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5. POSITION WITHIN THE ECOSYSTEM

5.1. ECOSYSTEMS WITH LEMNACEAE

Growing in dense mats on the surface of the water, Lemnaceae form a relatively simple ecosystem, which is rather easy to investigate in terms of the different organisms present, their interrelationships, and the environmental factors affecting the ecosystem. The factors necessary to develop a Lemnaceae ecosystem are described in chapter 4. However, it has to be kept in mind that the Lemnaceae ecosystem is influenced by other overlapping ecosystems which affect available light and nutrients and interfere in many ways. For instance, the productivity of the Lemnaceae cover is much dependent on the development stage of the surrounding plant communities (cf. JERVIS 1969).

In this chapter we shall look at

- the influence of Lemnaceae on abiotic factors within the ecosystem.
- the interrelationships of the Lemnaceae with other organisms.
- the interrelationships between the different species of Lemnaceae.
- the ecological and geographical differentiation within the Lemnaceae ecosystem.

REJMANKOVA (1981) gave an example of the mass and energy flow of a Lemnaceae ecosystem (fig. 5.1). She (1973, 1981) also investigated the seasonal changes of the biomass and the relative growth rate of two mixed Lemna minor and S. polyrrhiza communities.

The nutrients in Lemnaceae ecosystems are transported from the Lemnaceae fronds to the young fronds, to consumers by feeding, or back to the water after death of the fronds. LAUBE and WOHLER (1973) observed that at least 20% of the dry weight of oven-dried fronds is decomposed within a week if returned to a pond. After three weeks, 50% of the Mn, Mg, and Na are dissolved in the water. REJMANKOVA (1979, 1982) reports of the rapid decomposition of duckweed detritus. The biomass decreased to about half the weight within ten to twenty days. The half time of decomposition increases exponentially with decreasing air temperature. PATIENCE et al. (1983) describe the decomposition of L. aequinoctialis under anaerobic conditions. Short-chain carboxylic acids and ammonia were generated in

considerable amounts reaching a maximum of 30% of the original dry weight after 71 days. No carboxylic acids are present in the fresh homogenate. Within the 71 days no aerobic decomposition could be established. The concentrations of the carboxylic acids acetate, propanoate, butanoate, and pentanoate in decaying *L. aequinoctialis* reached a concentration of 7.5, 1.7, 1.0, and 0.6 mM, respectively, after three days, and a concentration of 2.5, 0.5, 0.4, and 0.2 mM, respectively, after 71 days. The corresponding concentrations of free amino acids and free sugars reached 3.7 mM and 0.01 mM after three days and 0.5 mM and 0.00 mM after 71 days (THOMAS et al. 1984). These organic substances are eaten by small animals (e.g. snails) or decomposed by microorganisms. Certain investigations have been made concerning the influence of herbicides on the Lemnaceae ecosystem. KANAZAWA et al. (1975) report a very high bioaccumulation of methylcarbamate (carbaryl) in Lemnaceae and algae (2000 to 4000 times the concentration in the water). Similar inves-

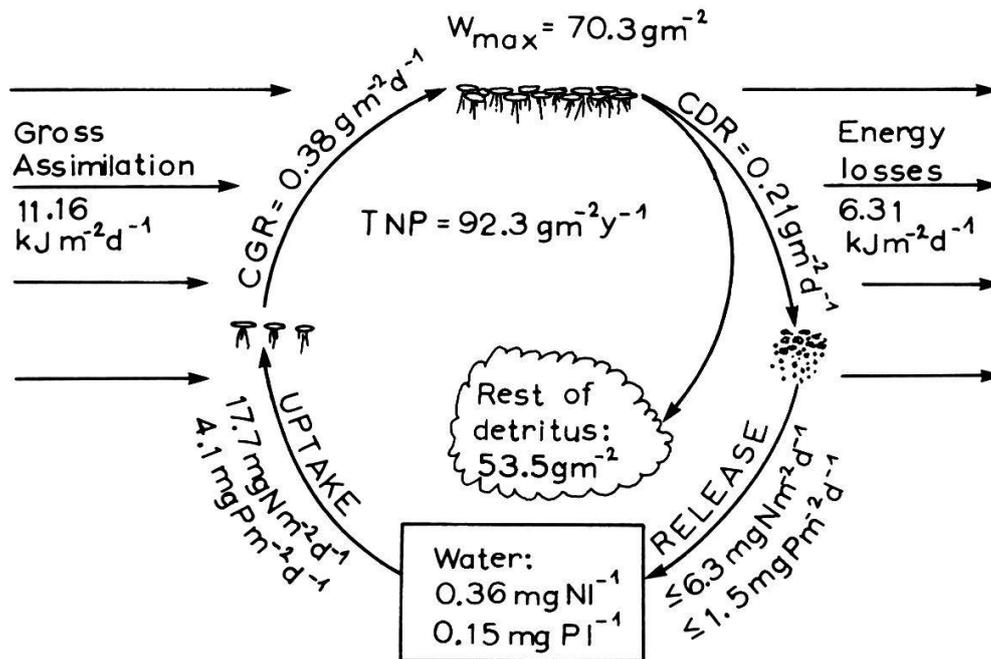


Fig. 5.1. Mass and energy flow in a duckweed system (according to REJMANKOVA 1981, constructed on the basis of data from the Pavelec fry pond, CSSR, April 30th to November 1st, 1977)

CDR	crop decomposition rate	TNP	total netto productivity
CGR	crop growth rate		(CGR + CDR)
W _{max}	maximum biomass		

tigations were made by MUIR et al. (1985) with the insecticide deltamethrine. For other effects of pesticides, see vol. 2, chapter 2.3.3.5.8 (LANDOLT and KANDELER 1987).

The water layer below a Lemnaceae cover contains much fewer producers but more detritivores and carnivores than that found in waters without Lemnaceae. The chlorophyll content below a Lemnaceae cover is about 1/30, while the protein content is 2/3 (POURRIOT 1972).

5.2. SPECIFIC ABIOTIC FACTORS IN ECOSYSTEMS WITH LEMNACEAE

Dense mats of Lemnaceae induce a change in the following conditions:

1. The temperature fluctuations of water beneath Lemnaceae cover are reduced. At 25 cm below a Lemnaceae cover, POURRIOT (1972) measured a 2-4°C lower average temperature than that determined in water without Lemnaceae between June and September. The daily fluctuations reached 4.5°C in water with Lemnaceae and 6.5°C in water without Lemnaceae. Similar results are reported by KLOSE (1963) and BOYD (1975), with KLOSE mentioning differences of up to 4°C in the daily fluctuations. At 25 cm below the surface covered with Lemnaceae the temperature is still 1 to 2°C lower during summer time, and also the amplitude of daily and monthly maximum and minimum temperatures is lower (POURRIOT 1972).
2. During periods of sunshine, the temperature at the surface of the water reaches much higher values in waters with Lemnaceae cover than in water without. This is due to the higher heat conductivity of the water rather than of Lemnaceae mass. In addition, the evaporation rate of open water is about 10% faster than the evapotranspiration rate of Lemnaceae cover; Lemnaceae have therefore a smaller cooling effect than the open water surface. According to DALE and GILLESPIE (1976), temperatures in the Lemnaceae cover are up to 4-11°C higher during daytime than on the open water surface, and up to 12°C higher than in the surrounding air. BOYD (1975) and DOCAUER (1983) have measured temperatures in Lemnaceae cover 3-4°C higher than those found on the open water. Similar results are reported by KLOSE (1963) and REJMANKOVA (1973). During night-time, the temperature of the Lemnaceae cover is lower than that of the open water due to the lower conduction of the heat in the Lemnaceae cover. DOCAUER (1983) mentions a difference of 4 to 5°C.
3. The light intensity is very low below a Lemnaceae cover. A cover of one Lemna layer absorbs about 93% of the light (GESSNER 1955). According to BOYD (1975), a Wolffia columbiana layer transmits 20-40% of light, a S. polyrrhiza layer only about 1%.
4. The oxygen content of the water is reduced below a Lemnaceae cover. Due to the small amount of light that can penetrate through the Lemnaceae cover, the assimilation of phytoplankton decreases to 5-30%

below a W. columbiana layer and to 2-5% below a S. polyrrhiza layer. The oxygen content does not rise during day-time and amounts to 4-8.5 ppm below a Wolffia cover and 3-5 ppm below a Spirodela cover. In water without Lemnaceae cover, it reaches 8-14 ppm (BOYD 1975). RIPL (1976) has measured an O₂ content of 1 ppm below a Lemnaceae cover and DUFFIELD (1981) 0.6-1.9 ppm. Other authors (STEPHANOVA 1928, LEWIS and BENDER 1961, MORRIS and BARKER 1977, DUFFIELD 1981, KORSAK and MYAKUSHKO 1980, CLARE and EDWARDS 1983) have also found much lower oxygen content below a Lemnaceae cover than that of uncovered water. MORRIS and BAKER (1977) measured an aeration rate of the water below a Lemnaceae mat between 4 and 47% of the estimated gas exchange rate in open water. The Lemnaceae cover slows the movement of water, preventing an intermixing of water with oxygen of the air. L. minor and S. polyrrhiza did not release any oxygen in the nutrient solution during the period of photosynthesis (POKORNY and REJMANKOVA 1983). The low oxygen content is unfavourable for many fish and other animals (e.g. LEWIS and BENDER 1961).

