and in a limited and controlled dosing.

Water in the Aquarium

THE INTERRELATIONSHIP OF CARBON COMPOUNDS, PH-VALUE AND CARBONATE HARDNESS

Carbon constitutes a vital element for the nutrition of higher plants. In contrast to terrestrial plants which obtain their carbon requirements exclusively from the carbon dioxide content of air, aquatic plants supply themselves with this nutritional element essentially from the different inorganic carbon compounds in water (CO_2 = carbon dioxide, H_2CO_3 = carbonic acid, HCO_3 = hydrogen carbonate, CO_3^{2-} = carbonation, $Ca(HCO_3)_2$ = calcium hydrogen carbonate).

Carbon dioxide, which transforms to carbonic acid by combining with water, constitutes one of the most essential nutrients for the plant's photosynthesis. With a low pH-value there are predominantly both free carbon dioxide and carbonic acid present. If carbon dioxide is extracted from the aquarium water through the plants' assimilation process this will—next to other factors, for example, the fish's respiration—result in an increase in the pH-value. As soon as the free carbon dioxide in the water has been exhausted, the plants will behave very differently. Whereas in some species growth will cease (for example, in all *Fontinalis antipyretica* studied so far), other aquarium plants are able to also assimilate and utilize the hydrogen carbonate ions (biogenic decalcification), resulting in a further increase in the pH-value. The outcome is a precipitation of the insoluble calcium carbonate ($CaCO_3$) which becomes visible by the lime crusts on the plants' leaf surfaces. Scientific research has proven that the pH-value can be increased to about 11 through the consumption of hydrogen carbonate ions by aquatic plants. Many species that depend on the supply of free carbon dioxide, will, however, cease their growth already at an earlier stage. Previous failures in the cultivation of rare species adapted to specific living conditions possibly have their cause in this.

Numerous studies of natural biotopes show that most aquarium plants live in a weak acid, calcium- and salt-deficient water which contains a sufficient supply of free carbon dioxide and carbonic acid. Even though many of these plants are adaptable within certain limitations and have a relatively wide pH-tolerance, they probably still prefer an environment as described above. Other aquatic plants, however, due to their extreme dependency on free carbon dioxide, are not, or are only to a limited degree, able to extract hydrogen carbonate from the water. For their photosynthesis a sufficient supply of free carbon dioxide, above all, is essential in the aquarium. Only a relatively small number of tropical aquatic plants populate natural habitats with calcium-rich water and an alkaline pH-value. Plants in these waters are generally characterized by their ability—during photosynthesis—to additionally extract the necessary carbon dioxide from the present calcium hydrogen carbonate ions. The consequence from these chemical-biological connections, which result from numerous biotope and laboratory studies, is the necessity to set and adjust a pH-value in the aquarium which can meet the different requirements of the largest number of plants possible. Such a pH-value should lie roughly in the range between 6.2 and 7.2.

Strongly assimilating aquarium plants consume a lot of CO_2 which is why it is often necessary to add this nutrient and furthermore to maintain the pH-value in the above range. To enable fertilization with CO_2, dealers offer different apparatus. It has to be stressed, however, that a necessity for additional CO_2 supply is given only when the aquarium is densely planted as well as illuminated and the natural production of carbon dioxide, e.g., through the respiration of the fish and oxidation processes, is insufficient for the nutritional upkeep of the plants, which is indicated by a calcium-lime precipitation. Regular testing and control of the pH-value demonstrate the value of CO_2 fertilization. It is important to know in this context that high concentrations of carbon dioxide are toxic for fish and that there also are fish species that cannot handle low pH-values. Regular measurements using CO_2 tests (follow instructions issued by the manufacturer) are, therefore, essential in maintaining an optimum CO_2 content.

However, for the cultivation of aquarium plants, not only familiarity with the interrelationship between pH-value and the water's carbon dioxide content is important, but also the connection between carbonate hardness (also referred to as alkalinity or acid-binding capability) and carbon dioxide. The higher carbonate hardness the more carbon dioxide is required to maintain the calcium hydrogen carbonate in soluble form, in other words to prevent the precipitation of lime. For this reason it is often useful to remove the mostly high carbonate hardness from the tap water. For instance, partial desalination through a weak acid cationic exchanger or full desalination is recommended. The treated water can be balanced to a favorable pH-value between 2 and 8 °dH by mixing it with tap water. Aquarium water with an even lower carbonate hardness has a very low pH stability and is primarily required for the breeding of some soft water fish species, but not for the cultivation of most aquarium plants. Waters with a carbonate hardness above 15 °dH generally constitute an unfavorable living environment for optimum plant growth because the pH-value can only be adjusted to a small degree due to its high stability.

THE SUPPLY OF NUTRIENTS IN THE AQUARIUM

Always typical of natural waters with rich plant populations is the presence of all the vital nutrients important for growth. If even a single nutrient is missing or is present in insufficient supply it will, according to Liebig's Minimum Law (1855), constitute the one growth-impeding factor. In contrast to natural water, tap water contains many of the essential nutrients for plants—such as iron, potassium, manganese, sodium, etc.—in inadequate quantities or not at all. Other nutrient components, on the other hand, like nitrogen and phosphorus, are present in mostly high concentrations. Therefore, it is occasionally necessary to add fertilizer to the aquarium water which contains all available nutrients for plant growth in a favorable combination. Furthermore, it is occasionally necessary to remove existing deficiencies—e.g., iron deficiency—through a special fertilizer containing trace elements. Because the range of commercially available fertilizers is large, a specific recommendation cannot be given. Basically, though, the application of such preparations should be done carefully and sparingly. Initially a dose smaller than that recommended by the manufacturer should be administered and the reaction monitored. An excessive supply of nutrients often leads to a catastrophic growth of algae.

Finally, it should not be forgotten that nutrients are absorbed in different quantities and composition by every plant species. To determine the nutrient requirements of a specific aquarium plant, scientific laboratory experiments are necessary, which until now, had mostly not been conducted. The results could form the basis for an optimal nutrient supply (which until now has been impossible to precisely target) and facilitate the easier detection of occurring deficiency symptoms in aquarium plants. A forward-looking and progressive aquaristics is called upon to confront such questions with more vigor.

WATER CIRCULATION

As explained in detail on pp. 14–16, water movement has an important function for the plants' photosynthesis. For this reason—and contrary to all other recommendations—care has to be taken that sufficient water movement is provided in planted aquariums. It becomes especially important when the aquarium is only thinly populated by fish and water circulation stagnates. Attention also has to be paid to the fact that, regarding water movement, the requirements of individual aquarium plants differ widely as well. Conclusions can be drawn from ecological data found in the descriptions of the individual species.

The required water movement is generally best achieved through the use of a filter with a low to medium output. In aquariums of more than 500 L contents, the installation of two filters is recommended, one of which runs very slowly and functions on a biological basis, whereas the second one primarily looks after the mechanical cleaning of the water and at the same time results in good water circulation. Switching off the filter overnight, as is occasionally recommended, not only constitutes animal torture due to a rapidly developing oxygen deficiency, especially in densely planted aquariums, but also has negative effects on the gas exchange and plant metabolism due to the stagnation of the water.

THE IMPORTANCE OF OXYGEN

It is undisputed that oxygen has an important function in the aquarium. In the aquarium oxygen producers stand opposite oxygen consumers, the latter including mainly the plants during the dark phase as well as all

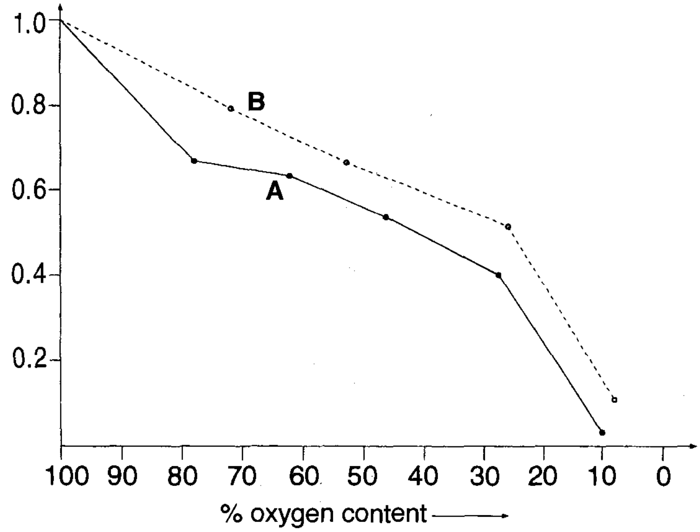


Diagram 3 Relative respiration intensity in higher aquatic plants under conditions of a decreasing oxygen content. A. *Fontinalis antipyretica*; B. *Lagarosiphon major* (according to Gessner and Pannier 1959).

microorganisms. The share of the oxygen consumed by fish is, in contrast, comparatively negligible. During the day the aquarium's oxygen content will increase essentially as a result of the plants' assimilatory activity and will peak in the evening. Furthermore, oxygen absorption by the water through movement on the water surface can occur. As a result of intensive assimilation by the plants, an occasional high over-saturation of the water by several hundred percent can take place. For example, the author registered an oxygen content of 198% in a pond densely populated with *Elodea canadensis*. This value, however, indicates an imbalance, namely the fact that the formation of assimilatory oxygen takes place quicker in water than the oxygen release into the atmosphere and the oxygen consumption by the organisms in the water. Such an over-saturation is, however, never achieved in an aquarium.

