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4. HABITAT DEMANDS AND ECOLOGICAL BEHAVIOUR

4.1. GENERAL

The demand for suitable climatic and nutrient conditions as well as the possibilities of reproduction, of spreading, and of surviving unfavourable conditions are important characteristics of the species of Lemnaceae which can explain their occurrence or absence in different regions of the world. There are three different means to learn about the ecophysiological behaviour:

- observations and ecological measurements in nature
- cultivation experiments under controlled conditions
- recording of the climatic conditions within the distribution area.

Cultivation experiments and a survey of the climatic conditions within the distribution area will be treated in more detail in volume 2, chapter 2 (LANDOLT and KANDELER 1987) and in chapter 6.3 of this volume. Only a short summary will be given here.

Many observations and ecological measurements of the habitat of the Lemnaceae are available from the literature, and there are many records of our own. Also, results of physiological experiments can be found quite frequently in the literature. Nevertheless, the exact ecological demands of the different species of Lemnaceae are not known satisfactorily. This is mainly due to the fact that the important ecological factors do not operate independently. In addition, most factors vary during the year at the same place. As McLAY (1973) showed L. aequinoctialis is able to use nutrients in dust washed from the stems of Scirpus which grows together with the Lemna. Also salt leached from the same source may be taken up.

4.2. VEGETATIVE GROWTH

4.2.1. Physical characteristics of the water body

Lemnaceae as typical pleustophytes mostly float on or near the surface of the water. Therefore, they are very sensitive to movements of the water caused by current, waves, or wind. Fast flowing waters are free of Lemnaceae or only carry some colonies that have been washed off. Slowly flowing waters contain Lemnaceae solely if they have anchoring possibilities for the fronds: rooted waterplants, driftwood. The fronds will accumulate in small quiet basins. According to DUFFIELD and EDWARDS (1981), Lemna plants float in a channel without rooted plants with a velocity of 70-100% of water movement within 0.01 and 0.1 m/s velocity. In dense stands of Phragmites, Lemnaceae are not moved at all if water velocity does not exceed 0.08 m/s. Winds do not move the surface film of water within stands of Phragmites below a velocity of 8 m/s. The authors created a model to predict the distribution of Lemna plants in a complex system of drainage channels. Waters with strong fluctuations are avoided because the fronds are washed away during high waters and are deposited on shore when the water sinks. Very slowly flowing ditches and channels where fronds driven away are replaced by fast reproduction are most favourable. Often these places are crowded with Lemnaceae. In stagnant waters there may be problems with waves and wind. By the movement of the surface water the fronds can be thrown on the shore where they dry out. They can also be pushed together in some quiet areas where they can form layers up to 20 cm thick (KLOSE 1963). In this case most fronds do not get enough light and nutrients and will eventually die. Large waters and windy places are therefore void of Lemnaceae except between reeds or in quiet basins. MURPHY and EATON (1983) could not find Lemnaceae in England in canals with heavy pleasure-boat traffic.

The depth of the water influences the occurrence of Lemnaceae in different ways. Relatively deep waters are more suitable in regions with very high radiation and high temperatures and with high evaporation. The danger of temperatures being too high or of drying out are much less in deep waters. In regions with cold winters, the waters with Lemnaceae must be so deep as to not freeze to the bottom where the resting fronds of the Lemnaceae are. Fronds of Lemnaceae are not very frost-tolerant.

However, most species of temperate regions are able to survive freezing in ice for shorter periods (KRONBERGER pers. comm., also many other observations of field botanists). DALE and GILLESPIE (1976) observed L. trisulca in waters up to 3 m, OZIMEK (pers. comm. 1985) up to 5.5 m deep. Waters that are too deep are unfavourable in cold regions because they warm up too late in summer. Considering the nutrient supply, shallow waters are more convenient for Lemnaceae. Most nutrients are concentrated near the bottom of the water; the nearer the Lemnaceae cover is to the nutrient pool the better is the supply through diffusion or intermixing (KLOSE 1963).

Temporary waters are rarely populated by species of Lemnaceae. The fronds dry out and die within a few hours if kept outside the water. According to KEDDY (1976) fronds of L. minor are dead after two and of L. trisulca after 1 1/4 hours exposure to air of 70% moisture and 25°C. Wolffia species are still more sensitive (own observations). Many authors working with Lemnaceae report similar observations. Even turions dry out within a short time outside the water (JACOBS 1947, DAS and GOPAL 1967 for S. polyrrhiza, LANDOLT unpubl. for S. polyrrhiza and L. turionifera, GODZIEMBA-CZYK 1970 for W. arrhiza). However, if turions of S. polyrrhiza are completely covered by mud or silt and are allowed to dry out slowly, they remain alive and begin to reproduce again when they are covered with water (DAS and GOPAL 1967, GOPAL pers. comm. 1984). S. polyrrhiza is therefore able to survive, under certain circumstances, in temporary water. This is probably only the case in tropical and subtropical regions with regular dry periods. The survival of dry periods by fruits or seeds is well documented for some species. Seeds of the following species are known or supposed to withstand desiccation: S. punctata (own observations in Australia), L. gibba (many records, e.g., HEGELMAIER 1868, LANDOLT 1957, WITZTUM 1977), L. disperma (own observations in Australia), L. aequinoctialis (many records and observations from all over the world), W. hyalina, W. repanda, W. Welwitschii, W. microscopica and W. globosa (from herbarium indications). Lemnaceae were observed in the following temporary waters: small lakes and ponds in regions with regular dry and wet periods, fish ponds, rice fields (see also chapter 4.4.2). In regions with perennial waters, Lemnaceae can be regularly introduced to temporary waters in the surroundings.

There are several rare conditions, where Lemnaceae grow outside of a water body. They may occasionally flourish on wet muddy shores. GUPPY

(1894) was able to cultivate Lemnaceae on wet mud for 20 months. In test tubes it has been possible to cultivate Lemnaceae on agar medium (except some Wolffiella species) here in Zürich for more than 30 years. More striking are Lemnaceae growing in the drip of waterfalls or on wet



Fig. 4.1. Lemna minor growing in the drip of a waterfall in Semien, Hara, Ethiopia (photo F. Klötzli, Zürich)

rocks. The occurrence of L. minor is known from waterfalls in the Kaukasus (from Abastumani in herb. STU and from Batum in herb. MPU), the Semien mountains (F. KLOETZLI and J. BURNAND, Zürich, pers. comm. 1973, see fig. 4.1.), and Madeira (Tutin in herb. BM). O. DEGENER, Honolulu (in lit. 1980), made a similar observation in Massachusetts, U.S.A. (the species was not determined). Lemnaceae living in waterfalls hang closely together by the roots. Only species with long roots (species group of L. minor) are able to utilize this ecological niche. KOLKWITZ (1933) observed moist rocks near Rio de Janeiro partly covered with a species of Lemna. The indications are corroborated by the present author who discovered green strips of L. valdiviana (together with Azolla caroliniana). The Lemna fronds stick to the rough and permanently moist granitic rock south of Rio in southern (shady) exposition (plate XVIId). A similar observation was made by Maas et al. (herb. U) in Ecuador (Tandapi) at 1450 m altitude with L. minuscula and by F. HALLE (in lit.) in Africa (Forêt de la Djoumouna near Brazzaville) with L. aequinoctialis.

4.2.2. Temperature conditions

4.2.2.1. General remarks

Lemnaceae are found in waters of all temperatures except in arctic and antarctic climates (see chapter 6.3.2.). In general, waters in climatic regions with an average temperature of the warmest three months of less than 10°C are not occupied by Lemnaceae. In the tropical mountains at an altitude of 3500-4000 m, the average monthly temperature is less than 8°C, but the average temperature of the water becomes much higher during day-time. L. gibba and L. minuscula, and to a lesser extent L. minor and L. valdiviana, are especially adapted to this climate. A similar cool, but never cold, climate occurs at the southern tip of South America where S. punctata was found.

Lemnaceae grow in the hottest regions of the world. The highest temperature measured in waters with L. aequinoctialis was 37°C in ricefields of the Central Valley of California. In a hot spring covered with L. minuscula, the water temperature was constantly 35°C (LANDOLT 1957) but the air temperature mostly lower. As is shown in chapter 6.3.2., there are differences in the demand and tolerance of temperatures between the species of Lemnaceae.

4.2.2.2. Optimum and maximum temperatures

A more detailed survey of the physiological investigations on the influence of water temperatures on growth of Lemnaceae is given in volume 2, chapter 2.3.4. (LANDOLT and KANDELER 1987). Optimum temperatures for the growth of Lemnaceae are above 24°C for all investigated species. At low light intensities, the optimum temperatures are generally lower than at high light intensities or in solutions with sugar. According to LANDOLT (1957) the growth rate is nearly the same at a constant temperature and at the same mean temperature varying several degrees. The growth rate at day temperatures of 26°C (16 hours) and night temperatures of 14°C (8 hours) showed only slight deviations from the growth rate at a constant temperature of 22°C. Somewhat higher growth rates were measured in L. turionifera, a rather continental species. L. gibba, L. minor, and L. minuscula which are distributed in more oceanic climates showed a slightly lower growth rate. In S. polyrrhiza, there was no difference. SHARITZ and LUVALL (1978) did not find any difference in the growth rate of S. punctata grown at temperatures of a constant 17.5°C and at alternating temperatures of 10°C and 25°C. LANDOLT (1957) compared the growth rate of 11 species at temperatures of 21°C, 26°C, and 30°C. The highest growth rate was measured at 30°C for the following species: S. polyrrhiza (3 clones), L. aequinoctialis (3 clones), and W. globosa (2 clones), all of which are widely distributed in tropical regions. All the other species showed the highest growth rate at 26°C. Of these species the following had higher growth rates at 30°C than at 21°C: L. turionifera (3 clones), L. minor (7 clones), W. arrhiza (1 clone), W. columbiana (1 clone). Lower growth rates were measured for the following species: S. punctata (1 clone), L. gibba (4 clones), L. trisulca (2 clones). L. minuscula included 4 clones with growth rates higher at 30°C, 5 clones with growth rates lower at 30°C than at 21°C. Below 20°C the growth rate decreases relatively quickly. Some species do not grow anymore at long lasting temperatures of 30°C (or less) (e.g. L. trisulca), 32-33°C (most clones of L. gibba, L. turionifera, L. minor, L. minuscula, W. gladiata, W. arrhiza, W. columbiana), and 36°C (S. punctata, L. aequinoctialis, W. globosa). Clones of S. polyrrhiza are the only ones still found growing at 36°C. DOCAUER (1983) found growth stop at temperatures of 32.5°C for L. minor, 34°C for L. turionifera, 35°C for W. borealis, 36°C for W. columbiana, and 38°C for S. polyrrhiza. Most species are able to stand

much higher temperatures for a short time (up to 40°C, see also STANLEY and MADEWELL 1976b). EL DIN (1982) observed L. gibba growing at air temperatures of 30-40°C (air humidity 30-50%). Turions of S. polyrrhiza survive temperatures of 50°C for 24 hours (JACOBS 1947). It is interesting to note that the species with the lowest maximum temperature (L. trisulca) is restricted to regions with relatively cool summers whereas the species with a high temperature tolerance are able to grow in the warmest regions of the world (S. polyrrhiza, L. aequinoctialis, W. glombosa). The species with a medium heat tolerance (L. gibba, L. turionifera, L. minor, L. minuscula, W. gladiata) do not occur in very warm regions. During the warm season, they may be replaced by other species as was reported of L. minor by SJOGREN (1968) from Southern California when air temperatures reach 35°C.

4.2.2.3. Minimum temperatures

It is important to distinguish between the effect of long lasting low temperatures which still enable a slow growth rate (minimum temperatures for growth), and the low temperatures which damage the plants (tolerance to deep temperatures).

There are two possibilities of surviving during cold temperatures: 1) actual tolerance to deep temperatures or 2) ability of sinking to warmer waters at the bottom. Not much is known about the frost tolerance of the different species. A temperature of -10°C is probably deadly for all species. In an overwintering study in Zürich, LANDOLT (1957) observed that all fronds of the 14 investigated species died on the surface of the water after the first frost of about -10°C. Turions of S. polyrrhiza are able to stand temperatures of -4°C for at least three weeks but of -12°C only for 24 hours (JACOBS 1947). DAS and GOPAL (1969) reported the loss of viability of S. polyrrhiza turions after 12 hours of temperatures between -5°C and -7°C (clones of subtropical regions). Normal fronds and turions of W. arrhiza die if exposed to temperatures of +1°C for 14 to 20 days and of -2°C for 6 to 10 days (GODZIEMBA-CZZY 1970). According to our own observations, L. gibba, L. minor, L. trisulca, and L. minuscula are able to survive enclosed by and under an ice cover of a temperature of a little below zero for several days. KRONBERGER (pers. comm.) made similar observations with L. minor in Austria. Differing observations are reported by LOHAMMAR (1938). He kept fronds of S. poly-

rrhiza, L. minor, and L. trisulca in bottles outdoor during winter time. The temperatures dropped down several times to temperatures below -10°C (once even to -22°C). Of the investigated species only S. polyrrhiza did not survive (some fronds were still living after one month).