5. The amount of organic substances is higher below a Lemnaceae cover. Because of the low oxygen content, the decomposition of dead organisms is retarded, causing the accumulation of organic substances (RAO 1953, GANNING and WULFF 1970). The outstanding accumulation of organic matter in the system with a Lemnaceae cover is pointed out by FLORES (1981). HARRISON and BEAL (1964) report that Lemnaceae occur only in waters that are rich in organic matter. However, the richness in organic matter is probably the consequence of the low oxygen content and not the cause of the occurrence of Lemnaceae. In general, water plants release about 4% of the organic carbon photosynthesized in water, which stimulates epiphytic and microbiotic activities (WETZEL and MANNY 1972), but may also enable submerged Lemnaceae to grow. The total of organic substances (especially glycerol and some sugars such as arabinose) released into the surrounding solution within a flask was more than 100 mg/l for L. minor and more than 300 mg/l for L. gibba after 50 days (AMBROSE 1978). Some of the organic substances in the water produced by Lemnaceae are tannins and other phenolic substances, which cause a brownish colour in water. The amount of these substances is distinctly greater in water with Lemnaceae than in Lemnaceae-free water (but with phytoplankton). It amounts to 0.40 ppm under a Spirodela cover and 0.65 ppm under a Wolffia cover compared

- with 0.14 ppm in the control without Lemnaceae (BOYD 1975). Under anaerobic conditions, L. aequinoctialis gets decomposed by rod-shaped and coccoid bacteria. Mostly ammonium acetate is released (PATIENCE et al. 1983). Contrary to water plants rooting in the soil, a Lemnaceae cover does not release detectable amounts of methane (CH_4) to the surroundings (SEBACHER et al. 1985).
6. The H_2S content is higher in water with a Lemnaceae cover than in water without. The anaerobic decomposition of dead organisms in Lemnaceae ecosystems produces H_2S . KLOSE (1963) measured up to 5 ppm H_2S in a pond, 20 cm below a Lemnaceae cover.
 7. The pH might be lower in the water beneath a Lemnaceae cover. BOYD (1975) reports differences in pH of up to 2.5, primarily due to the high CO_2 content (up to 50 ppm) found below a Spirodela cover. A reduction of the pH by 0.1-0.5 and a reduction of the degree of hardness by 0-0.2 under a Lemnaceae cover was observed by KNAPP and STOFFERS (1962), as compared to Lemnaceae-free waters. However, HIMES et al. (1967) point out that a well-buffered system with Lemnaceae does not change the pH.
 8. A reduction in evapotranspiration rate by 10-15% was observed in waters with Lemnaceae, when compared with waters without Lemnaceae (BOYD 1975, RYTHER et al. 1980, DEBUSK 1980). ORON et al. (1984) measured a reduction of 25-30%.
 9. There is a possibility that denitrification occurs below a cover of Lemna (HARVEY and FOX 1973).

5.3. RELATIONSHIP OF LEMNACEAE TO OTHER ORGANISMS

5.3.1. Herbivores and parasites

Lemnaceae are used as food by many different organisms:

1. **Mammals.** Beavers, rats, muskrats, racoons and wild boars are the mammals usually observed feeding on duckweeds (HICKS 1937, JACOBS 1947, FASSETT 1972, p. 347-348), but also other mammals such as cows, horses, and pigs sometimes feed on Lemnaceae. The feeding on Lemnaceae by mammals never becomes so intensive as to prevent the thriving and spreading of plants. However, small mammals are of some importance for dispersing Lemnaceae to neighbouring water.

2. **Birds.** Many kinds of water birds, especially ducks, but also geese, chickens, and pheasants, feed extensively on Lemnaceae (RIDLEY 1930, SCHULZ 1962, FASSETT 1972, p. 347-348). SCHWABE-BRAUN and TUEXEN (1981b) mention the following ducks: Anas strepera, A. crecca, A. discors, A. platyrhynchos (cf. JORDE et al. 1983), A. clypeata, Oxyura jamaicensis, and other birds: Aythya ferina, Fulica atrata, F. americana, Aix sponsa, Podilymbus podiceps, Gallinula chloropus, Porzana carolina and Philomachus pugnax. However, DYLIK et al. (1979) remark that Aythya ferina (contrary to Anas platyrhynchos) feeds on duckweeds only to a small degree (see also volume 2, chapter 3.4.4, LANDOLT and KANDELER 1987). Water birds are very important for the dispersion of Lemnaceae (see chapter 4.6).

3. **Reptiles.** The turtle (Kachuga tectum) was shown to feed on water plants, included L. trisulca (SHAH and TYAGI 1985).

4. **Fish and Crustaceae.** Carp and many other fish feed mainly on duckweeds. In some places they may be able to completely eliminate the Lemnaceae or prevent Lemnaceae from colonizing new areas (KRULL 1969). Grass carp is used to control or remove duckweeds in irrigation canals and reservoirs (NEWTON et al. 1979, TSUCHIYA 1979). In an aquarium, one can observe that of all species of Lemnaceae the genus Spirodela is less favourite by the fish, probably because of the richness in oxalate (druses). Gammarus pulex feeds on Lemnaceae but mostly takes fronds infected by fungi (PANDIT et al. 1978). Water shrimps (Macrobrachium) and some crayfish also eat Lemnaceae (GODFRIAUX et al. 1975, CULLEY et al. 1981) (see also volume 2, chapters 3.4.5.1 and 3.4.5.2, LANDOLT and KANDELER 1987).

5. Gastropoda (snails). SCHULZ (1962) mentions many different kinds of snails that are associated with Lemnaceae though not all of them feed on Lemnaceae. In North Germany, ten species of Gastropoda frequently live in Lemnaceae ecosystems; some are very specific for different associations (SCHROEDER 1977). For the Lemnon minoris (Riccietum fluitantis, Lemnetum trisulcae, Spirodeletum polyrrhizae), Anisus vortex is typical; in Lemnon gibbae (Lemnetum gibbae), Stagnicola palustris is usually found. In addition, Planorbis planorbis occurs in Riccietum fluitantis and Physa fontinalis in the Lemnetum trisulcae. Radix pereger can be found in all four associations investigated, except in Riccietum fluitantis. Five other snails (Lymnaea stagnalis, Bithynia tentaculata, Segmentina nitida, Planorbis corneus, Bathyomphalus contortus) are found rather infrequently. VAILLANT (1982) reports that Planorbis corneus devoured in a water basin all water plants, except Lemnaceae and Ceratophyllum demersum. STAHL (in SCHULZ 1962) assumes that the raphides in the Lemnoideae effectively prevent the plant from damage by snails. LUDWIG (1909) thinks the same of the tannins found in the pigment cells of Spirodela. An experiment by FROEMMING (1952) with Lymnaea stagnalis shows that at least the raphides do not prevent snails from feeding on duckweeds, for raphides could be identified in the excrement of the snails. In a similar investigation, Planorbis corneus, which usually feeds on detritus, was able to completely feed duckweeds when no other food was available. SAHAI and ROY (1977) report that Lymnaea luteola f. impura is able to feed on S. polyrrhiza. Fifty snails managed to consume 25 g of S. polyrrhiza within seven days.

Limnaea sp. is also reported to graze on green fronds of Lemnaceae in Kashmir (PANDIT et al. 1978). VAILLANT (1982) observed the action of newly introduced Limnaea stagnalis into an artificial pond ecosystem with a cover of Lemnaceae. Within a few months all Lemnaceae species disappeared due to the intensive feeding by Limnaea.

It is possible that some snails avoid Lemnaceae because of raphides or tannins whenever enough other food is available. Moreover, it is sometimes very difficult for larger snails to feed on duckweeds because the fronds do not offer a stable crawling support. On the other hand, STERRY et al. (1983) showed that L. aequinoctialis (especially decaying fronds) release strong attractant and arrestant substances of low molecular weight (1000) for the pulmonate water snail Biomphalaria glabrata. This snail is not a real herbivore but a detritivore which feeds on dead decom-

posing fronds. The snail is supposed to take up carboxylic acids (STERRY et al. 1985).

6. Arthropoda. SCOTLAND (1934, 1940) lists more than 40 insect species belonging to very different systematic groups (Diptera, Trichoptera, Lepidoptera, Anoplura, Coleoptera, Collembola) which feed and develop on Lemnaceae either facultatively or obligately. Larvae of the flies Hydrellia albilabris and Lemnaphila scotlandae, the louse Rhopalosiphum nymphaeae, the beetles Tanysphyrus lemnae and Podura aquatica, and the Collembola Sminthurus aquaticus are especially frequently associated with Lemnaceae. Mites (e.g. Notaspis lacustris) also can often be observed with Lemnaceae. Immature stages of the oribatid mite Hydrozetes lemnae feed specifically on L. gibba in Argentina. In the duckweed population the instantaneous rate of mortality never exceeds 28%. The predator does not have a notable depressive effect on the L. gibba population. The interspecific relationship of Hydrozetes and L. gibba is an interesting example at the limits of parasitism and predation (ATHIAS-BINCHE and FERNANDEZ 1986). In many publications certain insects are cited as characteristically feeding on Lemnaceae. Bagous (Curculionidae) feeds, in India, on S. polyrrhiza making small holes in the frond (SAHAI and ROY 1977). The larvae of the lepidopteran Synclita tinealis feeds predominantly on Lemnaceae (KINSER and NEUNZIG 1981), as do the chironomid Corynoneura lemnae (NAUMANN 1965), the trichopteran Limnephilus lunatus (especially on L. trisulca: VAILLANT 1982), and different weevils. The weevil Ochetina bruchi feeds on Lemnaceae, but the larvae need to develop on other water plants (CORDO et al. 1981). The larvae of the smallest (1-1.5 mm) aquatic weevil (Tanysphyrus lemnae, family Curculionidae) mine inside the fronds of duckweed (BUCKINGHAM et al 1986). Larvae of Parapoinx stratiotata (Pyralidae, Lepidoptera) construct cases from L. trisulca but do not feed on it (HABECK 1983). The larva of the butterfly Cataclysta lemnetea also makes a casing out of Lemnaceae fronds; in contrast to Parapoinx it feeds on Lemnaceae (VAILLANT 1982); other water plants (Elodea, Potamogeton, Nymphoides) are only accepted when Lemnaceae are missing (VAN DER VELDE 1979). The larvae of Tipula aino feed on roots of Lemna species (QUIAN 1982). A moth (Nymphula responsalis) behaves the same way in India (McCANN 1942).

7. Nematodes. Aphelenchoides fragariae was observed in Lemna cultures from Florida (SMART and ESSER 1968).

8. Fungi. The hypochytridiomycetes Reessia amoeboides and Reessia lemnae

live endobiotically in dying Lemnaceae, according to WAGNER (1969) and KANDELER (1979). COLBAUGH (1981) reports of a lethal foliar blight of Lemnaceae in water cultures, which is caused by the oomycete Pythium aphanidermatum. The reduction occurs due to foliar blight and dying of the fronds. Greatest foliar blighting activity occurs at temperatures of 24°C and 27°C (better than at 18°C, 21°C, and 30°C). REJMANKOVA et al. (1986) isolated Pythium myriophyllum from L. gibba growing in a dairy farm of Louisiana. The authors were able to show that this fungus is the cause of duckweed kills. Under natural conditions and temperatures above 22°C the amount of duckweeds killed by the fungus grows exponentially and the whole stand dies within several days. Six species of Lemnaceae have been tested in the laboratory: L. gibba, L. minor, and S. polyrrhiza proved to be most susceptible to the fungal infection. L. valdiviana showed more resistance whereas L. aequinoctialis and S. punctata never exhibited symptoms of disease. Optimum temperature for infection was about 32°C. It is interesting to note that the susceptibility to a fungal disease might be a factor limiting the distribution of certain Lemnaceae species. Rhizoctonia solani is able to infect L. minor, but the plants only get small irregular lesions (JOYNER and FREEMAN 1973). A smut, Tracya lemnae, is known from Spirodela (FISCHER 1953, ZOGG 1985).