The organisms' oxygen needs increase with temperature because the respiration intensity also increases with temperature. On the other hand the saturation value of oxygen in water is highly dependent on temperature. This saturation value registers at 9.4 mg/L at 20 °C, 8.6 mg/L at 25 °C and −8.0 mg/L at 30 °C.

Since the mid 1980s the importance of oxygen in the aquarium and its effect on plant growth has and is being controversially debated. One specific author repeatedly voiced a certain unsupportable opinion, even though numerous experts have countered with convincing arguments on many occasions. Still this author has continued to repeat this dubious and dangerous thesis even in most recent times (Krause and others 1990) in magazine articles and books in a rather stubborn way. In the following I would like to outline the most important arguments and statements he used in support of his thesis:

A low oxygen content apparently considerably enhances growth in submersed aquatic plants and also is the most conspicuous feature of aquariums with a prospering plant population. In aquariums with a high oxygen content nutrient gaps and growth stagnation are very likely to occur. Aquariums with well-growing plants will regularly show a very low oxygen content between 3 and 4 mg/L (mornings) and 6 mg/L (evenings). An oxygen content that does not exceed 5 mg/L in the evening is targeted because plants can suffer under a high oxygen content. If the oxygen content is above the value it is recommended to let the filter run more slowly, to reduce light intensity, to generously feed and to plant more densely in order to enhance mutual shading. This author has discovered through testing of her own that tropical plant biotopes regularly display low oxygen contents (between 3.5 and 5.5 mg/L). He further stipulates that most aquarium fish are accustomed to surprisingly low oxygen content. Lush populations of aquatic plants in nature are, according to him, mostly coupled to the outflow of groundwater because the cause lies in the high nutrient supply of the nearly oxygen-free groundwater. Sensitive nutrition gaps form downstream which prevent further plant growth. So much for a brief summary of the most important assertions.

In the following, counter-arguments are given that will contradict these assumptions. They are, for one, based on secure scientific data as well as on numerous tests which were conducted in aquariums as well as many natural habitats by several authors, including this author. Furthermore, the effects of a targeted increase in the oxygen content, effected by oxidators, on plant growth in the aquarium was observed over a period of many years.

The counter-arguments:

- Scientifically conducted studies on numerous aquatic plants show that the respirational intensity of higher aquatic plants is dependent on the water's oxygen content. Their respiration will drop off when the oxygen content drops, whereas water over-saturated with oxygen will lead to a distinct increase in respiration on the part of the aquatic plants (Gessner 1959). The respiration of the roots behaves likewise for which the oxygen content can quickly turn into a limiting factor which is why good aeration of the substrate (not only with terrestrial plants but also with most aquatic plants) has to be ensured. Since the respiration intensity of a plant is an indicator for its metabolism, i.e., also for its speed of growth, a high oxygen content in the aquarium water will have a favorable effect.
- The assertion that tropical plant biotopes are mostly oxygen-deficient is incorrect. Numerous tests have shown that natural waters with dense plant growth can display not only a low but also a very high oxygen content which lies above saturation (between 4 and 14 mg/L, in black water streams also between 2.3 and 3.5 mg/L, see also Horst 1986). Furthermore, the assertion that especially lush plant growth is mostly coupled to groundwater sources has to be firmly contradicted. The author observed countless biotopes without groundwater sources, e.g., small temporary waterways featuring dense plant populations or rivers which displayed a continuous, massive presence of aquatic and marsh plants over a distance of several kilometers.
- During the dark phase plants are reliant on an external oxygen supply. If the oxygen content of the aquarium is very low overnight, it can drop to levels not only fatal for fish, but also have a negative impact on the growth of plants due to reduced respiration.
- Due to their strong assimilation a high oxygen concentration will always be the result of many fast-growing plants in the aquarium; the latter can be considered a

barometer for an optimum aquarium. Oxygen readings in so-called "Dutch aquariums," famous for their excellent plant growth, show—under conditions of a normal technical input but intensive lighting and CO_2 fertilization—an increase in the oxygen content of about 70% in the morning to up to 130% saturation in the evening. With these observations, though, it has to be differentiated and taken into consideration that the differing growth speed of the individual plant species influences the oxygen content in varying degrees. An aquarium with predominantly slow-growing species will display a lower oxygen production than one featuring exclusively fast-growing species. .

- Nutrient deficiency can occur both with lower as well as higher oxygen values. The oxygen content of several aquariums was artificially increased by using oxidators. The aquariums were then observed over several years. Not only was a visibly improved plant growth registered but another positive side effect developed, namely the growth of blue-green algae being completely terminated in a few cases. This context is clearcut; the reasons for it, though, remain unexplained. In the studied aquariums only an occasional fertilization (every 4 weeks at the most) was necessary, and not as a consequence of nutrient oxidation but because of an increased nutrient consumption due to the strong growth of the plants.
- A reduction of precipitated nutrients as well as an improved availability of plant nutrients will only occur under oxygen values so low that they are dangerous and often fatal for all the aquarium's organisms. Today's fertilizers for aquatic plants contain chelating agents (complexing agents) which bind slightly oxidating nutrients.
- It has been scientifically proven for many years that a high oxygen content in water has a directly enhancing influence on plant growth and is an important factor for the propagation and biotope attachment of individual species. The occurrence of species from the Podostemaceae and Hydrostachyaceae families is, for example, restricted to tropical waterfalls because their respiration intensity and their oxygen requirements are exceptionally high. The plants will die if oxygen values are too low, the most important cause for the failure of cultivation experiments in the aquarium. *Aponogeton madagascariensis* (Kiener 1963), too, only grows in clear, fast-flowing waters and not in stagnant ones because of its high oxygen needs. It can be assumed that many aquatic plants preferring to live in rapid-flowing water also display this biotope attachment or link due to their high oxygen requirements.

The following point also underlines the necessity for a high oxygen content in the aquarium:

The oxygen content of water is of fundamental importance for the activity and reproduction of microorganisms (e.g., bacteria) since these are responsible for the self-cleaning process of waters (oxidation of toxic substances to nontoxic end products). With an increasing O_2 content their reproduction rate will also increase and with it oxygen absorption as well. In a high oxygen content environment in an aquarium, plant and animal waste products (fish feces, food scraps, and dead plant matter) are thus oxidated more rapidly to form nontoxic substances. A high oxygen content is, therefore, desirable.

All consumers of oxygen in the aquarium (plants, fish, microorganisms, etc.) produce carbon dioxide, one of the most important nutrients for plant growth. A high oxygen consumption, however, is only made possible by a high oxygen content. High oxygen usage improves not only the nutrient climate but simultaneously leads to a reduction of the pH-value which is generally desirable in most instances.

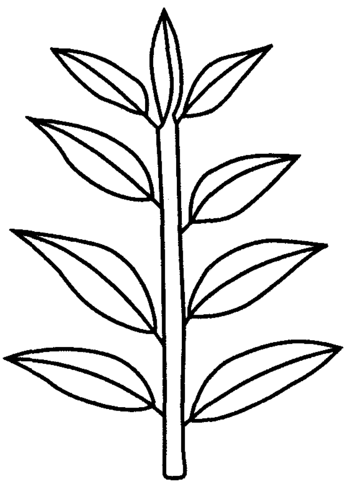
There are, however, a few fish species where it was proven that they do exist in a low oxygen environment. But since a variety of fish species are kept in the aquarium the oxygen level has to conform to the highest requirements and not the lowest. When oxygen content is too low it creates stress conditions for many fish and has to be interpreted as animal cruelty. A sudden filter breakdown will then quickly lead to the fish's demise.