To avoid low temperatures, most species in regions with cool seasons sink to deeper layers of the water where the temperatures are above zero. This may be done in the following ways:

- normally submerged species become more compact and sink to deeper layers (L. trisulca). Wolffiella species are able to sink further down, but, only W. gladiata is able to survive for a longer time at temperatures around zero.
- some species form true turions which sink to the bottom of the water: S. polyrrhiza, L. turionifera, some races of L. aequinoctialis (BEPPU and TAKIMOTO 1981c), and many Wolffia species.
- some species die after the first frost and sink to the bottom of the water still protecting some living buds in their pouches: S. punctata, L. gibba, L. minor, L. japonica, L. minuscula, L. valdiviana.
- a few species (e.g. L. perpusilla, L. gibba and L. aequinoctialis) are able to survive as seeds. The seeds of L. perpusilla do not germinate when ripe, they require a cold period of several weeks before germinating (KANDELER 1975, own observations).

Seeds of L. gibba and L. aequinoctialis germinate readily. Therefore, the seeds can only survive in a dry estate. Especially in rice fields, which dry out in early fall, one can observe germinating seeds of L. aequinoctialis in spring in newly watered fields. If the water cools down rapidly, seeds of L. aequinoctialis may stay dormant. It is known that they generally do not germinate at temperatures below about 10°C (GLICKMAN and POSNER 1966).

The minimum growth temperature is species specific. It varies between different clones of the same species. According to LANDOLT (1957 and unpublished) the 13 investigated species still grow at the following temperatures (lowest growth temperature for the clone):

4°C	: <u>L. gibba</u> (6 clones), <u>L. minor</u> (3 clones), <u>L. trisulca</u> (3 clones),
$6-9^{\circ}\text{C}$: <u>S. punctata</u> (2 clones), <u>L. minor</u> (5 clones), <u>L. turionifera</u> (5 clones), <u>L. trisulca</u> (1 clone), <u>L. minuscula</u> (8 clones)
$9-13,5^{\circ}\text{C}$: <u>S. polyrrhiza</u> (1 clone), <u>L. valdiviana</u> (1 clone),

L. minuscula (2 clones), W. gladiata (1 clone)
13.5-16.5°C: S. polyrrhiza (2 clones), L. aequinoctialis (4 clones),
W. arrhiza (1 clone), W. columbiana (1 clone), W. globosa
(1 clone)
16.5-20°C : S. polyrrhiza (1 clone), L. aequinoctialis (1 clone).

DOCAUER (1983) measured the following minimum growth temperatures: 5°C for L. minor, 9°C for L. turionifera, and at least 12-13.5°C for S. polyrrhiza, W. columbiana, and W. borealis.

The results cited explain the fact that the species which grow only at temperatures above 13.5°C do not, or only very rarely, occur in regions with mild winters and cool summers (e.g. western Ireland, Norway) and in the higher mountains of the tropics where the temperatures are never very warm. In mediterranean climates with mild but not very warm winters and warm summers, S. polyrrhiza and Wolffia species are rare. Frequent species such as L. gibba and L. minor are able to grow well during the relatively cool winter time whereas S. polyrrhiza and Wolffia wait, in form of turions, at the bottom of the water for warmer temperatures.

The overwintering experiment of LANDOLT (1957) gives some indications of the possibilities of different species. From the beginning of October 1955 until the end of April 1956 the mean temperature at Zürich was below 10°C, from November to March the mean temperature did not reach 5°C and mean minima were about zero or less. The ice cover in the water basins reached a thickness of 30 cm in February for some weeks (mean temperature -8.7°C). But the bottom of the water was never frozen. The following species survived successfully: S. polyrrhiza (2 clones), L. gibba (2 clones), L. turionifera (1 clone), L. minor (1 clone), L. trisulca (1 clone). The following were noted with a low survival rate: S. punctata (1 clone), L. minuscula (2 clones out of 5). No living fronds were observed in: L. obscura (1 clone), L. aequinoctialis (1 clone), W. arrhiza (1 clone), W. columbiana (1 clone), W. globosa (1 clone), W. lingulata (1 clone), and W. gladiata (1 clone). The two Wolffielas and the Wolffias (except W. globosa) had only about 100-400 fronds at the beginning of October. It cannot be excluded that they would have a better chance of survival if they had a start with many more fronds. In spring, L. gibba, L. minor and L. trisulca appeared at the surface of the water about three weeks before most of the other species. Under competing conditions, they would have a better chance to spread at the given climate.

Of the other surviving species, S. punctata appeared only 6 weeks later having no chance to produce enough new fronds during the short vegetation period to survive a second winter. According to DOCAUER (1983) L. minor grows much faster at temperatures below 20°C than L. turionifera, S. polyrrhiza, W. borealis, and W. columbiana. In spring L. minor is the first species to develop. The turions forming species showed up much later, L. turionifera about two weeks before the other species. These findings corroborate the observation that L. minor has a more oceanic distribution and is not dependent on high summer temperatures as the other four species are. In two rivers of Wisconsin L. turionifera (named as L. minor) did not develop before beginning of June, according to MADSEN and ADAMS (1985). L. minor begins the development in April under similar temperature conditions.

4.2.3. Light conditions

Lemnaceae can be found in sunny as well as in shady situations. Shady places are often more favourable for the growth of Lemnaceae in spite of the low light intensity because the supply of nutrient and organic matter is normally better, due to the many falling leaves and organic litter, also, shady places are not so much exposed to wind, and the temperatures are not so extreme. Especially in hot regions, the temperatures in a cover of Lemnaceae in the sun can rise to more than 40°C which might eventually damage the fronds. On the other hand, the temperatures of water in shady places can be too low for the growth of Lemnaceae in cold regions. Lemnaceae frequently occur in forest pools if nutrient supply is sufficient. EWEL (1984) reports that in Florida a disposal of secondary treated waste water into cypress domes results in the formation and persistence of a layer of duckweeds on the water surface. Within the reed belt (Phragmitetum) PANKNIN (1945) measured a light intensity of 2.5% of the intensity in sunny places in which L. trisulca still covered the water at 80-100%. LANDOLT (1957) found Lemnaceae in California in situations where the light intensity in the sun at noon did not exceed 500 lux, which corresponds to about the same percentage (taken in account that the intensity is much less on cloudy days). It is known that Lemnaceae can be grown in complete darkness if organic substances such as sugars are added to the nutrient solution. In nature, it is

probable that Lemnaceae are also able to supply their energy demands from dissolved organic substances. The lower fronds of thick covers of Lemnaceae, which can last for many months, do not get any light but probably receive some sugars secreted by the fronds of the upper layers. According to my own observations in Argentina, L. valdiviana, W. lingu-lata, and W. oblonga sometimes live heterotrophically below a solid cover of water plants (e.g. Pistia, Eichhornia, Scirpus cubensis). Similarly in some situations, L. trisulca which is very tolerant to shade (WOHLER 1966) is probably dependent on organic substances for its energy supply. VALLENTYNE and WHITTAKER (1956), SAUNDERS (1957), HARTMAN (1960) and WALSH (1965a,b) showed that sugars and other organic substances are present in lake waters.

According to LANDOLT (1957), the light saturation is not so much dependent on the species but on the clone and varies at 24°C and continuous illumination between 4000 lux and at least 15000 lux. It is higher at high temperatures and lower at low temperatures. It may also be higher at shorter illumination periods. LANDOLT compared the growth rate at 2500 lux with the maximal growth rate (measured at 9000 lux in solutions with sucrose). The following percentage of the growth rate at 2500 lux compared to the maximal growth rate was observed: S. polyrrhiza 50-55% (5 clones), S. punctata 58% (1 clone), L. gibba 53-63% (5 clones), L. minor 57-63% (7 clones), L. turionifera 48-63% (5 clones), L. aequinoctialis 59-75% (4 clones), L. valdiviana 70% (1 clone), L. minuscula 66-86% (8 clones), W. arrhiza 56% (1 clone), W. columbiana 48% (1 clone), W. globosa 64% (1 clone). Some clones of L. aequinoctialis, L. valdiviana, and L. minuscula which originate from shady places show the lowest optimum light intensity and are therefore most shade tolerant. It was not possible to measure a true percentage for the submerged species L. trisulca and Wolffielia which do not get enough CO₂ in solutions without sugar. The relation between light and growth and development of Lemnaceae is represented in more detail in volume 2, chapter 2.3.5 (LANDOLT and KANDELER 1987).

4.2.4. Chemical composition of the water

4.2.4.1. General remarks

The occurrence and composition of species of Lemnaceae in different lakes and ponds of the same region (with the same climate) may vary considerably. Though many differences in the composition of the species are merely accidental as was shown in WOLEK (1983), the chemical composition of the water is responsible in many cases. In addition, competition by other water plants, presence or absence of fish and other animals feeding on duckweed, occasional drying out, and use of herbicides play an important role. In spite of many field investigations with water analysis and extensive cultivation experiments, little is known about the optimal chemical composition which selects different species in nature. This may be due to the following facts:

- the nutrient content of the water changes during the year; to be able to compare the different locations, it is necessary to make several measurements during the course of the year;
- the nutrients of the ecosystem are only partly in the water; many nutrients may be stored in the biomass of a thick Lemnaceae cover;
- some of the nutrients in the water (e.g. Fe, Mn) may not be accessible for the Lemnaceae due to precipitation at a pH which is too high, and due to the absence of chelating organic substances;
- dust and clay particles in the water may contain some nutrients accessible for Lemnaceae (MCLAY 1973, HEALY and MCCOLL 1974b); these particles are filtered off before analysing the water and are therefore not measured.

In general, Lemnaceae avoid oligotrophic water. In regions with high precipitation, Lemnaceae are rare and found neither on granitic soil and limestone, nor on very old soils which are poor in most nutrients. Exceptions are waters heavily contaminated by waste water (KURIMO 1970, PIP 1979). On the other hand, excessive eutrophication may lead to the disappearance of more sensitive species, e.g. L. trisulca in Finland (TOIVONEN 1985) or Wolffia species in California (own observations). Table 4.1 gives a survey of the chemical composition of waters with Lemnaceae. In table 4.2 the lowest yearly mean of certain nutrients in water with a constant occurrence of Lemnaceae in central Europe is given.

Table 4.1. Range of nutrient content in waters with Lemnaceae (chemical elements in mg/l, conductivity in $\mu\text{S}/\text{cm}$) (according to KADONO 1982, LANDOLT 1981, LANDOLT results not publ., LANDOLT and WILDI 1977, LANDOLT and ZARZYCKI in prep., DE LANGE and SEGAL 1968, LUEOEND 1983, ROELOFS 1983, WIEGLEB 1978b)

characteristics of the water mineral content	absolute range	range of 95% of the samples
pH	3.5 - 10.4	5.0 - 9.5
conductivity	10 - 10900	50 - 2000
Ca	0.1 - 365	1.0 - 80
Mg	0.1 - 230	0.5 - 50
Na	1.3 - >1000	2.5 - 300
K	0.5 - 100	1.0 - 30
N	0.003 - 43	0.02 - 10
P	0.000 - 56	0.003 - 2
HCO_3	8 - 500	10 - 200
Cl	0.1 - 4650	1 - 2000
S	0.03 - 350	1 - 200

Table 4.2. Lowest yearly mean of some nutrients in waters of Central Europe with Lemnaceae species (data from LUEOEND 1983)

46 waters were investigated for three years. The Lemnaceae cover of the water was noted and the water analyzed from March to October once each month. In addition, 33 waters were observed less intensively. The number of occurrences of each species are as follows: S. polyrrhiza 18 times, L. gibba 16 times, L. minor 59 times, L. trisulca 15 times, and L. minuscula 28 times.

nutrients in mg/l	<u>S. poly- rrhiza</u>	<u>L. gibba</u>	<u>L. minor</u>	<u>L. tri- sulca</u>	<u>L. minus- cula</u>
P	0.007	0.027	0.006	0.010	0.012
N	0.04	0.22	0.04	0.04	0.18
K	1.3	2.6	0.9	2.0	1.5
Ca	18.8	23.7	11.6	40.0	18.6
Mg	1.1	4.5	1.1	4.6	1.1

4.2.4.2. pH values (table 4.1)

Measurements of pH values in water with Lemnaceae are relatively frequent though not very significant (e.g. HICKS 1932b, MOYLE 1945, LANDOLT 1957, HARRISON and BEAL 1963, KLOSE 1964, SEGAL 1966, DE LANGE 1972, McLAY 1976, LANDOLT and WILDI 1977, WIEGLEB 1978b, PIP 1979, LANDOLT 1981 and LANDOLT and ZARZYCKI in prep.). The pH of the water in the field varies according to the time of day and to the season. McLAY (1976) measured a pH between 7.35 and 9.7 in the same lake in California, the highest pH being a result of the high photosynthetic activity of Potamogeton stands during day-time. Therefore, field measurements show only a momentary stage. Also, the content of chelating agents in the water determines whether Lemnaceae are able to grow at extreme pH values. The pH of waters with Lemnaceae in the field ranges between 3.5 and 10.4 (LANDOLT 1957, LANDOLT and WILDI 1977). In nature, Lemnaceae are rarely found in waters with pH lower than 5. This is probably due to the poorness in nutrients of most waters with a low pH.