9. **Phanerogams.** ROBERTS (1972) observed, in Lake Erie, W. columbiana and W. borealis in the traps of Utricularia vulgaris. It is not sure if the Wolffia fronds are digested in the traps.

5.3.2. Mutualists, commensalists, and amensalists

The Lemnaceae cover offers a well protected biotope for many organisms. The secretions of sugar and other organic substances rich in energy by Lemnaceae provide nourishment for other organisms (WETZEL and MANNY 1972). Therefore, it is not surprising that so many small organisms are associated with Lemnaceae.

5.3.2.1. Mutualists

True mutualism is very rare. There are some nitrogen-fixing, blue-green algae and bacteria associated with Lemnaceae. This relationship points to a loose facultative symbiosis from which Lemnaceae profit by getting

more nitrogen and the algae by using the duckweed as physical support, as protection against direct sunlight and as source of carbohydrates and growth factors. PARK and YATAZAWA (1979) have identified Caltrix sp. and Microceate sp. Anabaena, which grows together with Azolla, was not detected. According to ZUBERER (1981, 1982), mats of Lemnaceae contain up to 10^5 cells of nitrogen-fixing heterotrophic bacteria (e.g. Klebsiella) and up to 10^5 propagules of cyanobacteria per gram wet weight. Azotobacter is not present. The nitrogen-fixing organisms are able to deliver up to 15-20% of the nitrogen needed by the Lemnaceae. If Azotobacter is added to the culture solution, Lemna minor is able to use a certain amount of the nitrogen fixed by Azotobacter after a few days (VISSER 1971). DUONG and TIEDJE (1985) report that 26 of 29 investigated Lemnaceae populations in Michigan, USA, showed acetylene reduction activity which is proportional to nitrogen fixation. The activities correspond to nitrogen inputs of $3.7-7.5 \text{ kg N}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$ (for dense L. trisulca stands, the values might be up to 10 times higher). The following cyanobacteria could be observed attached to the lower epidermis and to the reproductive pouches of the frond (but not to the roots) of Spirodela and Lemna (no cyanobacteria could be found on Wolffia): Noctoc, Gleotrichia, Anabaena, Calotrix and Cylindrospermum. This kind of nitrogen production seems to be generally distributed in freshwater macrophytes (FINKE and SEELEY 1978).

5.3.2.2. Commensalists

Many commensalists which take advantage of the Lemnaceae without damaging it are present in the Lemnaceae ecosystem. Some of these organisms may have a positive effect on Lemnaceae, but this had rarely been definitely proven. As an example the tubificid Branchiura sowerbyi is cited which is able to accelerate the diffusion of dissolved substances in the water of rice fields and, thus, to enhance the biomass of L. aequinoctialis (and algae and zooplankton) (KIKUCHI and KURIHARA 1981, 1982).

Algae, bacteria and yeasts. Epiphytic algae are common on Lemnaceae. HEGELMAIER (1868) already mentions mats of Coleochaete on W. Welwitschii, but also many free floating microorganisms are dependent on, or in relation to, Lemnaceae. Relatively few bacteria and diatoms have been observed on the upper surface of living L. aequinoctialis ($7.5\cdot 10^4$ bacteria, $4.6\cdot 10^4$ diatoms, and no yeasts, all per g fresh weight). On the

surface of decaying fronds the number of bacteria, diatoms, and yeasts per g fresh weight amounts to $3.7 \cdot 10^8$, $6.5 \cdot 10^6$, and $6.0 \cdot 10^7$ individuals, respectively. In addition, $1.5 \cdot 10^8$ individuals of other algae have been counted (STERRY et al. 1985). BOWKER and DENNY (1980) showed a strong seasonality of the epiphytic algal community in the phyllosphere of L. minor in southern England. The seasonal changes are related to changes in physico-chemical environmental conditions. Cyanophyta were numerically dominant on the roots of moribund and senescent fronds between August and January. Chlorophyta were most abundant on living fronds in May and June. Bacillariophyta produced seasonal maxima in March and April.

ZUBERER (1984) examined S. punctata and L. obscura (named as L. minor) by scanning and transmission electron as well as light microscopy. He observed the frond and root surfaces well colonized by bacteria and cyanobacteria as well as other microorganisms. Bacteria were also detected in the intercellular spaces of apparently healthy roots. RHO and TAYLOR (1981) compared bacterial populations associated with fronds and roots of duckweeds with populations of the surrounding pond water. Total heterotrophs and bacteria capable of ammonification were highest on the phylloplane, while acid-producing and denitrifying bacteria were higher on the rhizoplane. Bacterial isolates from phylloplane consisted of 53% chromogens and 18% IAA producers; those from rhizoplane were 44% and 41%, respectively. It is believed that plant roots and fronds stimulate certain bacteria selectively and that these bacteria, in turn, have an effect on the growth and development of duckweeds. HOSSEL and BAKER (1979a,b) reported the average number of bacteria from a 20-day old L. minor frond as about $0.1 \cdot 10^6$ per cm^2 on the upper side, $9.4 \cdot 10^6$ on the lower side, and $4.4 \cdot 10^6$ along the roots. According to BAKER and ORR (1986) the average number of bacteria on the upper frond side of L. minor is $0.3 \cdot 10^6$ per cm^2 and the lower side $10.5 \cdot 10^6$ per cm^2 . ANTIPCHUCK (1974) counted 10^5 bacterial cells per gram fresh weight with S. polyrrhiza.

According to KUCHAR (1954), the bacterial genera Sarcina (Micrococaceae) and Leptothrix (Clamydobacteriales) are very typical for water covered with Lemnaceae. In a Lemnaceae cover in England, BOWKER and DENNY (1980) identified 18 species of Cyanophyta, 21 of Chlorophyta, 1 of Euglenophyta, 15 of Bacillariophyta, and 2 of Chrysophyta. Twenty-two species were restricted to fronds and 5 to roots; young growing fronds were not as infected as the older ones. The composition and density of

algal flora of L. minor plants change during the year. The highest density of individuals was reached in March (700 per mm² on the upper side and 900 per mm² on the lower side). Between April and February the cover of algae was much less. On the other hand, the highest number of individuals along the roots (1400 per mm²) was found in December and January. In May and June, more than 70% of the algae belonged to the Chlorophyta species, whereas between August and January more than 80% of the flora consisted of Cyanophyta. In February and March, up to 40% Diatomae appeared (less than 8% during the other months).

Typical algae for Lemnaceae are the chlorophytes Tetraciella adhaerens and Protoderma viride growing on Lemnaceae as epiphytes and Chlorochytrium Lemnae as endophytes in the intercellular spaces of Lemna. Chlorochytrium and Lemna are growing well if separated; apparently they are not dependent on each other (LEWIN 1984). According to EHRLICH (1966), significant reductions in algae and bacteria were obtained in Lemna-covered containers at a detention period of 15 days. STANGENBERG (1967) reports of some bacteriostatic effects of substances excreted by L. minor plants or released by decaying fronds.

KLOSE (1963) lists more than 90 species of algae and bacteria in ponds with Lemnaceae. The species belong to bacteria, cyanophytes, Cryptophyceae, Chrysophyceae, Euglenophyceae, Volvocales and Diatomeae. The bacteria content is especially high in the deeper layers of water covered with Lemnaceae. KLOSE (1963) counted up to $2.1 \cdot 10^6$ individuals per ml water, including 7 species of sulphur bacteria. Under comparable conditions in ponds without Lemnaceae, the number was only 1/20 of this amount. VARELA et al. (1978) list three species of Cyanobacteria and ten species of other algae from a S. intermedia cover in Argentina. Most frequent species are: Microcystis aeruginosa (Cyanobacteria), Rhipidodendron sp. (Chrysophyceae), Meliora granulata and M. varians (Diatomeae). GOLDSBOROUGH and ROBINSON (1985) describe the annual sequences of biomass, species diversity and community composition of epiphytic diatoms on a dense mat of L. minor. Maximum biomass occurred in early spring while diversity reached relative maxima in early summer. Achnanthes hungarica, Amphora veneta, and Navicula twymaniana are supposed to be specific to the Lemna microhabitat.

In a dairy waste lagoon covered with Lemnaceae AMBORSKI and LARKIN (1980) observed 10^5 organisms per ml water, including 10^3 fecal coliforms, 10 fecal Streptococci and less than 0.3 Salmonella and Shigella

propagules. They had some indications that viruses were also present. In India, RAO (1953) identified most algae in Lemnaceae-containing water as Mixophyta and Cyanophyta. The main algae associated with a dairy waste lagoon system containing Lemnaceae are reported by KELLY (1980) as Trachelomonas, Agmenellum, Pandorina, Anacystis, Gomphosphaeria and Oscillatoria.

HERBST and HARTMAN (1981) have reported on the influence of Lemnaceae cover on the phytoplankton of a pond in Texas. Besides light intensity, the temperature pattern and the content of dissolved organic matter, which are dependent on the amount of Lemnaceae cover, the light quality and the day length, and, to a much less extent, the pH, the O₂ and CO₂ content have important effects on composition of the phytoplankton.