CONCLUSION

The oxygen content of water exerts an important influence on the life of plants, animals and microorganisms because it quite often constitutes the deciding factor for their survival. Through optimal plant growth oxygen values of up to 130% of saturation can be registered in the aquarium. This value represents a level which is not damaging to fish or plant growth. On the contrary, it is scientifically indisputable that a high oxygen content has a positive effect on all forms of life in the aquarium and that an extremely low oxygen level in water is always an indicator for a negative, harmful environment.

A high oxygen content in a plant aquarium requires a resupply of nutrients more often. This resupply, however, is conditional on the optimal thriving of the plants, which results in an increased nutrient consumption, and to a lesser extent on the precipitation of nutrients.

Oxygen reduction always entails a deterioration in the environmental conditions of all organisms. Therefore, all measures taken to intentionally reduce the oxygen level are dangerous, unbiological and are to be rejected outright. A stable oxygen content must be aimed for, with minimum levels of 5 mg/L in the mornings and 8.6 mg/L in the evenings, which corresponds to about 60 and 100% saturation at 25 °C. This high oxygen content can primarily be achieved through the optimum assimilation of the plants. Other supporting measures are, for example, the removal of dying and decaying plant matter, a regular water exchange, etc.



Flower Morphology

It has become increasingly evident over the last couple of years that the general interest shown by aquarists in plant biology and flower morphology has increased strongly. This is due to a variety of reasons. Flower formation is, on the one hand, seen as the ultimate crowning achievement of a successful cultivation process. Flower characteristics, on the other hand, also constitute indispensable identification aids. The following chapter is designed to provide the reader with a simple description of the flower structure and different forms of inflorescence, essential for a wider understanding of the subject.

Flower Structure

Complete flowers consist of sepals, petals, stamens as well as carpels. Sepals, which are usually of a green color, primarily serve to protect the internal flower organs during the budding stage. Petals are usually very conspicuous in form and color, thus functioning as a lure for pollinating insects. Calyx and corolla together form the perianth. If sepals and petals are similar in structure the perianth is called perigon and its constituting parts are referred to as tepals (e.g., in *Aponogeton*). In a gamophyllous corolla one differentiates be-

Flowers of *Lobelia cardinalis* are especially conspicuous in their coloration.

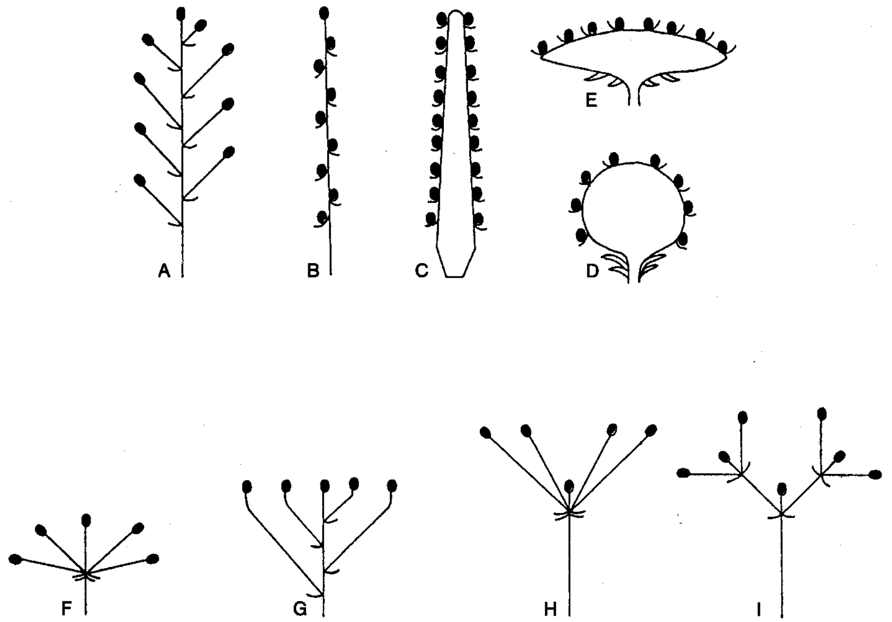


Diagram 4 Simple inflorescences. A = raceme, B = spike, C = spadix, D = capitulum, E = calathium, F = umbel, G = umbelliferous raceme, H = pleichoasium, I = dichasium.

tween the tube, the edge, which is often partitioned into sections, and the throat (e.g., in *Bacopa*, *Lindernia*, and *Hemianthus*). Sepals as well as petals can be free or adnate. The stamens are made up of the filament and the anther. The latter is divided into two compartments (thecae), each theca again being partitioned into two pollen sacs in which the pollen is produced. The two thecae are linked through a connecting piece (connective) to which the filament is attached. In the interior of the flower we find the pistil which in turn consists of the ovary, the style and the stigma. The ovary accommodates the ovules which will develop into seeds after fertilization. The ovary will then swell and the fruit will begin to form.

Flowers which have the full complement of reproductive organs—including stamens and carpels—are referred to as being *bisexual*. If either stamens or carpels are absent the flower is referred to as being *unisexual*. In this case flowers are *male* (without carpels) and *female* (without stamens). Usually both male and female flowers are found on one and the same plant, which is then called *monoecious* (e.g., *Cryptocoryne*). If, however, they

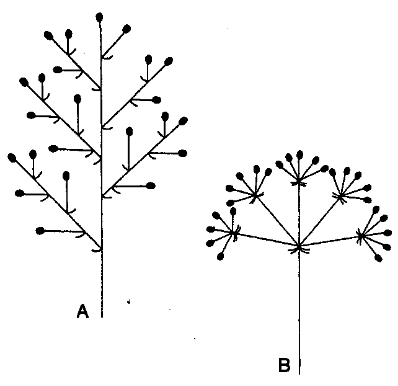


Diagram 5 Composite inflorescences. A = panicle, B = compound/composite umbel.

are distributed over different plants, they are called *dioecious* species (e.g., *Vallisneria*).

Forms of Inflorescence

In most instances several flowers are united in forming inflorescences, only occasionally are they arranged individually. One differentiates between *racemic inflorescences*, featuring one main axis, and *cymosic inflorescences* with several axes.

The *raceme* belongs to the category of racemic inflorescences in which petiolate flowers of roughly the same length are arranged on one main axis. In contrast to the raceme the *spike* features sessile flowers, from which the *spadix* can be distinguished by a thickened main axis. A shortening of the main axis leads to a capitulum, also called calathium, when it is a lot wider and surrounded by involucral leaves. A raceme in which all flowers are roughly found at the same height, is called a *corymb*. In contrast a shortened main axis results in an *umbel* if all solitary flowers are petiolate and stem from one central point in a radial way. Through the branching of the side axes the raceme becomes a *panicle*. This is called a *corymbose cyme* if all flowers are located on the same level. If, in an umbel, all solitary flowers are exchanged for umbels, the result is referred to as a *compound umbel*. A *compound spike* exists when the side axes display the shape of spikes.

In *cymose inflorescences* the main axis ends with a terminal flower and is also shorter than the side axes which originate at a point below and are able to branch out.

Depending on the number of side axes one differentiates between other forms of inflorescence: *monochasium* with one side axis, *dichasium* with two side axes, and *pleiochasium* (often referred to as cyme) featuring more than two side axes.

Flowers of *Utricularia foliosa* are set in a raceme.

Flower Biology

The flower biology of many aquatic plants is unique within the flora. The following chapter is designed to provide an insight into the often fascinating pollination mechanisms and also to be an incentive to delve further into this very interesting topic.

Pollination by Animals, Wind, Water

Pollination is defined as the transfer of the pollen onto the stigma of the carpels. It generally occurs through animals as well as wind or water. If a flower is pollinated with pollen from another flower *cross-fertilization* takes place. *Self-pollination* occurs if a flower is pollinated by its own pollen or by pollen from the same plant.

Flowers are commonly pollinated by insects such as bees, butterflies, and others (*zoidiogamy*). They are attracted by the color of the flowers and conspicuously shaped floral organs (visual stimulants) as well as odorous substances. When visiting a flower insects will, in most cases, discover pollen and nectar, which serve as nutrition, thereby quite unintentionally conducting pollination.

Anemogamy or *wind pollination* is another frequent occurrence in the plant world during which pollen is transported through wind. A prerequisite for this method is, for example, a smooth and dry pollen which has to be produced in large quantities in order to ensure that pollination takes place.