According to field observations, the following species occur in water with pH 5 or lower: L. minor (HICKS 1932b, LANDOLT 1957), L. turionifera (LANDOLT 1957), L. aequinoctialis (LANDOLT 1957), L. minuscula (LANDOLT 1957), W. gladiata (HICKS 1932b), W. globosa (LANDOLT 1957). The following species were found in water with pH 9 or higher: S. intermedia (LANDOLT and ZARZYCKI in prep.), S. polyrrhiza (LANDOLT and WILDI 1977), L. gibba (LANDOLT and WILDI 1977, LANDOLT and ZARZYCKI in prep.), L. turionifera (LANDOLT and WILDI 1977), L. aequinoctialis (LANDOLT and WILDI 1977), L. minuscula (LANDOLT and WILDI 1977, LANDOLT and ZARZYCKI in prep.), W. oblonga (LANDOLT and ZARZYCKI in prep.), W. brasiliensis (LANDOLT and ZARZYCKI in prep.), W. columbiana (LANDOLT and WILDI 1977, LANDOLT and ZARZYCKI in prep.).

As will be shown in volume 2, chapter 2.3.3.3. (LANDOLT and KANDELER 1987), most Lemnaceae grow in adequate solutions of a pH lower than 4, a few species even at a pH near 3. The lower growth limit of pH is species and clone specific. In culture, the following species (at least some clones) tolerate a pH between 3.2 and 3.5: S. punctata, L. turionifera, L. minor, L. aequinoctialis, L. perpusilla, L. valdiviana, L. minuscula, W. neotropica, W. lingulata, W. oblonga, W. gladiata, W. denticulata, and W. angusta. Species of which most clones do not tolerate a pH lower than 4 are: S. polyrrhiza, L. gibba, L. disperma, L. trisulca, W. hyali-

na and W. microscopica. In nature these species are mostly found in carbonate rich water.

4.2.4.3. Specific conductance (conductivity) (table 4.1)

The specific conductance is not directly correlated with the amount of nutrients present in the water but with the concentration of all ions. Since it is easy to measure, there are many records. It must be remembered that the measurements given are momentary values and not necessarily representative for the whole vegetation period. SCOPPOLA (1982) reports variation of conductance of a ditch in Italy within the same year between 688 and 1103, and 1153 and 2030 $\mu\text{S}/\text{cm}$. Similarly, CONGDON and MCCOMB (1976) give yearly variations of 1500 to 4500 $\mu\text{S}/\text{cm}$ from a lake with L. disperma (named as L. minor) in Western Australia. The highest specific conductance measured in water with Lemnaceae was 10900 $\mu\text{S}/\text{cm}$ (KADONO 1982), the lowest 10 $\mu\text{S}/\text{cm}$ (DE LANGE and SEGAL 1968). Most waters with Lemnaceae are within a range of 50-2000 $\mu\text{S}/\text{cm}$. According to our own records, there is only a slight difference in tolerance to the conductance of the water between different species. L. gibba, L. turionifera, L. obscura, L. trisulca and L. perpusilla were not found in waters below 100 $\mu\text{S}/\text{cm}$. On the other hand, L. gibba and L. minuscula often occur in waters with a specific conductance above 2000 $\mu\text{S}/\text{cm}$. As is shown by investigations of Lemnaceae associations in Europe, the main occurrence of L. gibba is in waters with high specific conductance: 940-3370 $\mu\text{S}/\text{cm}$ (MERIAUX 1978), 450-1244 $\mu\text{S}/\text{cm}$ (POTT 1980), and 360-1258 $\mu\text{S}/\text{cm}$ (STARFINGER 1983) for the Lemnetum gibbae. In comparison, the water of the Spirodeletum polyrrhizae (with abundant S. polyrrhiza) shows 485-647 $\mu\text{S}/\text{cm}$ (POTT 1980), and 202-714 $\mu\text{S}/\text{cm}$ (STARFINGER 1983), the Lemnetum trisulcae (with much L. minor and L. trisulca) 151-435 $\mu\text{S}/\text{cm}$ (POTT 1980), and 118-1272 $\mu\text{S}/\text{cm}$ (STARFINGER 1983). Water of the Ricciatum (with Riccia and some L. minor) have a specific conductance between 52 and 278 $\mu\text{S}/\text{cm}$ (POTT 1980), and 680-1089 $\mu\text{S}/\text{cm}$ (STARFINGER 1983). Similar measurements were made by WIEGLEB (1976). Contrary to Lemnaceae, other floating water plants such as Eichhornia, Pistia, and Utricularia are able to grow in water with a specific conductance of 11-27 $\mu\text{S}/\text{cm}$ (JUNK 1982). The first two genera have long root hairs and therefore a much larger absorbing surface. Utricularia is able to catch insects to supply itself with nutrients. Similarly, Salvinia can be

found in water with a low specific conductance (own observations).

2.2.4.4. Calcium (Ca) and magnesium (Mg) content; total hardness
(table 4.1)

The **total hardness** is strongly correlated with the amount of calcium and magnesium in the water. It varies in waters with Lemnaceae between 0.22 and 50 (LANDOLT and ZARZYCKI in prep.). If the total hardness falls below 0.5, the occurrence of Lemnaceae is mostly restricted to submerged species (L. valdiviana, Wolffia) (LANDOLT and ZARZYCKI in prep.). The calcium and magnesium content may vary within a year, especially in regions with dry periods. CONGDON and McCOMB (1976) report of a variation of 44-57 mg/l Ca and 21.5-43.5 mg/l Mg in a lake of Western Australia with L. disperma during the year. The variation is sometimes considerable between different years. LUEOEND (1983) showed that the average value of many waters may vary from year to year from zero to 30%.

The **calcium content** in waters with Lemnaceae is reported for North America to be from 1-145 mg/l (LANDOLT and WILDI 1977, LANDOLT 1981), for South America from 0.1-104 mg/l (LANDOLT and ZARZYCKI in prep.), for Malaysia from 1.2-48 mg/l, for Australia 4.5-100 mg/l (LANDOLT unpubl. results), for Japan from 7.8-78.6 mg/l (KADONO 1982), and for Europe from 9-243 mg/l with the main range between 1 and 80 mg/l (WIEGLEB 1978b). Already JACOBS (1947) reported that S. polyrrhiza needs a certain minimum of calcium and magnesium and that therefore it does not occur in the rather oligotrophic waters of the granitic region north of Lake Superior with less than 20 mg/l Ca. MOYLE (1945) found about the same limit in Minnesota. A similar value is given by LUEOEND (1983) (table 4.2.). L. minor is found in the Netherlands in waters with a Ca content between 5 and 37.5 mg/l (90% of the localities) (ROELOFS 1983). FELZINES (1977) observed L. minor in Central France in waters with 5-40 mg/l Ca and L. trisulca and S. polyrrhiza in waters with 40-80 mg/l Ca. LANDOLT and WILDI (1977) did not find L. gibba in waters with less than 6.5 mg/l Ca. But, in Argentina, the Ca content of waters with L. gibba sometimes had much lower values (LANDOLT and ZARZYCKI in prep.). LUEOEND (1983) checked the nutrient content of waters with Lemnaceae over three years (table 4.2). She found the lowest average value for L. minor with 11.6 mg/l Ca, for L. minuscula with 18.6 mg/l, for S. polyrrhiza with 18.8 mg/l, for L. gibba with 23.7 mg/l, and for L. trisulca with 40.0 mg/l.

The **magnesium content** in waters with Lemnaceae varies between 0.7 and 230 mg/l in North America (LANDOLT and WILDI 1977), in South America between 0.46 and 145 mg/l (LANDOLT and ZARZYCKI in prep.), in Malaysia between 0.14 and 78 mg/l, in Australia between 0.3 and 38 mg/l (LANDOLT unpubl. results). According to LUEOEND (1983) the lowest average value of Mg was for L. minor, L. minuscula and S. polyrrhiza 1.1 mg/l, for L. gibba and L. trisulca 4.5 mg/l.

The Lemnetum gibbae grows in waters with the highest content of Ca and Mg of all Lemnaceae associations (WEBER-OLDECOP 1969) in northern Germany. The water of this association also shows the highest total hardness (STRASBURGER and HOMANN 1982). According to MERIAUX (1978) water with Lemnetum gibbae in Northern France contain 47-365 mg/l Ca and 20-130 mg/l Mg, in Berlin 40-138 mg/l Ca and 3.4-23 mg/l Mg (STARFINGER 1983). STARFINGER (1983) measured 21-73 mg/l Ca and 1.6-8.2 mg/l Mg in the Spirodeletum, 13-152 mg/l Ca and 0.9-30 mg/l Mg in the Lemnetum trisulcae, and 16-111 mg/l Ca and 2.3-13 mg/l Mg in the L. minor association.

BEYER (1983) measured the limits of growth of some Lemnaceae (S. intermedia, L. gibba, L. disperma, W. hyalina, W. neotropica, W. australiana, and W. angusta) in relation to the Ca and Mg content of the culture solution. Optimal growth occurred between 2.1 and 6 mg/l Ca minimum and between 600 and 1800 mg/l Ca maximum. The lowest Mg content for optimal growth was between 0.06 and 0.2 mg/l and the highest Mg content for optimal growth was between 250 and 850 mg/l. L. gibba, L. disperma, and W. hyalina had a high demand for Ca and Mg and also a high tolerance, whereas W. neotropica and W. australiana had the lowest demand and W. neotropica the lowest tolerance for Ca and Mg. This corresponds to the occurrence in nature, the first group of species growing in partly dry regions, the second in regions with heavy precipitations. The upper limit measured by BEYER (1983) is practically never reached in nature. However the lower limit values are often found in nature and might be a very important limiting factor.

In nature the **ratio of calcium to magnesium** found in waters with Lemnaceae varies between 0.15 and 13. In waters with a ratio less than 0.3, only L. gibba, L. turionifera, L. minuscula, W. oblonga, and W. columbiana were found (LANDOLT and WILDI 1977, LANDOLT and ZARZYCKI in prep.). BEYER (1983) observed growth of Lemnaceae in culture solutions with a Ca/Mg ratio between 0.07 and 520.

PEARSALL (1921) saw Lemnaceae only in waters with a low ratio of K+Na/

Ca+Mg (lower than 0.5). Probably not the low content of Na and K but the high need for Ca and Mg in Lemnaceae is important. In our own investigations, a ratio of up to 10 was observed.

4.2.4.5. Sodium (Na) and potassium (K) content (table 4.1)

It is interesting to note that Lemnaceae are mostly found in waters with a higher sodium than potassium content (own observations). Also PIETSCH (1972) writes that the sodium content is higher than the potassium content in waters rich in Lemnaceae. However, as most waters in nature have a higher sodium content this finding possibly has no meaning. The content of Na and K is subject to variations within a year, especially in regions with dry periods. CONGDON and MCCOMB (1976) report of a yearly variation of 140-513 mg/l Na and 8-20 mg/l K in a lake with L. disperma (named as L. minor) from Western Australia and HOWARD-WILLIAMS (1979) of lower than 10 mg/l Na up to 600 mg/l Na in Lake Chilwa (East Africa). The variation of the yearly mean of potassium content varies such more than the calcium or the magnesium content from year to year. LUEOEND (1983) found for instance the following yearly means of K for two ponds in 1979, 1980, and 1981: 2 mg, 9 mg, 1 mg/l and 2 mg, 2 mg and 18 mg/l. These great variations may be the result of agricultural management.