Small animals. Many small animals that feed on bacteria and algae find favourable conditions within a Lemnaceae cover (cf. SCHULZ 1962). The average number of invertebrates in a Louisiana cypress tupelo wetland was highest in the floating mats of Lemna species. SKLAR (1985) counted 10500 individuals per m². MADONI and VIAROLI (1985) observed many ciliated Protozoa living in the L. minor cover. Special affinities to L. minor were noted for Vorticella convallaria, V. microstoma, Pyxidium invaginatum and Chilodonella uncinata. A high degree of association was found between L. minor and zooplankton (Cyclopoida, Calanoida, Cladocera, Bosmina, Ostracoda, and Amphipoda) (McCRADY et al. 1986). Hydra sp. (Hydra vulgaris, H. viridis, Chlorohydra viridissima), Rhizopoda, Ciliata, Nematodes, Plathelminthes (according to REHMEL 1974, Dugesia sp. is very often associated with Lemnaceae), Hirundineae, Oligochaeta, Turbellaria (e.g. Planaria), Rotatoria, Bryozoa (e.g. Cristatella mucedo and Lophopus cristallinus) and many Arthropoda (Collembola, insects, spiders, Crustaceae) do not feed Lemnaceae but live within the cover. VARELY et al. (1978) identified the following groups of animals (with species number) from a S. intermedia cover in Corrientes, Argentina: Nematoda (1), Rotifera (5), Oligochaeta (6), Hirudinea (1), Cladocera (4), Ostracoda (1), Copepoda (2), Amphipoda (1), Acari (2). PARDY and GLIDER (1984) showed that the amount of light transmitted by duckweed fronds, to which Hydra attach, is sufficient to promote symbiont photosynthesis (of intracellular algae) at levels approaching saturation. Pectinatella burmannica, an ectoproct (Coelomata), is attached to the lower frond surface of the roots of S. polyrrhiza in India (TONAPI and VARGHESE 1983). Out of the Arthropoda many Crustaceae groups can be named: Phyl-

lopoda, Ostracoda, Amphipoda and Isopoda. The Tardigrada (e.g. Macrobiotus macronyx) is another group living with Lemnaceae. Fasciolopsis buski, a Trematoda, is found very often within Lemnaceae in Vietman before being transferred to animals feeding on duckweeds (NGUYEN 1978). The growth of Daphnia especially is promoted under a cover of Lemnaceae (EHRlich 1966, DINGES 1973). ALIKHUNI et al. (1952) state that Daphne is not able to grow well in ponds without Lemnaceae in India.

Species of mosquito genus Mansonia which communicate filariasis, breed on the lower surface of duckweeds (besides Pistia, Eichhornia, and Azolla) (FOOTE and COOKE 1959). Mansonia uniformis was found to develop best in Lemna covered swamps (data from Natal, South Africa: APPLETON and SHARP 1985). Larvae of the mosquito Aedeomyia squammipennis which does not bite man but is an important vector transmitting malaria to birds, are able to hide beneath the fronds of S. intermedia in Venezuela (GABALDON et al. 1983). On the other hand, a close cover of Lemnaceae prevents the development of some mosquito larvae (e.g. Anopheles, Aedes, Culex (see also next section on amensalists and volume 2, chapter 3.8.4 LANDOLT and KANDELER 1987).

COLER and GUNNER (1969) compared the density of microorganisms growing on the surface of Lemna and glass walls. The populations found on Lemna were up to 100 times larger. The authors counted up to 47 metazoic organisms (predominantly Rotatoria) on the Lemna surface. They assumed that Lemna secreted organic substances, mainly amino acids, that were responsible for the higher populations. On L. trisulca, KOBUSZEWSKA (1973) counted an average of 1674 individuals of microfauna per m² water surface; on S. polyrrhiza, 155; and on L. minor, 590.

Detritivorous snails are often associated with Lemnaceae (see chapter 5.3.1).

The guppy (Lebistes), a fish that feeds on Lemnaceae, has no influence on the composition of the microfauna of the rhizosphere of Lemnaceae, but the development of Oscillatoria may reduce most of these microfauna organisms and favour the development of bacteria, probably due to the secretion of a toxin (COLER and GUNNER 1971).

5.3.2.3. Amensalists

Lemnaceae very often have a negative effect on the development of the larvae of mosquitoes, because of the lowered oxygen content in the water

below Lemnaceae cover. According to ANCONA (1930) Lemnaceae together with Azolla, but not alone, are able to prevent mosquito breeding. 76% of the larvae of mosquito Aedes aegypti die below a L. minor cover as opposed to 14% in controlled experiments without Lemna (ANGERILLI and BEIRNE 1974). The authors assume that juvenile hormones are secreted by Lemna. Extracts of L. minor had only a slightly toxic effect on adult mosquitoes, but prevented them from depositing their eggs into the water (ANGERILLI 1980b). Similar results were obtained with other mosquitoes (Culiseta inornata, Culex pipiens: ANGERILLI 1980a). Further reports of preventing mosquito breeding came from MATHESON and HINMAN (1929), SMITH and ENNS (1967), and FURLOW and HAYS (1972), who obtained complete inhibition of mosquito breeding (Culex, Anopheles, Uranotaenia) below a cover of S. punctata.

The influence of a Lemnaceae cover on fish is variable. SCHULZ (1962) reports of perch ponds which develop such a thick layer of Lemnaceae that the fish did not survive. Fish that require oxygen-rich waters are especially endangered by Lemnaceae. This is why fishermen often remove Lemnaceae from the water (cf. "operation duckweed" by HARGROVE 1976). On the other hand, there are many examples where the Lemnaceae cover has had a very positive effect on fish (SCHULZ 1962). In many ponds with Lemnaceae the fish population is much larger than in ponds without Lemnaceae; the Lemnaceae enlarge the feeding potential (KOBUSZEWSKA 1973), see also volume 2, chapter 3.4.5.1 (LANDOLT and KANDELER 1987).

STANGENBERG (1967) was able to demonstrate bacteriostatic effects of L. minor extracts. An algicide effect (against a unicellular chlorophyte) of W. globosa was detected by HILLMAN (in lit. 1979) in Petri dishes on nutrient agar.

5.3.3. Competitors

The main competitors of Lemnaceae plants are plants of the same growth form (other Lemnaceae, Azolla, Salvinia, etc.) (see chapter 5.4).

Other producer plants that compete for light and nutrients are mostly water plants that root in the bottom soil. Algae, forming dense covers on the surface of the water, compete with Lemnaceae, too. It is not investigated if water plants excrete allelopathic substances toxic to Lemnaceae as it is known from Hydrilla affecting Ceratophyllum (KULSHRESH-

THA and GOPAL 1983). Extracts of some blue algae are known to inhibit growth of L. minor (ENTZERTH et al. 1985). Cyanobacterin which is released by the blue green alga Scytonema hofmanni inhibits the growth of Lemna (GLEASON and CASE 1986). There are some observations that Lemnaceae do not occur at places with other water plants e.g. Myriophyllum spicatum (SCOTTER Ch., Cardiff, U.K. in lit.).

5.3.3.1. Water plants that root in the soil

In competing with rooting water plants, Lemnaceae have the following disadvantages:

- fewer possibilities of anchoring; at the beginning of the colonization of a pond, Lemnaceae are easily swept away if they cannot attach to some rooting water plants.
- difficulties in obtaining enough nutrients; for Lemnaceae, nutrients are only accessible in the uppermost layer of the water; whereas rooting plants may get nutrients from the soil or from any layer within the whole water body.
- possible damage caused by direct exposure to cool or hot air temperatures, heavy rains or hail; Lemnaceae have in general no reserve organs in a protected place.

However, there are also advantages for Lemnaceae:

- easy transport to other waters by water movement or animals.
- better utilization of daylight and solar radiation at the water surface.

Lemnaceae have a good chance to compete with rooting plants in the following environment: small quiet waters, rich in nutrients, in a rather mild climate. In these waters, Lemnaceae can form closed covers. Only species with enough nutrient reserves and the ability to grow over the water surface or to form big leaves on the surface of the water, have a chance of living together with Lemnaceae: Phragmites, Typha, Carex, Eichhornia, Nymphaea etc.). Under these conditions submerged species are very rare and need to live partly heterotrophically. The only submerged species found rather frequently together with Lemnaceae covers is Ceratophyllum demersum (cf. JACOBS 1947, LEWIS and BENDER 1961, MOORE 1962, WIEGLEB 1978a). On the other hand, in waters low in nutrients or with strong currents, Lemnaceae have no chance to compete with rooting plants and are either missing or scattered, growing rather locally.

The shadow of other water plants emerging above the surface of the water (e.g. Eichhornia, Pistia, Phargmites, Typha, Carex, Scirpus) inhibit the growth of Lemnaceae especially if the water is poor in dissolved organic substances.

5.3.3.2. Algae

Algae are most competitive with Lemnaceae in nutrient-rich waters. Fili-form algae, which form dense mats on the surface of the water (e.g. Spirogyra) especially can prevent Lemnaceae from spreading successfully. Very often, the algae cover is raised by development of gas, thus breaking the contact of the Lemnaceae with the water and causing the drying of fronds. It is not known how important the production of toxic substances are in the interrelationship between the different species of algae and Lemnaceae. The high turbidity in a shallow water area in New York caused by a mass development of Anabaena and the action of carps was considered responsible for the disappearance of L. trisulca (KRULL 1969). On the other hand, KNAPP and STOFFERS (1962) showed that much less algae grow in waters with L. trisulca than in waters without L. trisulca.

If nitrogen is a minimum factor in the water, L. minor and other water plants are able to prevent the development of plankton and epiphytic algae (FITZGERALD 1969).

KNAPP and STOFFERS (1962) investigated the influence of solutions in which various vascular water plants and algae had been grown on the growth of L. minor (and Elodea canadensis). They observed some retardation of growth (up to 30%), especially in solutions that had been used to grow L. trisulca cultures. However, the authors were not able to determine whether this effect was due to the lack of nutrients or the presence of toxic metabolic products.

5.4. RELATIONSHIP BETWEEN MEMBERS OF THE FAMILY OF LEMNACEAE AND OTHER SMALL, FREE-FLOATING, VASCULAR PLANT SPECIES

The similar life forms of Lemnaceae organisms and their mostly vegetative, very fast propagation ability lead to a very intensive interrelationship and competition. The number of individuals may reach as much as 200,000 Spirodela, 800,000 Lemna and 2,000,000 Wolffia fronds per m² (HICKS 1937). Under optimal conditions the competition between two species of similar forms may result in the displacement of one species within a relatively short time. This is probably why some Lemna species are strongly allopatric: e.g. L. gibba, L. disperma and L. obscura or L. minor, L. obscura and L. japonica, or W. arrhiza, W. columbiana (and W. globosa).