In most aquarium plants, the majority of which are marsh plants and flowers or inflorescences which are formed outside the water, pollination occurs through insects and/or wind. The author was able to observe butterflies, flies, beetles and bees during pollination of the *Echinodorus*, *Nymphaea* and *Sagittaria* genera in their native habitats. Interesting, too, is the impressive pollination mechanism of *Victoria amazonica*. If one opens a white, day-old flower at the natural location in the Amazon region (on the second day it will have turned a deep red), one will often find large beetles within them. These are attracted by odorous substances, the conspicuously white flower color as well as a temperature higher by about 10 °C (due to increased respiration) compared to the surrounding temperature. They enter the flower on the first evening once it has opened. Because the flower closes during the day, thereby trapping the beetles inside, they are only able to continue on to another flower the next evening, where they will deposit the foreign, imported pollen onto the stigma. Cross-pollination thus takes place, because the stigma will only be receptive to pollen during the first night. The pollen of its own flower will only mature when the stigma have again lost their susceptibility.

In some "genuine" aquatic plants, e.g., *Potamogeton* and *Myriophyllum*, which form their inflorescences close above the water surface, wind pollination will often occur in their natural environment. It is worth noting that flowers and inflorescences in such species are very inconspicuous and far less specifically shaped than plants reliant on pollination through insects, as is the case in the *Nuphar* and *Nymphaea* genera.

Pollination through water (hydrophily) occurs in very few aquatic plants. Adaptation to this medium developed in the course of evolution in the form of a strong specialization, which is specifically evident in the fact that luring and stimulation features (such as flower color, shape, and size) as well as the number of flowers and floral organs are very limited or reduced. Occasionally the flowers don't even disseminate odorous substances; they have entirely lost their function as instruments of attraction for insects.

Only in a few aquatic plants, e.g., *Ceratophyllum* and *Najas*, is the pollen floating in water actually transported by water to the (female) stigma. The perianth in these species is either greatly reduced (*Ceratophyllum*) or entirely absent (*Najas*). In other aquatic plants the water only serves as a method of transportation for the pollen or the male flowers which float on the water surface and are driven to the female stigma by wind. In some species, which raise their unisexual flowers above the water surface, pollination occasionally also takes place through rainwater.

During cultivation of aquarium plants in paludariums or in greenhouses the natural pollinating agents will usually be absent so that artificial pollination has to be conducted in order to achieve seed development. Transmission of pollen is easily completed using a fine brush or finger. In some *Aponogeton* seed formation was also achieved through the use of fruit flies which were encased in a plastic bag over the inflorescence.

The flowers of *Victoria amazonica* are pollinated by large beetles (photographed on the Amazon near Manaus).

Flower Biology in Hydrocharitaceae

Unique in our flora is the secretive flower biology within the Hydrocharitaceae family, well-known to aquarists through the genera *Egeria*, *Elodea*, *Hydrilla*, *Lagarosiphon*, *Ottelia*, and *Vallisneria*. Within the 16 genera and more than 100 species, which are exclusively aquatic plants, one will discover entirely different mechanisms of pollination, the research and study of which has not been completed to this day.

The regularly noticeable unisexuality of the flowers and the often occurring dioecious plants are conspicuous. There are, however, also species which are either male or female or even display bisexual flowers, as is the case in *Ottelia alismoides*. It is interesting to note that despite a considerable reduction in the flower organs the flowers of some species still have the ability to perform pollination and produce seeds (cleistogamous), even though the flowers do not open under water.

The appearance of cleistogamous flowers in *Ottelia alismoides* and *Blyxa aubertii* is well-known to aquarists, but also in other species in other genera, e.g., *Barclaya longifolia* (Nymphaeaceae).

Many flowers within Hydrocharitaceae are comparatively small and inconspicuous. They are nevertheless visited regularly by insects which are lured by odorous scents leading them to trigger pollination. The insects are often rewarded with nectar which is secreted

The conspicuous coloration of *Nymphaea rubra* flowers, found in a thermal lake near Héviz (Hungary), serves to lure insects.

by special glands. Sometimes, though, e.g., within the species belonging to the *Blyxa* genus, insects are not attracted or rewarded with any nectar.

In nearly all Hydrocharitaceae the visit by insects plays a vital role in the pollination process. Substantiated observations, though, regarding the species of the pollinating insects are only available for a few plants. Occasionally small flies were seen to visit the flowers of various species. The only species within this cognate circle which are pollinated through the wind, and not insects, are *Limnobium spongia* and *L. laevigatum*, this fact having been established through observations during cultivation and in the plants' native habitats.

A pointer to wind pollination occurring in these species is also the absence of odorous substances and nectar, as well as a very dry pollen which is easily transported and carried away by wind movement.

The flowers in Hydrocharitaceae are very delicate. To prevent them from being destroyed by wave movement the plants have specifically adapted to the medium water and developed special features. If, for instance, the female flowers of *Hydrilla verticillata* are submersed by water, the petals will close and the stigma will remain dry due to an enclosed air bubble. In *Egeria* the flowers are lifted above the water surface if water movement is very strong.

Within the Hydrocharitaceae family only few species utilize water as a method of transport to perform pollination. In *Elodea* the unmoistened pollen floats on the water surface and is carried by water movement to the female flowers which also float on the water surface. The female flower is surrounded by a small depression which helps in attracting male pollen.

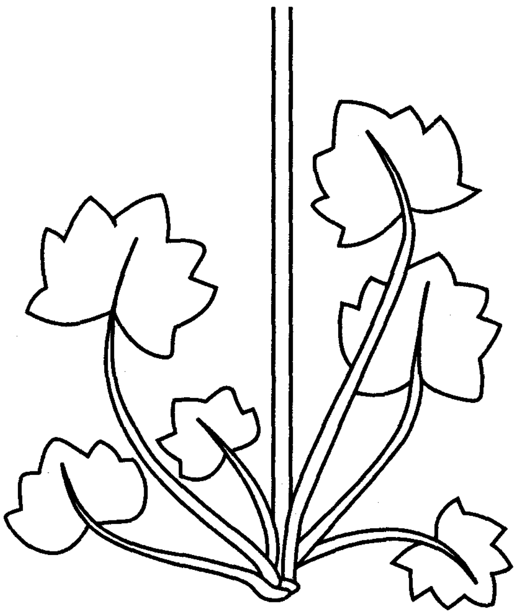
In the well-known genera *Vallisneria* and *Lagarosiphon* the male flowers themselves constitute the method of transportation and transmit the pollen directly onto the stigma belonging to the female flowers floating on the water. Water is indirectly part of the pollination procedure. In *Vallisneria* var. *americana*, a multitude of male flowers is released from a short spathe which then rises to the water surface as buds. There they will open, their tepals bending back, with the male flowers now being driven by water movement towards the female flowers. The female flowers float individually on the water surface on a long, spirally twisted pedicel. Because the stigma are arranged sideways, they are unreachable for the pollen. Only under the water's wave movement will the pollen access the stigma.

As outlined for *Vallisneria* the male flowers of the *Lagarosiphon* genus float on the reflexed tepals on the water surface. Three fertile stamen are horizontally arranged; three staminodes (sterile stamen) in an upright position form a "sail." Using this they drift towards the female flowers which lie slightly depressed (or in a small depression) on the water surface and thereby transmit the pollen onto the stigma.

Among aquatic plants the pollination mechanisms of the monotopic genus *Hydrilla* are unique, which is why they are worth being mentioned here as well. Each male spathe contains only one male flower. To mature the spathe will break open; the gas-filled bud will rise to the water surface and will float on the water for about 1.5 hours. It then opens abruptly through an interesting unfolding mechanism and flings its pollen in a radius of about 20 cm. The female flower will form a broad funnel on the water surface, which is positioned in such a way that only the top edges touch the water surface. The interior of this funnel contains the stigma. If the pollen is then thrust out of the anther of the male flower, a part of it will fall directly into the funnel of the female flower and is thereby transmitted to the stigma.

Even though the Hydrocharitaceae have developed very complicated pollination mechanisms, fruit are only rarely found in their natural habitats, which is generally due to the irregular distribution of the sexes.

The fascinating pollination mechanisms of Hydrocharitaceae described above are, in part, even more complicated than in the brief description given. Further study of this interesting topic can provide a more detailed insight into the secretive diversity of the flower biology of aquatic plants. Publications by C.D.K. Cook (1982 and 1994/1995) are highly recommended for further reading.



Sexual Propagation of Aquarium Plants

Sexual propagation is understood to mean reproduction by sexual means, occurring through seeds in flowering plants as well as other higher plants. Prerequisites for sexual propagation are flower formation, pollination, fertilization, as well as the production of fruits and seeds (refer also to the chapters "Flower Morphology" and "Flower Biology").