Sodium is present in waters with Lemnaceae from 1.3 mg/l (ROELOFS 1983) up to more than 1000 mg/l (LANDOLT and WILDI 1977). This corresponds to salt concentrations of about 0.004 to 2.5 o/oo. In Finland, LUTHER (1951) found L. trisulca in waters with a salinity of up to 2.5 o/oo (L. minor up to 2.3 o/oo) or, temporarily in waters up to 4 o/oo. In Denmark, OLSEN (1950) observed L. minor, L. gibba, and L. trisulca in waters with up to 8 o/oo salinity, but such high salinities in waters with Lemnaceae are exceptions and probably only temporary. According to VIERSSEN and VERHOEVEN (1983), L. gibba and L. trisulca grow in the Netherlands in waters with a salinity maximum in summer of 5.4 o/oo and with a highest yearly mean maximum of 3.6 o/oo. L. disperma (named as L. minor) grows in Western Australia in waters with a salinity of 0.3 to 8 o/oo, and S. punctata of 0.6-2.5 o/oo (BROCK and LANE 1983). L. minor died if transferred to salt water of the North Sea for one day (GUPPY 1894). Lemnaceae are found only rarely in waters with less than 4 mg/l Na.

STANLEY and MEADWELL (1976a) report an optimal growth of L. obscura

(named as L. minor) between 600 and 1400 mg/l Na if cultivated on nutrient solution. A content of 2300 mg/l Na retarded growth. HALLER et al. (1974) received similar results with the same species. The lethal concentration of Na was 4000-6000 mg/l. According to STRAUSS (1976) the lower limit of optimal growth of L. minor is around 115 mg/l Na. At 460 mg/l Na, there was already a decline of the growth rate in this species. HOWARD-WILLIAMS (1979) investigated the growth rate of S. polyrrhiza, L. aequinoctialis and W. hyalina from Lake Chilwa under different concentrations of Na (5, 20, 100, 250, 500, 750 and 1000 mg/l). S. polyrrhiza showed best growth at 250 mg/l, L. aequinoctialis at concentrations below 100, and W. hyalina at 1000 mg/l.

Although relatively high concentrations of sodium stimulate the growth of Lemnaceae, the necessary amount of sodium in nature seems to be much lower.

The **potassium** content of waters with Lemnaceae varies between 0.5 and 100 mg/l (LANDOLT 1981, LANDOLT and ZARZYCKI in prep.). Lemnaceae are rarely found in waters with a potassium content of less than 1 mg/l (LANDOLT 1981, WIEGLEB 1978b). 90% of the localities with L. minor in the Netherlands contained between 1.95 mg/l and 29.5 mg/l potassium (ROELOFS 1983).

LUEOEND (1983 and pers.comm.) measured the potassium content of waters with Lemnaceae in Central Europe over a period of three years. She found the following average minimum value for potassium in waters containing species of Lemnaceae (table 4.2): 0.9 mg/l for L. minor, 1.3 mg/l for S. polyrrhiza, 1.5 mg/l for L. minuscula, 2.0 mg/l for L. trisulca, and 2.6 mg/l for L. gibba. In North America, L. gibba, L. obscura, and L. turionifera occur only in waters with a potassium content higher than 3 mg/l. As the waters containing these species usually have a higher concentration of magnesium, and as magnesium ions hamper the absorption of potassium (AYADI et al. 1974), the apparent greater need for potassium may be caused by the high concentration of magnesium.

MERIAUX (1978) found in the waters of the Lemnetum gibbae 9.8- 35.2 mg/l K, in the Lemnetum trisulcae 3.3-7 mg/l K. STARFINGER (1983) observed in waters of the Lemnetum gibbae 7.6-42 mg/l K, of the Spirodeletum 6-50 mg/l K, of the Lemnetum trisulcae 5.4-38 mg/l K, and of the L. minor association 9.4-27 mg/l K.

STRAUSS (1976) reported optimal growth for L. minor in cultures with the addition of 20-400 mg/l K. According to EYSTER (1966) S. polyrrhiza

needs 40-800 mg/l K for optimal growth; at 0.2 mg/l K, it does not grow anymore. Many waters in nature have too little potassium for growth of Lemnaceae. The highest potassium content found in nature was always far below the tolerance for Lemnaceae.

4.2.4.6. Nitrogen (N) content (table 4.1)

The nitrogen content of water in nature is subject to great variation during the year. In Italy, SCOPPOLA (1982) found, at the same place, variations between 0.0 and 3.1 mg/l ammonium nitrogen and between 0.15 and 17 mg/l nitrate nitrogen in the course of the same year. In Germany, according to POTT (1980), the nitrate nitrogen content diminishes during summer from 1.2 mg/l to 0.3 mg/l in the Lemnetum gibbae and in the Spirrodeletum polyrrhizae, and from 1 mg/l to less than 0.005 mg/l in the Lemnetum trisulcae. KLOSE (1963) measured in four ponds with Lemnaceae in GDR the highest nitrogen from June to October (c. 15 mg/l) and the lowest from November to March (c. 5 mg/l). Also for nitrogen the variation of the mean yearly value can be surprisingly high. LUEOEND (1983) measured in 1979, 1980, and 1981 nitrogen content at the same place of 0.3, 0.06, and 1.2 mg/l, respectively.

From field investigations, it does not seem very important if the nitrogen is present as ammonium ion or as nitrate ion, since Lemnaceae grow in waters where the one or the other ion is missing. MELZER (1980) refers to L. trisulca as having a very low nitrate reductase activity even in waters rich in nitrate, this could mean that the species prefers ammonium as a nitrogen source. In waters with the Lemnetum trisulcae POTT (1980) found a relatively high content of ammonium (0.4-2.0 mg/l nitrogen) which could corroborate the findings of MELZER (1980). On the other hand, L. trisulca grows very slowly due to the lack of CO₂ in this water so that this may be the reason for the low nitrate reductase activity.

The highest total nitrogen in waters with Lemnaceae was measured by LANDOLT and ZARZYCKI (in prep.) with 43 mg/l N (in form of nitrate; the highest amount of ammonium was 34 mg/l N, according to ROELOFS 1983). The lowest content seems to be less than 0.001 mg/l N (LANDOLT unpubl. results). A nitrogen content below 0.02 mg/l is very rare in waters with Lemnaceae. In Thailand, W. globosa still grows in waters with less than 0.04 mg/l nitrate and nitrite nitrogen (CHOMCHALOW 1971). The author

supposes that the plants are in symbiosis with nitrogen fixing organisms similar to the relationship Azolla-Anabaena (see also chapter 5.3.2). L. gibba is reported as using nitrate nitrogen from solutions with 0.15 mg/l and higher (INGEMARSSON et al. 1984). In general, waters with Lemnaceae are relatively rich in nitrogen. This is especially true for L. gibba in Europe. WIEGLEB (1978b) measured a significantly higher nitrogen content in waters with the Lemnetum gibbae than with other water plant associations. POTT (1980, 1981) and (in brackets) STARFINGER (1983) give values of 2.1-9.8 (1.2-2.0) mg/l in the Lemnetum gibbae compared with 1.2-7.8 (0.7-2.3) mg/l in the Spirodeletum polyrrhizae, 0.4-5.8 (0.7-4.3) mg/l in the Lemnetum trisulcae, and 0.4-2.7 (1.1-1.4) mg/l in the Ricciatum. DENNY et al. (1978) and WELSH and DENNY (1978) showed that in Lake Chilwa (Tanzania) the southern part with a nitrogen content of 0.01-0.04 mg/l is free of Lemnaceae whereas in the northwestern part with 0.03-0.04 mg/l S. polyrrhiza is found and the northeastern part with 0.08-0.15 mg/l is covered with L. gibba, L. aequinoctialis, and in addition W. hyalina. Similar observations are frequent. ULLMANN and VAETH (1978) report that L. gibba occurs in waters most rich in nitrogen. The same result was found by LUEOEND (1983), she measured the following lowest average yearly values of nitrogen for the waters of different Lemnaceae species (table 4.2): 0.04 mg/l for S. polyrrhiza, L. minor, L. trisulca, 0.18 mg/l for L. minuscula, and 0.22 mg/l for L. gibba. Also in North America, L. gibba grows in waters with a significantly higher content of nitrogen than the other species of Lemnaceae (LANDOLT and WILDI 1977).

Optimal growth of Lemnaceae in culture was observed in solutions with a nitrogen content from 0.6 mg/l (L. gibba, L. minuscula), 2.8 mg/l (L. minor), and 14 mg/l (S. polyrrhiza) up to more than 70 mg/l (all species) (LUEOEND 1980, 1983). MUELLER (1983) gives the following upper limit of nitrogen concentration for growth of Lemnaceae: 420-700 mg/l (L. minuscula), 1120-1680 mg/l (S. punctata), 1400-1680 mg/l (S. polyrrhiza), 1400-2100 mg/l (L. minor), 2100-2800 mg/l (L. gibba and L. turionifera). According to STANLEY and MADEWELL (1976a) the 50% inhibitory level of NH_4 nitrogen is 700 mg/l for L. obscura. L. aequinoctialis showed symptoms of toxicity at 1400 mg/l nitrate nitrogen (FERNANDEZ and BALDOS 1981). In natural waters the upper limit of nitrogen is never reached. At nitrogen concentrations of 0.56 mg/l or lower, S. polyrrhiza forms turions. It does not grow any longer at concentrations lower than

0.1 mg/l. L. gibba still grows slowly at 0.02 mg/l N, L. minor and L. minuscula even at 0.004 mg/l N (LUEOEND 1983). According to INGEMARSSON et al. (1983) the nitrate is taken up by L. gibba at the same constant rate at concentrations down to 0.6 mg/l. It may be concluded that this concentration is the lower limit of nitrate content for optimal growth of L. gibba which is in agreement with the results of LUEOEND (1980, 1983) (table 4.2) who measured a somewhat lower mean nitrogen value for L. gibba occurrence of 0.22 mg/l.

4.2.4.7. Phosphorus (P) content (table 4.1)

In nature phosphorus probably plays the leading role in limiting the growth of the Lemnaceae. According to FEKETE et al. (1976), neither the content of phosphate phosphorus nor the content of soluble total phosphorus are unequivocal values of the available phosphorus for Lemnaceae because different phosphorus compounds are not absorbed from the same minimal concentration. Another difficulty in analysing the available phosphorus content of waters is that Lemnaceae are able to utilize phosphorus which is bound to clay particles and therefore usually not measured in water samples (HEALY and MACCOLL 1974b; see also vol. 2, chapter 2.7.6 on phosphate acquisition by release of phosphatases). In addition, the availability of the phosphorus depends on the pH and the calcium content. Phosphorus can precipitate at pH 8 and higher.

Similarly to the nitrogen content, the phosphorus content varies during the year and between different years (LUEOEND 1980). SCOPPOLA (1982) observed values for the phosphorus content between 0.2 and 1.7 mg/l at the same locality, STARFINGER (1983) between 0.037 and 0.73 mg/l and KLOSE (1963) between 0.02 and 0.19 or 0.004 and 0.16 mg/l. The lowest average phosphate value was measured by POTT (1980) in Europe in April (0.8 mg/l P in the Lemnetum gibbae and much lower values in other associations), the highest in November (2.8 mg/l P in the same association).

In the Netherlands in 90% of the waters with L. minor, the phosphorus content varied between 0.003 and 0.62 mg/l (ROELOFS 1983). Still lower values are considered as only temporary or are possible due to changes in the phosphorus content during transport of the samples for water analysis. LUEOEND (1983) found the following lowest average yearly values of phosphorus content in waters of Central Europe with Lemnaceae (table

4.2): 0.006 mg/l for L. minor, 0.007 mg/l for S. polyrrhiza, 0.010 mg/l for L. trisulca, 0.012 mg/l for L. minuscula, and 0.027 mg/l for L. gibba. In northern Europe IVERSEN and OLSEN (1946) recorded 0.012 mg/l P as the lowest value for waters with L. minor and L. trisulca. In Germany the highest phosphorus content of waters with Lemnaceae amounts to 25 mg/l (WIEGLEB 1978b), and in Malaysia to 56 mg/l (LANDOLT unpubl. results).

POTT (1980, 1981) and (in brackets) STARFINGER (1983) found Lemnaceae associations within the following limits of phosphorus content: 0.9-3.0 (1.0-2.3) mg/l (Lemnetum gibbae), 0.4-2.7 (0.1-0.5) mg/l (Spirodeletum polyrrhizae), 0.2-1.4 (0.14-0.8) mg/l (Lemnetum trisulcae), and 0.0-0.2 (0.7-0.8) mg/l (Ricciatum fluitantis).