There are some experimental investigations on the interactions between European species of Lemnaceae. CLATHWORTHY and HARPER (1962) studied the competition for light between S. polyrrhiza, L. gibba, L. minor and Salvinia natans, keeping a constant nutrient concentration in the cultures. In mixed cultures, L. gibba and Salvinia were able to thrust aside S. polyrrhiza and L. minor. L. minor and S. polyrrhiza coexisted without dominating each other. Success in competition was not correlated with growth rate in pure cultures, but rather with morphological characteristics such as presence of aerenchyma (L. gibba) and the possession of a connecting stem between the fronds and the presence of stiff hairs (Salvinia), which enables the plants to grow over the flat fronds of other species. IKUSIMA (1955) and IKUSIMA et al. (1955) investigated the growth of S. punctata and L. minor in pure and mixed cultures. No distinct competition effect was detected.

REJMANKOVA (1975a,b) studied the competition for light between L. minor and L. gibba under field and laboratory conditions. Especially with higher temperatures, L. gibba had a definite advantage of being able to cover the flat fronds of L. minor with its gibbous fronds.

BORNKAMM (1970b) and KEDDY (1976) investigated the competition between L. minor and L. trisulca. In the experiments of BORNKAMM (1970b) L. minor became dominant in mixed cultures. L. trisulca developed a lower dry matter and protein production and a higher carbohydrate/protein ratio in mixed than in pure culture. KEDDY (1976) got similar results. Though L. minor is much faster reproducing and is able to shade L. trisulca

completely, L. trisulca still grows at a reproduction rate of 70% of the control rate when shaded by L. minor, whereas the growth rate of L. minor slows down to zero when shaded.

The competition for nutrients was studied by WOLEK (1974b, 1979). He cultured S. polyrrhiza, W. arrhiza, L. gibba and L. minor in different combinations. The ability to compete was not directly related to the growth rate in single cultures, but, according to his interpretation, to the possibility of making use of the nutrients offered. The larger the absorbing surface in the water and the deeper the absorbing organs, the better the competitive position. The following sequence in competitive ability for nutrients was shown: S. polyrrhiza, L. gibba, L. minor, W. arrhiza. S. polyrrhiza, with its many roots, was able to use the largest water body for nutrients per dry weight; W. arrhiza, the smallest. L. gibba and L. minor, with one root each, were between, the gibbous fronds of L. gibba having a larger absorbing surface than the flat ones of L. minor. The investigations of WOLEK also show that the different species release specific metabolic substances in the solution which, in small doses, promote the growth of fronds but at higher concentrations, slow down the growth rate. Most sensitive to these metabolic products is S. polyrrhiza, which is forced to produce turions, and to a lesser extent L. gibba. The metabolic substances are believed to affect the nitrogen metabolism: fronds in solutions with metabolic substances have a higher NO₃ content per mg dry weight than fronds in solutions where the substances have been removed by coal absorption. However, DOCAUER (1983) did not detect any allelopathic effect between S. polyrrhiza and L. turionifera (table 5.1).

The experiments on competition supplemented by some of our observations (LANDOLT unpubl.) give the following results for the European species of Lemnaceae:

- a. In waters with a good nutrient supply and suitable climatic conditions (average winter temperatures higher than -1°C; average summer temperatures lower than 26°C), L. gibba dominates.
- b. In waters with partial, but not optimal nutrient supply (e.g. in regions with high precipitation), S. polyrrhiza dominates in regions with warm summers, L. minor dominates in regions with cool summers.
- c. In waters with constantly low concentration of phosphorus during the growth period L. trisulca may dominate since it is first able to take up the phosphorus released by the sediment.

d. In waters with a temporarily insufficient nutrient supply, W. arrhiza has an advantage in regions with mild winters and warm summers because it is still able to grow rather quickly at low concentrations (in contrast to L. gibba), and can avoid the most unfavourable conditions by forming turions. These turions might be able to profit at the bottom of the water from the nutrients newly released by the sediment. On the other hand, once established in large masses, W. arrhiza is able to keep other species of Lemnaceae in control due to the growth-retarding effect of the metabolic products released into the water (cf. WOLEK 1974b).

In a later laboratory experiment, WOLEK (1984) showed that different clones of S. polyrrhiza have different competitive abilities in two-species cultures with L. minor. It has to be concluded that competition experiments with only one clone of each species do not give the whole competitive ability of the tested species.

Table 5.1. Competition for nitrogen (N) and phosphorus (P) between Lemna turionifera, Spirodela polyrrhiza and Wolffia borealis (according to DOCAUER 1983)

- 0 in monoculture
- a in competition with S. polyrrhiza
- b in competition with L. turionifera
- c in competition with W. borealis

N / P ratio	Growth rate			% of monoculture		
	150	2.7	0.2	150	2.7	0.2
L. turionifera 0	0.19	0.30	0.28	100	100	100
S. polyrrhiza 0	0.16	0.23	0.20	100	100	100
W. borealis 0	0.005	0.14	0.13	100	100	100
L. turionifera a	0.16	0.23	0.21	82	77	77
S. polyrrhiza b	0.09	0.15	0.15	58	67	78
W. borealis b	0.005	0.01	0.02	100	7	15
L. turionifera c	0.21	0.30	0.29	110	100	100

5.5. PLANT COMMUNITIES WITH LEMNACEAE

5.5.1. Characteristics of Lemnaceae communities and principles of classification

In a restricted sense (TUEXEN 1974), Lemnaceae communities are plant communities of phanerogams, ferns and Hepaticae floating on or below the water surface (pleustophytes) and consisting of a very simple structure (fig. 5.2). They live in a water layer of a few centimeters thickness and relocate only during resting periods, eventually to deeper layers of the water. Contrary to most other communities of water plants, Lemnaceae are not directly influenced by the soil conditions but are dependent on the water composition. Accordingly, they have a very low biomass (7-280 g dry weight per m²) as opposed to up to 10,000 g of a stand of Phragmites (VARFOLOMEEVA 1976, EWEL and ODUM 1978, HEJNY et al. 1981, see also volume 2, chapter 3.2., LANDOLT and KANDELER 1987). Lemnaceae communities can be found as independent mats in small ponds, pools, and

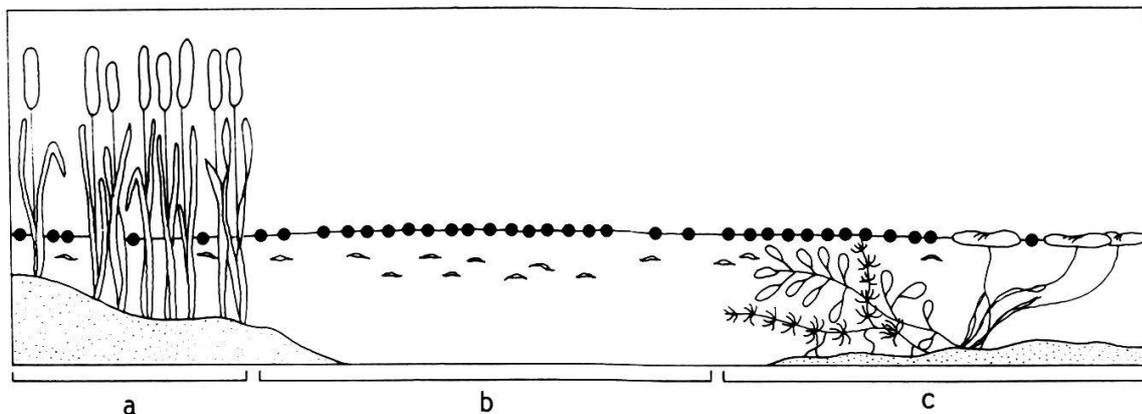


Fig. 5.2. Schematic presentation of a Lemnetea community in relation to other communities of water plants (from SCHWABE-BRAUN and TUEXEN 1981b)

- a. superposition of Lemnetea with Phragmitetea (reed vegetation)
- b. pure Lemnetea communities
- c. superposition of Lemnetea with Potamogetonetea (floating water plants that root)

- layer of pleustonic water plants (lemnaceous growth form)
- ▲ layer of submerged floating water plants (ricciellid growth form)

ditches, or they are overgrown by other plant communities (such as Phragmites or Potamogeton communities) on which they partially depend for anchoring purposes. Limits in the occurrence of Lemnaceae due to nutrient content of water are discussed in chapter 4.2.4.

Lemnaceae communities can be distinguished from other wetland vegetation with large-scale color infrared aerial photography. L. trisulca stands look different from stands of other Lemnaceae (LOVVORN and KIRKPATRICK 1982).

Lemnaceae grow together with the floating species of the following genera: Azolla, Salvinia, Pistia, Ceratopteris, Limnobium, Eichhornia, Hydrocharis, Stratiotes, Aldrovanda, Ceratophyllum, Utricularia, Trapa and the Hepaticae Riccia and Ricciocarpus. Some of these genera are able to grow in waters very low in nutrients (Utricularia, Aldrovanda); others are only occasionally free-floating (Hydrocharis, Stratiotes, Ceratophyllum, Limnobium) or have other different growth forms (Eichhornia, Pistia) with long roots and leaves and shoots rising above the water surface. Therefore, they are not typical for Lemnaceae communities. However, Lemnaceae very often grow together with members of these genera but ecologically and sociologically have another centre of occurrence. The characteristic genera that typically form communities with Lemnaceae are Azolla, Riccia and Ricciocarpus. Other free-floating species are associated as long as they do not rise above the water surface. Salvinia species must be considered as members of Lemnetea associations if they are not connected tightly to dense mats.

In many different climatic zones, Lemnaceae communities show definite periodic development with seasonal changes (table 5.2). It is a matter of opinion whether the seasonal changes can be considered a characteristic of one single association or whether different associations that replace each other according to the season can be distinguished. The different seasonal stages can be observed in some climatic places as independent associations. On the other hand, seasonal variation may be typical of a special environment; in a similar way, different seasonal aspects occur in many terrestrial communities. The example of table 5.2 was noted in California during 1954/1955 (LANDOLT unpubl.). In spring, the nutrient supply (especially of bases) is relatively low due to winter rains. The development of L. gibba is delayed, whereas L. minor is able to multiply. For the germination of the turions of W. globosa and L. turionifera, which were formed in the fall, it is still too cool.