Even though there are only a few aquarium plants that occasionally produce flowers in submersed cultivation, and propagation through seeds is predominantly conducted by aquatic plant nurseries, the topic of sexual propagation deserves a short chapter, especially due to the fact that some plants only reproduce sexually.

Sowing and Growing

The most important prerequisites for successful sexual propagation to take place are, obviously, mature and germinable seeds. The right point in time for the harvest of seeds is usually when the fruits open up and release the mostly brown seeds. For a variety of reasons an immediate sowing is sometimes undesirable. In such cases it is essential to know how long the seeds will retain their germinability. For many aquarium plants there is, however, insufficient information available about this. Comparative studies putting the age of the seeds in relation to the germination rate are so far unknown for aquarium plants. It is known that, for example, in some *Echinodorus* species, several seeds many years old are still germinable. In contrast, the seeds or fruits of *Aponogeton* and *Cryptocoryne* species will float for a short time on the water surface, where they will basically germinate immediately, otherwise losing their germinability rather quickly. Temperature, too, is a major factor for germination. In aquarium plants tropical temperatures of 30 °C and higher will often lead to higher germination rates than lower temperatures.

It seems surprising with the multitude of aquarium plants that fruit formation in cleistogamous flowers can only be seen in very few species. Aquarists are most familiar with the formation of fruit in *Barclaya longifolia* and *Ottelia alismoides*, but it also occurs in *Blyxa*, *Hydrothrix* and often in *Ludwigia* species. In *Barclaya* and *Ottelia* the mature fruit will suddenly burst open, with the seeds dispersing throughout the aquarium, where they will usually fail to germinate due to insufficient light. With the aid of a nylon stocking slipped over the fruit, the mature seeds can be easily collected in order to conduct controlled sowing at a later stage. This method can, of course, also be used for other species, e.g., *Aponogeton crispus*.

There are several different methods to perform sowing. In marsh plants the seeds are usually sown in moist soil and under conditions of high humidity. The substrate can also consist of a different soil if this contains sufficient nutrients. Good lighting is also essential. The seeds from aquatic plants are left to germinate in water. The mature seeds from *Barclaya* and *Ottelia*, for example, will develop roots and leaves after only a few days in water. The embryos are then set into small pots or bowls containing a loam-sand mixture and introduced into water under good lighting. With a little care a small pot can also be located on the aquarium's edge. This pot is covered with gauze or any other wide-meshed fabric to avoid snails and fish damaging the very tender and delicate small plants. With increasing plant size the gauze can be removed. After several weeks it can often be noted that the growth of the juvenile plants suddenly stagnates, possibly due to nutrient deficiency. In such cases the author was able to restimulate growth by removing the plants from the substrate and after trimming the roots, replanting them in a different location.

The sowing and growing of juvenile plants through seeds is generally protracted, laborious and rarely pays off in the end. For these reasons sexual propagation is used by aquatic plant nurseries in only a few species. It is, however, useful in cases where vegetative propagation is possible only in insufficient quantities, or where reproduction is possible only through seeds (e.g., *Aponogeton*).

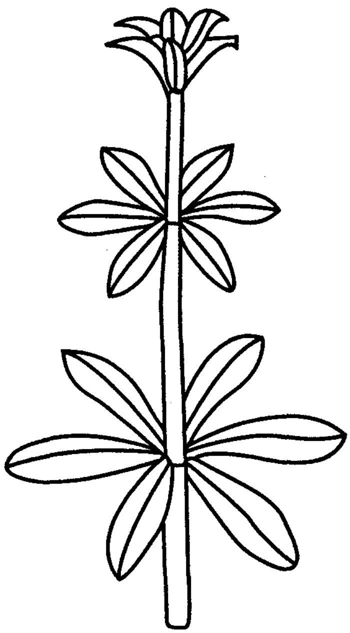
Cultivation of Aquarium Plants

Cultivation of aquarium plants is defined as a process of selection of variations which are genetically different. The aim of the cultivation of aquarium plants is to obtain new plants for aquaristic purposes which are conspicuously different in their coloration and appearance from the original species. In addition improved growth performance is desired. Such methods are well established in the cultivation of ornamental and useful plants; they are, however, relatively new in aquaristics. Often genetically different parent plants are used in the cultivation of hybrids

Breeding of *Isoetes velata* var. *sicula* through spores.

(well-known in *Echinodorus*). Furthermore, new plants can also be produced and selected through natural or induced mutation. *Cabomba caroliniana* 'Silver-Green' and *Echinodorus schlueteri* 'Leopard' have, for example, come about through incidental mutation.

Cross productions should be clearly marked as such by a multiplication symbol (×). The introduction of a cultivar name is also possible. A prerequisite for the introduction of a cultivar, though, is the genetic consistency of a plant, i.e., the transfer of all features from one generation to the next must be guaranteed. Cultivar names must be drawn from a living language and enclosed in single quotation marks.



Vegetative Propagation of Aquarium Plants

Vegetative propagation means reproduction by nonsexual means. In the following chapter different methods of reproduction will be described which are part of the daily practice of aquarium maintenance and which can also easily be performed by the layman without the use of any extra facilities.

Cuttings

A large number of aquarium plants form creeping or upright growing shoots. These stem plants can be split up into stem axis (stem) nodes, on which the leaves are arranged in differing phyllotaxis and internodes. Most stem plants are characterized in the aquarium by a very high degree of lateral branching which has its origin in the leaf axils. These lateral branches can be cut off and used as cuttings so that reproduction in general does not pose a problem. *Ludwigia* and *Hygrophila* species, for example, but quite a few other aquarium plants, too, count among those species featuring an intensive formation of lateral shoots.

The group of stem plants, however, also contains species that only develop lateral shoots but where, at the same time, a more intense reproduction is desired. To enhance the development of lateral shoots the strong stems can be cut into segments (part or shoot cuttings) each featuring two to four nodes. When partitioning the plant it is best to use a scissors or knife to cut just below the node where root formation will occur later on. Leaves are also removed from this node in order to prevent rotting in the substrate. The stem tip of the parent plant will continue to grow unbranched as a cutting. The remaining part cuttings are planted into the substrate where, after only a few days, they will generally form adventitious shoots usually at the highest node.

Trimming stem plants that have grown too high can be done easily in the aquarium. The shoot tip is severed and again planted; the rest of the stem can also be segmented or can remain in the soil where it will again branch out.

Species of the *Ceratophyllum*, *Egeria*, *Elodea*, *Hydrilla*, *Lagarosiphon* and *Najas* genera mostly grow below the water surface in their natural habitats and form no roots or only a few roots which they use to anchor themselves in the soil. Flooding growth causes the shoots to tend to branch out a lot, and they will reproduce through fragmentation (separation into part segments), so that vegetative propagation of the species mentioned is not complicated.

Runners

Reproduction through scions, too, which occurs on more or less long runners (lateral shoots with extended internodes) of strong parent plants, is of great relevance in aquaristics. Cryptocorynes, small-growing *Echinodorus* species as well as representatives of the *Vallisneria* and *Sagittaria* genera produce scions. Some floating plants, too, reproduce in this way. Known examples for an especially productive propagation are *Eichhornia* *crassipes* and *Pistia stratiotes*, but also *Trapa natans*, *Hydrocleys* and *Limnobium* species.

Propagation through scions rarely poses problems for the aquarist. Care must be taken, though, to ensure that the scions are not severed too early from the parent plant because this would lead to no or at least stunted growth. Whereas Cryptocorynes should be disrupted as little as possible in their growth, thinning out dense populations and replanting scions becomes necessary in *Echinodorus* and *Sagittaria* species.

Division

Numerous aquarium plants develop a more or less thickened rhizome, i.e., a rhizome which enables the survival of a disadvantageous vegetation period in natural habitats by acting as a storage organ. The rhizome in *Anubias barteri*, for example, is very long, comparatively thin and branches regularly. In contrast the rhizomes of the large-growing *Echinodorus* species are conspicuously thick, only a few centimeters long and a branching can only occasionally be seen in strong parent plants. To increase the reproduction rate long rhizomes may be divided using a sharp knife into 2–3-cm long segments which should display several plumules, if at all possible. These rhizome segments can float freely on the aquarium's water surface under intensive lighting until new plants develop from the dormant buds.

Propagation through the division of rhizomes is relatively productive in *Anubias* species; in *Echinodorus* species, however, it will not always be successful.