The lower limit of phosphorus content for the growth of Lemnaceae is probably higher than for most other floating water plants (e.g. Riccia, Salvinia, Pistia, Eichhornia). On the other hand, species of Lemnaceae compete well with other water plants, especially algae, in water with high phosphorus but relatively low nitrogen content (FITZGERALD 1969, LEWCOWICZ and LEWCOWICZ 1977).

Optimal growth of Lemnaceae in culture is possible between the following limits of phosphorus content (LUEOEND 1983): 0.4-10.9 mg/l for S. polyrrhiza and L. minor, 0.08-10.9 mg/l for L. minuscula, and 0.08-54.3 mg/l for L. gibba. The minimal concentration for growth is 0.03 mg/l for L. minor and L. minuscula, and 0.2 mg/l for S. polyrrhiza and L. gibba (LUEOEND 1983). The upper limit for S. polyrrhiza is about 1500 mg/l P (EYSTER 1966) which is more than a hundred times more than the values measured in nature. DOCAUER (1983) reported a high need of phosphate for W. borealis, higher than for other species in North America. In nature W. borealis can be found sometimes in lakes very poor in phosphorus. Since W. borealis is able to form turions during the whole summer (in contrast to W. columbiana which forms turions only in fall) the author concludes that the turions may be provided with phosphorus from the sediment layer after sinking to the bottom.

4.2.4.8. Content of inorganic carbon (HCO_3^-) (table 4.1)

Inorganic carbon in the water is only essential for totally or partly submerged species of Lemnaceae which are dependent on dissolved CO_2 or on bicarbonate: L. trisulca, L. tenera, L. valdiviana (if submerged),

most Wolffiella species, and some Wolffia species (e.g. W. columbiana). According to STEEMANN NIELSEN (1944, 1947), the dissolving of CO₂ in water surrounded by normal air (0.03% CO₂) is only about 0.6 mg/l which enables Myriophyllum, Ceratophyllum, and Elodea a very low rate of photosynthesis but is insufficient for survival. The plants mentioned are able to utilize bicarbonate but not carbonate. They reach about 50% of their maximal growth rate if supplied with 60 mg/l bicarbonate. At a pH of higher than 6.5 a greater amount of inorganic carbon is in solution in form of bicarbonate, at pH 7.5:10.8 mg/l bicarbonate; and at pH 9.5: 7.1 mg/l (RAVEN 1981). In Finland, submerged water plants grow in granitic regions only near the coast where the pH of the water is higher and the supply of bicarbonate better (STEEMANN NIELSEN 1954). L. trisulca is not able to grow at a pH of 6 in solutions without the addition of an organic carbon source (e.g. sucrose). But at higher pH, and especially if bicarbonate or carbonate is added, L. trisulca and W. gladiata grow well (LANDOLT results not publ.).

In waters with Lemnaceae WIEGLEB (1978b) found high values of bicarbonate (mostly between 30 and 200 mg/l). SEGAL (1966) reports values up to 503 mg/l bicarbonate, and in 90% of the waters with L. minor ROELOFS (1983) measured 12.2-1200 mg/l bicarbonate. PIETSCH (1972), too, measured, in waters with L. minor, a high bicarbonate content which was generally higher than the sulphide and the chloride content. The values of dissolved carbon dioxide in waters with Lemnaceae are also high. WIEGLEB (1978b) measured an average amount of 10 mg/l, ROELOFS (1983) an average of 45 mg/l. These high values are probably due to the fact that under a cover of Lemnaceae there are no green organisms which can assimilate the carbon dioxide.

Submerged species generally live in waters with a high bicarbonate content. In the Lemnetum trisulcae POTT (1980) measured 10-62 mg/l CO₂ compared with 8.0-11.2 mg/l in the Lemnetum gibbae. ELLIS (1955) recorded a content of over 100 mg/l bicarbonate in waters with W. gladiata and Riccia and more than 60 mg/l bicarbonate and carbonate in waters with other Lemnaceae.

4.2.4.9. Chloride (Cl) content (table 4.1)

The chloride content of waters with Lemnaceae amounts between 0.1 mg/l (HARRISON and BEAL 1964, LANDOLT and ZARZYCKI in prep.) and 4650 mg/l

(OLSEN 1950 for L. gibba and DE LANGE 1972 for L. trisulca). The chloride content may vary during the year at the same locality as was shown by SCOPPOLA (1982), and (in brackets) CONGDON and McCOMB (1976), e.g. between 28.4 and 136.2 mg/l or between 91.2 and 426 mg/l (212 and 655 mg/l). In general, the content of chloride was much higher than 1 mg/l in natural waters (HARRISON and BEAL 1964, DE LANGE 1972, KADANO 1982, STARFINGER 1983, LANDOLT and ZARZYCKI in prep., LANDOLT unpubl. results). In 90% of the waters with L. minor ROELOFS (1983) measured between 2.8 and 142 mg/l Cl.

MARTIN (1963a,b, 1965) showed that chloride ions are necessary for good growth of Lemnaceae. Optimal growth was obtained with a minimum chloride content of 0.5 mg/l for S. polyrrhiza, 0.03 mg/l for L. minor, and 0.01 mg/l for L. aequinoctialis. The need for minimal growth is at least 3-5 times lower. EYSTER (1966) achieved optimal growth of S. polyrrhiza between 0.3 and 30 mg/l chloride; at 350 mg/l, the growth was retarded, and at 3500 mg/l, the fronds died.

In nature the minimal chloride content very rarely seems to limit growth of Lemnaceae. It is possible that some species need even more chloride for optimal growth than S. polyrrhiza and avoid waters where the chloride content is too low. However, the upper limit is quite often reached in brackish water. In general, the high chloride content seems to limit the growth of Lemnaceae more than the high sodium content.

4.2.4.10. Sulphur (S) content (table 4.1)

Lemnaceae are found in waters with as low as 0.0-5 mg/l sulphate (LOHAM-MAR 1938, MOYLE and HOTCHKINS 1945, JACOBS 1947, SEGAL 1966, ROELOFS 1983, LANDOLT and ZARZYCKI in prep.) which corresponds to about 0.0-1.5 mg/l sulphur. Usually the sulphur content was higher than 15 mg/l (MOYLE and HOTCHKINS 1945) or 5 mg/l (LANDOLT unpubl. results). The highest sulphur content measured in waters with Lemnaceae was 200-350 mg/l sulphur (SEGAL 1966, POTT 1980, LANDOLT and ZARZYCKI in prep.). The occurrence of Lemnaceae in waters which smell of H₂S is reported by SEGAL (1966) for S. polyrrhiza, L. gibba, and L. trisulca from the Netherlands. A. KLEIN, Gelterkinden (pers.comm.) collected L. gibba, L. minuscula, and W. oblonga in sulphur-rich volcano lakes in the Andes of Peru. MERIAUX (1978) found the Lemnetum gibbae in northern France in waters with 20-230 mg/l sulphur, POTT (1980) and STARFINGER (1983) in Germany,

in waters with 23-67 mg/l sulphur. The waters of the Lemnetum trisulcae had 4-44 mg/l sulphur, the Spirodeletum 6-48 mg/l, and the Ricciatum fluitantis 0.03- 65 mg/l. EYSTER (1966) obtained optimal growth for S. polyrrhiza in culture solutions with 15-700 mg/l sulphur. Minimal growth was obtained by addition of 1.5 mg/l sulphur. At 2000 mg/l sulphur, growth almost ceased. Waters in which the sulphur content is too low to enable growth of Lemnaceae are probably rare in nature. On the other hand, too much sulphate or sulphide is reached only in sulphur springs.

4.2.4.11. Content of trace elements

Though many trace elements are necessary for the growth of Lemnaceae, no indications of limiting amounts in nature are known, since these elements are rarely analysed.

It is possible that too little accessible iron (Fe) sometimes limits growth in waters with high pH. According to DOCAUER (1983) ponds in Michigan with S. polyrrhiza contained less soluble iron than ponds with L. turionifera. POTT (1980) found 0.01-0.68 mg/l Fe in waters with Lemnaceae. About 1 mg/l Fe is necessary for good growth of Lemnaceae (STEINBERG 1946, EYSTER 1966), but much less is needed for survival. LOHAMMAR (1938) measured, in Swedish lakes containing Lemnaceae, less than 0.2 to 0.8 mg Fe/l and less than 0.01 to 0.9 mg Mn/l. He observed no limiting content of Fe or Mn.

KLOSE (1963) is of the opinion that manganese (Mn) may be a limiting factor in some waters. Manganese is needed in a concentration of at least 0.05 mg/l for good growth (STEINBERG 1946, EYSTER 1966). In waters from Argentina and Malaysia covered with Lemnaceae the manganese content was mostly below 0.05 mg/l (the lower level of sensitivity of the method of analysis) (LANDOLT and ZARZYCKI in prep., LANDOLT unpubl. results). The highest amount of manganese measured was 0.5 mg/l, still within the limits of the optimal growth which is according to EYSTER (1966) between 0.05 and 3 mg/l. KLOSE (1963) found Lemnaceae in Europe in waters of 0.0 to 1.1 mg/l manganese content.

Zinc (Zn) is needed in concentrations of about 1 mg/l for optimal growth of S. polyrrhiza (EYSTER 1966) and of 0.04 mg/l for L. minor (STEINBERG 1946). The upper limit of zinc content for growth of L. minor is about 30 mg/l (SAROSIEK and WOZAKOWSKA-NATKANIEC 1980), for L. obscura 65 mg/l (STANLEY and MADEWELL 1976a) and for S. polyrrhiza, according to EYSTER

(1966), 300 mg/l or higher. The toxicity of Zn is dependent on the nutrient composition of the solution. It is much higher if the Mg content is low (MARTIN 1955). In Argentina and Malaysia, the waters with Lemnaceae contained 0.01-0.2 mg/l Zn. Five stations with 0.2-102.6 mg/l Zn were free of Lemnaceae. Since the calcium and magnesium content of the same sample was not low in all samples, possible toxicity of the zinc is probably to be excluded.

The necessary amount of **boron (B)** for optimal growth of L. minor and W. arrhiza is at about the same level as for manganese (0.05 mg/l) (STEINBERG 1946, EICHHORN and AUGSTEN 1974). The lower limit of good growth is higher for S. polyrrhiza: 1 mg/l (EYSTER 1966). Other possible trace elements (Mo, Cu, Ni) are needed in such low concentrations that no deficiencies are known.

Lemnaceae are able to store trace elements. Therefore they can survive for a long time without supply.

4.2.4.12. Content of organic substances

Different authors (e.g. RAO 1953, HARRISON and BEAL 1964, LEUCHTMANN 1979, PIP 1979) measured a relatively high content of organic substances in waters with Lemnaceae: up to 21 mg/l. TOMASZEWCZ (1977) found the association Wolffietum arrhizae only in peat bogs. According to KRAUSE (1979) in central Germany, Lemnaceae are bound to organically contaminated waters. It is not known whether the high content of organic substances is the cause or the effect of the colonization by Lemnaceae. Since waters with Lemnaceae are generally poor in oxygen, the organic substances formed by dead organisms do not decompose and so accumulate. On the other hand, organic substances may play a role as buffering substances, chelating agents, suppliers of vitamins or energy for heterotrophic growth. The presence of sugars in natural waters and their meaning for the growth of Lemnaceae has been mentioned in chapter 4.2.3. Carboxylic acids, amino acids and sugars develop from decaying Lemnaceae (PATIENCE et al. 1983) and other organisms. SHAPIRO (1957, 1958, 1964) demonstrated the presence of chelating agents in lake water. According to SAUNDERS (1957), growth factors and vitamins can be shown in water of natural localities. He lists the following substances analyzed from natural waters and from lake sediment extracts: thiamine, niacin, biotin, three chlorophyll-like pigments, α - and β -carotene, lycopene, myxoxan-

Table 4.3. Lowest nutrient demand of some Lemnaceae species
(from different literature sources and own obeservations)

1 relatively low demand
2 medium demand
3 relatively high demand
(see table 4.4)

Species	Ca	Mg	K	N	P	C
<i>S. intermedia</i>	2	2				1
<i>S. polyrrhiza</i>	2	2	2	1	1	1
<i>S. punctata</i>	1	1				1
<i>L. gibba</i>	2	3	3	3	3	1
<i>L. disperma</i>	3	2				1
<i>L. minor</i>	1	1	1	1	1	1
<i>L. japonica</i>		2				1
<i>L. obscura</i>	1	1	3			1
<i>L. turionifera</i>		3	3	1	1	1
<i>L. trisulca</i>	3	3	3	1	2	3
<i>L. perpusilla</i>	1	1				1
<i>L. aequinoctialis</i>	1	2		2		1
<i>L. valdiviana</i>	2	1				2
<i>L. minuscula</i>	2	1	2	3	2	1
<i>W. hyalina</i>	2	3		3		1
<i>W. neotropica</i>	1	2				3
<i>W. Welwitschii</i>						3
<i>W. lingulata</i>	1	1				3
<i>W. oblonga</i>	1	1				3
<i>W. gladiata</i>	1	1				3
<i>W. microscopica</i>	1	3				1
<i>W. brasiliensis</i>	2					1
<i>W. borealis</i>		2	3	3	3	1
<i>W. australiana</i>	1	2				1
<i>W. angusta</i>	2	2				1
<i>W. arrhiza</i>	2	2				1
<i>W. columbiana</i>						2
<i>W. globosa</i>	2	2				2

Table 4.4. Three levels of approximate minimum nutrient requirements in Lemnaceae, in mg/l (see table 4.3)

	Ca	Mg	K	N	P	C
1	10	1.0	1.0	0.04	0.006	0
2	18	2.5	1.5	0.1	0.010	2
3	40	4.5	4.5	0.2	0.030	10

thine, rhodoviolascin, peptides, tryptophane, tyrosine, histidine, cystine, arginine, glucose, galactose, arabinose, xylose, ribose, dehydroascorbic acid, and a rhamnoside. As we know that Lemnaceae have very efficient systems to take up different kinds of amino acids and other organic compounds (DATKO and MUDD 1985), organic substances may play an important role for Lemnaceae to grow in shaded areas or in lower layers of a plant mat covering the water surface. However, there is no correlation between the occurrence of Lemnaceae and the amount of organic substances (organic carbon or organic nitrogen) in waters of northern Switzerland (LEUCHTMANN 1979). Lemnaceae are present in waters with 0.02 to 1.64 mg/l dissolved organic nitrogen (DON) and with 1.0-21.0 mg/l dissolved organic carbon (DOC) (PIP 1979).