During the warm summer, low in precipitation, the conditions for L. gibba are more favourable until certain nutrients (e.g. nitrogen, phosphorus) are exhausted. This is the time for development of W. globosa, which is favoured by high temperatures and able to utilize lower nutrient conditions than L. gibba. With the cooler temperatures in late fall, W. globosa forms turions and disappears from the water surface, thus giving way to Azolla. Azolla grows at even lower temperatures than W. globosa and manages to develop at a rather low nutrient content. Occasionally frost and dense rainfall during wintertime destroy the Azolla cover, enabling the more cold-tolerant L. minor to flourish. The three rather distinct seasonal stages are characterized by the mass development of L. minor, W. globosa and Azolla, successively. The stand has to be attributed to the L. gibba alliance because beside L. gibba, L. minuscula and Azolla filiculoides are typical species. On the other hand, L. trisulca, a characteristic species of the L. minor and the L. turionifera alliances, is not present.

This example shows that it is important to take relevés several times a year at one location to obtain knowledge about the habitat of the place. Similar examples of seasonal changes, although not so apparent, can be found in cooler regions, too. MERIAUX and GEHU (1978) show a seasonal

Table 5.2. Seasonal changes of the Lemnaceae vegetation in a pond near Fresno (California, USA). Relevés of Lemnaceae cover according to BRAUN-BLANQUET: + occasional (up to 1%), 1 very sparse (1-5%), 2 scarce (5-25%), 3 rather abundant (25-50%), 4 abundant (50-75%), 5 very abundant (75-100%). The vegetation consists of a rare association of L. gibba and W. globosa (1.5.3) in central California.

Species	Date								
	1954								1955
	1.4.	19.5.	9.7.	6.8.	7.9.	29.9.	8.11	4.12.	10.1.
Lemna gibba	1	1	2	2	2	2	1	+	+
Lemna minor	2	3	2	2	2	2	1	+	+
Lemna turionifera	+	+	1	2	2	2	+	+	+
Lemna minuscula	+	1	2	1	1	1	+	+	+
Wolffia globosa	+	2	4	5	5	5	2	1	+
Azolla filiculoides	+	+	+	+	+	+	1	3	5

change in the vegetation of a small lake in northern France. In the summer, Callitriche luxuriates but is succeeded by a mat of L. gibba in fall. Callitriche deteriorates in the autumn, releasing nutrients into the water. The higher nutrient level stimulates growth of L. gibba. PEDROTTI (1979) describes a seasonal change of a "Ricciocarpetum natan-tis" (winter and spring) to a "Lemnetum minoris" (late spring and summer) from central Italy due to the fluctuations of the nutrient content. Besides seasonal changes, there can be a succession of Lemnaceae communities from very simple, one-layered, single-species associations in waters of new origin or recently-disturbed waters to more complicated associations of several species in well-established, stable waters. Species of the first association type are named here "pioneer species" in contrast to later appearing "follower species". The pioneer species can colonize rather quickly; they have a high propagation rate and rather large fluctuations in population size (typical r strategy). The fronds of these species float on the surface of the water (fig. 5.3). In this category fall all Spirodela and Lemna species except L. trisulca, L. tenera and L. valdiviana, and from the other genera, Azolla and Salvinia. Of these pioneer species, a few are very characteristic for certain geographic and climatic zones. The principal species are L. minor, L. gibba, L. japonica, L. turionifera, L. obscura, L. disperma, L. aequinoctialis (L. perpusilla and S. punctata). All are about of the same shape and size ("L. minor type"). These principal species often exclude one another in their distribution. For a climatic characterization of the species distribution, see chapter 6.3. Due to their frequent occurrence and mainly allopatric distribution, the principal species are most suitable to use in classifying the Lemnaceae communities.

As the follower species are found only under relatively stable conditions, they do not propagate as fast as the pioneer species, have lower demands for nutrients and light, and are very often submerged. Under stable conditions, the nutrients of the ecosystem are mostly in the biomass, leaving only a few nutrients in the water; however, the CO₂ content of the water is much higher, enhancing photosynthesis for the submerged plants. The better these follower species grow, the fewer nutrients are available for the pioneer plants since the submerged species can obtain the nutrients diffusing from lower parts of the water; the pioneer plants starve and eventually die. The water of the stable association with follower species often shows a rather constant low level of

phosphorus (LANDOLT unpubl. observations). Phosphorus is released by the sediment and can be taken up by the submerged follower species. It is known that Lemnaceae release some organic substances into the water, enabling the fronds of deeper layers to develop even if they do not receive light. The final associations therefore consist of many submerged plants and a few scattered fronds on the surface of the water provided that no disturbances occur such as the addition of nutrients from outside or water movement. Very often the final associations are rather rich in species (up to 12). Communities of only one follower species may occasionally occur if the principal species die out in the final succession due to lack of nutrients or if the follower species are able to



Fig. 5.3. Lemna minuscula as a pioneer species in an outlet of a small spring near Bariloche, Argentina. The fronds are periodically washed away in the rainy season. (Photo E.L.)

grow in locations not suitable for growth of principal species (e.g. L. trisulca in cool regions with very short vegetation periods). Typical follower species are L. trisulca, L. valdiviana, W. neotropica, W. linguata, W. oblonga, W. gladiata, W. denticulata, and Riccia fluitans. The behaviour of the other species of Lemnaceae is somewhere between that of the pioneer and follower species or is not known. Pioneer species are characteristic for alliances, follower species for associations.

A special problem of community classification occurs when stands have only one species. Stands with one species may be grouped according to the following causes for their existence:

- pioneer stands: only one species has yet reached suitable water
- stands of follower species in the final succession where all other species of the association disappeared due to lack of nutrients
- stands with special conditions suited only for one species (at the ecological limits of an association)
- adventitious stands in waters suited only temporarily for Lemnaceae growth.

Except for the last type, classification of these one-species stands is justifiable. It is possible that such stands of one species belong to different sociological units according to their origins. Stands of pure L. trisulca, for instance, belong in Europe to a L. minor - L. trisulca association, in continental America to a L. turionifera - L. trisulca association, in East Asia to a L. japonica - L. trisulca association, and in Australia to a L. disperma - L. trisulca association. I agree with SCHWABE-BRAUN and TUEXEN (1981b) that it is not appropriate to name such stands individually (e.g. "Lemnetum minoris", cf. MUELLER 1977) because they are ecologically not identical at the different places of occurrence.

WOLEK (1983) tested the hypothesis that the occurrence of Lemnaceae species results from the random dispersal of propagules of the pool of potentially available species. According to his results of 1945 investigated phytosociological records from Poland, he is of the opinion that a natural plant community belonging to the Lemnetea class is a haphazard collection of species with nearly the same environmental requirements. WOLEK's results are understandable if one takes into account that he investigated a climatically not greatly differentiated region and that the Lemnaceae are easily distributed over short distances by birds. Also he

did not consider data of frequency of the different species at one place. However, his results do not exclude that differences in species-composition and species-frequency occur in a region due to different chemical composition of the waters. Most field botanists will confirm that stable and constant differences between the Lemnaceae cover of many ponds can be found which are not explainable by random distribution. Also, at least some of the chemical differences of the waters of different Lemnaceae associations are evident (see chapter 4.2). In addition, there is no doubt that climatic differences in the world result in different composition of pleustonic communities. Remarkably, the study of WOLEK (1983) shows that chance plays a more important role in the formation of pleustophyte associations than in terrestrial communities. An association cannot be characterized just by the frequency of occurrence throughout the year.

According to the system of BRAUN-BLANQUET, communities of dominating Lemnaceae can be classified as the class Lemnetea. However, SCHWABE-BRAUN and TUEXEN (1981b) are of the opinion that the class Lemnetea (minoris) W.Koch et R.Tx. (in lit. 1954) apud R.Tx. 1955 cannot be applied to all communities with dominating Lemnaceae because the only characteristic species of the class, L. minor, is not present in all regions where the Lemnaceae associations occur. They propose a class group Wolffio-Lemnea. However, it does not seem very reasonable to use the same narrow species concept for the characteristic species of the class as of an association. Since most species differentiate within larger areas of the world, this principle would lead to a splitting up of many classes as soon as characteristic class species are taxonomically investigated more closely. If we take species groups instead of species, we get two characteristic "species" for the class Lemnetea: S. polyrrhiza s.l. (with S. polyrrhiza and S. intermedia) and W. arrhiza s.l. (with W. arrhiza, W. columbiana, W. globosa, W. australiana and W. angusta). A further division in orders can be made with L. trisulca and L. minor s.l. (L. minor, L. turionifera, L. gibba, L. disperma, L. obscura, L. japonica, and L. ecuadoriensis) as a characteristic species of the first order and L. aequinoctialis of the second order. The first order corresponds to the Lemnetalia minoris W.Koch et R.Tx. (in lit. 1954) apud R.Tx. 1955; the second corresponds to the Lemnetalia aequinoctialis (as L. paucicostatae nomen ex SCHWABE-BRAUN and TUEXEN 1981b).

In the literature other orders have been distinguished as containing

Lemnaceae, but belonging to other classes. PASSARGE (1978), for instance, names two orders, Lemno - Utricularietalia and Hydrocharietalia, which mediate between Lemnetea and Utricularietea and between Lemnetea and Potamogetonetea, respectively. FEOLI and GERDOL (1982) compared the class Lemnetea in Europe to Potamogetonetea by cluster analysis. In contrast to earlier classifications (DEN HARTOG and SEGAL 1964, MUELLER 1977) and in agreement with SCHWABE-BRAUN and TUEXEN (1981b), they separated Hydrocharitetum morsus-ranae Van Langend. 1935 (part of Hydrocharietalia) from the Lemnetea class and put it in the Potamogetonion pectinati W. Koch 1926. In the following survey of the communities of Lemnaceae in the world, all communities with mass development of Pistia, Salvinia, Eichhornia and Hydrocharis will not be considered; nor will communities with good development of Utricularia, which is characteristic for oligotrophic and mesotrophic waters. Lemnaceae play only a small role in these communities, anyway. Moreover, not much sociological work has been done on these species (especially in the tropics).

For the European Lemnetea associations, a very careful and complete monograph by SCHWABE-BRAUN and TUEXEN (1981b) has been presented which is strongly based on the principles of the school of Braun-Blanquet. It contains an extensive amount of ecological informations and references and also includes some extra-European sociological investigations. ESKUCHE and ROMERO FONSECA (1982), ESKUCHE (1986) and LANDOLT and ZARZYCKI (in prep.) give some relevés from northern Argentina containing much Salvinia and/or Azolla or Pistia, which partly belong to other classes. Some relevés have similar composition of species as in associations of the Lemnetalia aequinoctialis but lack L. aequinoctialis.