Adventitious Plants

The formation of adventitious plants on leaves, petioles, roots and inflorescences of the parent plant is well-known to aquarists. Propagules on the margins can often be seen in ferns such as *Ceratopteris* and *Microsorum*, whereas in pond lilies, such as *Nymphaea micrantha* and *Nymphaea* × *daubenyana*, they are found on the leaf base, ensuring easy vegetative propagation in these species. In *Microsorum* shoots will also form in large quantities on the roots hanging in the water.

Detached leaves floating on the water surface will form adventitious plants at the fractures, which can be severed after attaining a sufficient size, e.g., in *Hygrophila* species, *Gymnocoronis spilanthoides* and others. Some species, for example *Samolus valerandi*, *Rorippa aquatica* and *Physostegia purpurea*, develop leaf axillary plants on the peduncles.

Especially important for a productive propagation is the formation of adventitious plants on the inflorescences of many *Echinodorus* species. Depending on the individual species these will form in differing quantities on the whorls (refer also to the induction of flowering in *Echinodorus* species on pp. 239–240). If peduncles form underwater on sword plants, it is recommended to press these below the surface, despite their attempt to protrude the water surface. The formation of adventitious plants will then usually occur quicker and more intensely than when above water where

Today many aquarium plants are being cultivated through tissue culture.

the plant offspring can easily dry out and not form any roots due to usually low temperatures and low humidity. After reaching a size of about 5 cm and producing a few roots, the adventitious plants may be severed and replanted.

Of the family of Aponogetonaceae, only *Aponogeton undulatus* displays this unusual vegetative propagation through propagules which are formed instead of the rare inflorescences.

Bulbils and Brood Tubers

Reproduction through bulbils and brood tubers is very common in the cultivation of ornamental and useful plants. Among aquarium plants tubers are known to occur only in the species belonging to the *Aponogeton* genus; in most cases, though, they are incapable of producing brood tubers.

Bulbils are occasionally formed on strong specimens of the *Crinum* genus; this form of reproduction, however, is rarely productive. The development of bulbils in the aquarium is more common especially in *Crinum calamistratum*.

Propagation of Certain Floating Plants

The vegetative reproduction of certain small-growing floating plants is quite interesting, which is the reason why they deserve separate discussion at this point. *Phyllanthus fluitans* as well as *Azolla* and *Salvinia* species develop numerous lateral shoots which will separate from the parent plant after reaching a certain length (fragmentation) or, alternatively, break up into their individual branches after their older parts have died off.

Lemna, *Spirodela*, *Wolffia* and *Wolffiella* display a very unusual propagation in that their daughter limbs grow from lateral or basal pockets on the parent plant. Under advantageous growth conditions the reproduction rate of these plants is very high, resulting in the water surface in the aquarium becoming overgrown and clogged up within a short time.

Propagation by Tissue or Meristem Culture

A modern method of vegetative propagation is achieved through the help of cultivation in test tubes, a practice that has already found application for a long time with useful plants (e.g., strawberries, beets, and orchids) and which is also being increasingly used in aquatic plant nurseries.

Reasons in favor of tissue culture in aquatic plant nurseries are, for one, the more rapid reproduction compared to conventional methods, and also the considerably reduced requirement for space. Furthermore, some rare species, for example, *Aponogeton* and *Crinum* specimens, which can only be produced in insufficient numbers or not at all under normal cultivation conditions, can be reproduced in such great quantities using tissue culture that any importation from native habitats will soon become unnecessary. Another important advantage in the application of tissue culture is that juveniles grown from meristems (growth tissue) are usually genetically identical (clones) and are identical to the original plant. This, for example, enables the reproduction in a test tube of especially decorative hybrids, which otherwise do not sexually reproduce, or in which a genetic splitting during seed reproduction might be expected, with the plants thus being able to be preserved. In the breeding of useful plants (e.g., in cloves) it is also of great importance that juveniles resulting from suitable meristems are virus-free.

The application of tissue culture demands a high financial outlay by the aquatic plant nurseries, based on the purchase of complicated apparatuses, laboratory instruments, which are required for sterile work practices, and air conditioned rooms. Above all a comprehensive biological knowledge base in the field of tissue reproduction is necessary because the individual aquatic and marsh plants differ in their reaction to the quantitative ratio of supplements and additives in the nutrient mediums, with a special series of experiments always being a necessary prerequisite for almost every species.

For this very reason only the larger plant nurseries in Europe (alongside some aquarists) are involved in this future-oriented and promising method of reproduction.

Practical Application of Propagation by Tissue or Meristem Culture

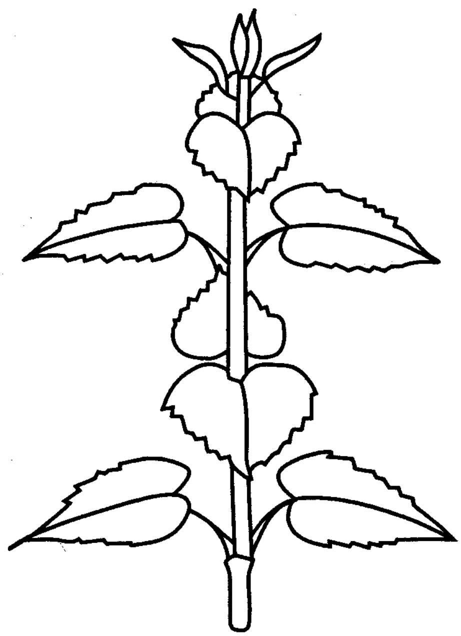
Suitable tissue, which has the capacity for continuous cell division, is removed from the parent plant. In most cases it is growth tissue from the stem or root tips. These meristems are disinfected so that they are free from fungi and bacteria, and are then transferred onto a sterile nutrient medium. The most important components of the nutrient solution are water, minerals, organic substances, as well as certain vitamins and plant hormones. By adding agar-agar (a colloidal substance extracted from red algae) the nutrient base is transformed into a gelatinous form so that the meristems are unable to drop to the bottom. The tissue parts now grow through cell division, resulting in a collection of nondifferentiated cells (callus tissue), called callus. These calli can, in turn, be cultivated further by transmitting them onto other nutrient media. If the nutrient solution contains a plant hormone which aids the formation of shoots, numerous very small plants will develop from these vegetatively reproduced single cells, which, after reaching a certain size, are transferred to another nutrient solution in order to enhance their root formation. Sometimes nutrient media are used which simultaneously trigger shoot and root growth. Once the little plants are big enough they are partitioned, either reapplied or removed from the petri dishes or test tubes and relocated from the sterile environment to the hot house where they continue to be cultivated until they are large enough to be sold. The biggest problems facing tissue culture are infections through microorganisms, such as bacteria and fungi, which can quickly destroy the cultures.

Tissue culture is by no means used exclusively for rare species or species which are difficult to reproduce by conventional, costly methods. It is also used for stem plants which in turn can easily be propagated vegetatively through cuttings. Next to the initially mentioned general reasons in favor of propagation through tissue culture, producers also list a more bushy and compact habitus of meristem plants compared to conventional methods, which is why meristem plants can be better marketed. This reason does not immediately seem rational, the differences are, however, clearly visible when comparing

Tissue section of a *Cryptocoryne* with shoot.

plants from normal propagation with those obtained through meristem culture.

Even though there are still many nurseries in Europe in which propagation through tissue culture is not practiced, this form of vegetative multiplication will, in the future, have the best chances in the market. There is also the legitimate hope that especially decorative but presently rarely kept plants, for example, the cross *Aponogeton* × *rigidifolius*, can be made available to a larger circle of hobbyists. Even today the demand for aquarium plants is increasingly being met through the application of tissue culture.



The Correct Choice of Aquarium Plants

The comprehensive range of plants available from dealers can mislead aquarists into selecting aquarium plants according to visual characteristics and not according to species requirements. Failures in cultivation are, therefore, often a consequence of such action. In order to be able to make the correct choice of aquarium plants it is necessary to familiarize oneself with the requirements and features of the individual species. To facilitate the right decision within the wide range of aquarium plants some general hints are provided in the following chapter.

Most plants kept in aquariums are marsh plants, usually originating from above-water cultivation in nurseries and being offered in this form in aquarium dealerships. Aquarists often, and quite unwarranted, view emersed cultivated plants very negatively, because many plants rid themselves of their emersed leaves during replanting underwater, which, of course, can lead to problems during the setting up of new aquariums. However, emersed cultivation of aquarium plants has big advantages over the submersed maintenance: on the one hand the marsh plants will grow considerably more quickly above water, and are less vulnerable or sensitive during and after the transfer into a different and new environment. On the other hand lower operating costs (heating and lighting) in nurseries also mean lower prices, which benefit the aquarist. Furthermore, European nurseries have to compete with the cheap mass imports from Asian and South American countries. Because emersed plants first have to adapt to a submersed lifestyle, it is useful, if possible, to also include acclimatized and established submersed cultivated and fast-growing species in the setting up of a new, larger aquarium. These can, for example, be obtained from aquarist friends, plant exchanges or fairs, regularly organized by aquarist associations in larger towns. When using "genuine" aquatic plants the problem of readaptation to a submersed environment will not occur, which is why they should be used in new aquariums.