Waters with Lemnaceae often contain ethylene which is responsible for the gibbosity of L. gibba (ELZENGA et al. 1980) and possibly of S. intermedia, S. punctata, L. disperma, and L. obscura. Gibbous fronds have an advantage in competition with flat fronds because they push their edges over the edges of the flat fronds and because they have a larger absorbing lower surface (see chapter 5.4). Lemnaceae are very sensitive to most herbicides and algicides as well as to many other pesticides (cf. KHARE 1977, 1979, EVANS and WALKER 1978, PRASAD 1981).

4.2.4.13. Characteristic demands of species (tables 4.3, 4.4)

Table 4.3 is an attempt to characterize the specific demands of some Lemnaceae species. For most species, the exact requirements are not known exactly. The approximate limits (average value throughout the year) for different nutrients are put together in table 4.4.

4.3. SEXUAL REPRODUCTION

4.3.1. Flowering conditions

4.3.1.1. General remarks

There are many observations on flowering Lemnaceae in nature. Since the flowers are very inconspicuous and therefore difficult to detect, the occurrence of flowers was carefully noted by many authors (e.g. GILLMAN 1881, KALBERLAH 1895, ROSTOWZEW 1905, SAEGER 1929, HICKS 1932a, GIARDELLI 1935, 1947, MASON 1938, LUTHER 1948, KURZ and CROWSON 1949, MAHESHWARI 1954, OBERMEYER-MAUVE 1966, JOVET and JOVET-AST 1967, ARMSTRONG 1982, MARTINSSON 1984, PECHENYUK 1985). Flowering in nature is known of all species except L. ecuadorensis, W. elongata, and W. australiana (see table 4.5). However, flowers of W. australiana have been observed in cultures (LANDOLT unpubl.). Table 4.5 gives a survey of flowering samples found in the field by the present author and in herbaria studied. From table 4.5, it is evident that the species of Lemnaceae can be divided into three groups according to their flowering behaviour (the species are enumerated in the sequence of decreasing flowering percentage):

1. Species which flower and fruit often (9-48% flowering samples)

L. perpusilla, W. hyalina, L. aequinoctialis, L. gibba, L. disperma, W. Welwitschii, and W. lingulata.

2. Species which flower occasionally (1.5-6% flowering samples)

S. punctata, W. globosa, L. minor, L. minuscula, L. turionifera, W. oblonga, W. gladiata, S. intermedia, L. valdiviana, W. arrhiza, W. columbiana, L. japonica, L. obscura, W. brasiliensis, W. angusta, L. trisulca.

3. Species which flower very rarely (less than 1% flowering samples)

S. polyrrhiza, W. borealis, W. australiana.

The behaviour of L. ecuadorensis, L. tenera, W. rotunda, W. repanda, W. neotropica, W. denticulata, W. elongata, and W. microscopica is not sufficiently known, due to the small amount of checked specimens (less than 40).

For most species, the occurrence of flowering in nature cannot be explained satisfactorily. There are so many ecological factors involved in

flowering that it is difficult to get a clear picture of the causing factors. In addition, it seems that different species and even different clones of the same species sometimes behave differently. In nature, it is possible to observe localities with several species flowering at the same time (e.g. GILLMAN 1871, SAEGER 1929, HICKS 1932a, GILBERT 1937, JACOBS 1947, LANDOLT 1957). This information indicates either that the environmental demands for flowering are similar for different species, or it reveals a transmission of flowering from one species to another. LANDOLT (1957, p. 317) was able to demonstrate flowering L. gibba in mixed cultures with flowering L. turionifera under low light intensity which was not sufficient for flowering of L. gibba in pure culture. The experiment was successfully repeated by LOCKHART, Pasadena (in lit.). It is assumed that the flowering species produce a higher level of ethylene which is able to induce the flowering of other species. On the other hand, flowering at a certain place may be restricted to some species only, to different seasons, or to different locations within the same water (LANDOLT 1957).

In the chapters 4.3.1.2 to 4.3.1.6, the special factors which seem to play a role in causing flowering are discussed. For more physiological details see vol. 2, chapter 2.4.3 (LANDOLT and KANDELER 1987).

It is evident that the behaviour in nature also depends on the geographical region and the time of collecting. That is why records of different regions may deviate from the results of table 4.5. In Poland WOLEK (1984) found during July (3rd to 16th July 1975) the following flower percentage in naturally growing Lemnaceae samples: S. polyrrhiza 0% (21 sites); L. gibba 12.5% (16 sites); L. minor 23.8% (42 sites); L. trisulca 8.7% (23 sites), and W. arrhiza 0% (3 sites). In Öland (Sweden) MARTINSSON (1984) detected between 23rd June and 1st August 1982 46% flowering L. minor (26 sites). The difference to the results of table 4.5 may be explained by the fact that both authors observed the Lemna stations only during the warmest periods, whereas the samples of table 4.5 were collected in the course of the whole year. It is interesting to note that in Poland only species with their main distribution in rather cool climates (similar to the areas studied) have a higher flowering percentage (L. minor, L. trisulca) whereas species occurring mainly in warm regions (S. polyrrhiza, L. gibba, W. arrhiza) flower more rarely during the Polish summer than worldwide. HICKS (1932a) observed 8% flowering L. minor (included L. turionifera) in Ohio which is slightly

higher than in table 4.5. Ohio with rather warm summers is probably more favourable to flowering of L. minor and L. turionifera than more oceanic and cooler regions.

Table 4.5. Flowering and fruiting percentage of Lemnaceae species in nature (data taken from herbarium specimens and own observations)

Species	estimated number of samples	number of flowering samples	number of fruiting samples	% flowering	% fruiting
<i>S. intermedia</i>	200	6	6	3	3
<i>S. polyrrhiza</i>	3500	12	3	0.3	0.1
<i>S. punctata</i>	550	30	17	5	3
<i>L. gibba</i>	1100	154	102	14	9
<i>L. disperma</i>	136	16	10	12	8
<i>L. minor</i>	1500	86	11	5	0.6
<i>L. japonica</i>	52	1	0	2	<2
<i>L. obscura</i>	450	9	6	2	1.3
<i>L. ecuadorensis</i>	2	0	0	(<50)	(<50)
<i>L. turionifera</i>	1750	64	21	4	1.2
<i>L. trisulca</i>	2500	37	10	1.5	0.4
<i>L. perpusilla</i>	300	145	137	48	45
<i>L. aequinoctialis</i>	2200	412	348	19	16
<i>L. tenera</i>	11	1	0	(10)	(<10)
<i>L. valdiviana</i>	500	13	7	3	1.6
<i>L. minuscula</i>	700	39	12	5	2
<i>W. hyalina</i>	62	20	15	32	24
<i>W. repanda</i>	3	2	2	(67)	(67)
<i>W. rotunda</i>	1	1	0	(100)	(<100)
<i>W. neotropica</i>	10	1	1	(10)	(10)
<i>W. Welwitschii</i>	86	8	6	9	7
<i>W. lingulata</i>	170	23	5	13	2.6
<i>W. oblonga</i>	230	9	1	4	0.4
<i>W. gladiata</i>	250	10	2	4	0.8
<i>W. denticulata</i>	9	1	0	(11)	(<11)
<i>W. microscopica</i>	10	2	1	(20)	(10)
<i>W. elongata</i>	4	0	0	(<25)	(<25)
<i>W. brasiliensis</i>	650	13	5	2	0.8
<i>W. borealis</i>	500	1	0	0.2	<0.2
<i>W. australiana</i>	44	0	0	<2	<2
<i>W. angusta</i>	46	2	0	4	<4
<i>W. arrhiza</i>	150	4	1	3	0.8
<i>W. columbiana</i>	1200	18	3	1.5	0.3
<i>W. globosa</i>	105	6	3	6	3

4.3.1.2. Crowding effect

Very often, flowers can only be observed under crowding conditions. Or, flowering is at least more intense in a dense cover of Lemnaceae than within scattered fronds. Sometimes, many species are flowering together at the same time under crowding conditions (observations of many field botanists, e.g. SAEGER 1929). FAERBER (1984) showed that crowding in L. gibba is able to stimulate ethylene production. Therefore, it is probable that a higher content of ethylene which promotes flowering (cf. SCHARFETTER et al. 1984) is responsible for the crowding effect.

4.3.1.3. Light intensity

Some authors report that sunlight favours flowering (e.g. HICKS 1932a for L. minor and L. trisulca, LUDWIG 1909 for L. trisulca, ARMSTRONG 1982 for W. borealis), others observed flowers mostly in the shade (e.g. GILLMAN 1881 for S. polyrrhiza, LUDWIG 1909 for L. minor). MARTINSSON (1984) saw flowering L. minor in southern Sweden in both sunny and shady localities, the shaded populations with later flowering than those exposed to the sun. Also ROSTOWZEW (1901) made the same observation with L. minor in the region of Moscow. According to LANDOLT (1957), L. turionifera flowers in culture only at relatively high light intensities; at low intensities, sucrose has to be added to induce flowering. L. gibba, too, flowered only at relatively high intensities (above 2500 lux) which is in accordance with observations made in nature. L. minuscula on the other hand, flowered preferably in the shade (LANDOLT 1957). L. aequinoctialis reacts differently, depending on the clone studied. Most clones needed high light intensities but others flowered also at somewhat lower intensities. If sucrose is added, some clones produce flowers even under almost dark conditions. It seems that a certain high light intensity is necessary so that the fronds produce enough energy reserves to be able to flower. The lowest intensity needed is dependent on the clone. Different temperatures at sunny and shady localities may also contribute to the different flowering behaviour.

HICKS (1932a) got flowers experimentally by ultraviolet radiation in L. minor, L. turionifera, L. minuscula, L. valdiviana, L. trisulca, and W. columbiana, but not in S. polyrrhiza and W. borealis. It is not clear if the effect of UV radiation is a direct energetic effect on some meta-

bolic processes or if there is a specific effect transmitted by a pigmentary system other than chlorophyll. The results of HICKS (1932a) have never been checked.

4.3.1.4. Duration of light

It is well known from many experimental investigations that flowering of most species of Lemnaceae are dependent on the length of the day. A survey of the experiments carried out hitherto is given by KANDELER (1983).

Long-day plants: L. gibba (KANDELER 1955, 1956, BENNINK et al. 1970, KRAJNCIC and DEVIDE 1980), L. turionifera (LANDOLT 1977 named as L. minor I, BENNINK et al. 1970 named as L. minor), L. minor (KRAJNCIC 1974b, KRAJNCIC and DEVIDE 1980), S. polyrrhiza (1 of 5 investigated clones: KRAJNCIC and DEVIDE 1982a), S. punctata (SCHARFETTER et al. 1978), W. brasiliensis (6 of 14 investigated clones flowered under a 15 hour day, 28°C day and 22°C night temperature, 12,000 lux, 1/3 Hutner solution with 1% sugar: LANDOLT unpubl. results) and L. aequinoctialis, S-type (BEPPU and TAKIMOTO 1981b). S. intermedia seems to flower under long-day conditions, too (KLICH and MUJICA 1985).