The following survey does not give an accurate list of the different sociological units since only very few sociological relevés are available. It is only provisional and not complete. From many field investigations and from identification of thousands of herbarium specimens, this author has obtained a fair amount of knowledge of the different species of Lemnaceae that grow together.

5.5.2. Survey of Lemnaceae communities

Single class: Lemnetea minoris W. Koch et R. Tx. (in lit. 1954) apud R.Tx 1955

Characteristic species of the class: S. polyrrhiza s.l., W. arrhiza s.l., Ricciocarpus natans s.l.

Distribution: Whole world, except Arctic, Antarctic and desert regions. The class contains at least two orders: Lemnetalia minoris in temperate regions and Lemnetalia aequinoctialis in subtropical and tropical regions.

1. Order of Lemnetalia minoris W.Koch et R.Tx. (in lit. 1954) apud R.Tx. 1955

Characteristic species of the order: L. trisulca, L. minor s.l., Azolla filiculoides s.l., Riccia fluitans s.l.

Distribution: Temperate and subarctic regions of the world, tropical and subtropical mountains.

The order consists of at least six alliances according to the six principal species: L. minor, L. turionifera, L. japonica, L. obscura, L. gibba, L. disperma.

1.1. Alliance of L. minor: Lemnion minoris W.Koch et R.Tx. (in lit 1954) apud R.Tx 1955

Characteristic species of the alliance: L. minor s.str.

Distribution: Temperate and subarctic regions with oceanic-suboceanic climate: Europe; southwestern Asia (eastwards to Kashmir); northern, eastern and southern Africa; North America; New Zealand; islands of the Atlantic Ocean.

The circumscription of the alliance does not exactly follow the definition of the Riccio fluitantis - Lemnion trisulcae of SCHWABE-BRAUN and TUEXEN 1981a,b) and of SCOPPOLA (1983). Besides the four associations of that alliance (Lemnetum trisulcae, Ricciocarpetum natantis, Riccietum fluitantis, Azollo carolinianae - Riccietum fluitantis), the following associations are included here:

- a) associations of the Lemno minoris - Salvinion natantis Slavnic 1956 em. Schwabe et R.Tx (where L. minor is well developed and Salvinia does not constantly dominate); it is assumed that during spring and early summer, L. minor and L. trisulca are the dominant species whereas Salvinia spreads in late summer.
- b) Spirodeletum polyrrhiza (where L. minor is better developed than L. gibba for the greater part of the year); SCHWABE-BRAUN and TUEXEN (1981b) and SCOPPOLA (1983) combine this association with the Lemnion gibbae.
- c. Two additional associations in North America, one association in South Africa, one in East Africa and one in New Zealand.

The classification of communities with L. minor in Europe is not generally agreed on. TUEXEN (1974) distinguishes 3 associations for northwestern Germany; WOLEK (1974a), 3 for Poland; SELISKAR (1983), 2 for Slovenia; KNAPP and STOFFERS (1962), 2 for Hessen (Germany); HILBIG (1971), 3 for the southern DDR; SCHOLZE (1986), 3 for Vorarlberg (Austria); and MUELLER and GOERS (1960), 5 for southwestern

Germany. Of the 17 associations with Lemnaceae described by PAS-SARGE (1978) for Central Europe, 11 belong to Lemnion minoris as it is described here. Taking into consideration the small number of species present in different associations and the seasonal changes that occur in species composition, it does not make much sense to have so many associations. The five associations of SCHWABE-BRAUN and TUEXEN (1981b) for the whole of Europe sufficiently cover the ecological variations. POTT (1981) reports on the value of the associations as bioindicators.

1.1.1. **Association of L. minor and L. trisulca: Lemnetum trisulcae (Kelhofer 1915) Knapp et Stoffers 1962**

Characteristic species: L. trisulca

Additional species: L. minor, S. polyrrhiza, (L. gibba, W. arrhiza, W. columbiana, Azolla filiculoides, Hydrocharis morsus-ranae)

Distribution: Europe (distribution map by SCHWABE-BRAUN and TUEXEN 1981b); southwestern Asia; northern and eastern Africa; North America (eastern and western part).

The association occurs frequently in rather deep, cool, mesotrophic to eutrophic waters that are relatively rich in bases. Very often there are pure stands of L. minor (pioneer stages). Under stable conditions, at the end of a succession, the association is characterized by good development of L. trisulca and moderate development of the pleustic species. This association is described extensively by SCHWABE-BRAUN and TUEXEN (1981b).

1.1.2. **Association of L. minor and Ricciocarpus natans: Ricciocarpetum natantis Segal 1963 em. R.Tx. 1974**

Characteristic species: Ricciocarpus natans

Additional species: L. minor, L. trisulca, (Riccia fluitans, S. polyrrhiza, W. arrhiza, W. columbiana, L. gibba, Utricularia sp.)

Distribution: Europe (distribution map by SCHWABE-BRAUN and TUEXEN 1981b, SCOPPOLA 1982), North America (Africa, southwestern Asia); regions with mild winters.

The association does not occur very frequently; it grows in warm, eutrophic waters that are often shaded by trees, Phragmites, rice, etc. According to SCHWABE-BRAUN and TUEXEN (1981b), it is typically found in waters low in phosphorus content. This association is described extensively by SCHWABE-BRAUN and TUEXEN (1981b).

1.1.3. **Association of L. minor and Riccia fluitans: Riccietum fluitantis Slavnic 1956 em. R.Tx. 1974**

Characteristic species: Riccia fluitans

Additional species: L. minor, L. trisulca, S. polyrrhiza, (Ricciocarpus natans, W. arrhiza, W. columbiana, L. gibba, Hydrocharis morsus-ranae)

Distribution: Europe (distribution map by SCHWABE-BRAUN and TUEXEN 1981b and SCOPPOLA 1982); North America (northern Africa, southwestern Asia).

The association occurs in waters with low nitrogen, low phosphorus and low mineral content. This association is described extensively by SCHWABE-BRAUN and TUEXEN (1981b). Relevés from warmer regions containing much Azolla caroliniana are described as a distinct association (Riccio fluitantis - Azolletum caroliniana) by AVENA et al. (1975) and SCOPPOLA (1982).

1.1.4. **Association of L. minor and Salvinia natans: Lemno minoris - Salvinietum natantis (Slavnic 1956) Korneck 1959**

Characteristic species: Salvinia natans

Additional species: L. minor, S. polyrrhiza, L. trisulca, Ceratophyllum demersum, Hydrocharis morsus-ranae, (Riccia fluitans, Azolla filiculoides, L. gibba, W. arrhiza, Aldrovanda vesiculosa)

Distribution: Eastern Europe (distribution map by SCHWABE-BRAUN and TUEXEN 1981b); southwestern Asia, Kashmir; rather continental regions with warm summers.

The association grows in rather warm, eutrophic waters. It is described extensively by SCHWABE-BRAUN and TUEXEN (1981b). These authors include it in an alliance of its own. However, TUEXEN (in an appendix in SCHWABE-BRAUN and TUEXEN 1981b) and SCOPPOLA (1982) distinguished three associations with Salvinia natans in Europe corresponding to the association 1.1.1., 1.1.3., and 1.1.5. superimposed by Salvinia. S. natans is a species of climatically rather continental areas. In the present treatment, the association contains only stands with good development of Salvinia. Since in Europe it contains mostly L. minor it is attributed to the Lemnion minoris.

1.1.5. **Association of L. minor, L. gibba, and S. polyrrhiza: Spirodeletum polyrrhizae (Kelhofer 1915) W.Koch 1954**

Characteristic species: L. gibba

Additional species: L. minor, L. trisulca, S. polyrrhiza, L. minuscula, Azolla filiculoides, Salvinia natans, W. arrhiza

Distribution: Europe (distribution map by SCOPPOLA 1982); northern, central and southern Africa; southwestern Asia; California; regions with warm summers and mild winters.

The association is frequent in eutrophic waters and forms a transition to the Lemnion gibbae alliance. It is described extensively by SCHWABE-BRAUN and TUEXEN (1981b), SCOPPOLA (1982) and SBURLINO et al. (1986) where it is placed in the Lemnion gibbae alliance. The much better development of L. minor than that of L. gibba in this association and the frequent occurrence and good development of S. polyrrhiza and L. trisulca, which usually occur rather rarely within Lemnion gibbae, suggest an allocation to Lemnion minoris. The almost identical contingency profiles of L. minor and S. polyrrhiza in Europe (WIEGLEB 1978a) also point in this direction. The Wolffietum arrhizae Miyaw. et Tx. is a variant partly of this association and partly of the L. gibba - L. minor association (1.5.1.) in which W. arrhiza temporarily reaches dominance. For an example see SZALMA and BODROGKOEZY (1985).

1.1.6. Association of L. minor, W. columbiana and W. borealis

Characteristic species: W. borealis, W. columbiana

Additional species: L. minor, S. polyrrhiza, L. trisulca, Riccia fluitans, (W. brasiliensis, L. turionifera)

Distribution: North America (northern and central states of the USA, southern Canada); regions with rather mild winters and warm summers.

The association is frequent in warm, eutrophic waters with relatively low Ca and Mg content.

1.1.7. Association of L. minor and L. perpusilla

Characteristic species: L. perpusilla

Additional species: L. minor, S. polyrrhiza, Riccia fluitans, (W. columbiana, W. borealis, W. brasiliensis, Azolla caroliniana, L. trisulca)

Distribution: Northeastern and central states of the USA.

The association is not frequent and grows in waters with relatively low Ca and Mg content.

1.1.8. Association of L. minor and W. australiana

Characteristic species: W. australiana, L. disperma

Additional species: L. minor, (S. punctata)

Distribution: New Zealand; regions with very mild winters.

The association is not very wide-spread and grows in rather eutrophic waters with relatively low content of Ca and Mg.

1.1.9. Association of L. minor and W. denticulata

Characteristic species: W. denticulata

Additional species: L. minor, W. arrhiza, S. polyrrhiza, (W. Welwitschii, S. punctata, Azolla pinnata, Ceratophyllum demersum, Utricularia sp.)