Don't be afraid of taking along a book on aquarium plants when making your purchase and making your selection according to the information provided. The dealer will be more capable of offering advice and suggestions if you can provide him/her with photos of the desired species as well as their scientific names.

Aquarium plants are often sold in bundles, and some aquatic plant nurseries have fortunately adopted the method of providing the bundles with a label indicating the name as well as tips on maintenance. This can certainly facilitate the choice for the purchaser.

Genuine Aquatic Plants

Only some of the aquarium plants available are so-called "genuine" aquatic plants which also exist continuously submersed in their native habitat. Some even flower underwater; others, in turn, form their inflorescences close to the water surface. The Hydrocharitaceae family, for example, with the genera of *Blyxa*, *Egeria*, *Elodea*, *Hydrilla*, *Hydrocharis*, *Lagarospihon*, *Limnobium*, *Ottelia*, *Stratiotes* and *Vallisneria*, contains exclusively aquatic plants. Representatives of this family which are kept quite often are the species belonging to the genus *Vallisneria*, which can all be recommended without exception. *Egeria densa* is also part of the permanent contingent available at dealers; this species, however, is mainly suited for cold-water aquariums or garden ponds. *Stratiotes aloides*, too, which is occasionally commercially available, is generally used as a cold-water plant. All other species belonging to these genera are, unfortunately, only rarely available.

Only real aquatic plants are available from the *Aponogeton* genus as well. Some fast-growing recommended species are *Aponogeton boivinianus*, *A. crispus* and *A. ulvaceus*, which are also suited for new aquariums because they develop numerous leaves in quick succession. *Aponogeton madagascariensis* is an exception and is very popular because of its lattice-like leaf structure but is very sensitive in cultivation.

Other recommended and commonly available aquatic plants are *Crinum thaianum* and *C. natans* as well as several different pond lilies (*Nymphaea*). Some floating plants occasionally found in dealerships have only limited use in aquariums because they will progressively grow smaller in cultivation. Among these are *Eichhornia crassipes*, *Pistia stratiotes* and *Salvinia* species.

A larger number of easy to maintain "genuine" aquatic plants, such as *Ceratophyllum*, *Potamogeton gayi*, *P. wrightii*, *Zosterella dubia*, *Utricularia*, *Najas* and *Nymphoides* species, are, regrettably, only rarely found. If the opportunity to purchase one of the above arises at some stage, it should definitely be grasped.

An impressive biotope on Bali with dense populations of *Ottelia alismoides*. The plants exist unshaded under intense sunlight.

Distinguishing Aquatic and Marsh Plants

Under close scrutiny some species, for instance *Ceratophyllum* and *Utricularia*, can already be identified as "genuine" aquatic plants by discovering the absence of any roots. In most cases they also have, as a typical feature, fragile, thin, often dissected and fine-structured aquatic leaves, the function of which is to enlarge the surface area. The submersed plants have only a very thin epidermis (outer skin), which enables the absorption of gas, water and nutrients. The supporting tissue in stems and leaves is accordingly usually weak. If one looks at a cross-section through a submersed stem—*Ammannia* or *Limnophila* are suitable examples—the clearly marked or pronounced form of the intercellular spaces is evident: air tubes and air storage spaces, which provide a solid gas diffusion, can be made out quite clearly. This feature, together with a little experience, enables the easy recognition of aquatic plants and submersed growing marsh plants.

A conspicuous characteristic of aquatic plants are the often transparent leaf blades found in several *Aponogeton* species. Other plants have quickly adapted their leaf structure to the fast-flowing water in their native habitats by developing ribbon-like and bullate leaves, for example, some species belonging to the *Crinum*, *Cryptocoryne* and *Vallisneria* species.

Fast-Growing Marsh Plants

Marsh plants make up the major part of the range of aquarium plants. In their natural habitats they grow both submersed (under water)

Anubias barteri var. _caladiifolia_ at a waterfall in Limbe (Cameroon). The plant is excellently suited for large aquariums holding cichlids.

as well as emersed (above water). Dependent on seasonal variations in the water levels many marsh plants develop differently structured leaves under water as an adaptation to their submersed existence to those formed above the water surface. A good example of this is *Hygrophila difformis* whose emersed leaves display an undivided shape whereas the submersed shoots appear totally different and have pinnatisected leaf blades.

As mentioned before, aquarium dealers mainly offer emersed cultivated plants. In order to choose the right aquarium plants it is necessary to learn how to distinguish between the forms living above and below the water surface. If one is not familiar with the individual species, this task seems exceptionally difficult at first. There are, however, several features that quickly indicate if the relevant plant has grown under water or not. The chapter on genuine aquatic plants has already pointed out the typical structure of aquatic leaves. Fast-growing marsh plants kept underwater also feature thinner and more delicate leaves compared to terrestrial forms, as well as a relatively soft and often sponge-like stem. If plants reared in the aquarium are removed, most species will let their leaves hang down limply, which also happens with the stem in stem plants. In contrast terrestrial plants usually display stiff upright leaves and stems.

Another conspicuous characteristic of submersed cultivated plants is the lacking pubescence. *Alternanthera reineckii*, *Bacopa caroliniana*, *Hygrophila difformis* and *Limnophila aquatica*, for example, only display a distinct pubescence above water, and are otherwise glabrous.

Fast-growing and recommended species

In its native habitat in Cameroon *Anubias barteri* var. *glabra* often grows emersed on stones. It will, however, adapt well to submersed conditions.

which are often commercially available and only require a short period of adaptation to a submersed environment are the representatives of the *Bacopa*, *Ceratopteris*, *Hygrophila*, *Limnophila*, *Ludwigia* and *Echinodorus* genera.

Other undemanding aquarium plants are *Heteranthera zosterifolia*, *Lobelia cardinalis*, *Rotala rotundifolia* and *Shinnersia rivularis* as well as several *Cryptocoryne* species.

Demanding but well-growing aquarium plants are *Ammannia* and *Nesaea* species as well as *Alternanthera reineckii*, *Didiplis diandra* and *Hemianthus micranthemoides*. They require a longer time to adapt and initially drop their emersed leaves during their period of adaptation to a submersed environment, but then proceed to rapidly resume growth under optimum conditions.

Slow-Growing Marsh Plants

Among this group are *Anubias* species which have been available over the last couple of years and which are especially suited to cichlid aquariums due to their hard leaf structure. When touching and feeling an emersed leaf the difference in aquatic leaves will quickly become evident: it is leathery and stiff, not transparent and unpartitioned. If *Anubias* is removed from the water the leaves will remain in their upright position and will not hang down in a limp fashion. Even though the *Anubias* species that are commercially available adapt well to a submersed environment care should be taken when purchasing specimens so that they grow slowly, the period of adaptation thereby taking considerably longer than with many fast-growing species. The same also goes for the popular ferns *Bolbitis heudelotii* and *Microsorum pteropus*. When setting up a new aquarium it is therefore recommended to initially begin with fast-growing species (also as a precaution to prevent the development of algae) which can then progressively be replaced with slow-growing species. Occasionally aquarium stores also stock *Lagenandra*, *Aglaonema* and *Spatiphyllum* species which are often confused with the *Anubias* species. These plants, however, generally do not grow under water (*Lagenandra praetermissa* is an exception being suitable only for higher aquariums), and their purchase is not recommended.

Plants Unsuitable for Aquariums

Even though the available range of well-growing aquarium plants has increased continuously over the last couple of years, species totally unsuitable for underwater cultivation continue to be made commercially available in aquarium shops. They will not grow submersed and will die after only a few days. Most of these plants are traded under exotic fantasy names, for example "underwater palm," and are conspicuous by their bright coloration which is why they continue to be bought by aquarists. The disappointment after discovering that they will not grow in the aquarium is usually great. Species unsuitable for submersed cultivation are offered from the following genera: *Chamaedorea*, *Chlorophytum*, *Commelina*, *Cordyline*, *Cryptanthus*, *Dracaena*, *Fittonia*, *Hemigraphis*, *Selaginella* and *Syngonium*. *Acorus* and *Lagenandra* species as well as *Alternanthera sessilis* and *Bolbitis heteroclita* are only temporarily suitable for submersed cultivation, but can be kept without complications in a paludarium (marsh aquarium).