Short-day plants: L. aequinoctialis, most clones, e.g. No. 6746 (HILLMAN 1958 and many other authors) and N-type strains of BEPPU and TAKIMOTO 1984. It is interesting to note that flowering of clone No. 6746 is only short-day dependent at higher temperatures (26°C-30°C for solutions with EDTA and 29°C-31°C for solutions without EDTA). At lower temperatures and in old cultures the clone 6746 of L. aequinoctialis behaves as a day-length neutral plant (HILLMAN 1959a,b, 1960a, CLELAND and AJAMI 1974). Further short-day species: L. perpusilla (KANDELER and HUEGEL 1974a), W. microscopica (MAHESHWARI 1963), W. brasiliensis (MAHESHWARI and CHAUHAN 1963, MAHESHWARI and SETH 1966b), W. angusta (LANDOLT unpubl. results), W. arrhiza (if cultured at long-day conditions before; therefore this plant is called a long-short-day plant: KRAJNCIC and DEVIDE 1980).

Day-length neutral plants: S. polyrrhiza (4 of 5 investigated clones: KRAJNCIC and DEVIDE 1980, 1982a). L. obscura (CLELAND et al. 1982), L. aequinoctialis K-type (BEPPU and TAKIMOTO 1981b).

It is interesting to note that long-day plants are species mainly distributed in the temperate climate, that short-day plants grow often in the tropics and subtropics, and that the day-length neutral S. poly-

Table 4.6. Flowering and fruiting time of Lemnaceae species in different regions of the world

Geographical areas (G.a.):

- 1 North America (Canada, USA, northern Mexico)
- 2 Eurasia (southwards to about 30° NL)
- 3 Southern South America (Argentina, Chile, Uruguay)
- 4 Southern Australia (northwards to about 30° SL)
- 5 Central and South America (except Argentina, Chile, and Uruguay)
- 6 Africa
- 7 Southern Asia and Northern Australia (between about 30° NL and SL)

Table 4.6. (continued)

species	G.a.	month											
		1	2	3	4	5	6	7	8	9	10	11	12
<i>W. neotropica</i>	5											1	
<i>W. Welwitschii</i>	5		1				2						
	6												2
<i>W. lingulata</i>	1	1	1		1	3	2	3	4	2	1	2	
	3												
	5												
<i>W. oblonga</i>	1		1		1				2		1		
	3						1					3	
	5												
<i>W. gladiata</i>	1		2	1	3	3							1
<i>W. denticulata</i>	6												
<i>W. microscopica</i>	7												1
<i>W. brasiliensis</i>	1					1	1		1	3			1
	3	1	1				1						1
	5							3					
<i>W. borealis</i>	1							1		1			
<i>W. angusta</i>	7									1			
<i>W. arrhiza</i>	2												
	6				1					1	1	1	
<i>W. columbiana</i>	1					1		2	4	1	1		
	3			1								4	
	5							1				1	1
<i>W. globosa</i>	6	1	1					1			1	1	

rrhiza is distributed throughout most climatic zones.

In addition the following species which have a clearly extratropical area may be long-day plants: *L. disperma*, *L. japonica*, *L. trisulca*, *W. oblonga*, *W. gladiata*, *W. denticulata*, *W. borealis*, *W. australiana*. Additional species with mainly tropical and subtropical distribution, and therefore possibly short-day plants, are: *L. ecuadorensis*, *L. tenera*, *W. hyalina*, *W. repanda*, *W. rotunda*, *W. neotropica*, *W. Welwitschii*, *W. elongata*. Furthermore species with a distribution throughout many climatic zones and probably either with a day-length neutral reaction, or short-day plants are: *L. valdiviana*, *L. minuscula*, *W. lingulata*, *W. columbiana*, *W. globosa*.

The necessary length of light and dark periods may vary within a species (e.g. for *L. aequinoctialis*: BEPPU and TAKIMOTO 1981b), also temperature and other conditions are able to influence the length of day necessary for flowering. In strain 381 of *L. aequinoctialis*, for instance, a lowering of the night temperature from 25°C to 20°C changes the critical

day length from 11 to 9 1/2 hours (BEPPU and TAKIMOTO 1981b). For further investigations on the rather complex interrelationship between day-length and flowering see volume 2, chapter 2.4.3 (LANDOLT and KANDELER 1987)

The flowering times of the species found in nature are put together in table 4.6. The data are taken from herbarium specimens and from our own field observations. In addition, the following publications were consulted, mainly because European herbarium material was not checked: LUTHER (1948) and MARTINSSON (1984) for flowering Lemnaceae in northern Europe, JOVET and JOVET-AST (1967) for flowering L. minuscula in France, JOVET (1968) for flowering W. hyalina in Chad, and GILBERT (1937) and ARMSTRONG (1982) for flowering W. borealis in U.S.A.

Table 4.6 shows that neither long-day plants nor short-day plants are restricted to their necessary day-length conditions for flowering in nature. Keeping in mind that the light-dependent flowering conditions may be variable within a species as well as within different temperature and nutrient conditions, it is understandable that in nature short-day and long-day plants are able to flower at almost any time of the year under otherwise favourable conditions. Especially in spring and autumn short-day, long-day, and day-length neutral plants may flower together at the same place. Some differences in the flowering behaviour of different species can be observed in table 4.6. Species with a short flowering time during the warmest summer months (S. polyrrhiza, L. turionifera, and to a lesser extent L. minor) are probably dependent on warm water. L. trisulca behaves similarly but evidently needs less warmth; therefore, it usually flowers in June. All other species, which grow in cooler regions, show some flowering preference in warmer months. Interestingly, L. perpusilla flowers mainly in September. Some of the late records of L. perpusilla in table 4.6 may actually concern samples with overwintering fruits, since no distinction was made between flowering and fruiting specimens from herbaria. Nevertheless, the late flowering of L. perpusilla is remarkable. It might be explained by the necessary short-day conditions. Since L. perpusilla overwinters in cooler regions with fruits still cohering to dead fronds, the late fruiting is understandable.

4.3.1.5. Temperature

According to table 4.6, species of Lemnaceae flower in cool climate zones only during warm seasons. LANDOLT (1957) was able to induce flowers of L. gibba and L. turionifera only at temperatures of 24°C or higher; especially L. turionifera flowers much better at temperatures of 30°C than of 26°C. For L. aequinoctialis, it was possible to get flowers at temperatures down to 16.5°C. Above 31°C the clone 6746 of L. aequinoctialis no longer flowers (CLELAND and AJAMI 1974). W. microscopica, a short-day plant, needs a temperature of 22°C for optimal flower induction (RIMON and GALUN 1968b). This corresponds to the temperatures in Central India during winter time. In table 4.6, some species can be detected which flower even in the cooler regions 1, 2, 3, or 4 during the winter. It is supposed that these species do not need high temperatures for flowering: L. perpusilla, L. minuscula, W. lingulata, W. oblonga, W. gladiata. ROSTOWZEW (1901) observed flowering of L. minor in the region of Moskow only in a year with cool summer. L. minuscula flowers in western France in December and January (JOVET and JOVET-AST 1967), and W. lingulata can be found flowering along the coast of California in January and February (LANDOLT 1957).

4.3.1.6. Chemical composition of the water

So far it was never possible to correlate the flowering of Lemnaceae in nature with the chemical composition of the water. The flowering seems to occur within a wide range of different nutrient content (see table 4.7). The effect of some chemicals on flowering under experimental conditions will be referred to in volume 2, chapter 2.4.3 (LANDOLT and KANDELER 1987). The pH seems to have no influence on flowering of cultures either. LANDOLT (1957) found flowering Lemnaceae (L. gibba, L. minor, L. turionifera, L. minuscula, and W. lingulata) at a pH lower than 6 (down to 4.7; not included in table 4.7). However, HICKS (1932a) reported experimentally induced flowering in L. minor and L. trisulca by enhancing the pH over 7 (with NaOH). It is difficult to understand his results, and they have never been checked successfully. If table 4.7 is compared with table 4.1, it is obvious that the content of Na, K, Ca, and Mg in waters with flowering Lemnaceae has about the same variation as in cultures of non-flowering Lemnaceae.

Table 4.7. Chemical composition of waters with flowering Lemnaceae. The samples originate from Argentina (27), Brazil (4), North Carolina (2), California (3), and Australia (3) (LANDOLT unpubl. results)

Flowering occurs even outside the 95% range. In flowering cultures, no high content of N and P was observed. GILBERT (1937) found, in Minnesota, flowering S. polyrrhiza, L. minor (incl. L. turionifera), L. trisulca, W. borealis, and W. columbiana in a year with abundant rains. It is not known if the rain was responsible for the frequent flowering. It is possible that the rain had an effect due to the cooler temperatures connected with it or due to the dilution of some elements in the water.

4.3.1.7. Flowering in culture (see volume 2, chapter 2.4.3, LANDOLT and KANDELER 1987)

Several authors report flowering of Lemnaceae samples when cultured at home. ROSTOWZEW (1901) mentions continuous flowering of L. minor from the field after cultivating at room conditions. This effect could only be observed if jars have been covered by a glass plate.

Some of our own clones showed flowers some weeks after arriving in Zürich from their natural habitat. Clones of 19 species flowered either regularly in the test tubes at normal room conditions (a few clones of L. aequinoctialis, L. perpusilla, W. lingulata, W. microscopica) or they developed flowers under experimental conditions. Different clones of the same species behaved differently, especially in response to light intensity, temperature, or addition of sugar. Flowering was observed partly under the following conditions: 24-28°C, 12-16 hours daylight, 3,000 to 25,000 lux, 1/3 or 1/5 Hutners solution, with or without sugar, and with the following species: L. aequinoctialis (about half of the clones), L. perpusilla (about half of the clones), L. gibba and L. disperma (about 85% of the clones), L. turionifera (about 2/3 of the clones), W. microscopica (the only clone), W. brasiliensis (nearly half of the clones). Flowering of L. obscura, L. valdiviana, and W. angusta was seen only in 1 or 2 clones each. More species flowered when EDDHA was added to the solution. The following number of clones flowered in the EDDHA experiments (in brackets the number of cultivated clones in the experiments): S. intermedia 2 (4), S. polyrrhiza 2 (2), S. punctata 0 (2), L. gibba 3 (5), L. disperma 2 (4), L. minor 1 (5), L. obscura 3 (4), L. japonica 3 (6), L. turionifera 0 (5), L. trisulca 1 (1), L. valdiviana 1 (4), L. minuscula 0 (4), W. hyalina 0 (2), W. neotropica 0 (2), W. Welwitschii 1 (2), W. lingulata 0 (2), W. oblonga 0 (2), W. gladiata 0 (3), W. denticulata 0 (2), W. brasiliensis 1 (1), W. borealis 0 (1), W. australiana 1 (1), W. columbiana 2 (4).

These preliminary observations show that probably all species may be brought to flower if the conditions are varied.

4.3.2. Pollination and fruit setting

The method of pollination in Lemnaceae has been the object of speculation for many botanists. ROSTOWZEW (1901, 1905) and MAHESHWARI (1954) think of pollination by wind or rain. TRELEASE (1882) and LAWALREE (1961) suppose that the fronds push together and scatter the pollen grains from the anthers on to neighbouring stigmas. According to COX (1983), L. trisulca is water-pollinated. He argues that the fronds form long chains which enhance the possibility of matching pollen grains floating on the surface of the water. He probably never observed flowering L. trisulca, because in contrast to the submerged vegetative fronds, the flowering fronds do not form chains; also, the stigma of flowering fronds is always well above the water surface before pollination, and therefore cannot be pollinated by pollen grains floating on the water surface. Pollination by snails is assumed by DELFINO (1882). The small number of pollen grains (20 in each locule of L. aequinoctialis) which often stick together, and the spiny surface structure of the pollen grains are definite arguments for zoogamy. As LUDWIG (1909) and BLODGETT (1923) suppose, pollination is most probably mediated by small flies, aphids, mites, small spiders, etc. As a matter of fact, it is easy to detect Lemnaceae pollen grains within the hairs of the lower surface of such animals moving on a flowering Lemnaceae cover, as it was already pointed out by LUDWIG (1909). By these small animals, the pollen grains are probably transferred from the anthers to the droplet of the stigma. It also seems possible that some of these little arthropods suck the sugar solution of the droplet and carry out pollination simultaneously. There is some confusion in the literature about the sequence of ripening of anthers and stigma (see chapter 2.6.4). From our own experience, there is no doubt that except for some few species such as L. perpusilla and L. aequinoctialis, most species are protogynous. It is possible that some species are partly or totally self-sterile. Since Lemnaceae propagate vegetatively very quickly, flowering fronds are mostly surrounded by fronds of the same clone. If the species is self-sterile, fruits rather rarely develop. This is the case in L. minor (in contrast to L.

gibba) (compare the percentage of flowering and fruiting in table 4.5). LUTHER (1948) could not detect any fruits within 30 flowering herbarium samples of L. minor from Northern Europe. In a preliminary experiment (LANDOLT unpubl.) the crossing of flowering fronds of two L. minor populations from Switzerland and northern Italy was attempted; 5 self crossings did not result in fruit setting. However, 2 fruits developed from 5 crossings between fronds of the 2 different populations. CALDWELL (1899) reports frequent degeneration of the embryo sac of L. minor before fecundation. On the other hand, in Vienna, LUDWIG (1909) frequently saw L. minor flowering and fruiting in the shade. Either different clones of L. minor behave differently or LUDWIG confused L. minor with temporarily introduced L. aequinoctialis. He also observed androgyny in his flowering fronds which is not otherwise known for L. minor.