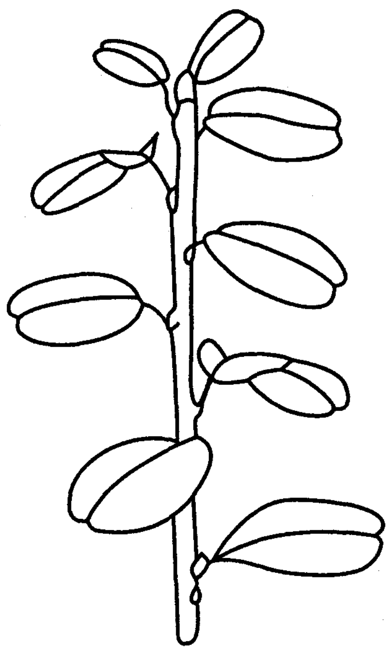
The following survey is designed to assist in making the right choice of aquarium plants:

Typical features of genuine aquatic plants, floating plants or submersed cultivated species:

- The leaves are lacerate, finely structured, strap-shaped, occasionally fragile and thin, sometimes transparent, bullate or cancellate.
- The stem is mostly soft (can it be compressed?) and, if it is fleshy, displays clearly visible air tubes and storage spaces (cross-section).
- Leaves, often the stems as well, will hang down limply after removal from water.
- The plants are glabrous or have minimal pubescence.
- The plants have air cushions (*Eichhornia crassipes* and *Limnobium*), float on the water surface or develop floating leaves.

Typical features of terrestrial plants, slow-growing marsh plants or species totally unsuitable for aquarium culture:

- The leaves are strong, leathery and not or hardly transparent.
- The stem is hard.
- Leaves and stems do not hang down limply after removal from the water but will remain upright instead (not in species displaying creeping growth).
- The plants often display pubescence.
- The plants have a conspicuous coloration.



The Design of Plant Aquaria

Before laying out a plant aquarium, one should first think about how to give it shape and where to place plants along the side panes and back wall. This is especially important for a harmonious effect. In order to make them natural looking, for example, structured plates made of pressed natural cork or synthetic resin are available in pet shops. Recommendable and, what's more, inexpensive, are polystyrene plates in which you can burn or melt a relief-like pattern and then paint black with nontoxic paint. Small-leaved forms of *Microsorum pteropus* and *Anubias barteri* var. *nana* can be used for planting on these decorative plates. The rhizomes are pinned down to the structured plates with short, curved pieces of PVC-covered wire. *Anubias*, *Microsorum* and *Bolbitis* can also be used for planting on stones and roots, as can mosses and algae balls. The latter can best be tied down with thin nylon thread. A fashionable, very effective planting is created with a cushion of commercially available *Riccia*, which, following the examples of Japanese aquarium art, is tied down with a hairnet.

Before choosing and buying the desired plants, it has proved useful to make a drawing (planting scheme) which indicates where the plants will be placed, either singly or in groups. In setting up the planting scheme, a plant street should first be planned, reaching diagonally from the front preferably far to the back in a sloping way. Such a street not only produces a striking three-dimensional effect, but also has a pronounced optical effect. In Dutch aquaria, which are often used as an example for plant lovers, the undemanding and slow-growing *Lobelia cardinalis* and the more light-requiring *Saururus cernuus* are often used in a plant street. Sometimes the fast-growing species *Alternanthera reineckii* and *Hygrophila corymbosa* are also used. With a bit of skill, species like *Isoetes velata*, which have a rosette-like growth, or the adventitious plants of *Echinodorus bleheri*, can be used in a plant street. Never plan the beginning of a plant street exactly in the middle of the aquarium as this divides the aquarium optically into two halves, harming the total effect. Furthermore, attention should be paid to designing a preferably dense and close grouping. Do not economize on plant material! An unusual and attention-drawing eye-catcher is formed by a second, parallel plant row consisting of plants clearly different in both color and shape.

The next thing to decide is which solitary plants should be used. Solitary plants are those species which are used singly and give good optical effects. All other species are always used in groups. Especially recommended as solitary plants are the large-growing sword plants, *Echinodorus bleheri*, *E. parviflorus*, *E. cordifolius*, and *E. uruguayensis*, and also some *Echinodorus* cultivars like *Echinodorus* 'Rubin', E. 'Ozelot', and E. 'Rosé'. The color forms of *Nymphaea lotus* and *Crinum* species are quite decorative. Some species of the genus *Aponogeton* also have great decorative value as solitary plants. In very small aquaria with a capacity less than 60 L, one usually has to refrain from using solitary plants as they dominate the aquarium. However, in larger aquaria, one should also be satisfied with only a few solitary plants.

Now to plant the aquarium's front section. This is a very difficult job since the choice of available fast-growing, but at the same time undemanding, foreground plants is not very large. Well suited are the stolon-producing species *Echinodorus tenellus*, *E. quadricostatus*, and *Sagittaria subulata*, which rapidly cover the bottom like a lawn. Just as undemanding are *Eleocharis acicularis* and various *Lilaeopsis* species; the latter should always be bought in large amounts as they grow slowly. *Crptocoryne parva*, *C.* × *willisii*, *C. wendtii*, and *C. walkeri* are also decorative and slow-growing, but are satisfied with an average lighting intensity. Absolutely recommendable as a foreground plant is *Anubias barteri* var. *nana*. Extremely light-demanding and therefore only fit for the experienced plant lover is the Australian *Glossostigma elatinoides*. The planting of small foreground plants often leads to the largest problems. Your patience will be especially put to the test with the fragile shoots of *Glossostigma* and *Marsilea*, since they become loose time after time. A pair of blunt tweezers can be of great help. At last, when planting the foreground plants, one will notice that sand or fine-grained gravel is more appropriate for planting than gravel with a diameter of more than 3 mm. It takes a lot of effort and time to plant the smallest sword plant, *Echinodorus tenellus*, because each small plant should be planted singly, not together with others in the same planting hole. This also applies to the somewhat bigger, stolon-producing species like *Echinodorus quadricostatus* and *Sagittaria subulata*.

After the plant street, solitary plants, and foreground plants have been drawn on the planting scheme, one needs to start thinking about which middle and background plants should be used. Strongly recommended, small-leaved stem plants for the middle parts are *Bacopa caroliniana*, *B. monnieri*, *Hygrophila polysperma*, *Hemianthus micranthemoides*, and *Heteranthera zosterifolia*. Ranking among the more tender and very light-demanding plants are *Didiplis diandra* and *Micranthemum umbrosum*. Depending on the size of the aquarium, the following species are fit for planting in the middle or background: *Limnophila* species, *Ludwigia* hybrids, *Rotala rotundifolia*, *Hygrophila difformis*, and various shape and color forms of *Hygrophila corymbosa*. Light-demanding and tender plants are *Cabomba* and *Myriophyllum* species, *Eichhornia azurea*, and the intense red-colored *Alternanthera reineckii*, *Ammannia gracilis*, and *A. senegalensis*.

Of the large number of species with a rosette-like growth, the following are especially well suited for middle and background planting: most of the *Echinodorus* species and cultivars, although many of them are very light-demanding. Others include almost all commercially available Cryptocorynes, which grow well at lower light intensities, but in the aquarium need several months to take root. Also highly recommended are *Vallisneria* and *Ceratopteris*.

In the realization of middle and background planting, a few basic rules must be followed. For example, stem plants will catch the eye only if planted in a gradually sloping way. A larger group always looks stronger than a smaller one. Fleshy-leaved, strong shoots (e.g., *Ammannia gracilis* and *Eusteralis stellata*) are planted singly and at such a distance that they will neither impede nor shade each other. Also most of the ground-covering species, like *Cryptocoryne* and the stolon-producing *Echinodorus*, should always be planted in larger groups in order to achieve a harmonious effect. To create a large contrast, similarly shaped or colored species should not be planted next to each other. For example, it is not wise to place the similarly shaped species of *Myriophyllum* and *Cabomba* together, or the red *Ammannia gracilis* next to the red-brown *Cabomba furcata*.

Therefore, the most important rule of planting is to create striking contrasts with the help of plant colors and shapes. Please note when buying plants that more money is spent for dense planting than for fish! Furthermore, take into consideration that most of the plant species (excluding solitary plants) will only catch the eye effectively if planted in larger groups. Therefore, always buy several bunches or pots of each species!