In culture, self-pollination was observed regularly in L. perpusilla and L. aequinoctialis whereas fruit setting in L. gibba was rather rare and restricted to a few clones. Other flowering species did not set fruits (LANDOLT unpubl.). From herbarium samples, we can distinguish three groups of fruit frequency within species of Lemnaceae:

1. Species which fruit often (at least half of the fertile samples show fruits): S. intermedia, S. punctata, L. gibba, L. disperma, L. obscura, L. perpusilla, L. aequinoctialis, L. valdiviana, L. minuscula, W. hyalina, W. repanda(?), W. neotropica(?), W. Welwitschii(?), W. microscopica(?), W. globosa(?).
2. Species which fruit occasionally (1/5 to 1/2 of the fertile samples show fruits): S. polyrrhiza, L. turionifera, L. trisulca, W. lingu-lata, W. gladiata, W. brasiliensis, W. arrhiza, W. columbiana.
3. Species which fruit rarely (less than 1/5 of the fertile samples show fruits): L. minor, W. oblonga.

The question mark means that the flowering occurrence is too rare to attribute the species definitely to a fruiting group. The fruiting behaviour of the following species is not known, due to the very rare occurrence of flowering: L. japonica, L. ecuadorensis, L. tenera, W. rotunda, W. denticulata, W. elongata, W. borealis, W. australiana, W. angusta.

The first two groups are probably self-fertile. WITTE (1985) confirmed the self-pollination of W. Welwitschii. At least members of the second group do not self-pollinate. BROOKS (1940) had to pollinate W. columbiana artificially to get fruits. It is evident that gene exchange within a

species and between species is rare due to either self-pollination or very rare flowering and fruiting. However, HILLMAN (1975a) was able to show that L. aequinoctialis No 6746 is heterozygotic.

Some times it can be observed in different species that the anthers do not appear. KLICH and MUJICA (1985) described this phenomenon in S. intermedia as cleistanthery. The lack of dehiscence of the anthers as well as of the secretion of the droplet on the stigma is probably due to unfavourable environmental conditions.

4.4. DISPERSAL AND SURVIVAL

4.4.1. Dispersal

Lemnaceae are free floating plants which can easily be removed or destroyed at their habitat. Therefore they mostly live as pioneer plants (cf. chapter 5.5.1 where the Lemnaceae species are grouped in pioneer and follower species; compared with species of the zonal vegetations, follower species are still in many characteristics pioneer species). In general, pioneer species are easily distributed. KEDDY (1976) explains the distributional ecology of Lemnaceae by the island biogeographic theory. The colonization capability of the two investigated species (L. minor and L. trisulca) was defined as its ability 1) to withstand desiccation, 2) to quickly populate a new habitat and 3) to inhibit the other species competitively. According to this author, L. minor was far superior to L. trisulca in the abilities 1) and 2) and superior or equal in 3).

Lemnaceae are small and not fixed. A dislocation by wind, wave action, or water current occurs often. In the southern states of the U.S.A., Wolffia fronds have been transported over several kilometres by a tornado. In Europe SCHULZ (1962) reported Wolffia fronds from the gutter of a house. It is supposed that they were transported by the wind. Wolffia fronds have also been found in the water of melted hailstones (LUDWIG 1909). DUFFIELD and EDWARDS (1981) gave a model of dispersal of L. gibba in slow flowing ditches in South Wales, taking into account wind action, water profile, other water plants, vertical velocity, and some other factors.

However, the main distributors of Lemnaceae are animals which live around the water: mammals (e.g. beavers, rats, muskrats, racoons), birds (waterfowl and other water birds), amphibians and reptiles (water-snakes, turtles), which become covered by fronds and carry them from one water to another. JAEGER (1964) showed that the most frequent occurrence of W. arrhiza can be observed along bird passages. The possible distance of distribution within one passage is limited by the time in which the Lemnaceae frond dries irreversibly. This takes according to WOLEK (1981) 2 1/2 hours for S. polyrrhiza, L. gibba, L. minor, and L. trisulca, and 20-30 minutes for W. arrhiza, at a temperature of 21-26°C and 60-70%

humidity. KEDDY (1976) observed for L. minor completely dead fronds already after 2 hours and for L. trisulca after 1 1/4 hours (25°C and 70% humidity). Under special conditions (low temperature, high humidity, and within relatively thick layers of fronds) Lemnaceae will certainly remain alive for a longer time. GODZIEMBA-CZYZ (1970) still detected living W. arrhiza fronds after up to 6 hours, and RIDLEY (1930) living fronds of L. minor after 12-22 hours out of the water. On the surface of the feathers of a bird, the conditions for Lemnaceae during a flight are normally not very favourable. In this case even the values of WOLEK are probably too high. JACOBS (1947) saw a water bird with mostly dead fronds after a flight of 6 minutes. Only a few fronds of L. minor were still alive. If we take these observations into account, Lemnaceae can be distributed by birds under normal conditions only for a few kilometers. But, if occasionally some fronds are covered by the feathers or if it is rainy during the flight, the distance of displacement may reach up to a hundred or more kilometres. In the form of seeds which are mostly drought resistant, Lemnaceae can be transported by the bird as far as the seeds or the fronds with seeds stick to the bird. It is not known, if seeds remain alive after having passed through the tract of digestion. Drought-resistant seeds are known of L. gibba, L. disperma, L. aequinoctialis, and L. perpusilla (see chapter 2.6.6). However, according to ROSTOWZEW (1901), L. minor seeds do not tolerate drying out. Perhaps, this statement bases on the fact that dry seeds of L. minor no longer germinate. It is possible that L. minor seeds behave like those of L. perpusilla and need a cold period before germinating.

CHABRECK and PALMISANO (1973) observed marshes of the Mississippi River in Louisiana before and after a hurricane passed over. Lemnaceae species occurring quite frequently in the region before the hurricane did not show up any more until more than a year later. This demonstrates that dispersal is sometimes not so easy and fast as it seems. GODWIN (1923) gives some examples of dispersal of pond flora. He investigated six ponds of different ages. A positive correlation was found between age and diversity of species. Only the two oldest ponds (more than 80 years old) had two species of Lemnaceae (L. minor and L. trisulca). However, this is not only a question of the speed of dispersal but also of the development of a suitable habitat (nutrient composition, content of organic substances, stability of the ecosystem etc.).

The present distribution of some species of Lemnaceae can only be ex-

plained if we assume transport of drought-resistant seeds or if we propose that the present occurrences are relicts of a previously much wider distribution. The biggest disjunction gaps of some species today are (see distribution maps in chapter 6): L. trisulca: 1500 km, S. polyrrhiza: 2500 km, L. aequinoctialis: 2500 km, L. gibba: 4000 km, S. punctata: 5000 km.

If L. minor, and possibly other species, do not form drought-resistant seeds, the distribution on some remote islands is difficult to explain. In some cases, dispersal by man is probable. For L. minor, the occurrence in New Zealand, in Australia, and on the Atlantic Islands might be anthropogenous. The dispersal with aquarium plants, fish tanks etc. is so easy and might have occurred already several hundred years ago. The present distribution gives some indications of the ecological demands of the species but no conclusions can be made whether or not they are indigenous. For further indications about possible dispersal of Lemnaceae species by man, see chapter 6.4.

4.4.2. Survival during unfavourable conditions

In many climates, there are some critical seasons for the occurrence of Lemnaceae. Three kinds of unfavourable situations may be of importance for the delimitation of the distribution of Lemnaceae; cold seasons, dry seasons, and rainy seasons. Warm seasons may also limit the occurrence of Lemnaceae species, but there is no other possibility for species which are not very heat tolerant to survive in warm regions than avoiding sun light.

a. **Cold seasons.** As it is shown in chapter 4.2.2.3 and in volume 2, chapter 2.3.4.4 (LANDOLT and KANDELER 1987), Lemnaceae fronds are not very resistant to cold. Long lasting temperatures below -10°C can probably not be tolerated by normal vegetative fronds of any species. Therefore, most species surviving in colder regions avoid the cold temperature at the surface of the water by sinking down to warmer layers. This is possible in the following four ways:

- 1) The fronds normally live submerged (L. trisulca, W. gladiata). During cold seasons they store more starch and reduce the aerenchymatic tissue. In this way their specific weight increases and they sink fur-

ther down. L. trisulca is able to survive (in the water) air temperatures down to at least -40°C . It was observed living in Canada below an ice cover of more than three metres (DALE and GILLESPIE 1976). The fronds of W. gladiata are most sensitive to cold and the growth in spring begins at higher water temperatures. That is why W. gladiata does not reach such cold climatic zones as L. trisulca, but for a Wolffia species, which are otherwise very frost sensitive and do not occur outside tropical and subtropical regions, the distribution is quite remarkable.

- 2) The fronds die during cold periods and sink to the bottom of the water still bearing some living buds within their pouches (L. gibba, L. minor). If the weather is not very cold, the fronds remain on the surface and are still able to grow at relatively low water temperatures (down to about 4°C).
- 3) The species produce special resting fronds (turions) with reduced aerenchym and high starch content (maybe reduced roots), due to their relatively high specific weight, they sink to the bottom of the water and stay there below the ice cover until the water reaches temperatures far above zero (mostly higher than 10°C). S. polyrrhiza, L. turionifera, and most Wolffia species belong to this group. If the turions are relatively cold-resistant the species will still occur in the coldest region of the world (S. polyrrhiza, L. turionifera). The Wolffia species are not so tolerant (see also chapter 2.5.).
- 4) The species form cold-resistant seeds which sink during the cold period either to the bottom of the water (L. perpusilla) or overwinter on the dry soil (e.g. of rice fields) (see also chapter 2.6.6).

VAN DER VALK and DAVIS (1978) counted 1500 turions of L. turionifera, 1200 turions of S. polyrrhiza, and 30 groups of L. trisulca on the average on each m^2 of the bottom of a small lake in Iowa (U.S.A.).

b. Dry seasons. There are only a few species which are able to regularly survive dry seasons as seeds: L. aequinoctialis (LANDOLT 1957, BEPPU and TAKIMOTO 1981b and many further observations), L. gibba (HEGELMAIER 1868, LANDOLT 1957, REJMANKOVA 1976, WITZTUM 1977), L. disperma (BROCK and LANE 1983). According to BROCK and LANE (1983) L. disperma is only able to live in places which are wet for at least 7 months. In contrast, seeds of L. minor are not able to survive dry periods (according to ROSTOWZEW 1901). L. aequinoctialis can be observed in rice fields which

regularly dry out. In southern France and northern Italy this species survives as dry seed from September to May (own observations). Other species, which can possibly stand dry periods are: W. hyalina, W. repanda, and W. microscopica. In Australia, S. punctata is able to survive dry seasons as seeds (personal comm. from Australian farmers). The turions of S. polyrrhiza may survive dryness if they are imbedded in clay (DAS and GOPAL 1969, GOPAL personal comm.). Up to now, this phenomenon has been observed only in India. Further investigations on its validity for other regions are necessary. It is interesting to note that S. polyrrhiza is very often associated with L. aequinoctialis in tropical and subtropical regions even in waters which are supposed to dry out periodically.

c. Wet seasons. During seasons with much rain, the water may get so poor in nutrients that growth and propagation of Lemnaceae are no longer possible. Also during high water and flooding the fronds on the surface of the water are washed away. Some species respond by forming turions (e.g. S. polyrrhiza, Wolffia species) and remain in a resting stage at the bottom of the water, others sink to the bottom of the water where the nutrient content is possibly higher (Wolffiella species, L. trisulca, L. valdiviana). From our own observations in Argentina, heterotrophous growth in these rather dark situations is very probable.