Distribution: Southern Africa (very localized in E. Cape, Natal, and southern Mozambique); in frost-free but rather cool regions. The association grows in mesotrophic waters under stable conditions; in the end stage, it is characterized by well developed W. denticulata and sparsely developed pleustic species. MUSIL et al. (1973) describe sociological stands from Pongolo River Pans, Natal, with W. arrhiza, S. polyrrhiza, Utricularia exoleta and Ceratophyllum demersum, which apparently lack L. minor.

1.1.10. Association of L. minor and W. Welwitschii

Characteristic species: W. Welwitschii

Additional species: L. minor, L. trisulca

Distribution: Eastern Africa, locally in the region of Lake Victoria.

1.2. Alliance of L. turionifera

Characteristic species of the alliance: L. turionifera

Distribution: Central and northeastern Asia (westwards to the Ural and Turkey); North America; in regions with continental climate.

The alliance of L. turionifera replaces the Lemnion minoris alliance in more continental climates. LOOMAN (1985) gives many relevés from Saskatchewan, Alberta and Manitoba which belong to this alliance. Unfortunately he did not distinguish between L. minor and L. turionifera. But most, or all, of his L. minor probably belong to L. turionifera for ecological and geographical reasons. However, he distinguishes in that region between W. columbiana and W. arrhiza. The present author checked the W. arrhiza of LOOMAN (1985) and identified it as W. columbiana.

1.2.1. Association of L. turionifera and L. trisulca

Characteristic species: L. trisulca

Additional species: L. turionifera, S. polyrrhiza, (W. columbiana)

Distribution: Central and northeastern Asia; northern part of North America.

The association corresponds to the L. minor - L. trisulca association (1.1.1.) of more oceanic regions; it is very widespread and occurs frequently.

1.2.2. Association of L. turionifera and Riccia fluitans

Characteristic species: Riccia fluitans

Additional species: L. turionifera, L. trisulca, S. polyrrhiza, W. columbiana, (L. valdiviana, W. borealis, Ceratophyllum demersum)

Distribution: North America and probably also Asia.

The association corresponds to the L. minor - Riccia fluitans association (1.1.3.) of more oceanic regions.

1.2.3. Association of L. turionifera and Ricciocarpus natans

Characteristic species: Ricciocarpus natans

Additional species: L. turionifera, S. polyrrhiza, L. trisulca, (W. columbiana, W. borealis, Riccia fluitans)

Distribution: North America; Asia (?); in regions with warm summers.

The association corresponds to the L. minor - Ricciocarpus natans association (1.1.2.) of the more oceanic regions.

1.2.4. Association of L. turionifera, W. columbiana and W. borealis (plate XVIa)

Characteristic species: W. columbiana, W. borealis

Additional species: L. turionifera, S. polyrrhiza, L. trisulca, Riccia fluitans, (W. brasiliensis, Ceratophyllum demersum, Ricciocarpus natans)

Distribution: North America (central states of the USA).

The association corresponds to the L. minor - W. columbiana - W. borealis association (1.1.6.) of more oceanic regions. In the

northernmost part of the area of the association W. borealis is missing.

1.2.5. Association of L. turionifera, L. minuscula and L. gibba

Characteristic species: L. gibba, L. minuscula

Additional species: L. turionifera, S. polyrrhiza, (L. trisulca)

Distribution: Southwestern USA, and without L. minuscula in Turkey and southern Central Asia.

The association corresponds to the L. minor - L. gibba association (1.1.5.) of more oceanic regions; it is not widespread.

1.3. Alliance of L. japonica

Characteristic species of the alliance: L. japonica

Distribution: Eastern Asia; in oceanic regions with rather mild winters.

The alliance of L. japonica replaces the Lemnion minoris alliance in eastern Asia; it extends to slightly warmer regions.

1.3.1. Association of L. japonica and L. trisulca

Characteristic species: L. trisulca

Additional species: L. japonica, S. polyrrhiza, (W. globosa)

Distribution: Eastern and southern China; Korea; northern Japan.

The association corresponds to the L. minor - L. trisulca association of Europe and North America. There are probably associations also with Riccia fluitans and Ricciocarpus, but thus far there are no definite indications of this.

1.3.2. Association of L. japonica and W. globosa

Characteristic species: W. globosa

Additional species: L. japonica, S. polyrrhiza, S. punctata, (L. trisulca, L. aequinoctialis)

Distribution: Central China and central Japan; in regions with mild winters.

The association grows in warm, eutrophic waters.

1.4. Alliance of L. obscura

Characteristic species of the alliance: L. obscura, L. valdiviana

Distribution: Southeastern and south central states of the USA; in regions with mild winters and warm summers.

The alliance replaces the Lemnion minoris alliance in warmer regions of eastern North America.

1.4.1. Association of L. obscura and W. gladiata:

Lemno valdivianae - Wolffielletum gladiatae Landolt 1981

Characteristic species: W. gladiata, Limnobium spongia

Additional species: L. obscura, L. aequinoctialis, L. valdiviana, S. polyrrhiza, W. brasiliensis, W. columbiana, Riccia fluitans, (Azolla caroliniana, Utricularia purpurea)

Distribution: Southeastern states of the USA and Mexico; regions with very mild winters and warm summers.

The association grows in mesotrophic waters with rather low content of Ca and Mg. Under stable conditions the association is very rich in species (7-10) and characterized by well-developed W. gladiata. The association is described by LANDOLT (1981).

1.4.2. **Association of L. obscura, S. polyrrhiza, Ricciocarpus natans, and W. brasiliensis**

Characteristic species: Ricciocarpus natans

Additional species: L. obscura, S. polyrrhiza, W. brasiliensis, W. columbiana, L. valdiviana, (L. aequinoctialis)

Distribution: Southeastern and south central states of the USA.

The association with well-developed L. obscura and S. polyrrhiza grows in more eutrophic waters than 1.4.1. and is rather widespread in the regions where it is found.

1.4.3. **Association of L. obscura and W. oblonga**

Characteristic species: W. oblonga, W. lingulata

Additional species: L. obscura, S. polyrrhiza, L. valdiviana, W. columbiana, W. brasiliensis, L. aequinoctialis, (W. gladiata, Riccia fluitans, Ricciocarpus natans, L. minuscula, L. gibba)

Distribution: Florida, Louisiana, Texas, Mexico; regions with very mild winters (only slight frosts) and warm summers.

The association replaces the Lemno valdivianae - Wolffielletum gladiatae (1.4.1.) in warmer regions with more eutrophic waters. SCHWABE-BRAUN and TUEXEN (1981b) cite some relevés of this association from Mexico.

1.5. **Alliance of L. gibba: Lemnon gibbae R.Tx. et A. Schwabe 1974 apud R.Tx. 1974 p.p.**

Characteristic species of the alliance: L. gibba, L. minuscula, Azolla filiculoides

Distribution: Western and southern Europe; southwestern Asia (eastwards to Kashmir); northern, eastern and southern Africa; southern North America (Mexico, southwestern states of the USA); South America (Andes, Chile, Argentina, Uruguay, southern Brazil); mostly found in regions with a mediterranean climate.

The alliance is well documented in Europe (SCHWABE-BRAUN and TUEXEN (1981b). Associations with well-developed L. trisulca and S. polyrrhiza are not placed within this alliance since L. gibba is rarely associated with these two species in its worldwide distribution.

1.5.1. **Association of L. gibba and L. minor: Lemnetum gibbae (W.Koch 1954) Miy. et J.Tx. 1960**

Characteristic species: L. minor

Additional species: L. gibba, (S. polyrrhiza, L. trisulca, L. minuscula, W. arrhiza, Azolla filiculoides)

Distribution: Europe (distribution map by SCHWABE-BRAUN and TUEXEN 1981b and SCOPPOLA 1982); southwestern Asia; northern, eastern and southern Africa; California; in regions with summers that are not very warm.

The association is widespread in the contact zones between the Lemnion gibbae and the Lemnion minoris, in rather eutrophic waters. SCOPPOLA (1982) described a distinct association of Azolla filiculoides and Riccia fluitans from Italy with extensive development of these two species. The association stays between the Lemnetum gibbae and the Riccietum fluitantis (1.1.3.).

1.5.2. **Association of L. gibba and L. turionifera**

Characteristic species: L. turionifera

Additional species: L. gibba, L. minuscula, L. minor, S. polyrrhiza, (Azolla filiculoides)

Distribution: California, Nevada, Arizona, New Mexico.

The association replaces association 1.5.1. in more continental climates.

1.5.3. **Association of L. gibba and W. globosa (table 5.2)**

Characteristic species: W. globosa

Additional species: L. minor, S. polyrrhiza, L. gibba, L. turionifera, L. minuscula, Azolla filiculoides

Distribution: Central California (very localized, in regions with warm summers and mild winters).

The association grows in warm, rather eutrophic waters, with a relatively low Ca and Mg content.

1.5.4. **Association of L. gibba and W. oblonga (fig. 5.4, plate XVIc)**

Characteristic species: W. oblonga, W. columbiana

Additional species: L. gibba, L. minuscula, (S. intermedia, Azolla filiculoides, L. valdiviana, W. brasiliensis, Limnobium laevigatum, Utricularia gibba)

Distribution: South America; in warm temperate regions with very mild winter temperatures (only slight frosts).

Under stable conditions the association is characterized by good development of Wolffiella and less developed pleustic species. OBERDORFER (1960) describes a fragment of this association from Chile under the name Lemno - Azolletum chilense. In waters poor in nutrients, L. valdiviana prevails and Utricularia gibba is regularly occurring. The association probably has to be subdivided.

1.5.5. **Association of L. gibba, W. lingulata, and S. polyrrhiza**

Characteristic species: W. lingulata

Additional species: L. gibba, L. minuscula, S. polyrrhiza, L. minor, L. turionifera (L. aequinoctialis, L. valdiviana, W. oblonga, Azolla filiculoides)

Distribution: California; in warm temperate regions with very mild winter temperatures and dry summers.

The association is a geographical variant of 1.5.4. Due to pollution it has become very rare within the last 30 years.

1.5.6. **Association of L. gibba and L. obscura**

Characteristic species: L. obscura, W. gladiata, L. valdiviana

Additional species: L. gibba, W. columbiana, W. lingulata (W. brasiliensis, L. minuscula, W. oblonga, L. trisulca, S. polyrrhiza)

Distribution: Mexico (region of the capital); warm temperate regions with very mild winter temperatures and humid summers. The association which is documented in many herbarium samples (e.g. Hahn, Schaffner) and in relevés by BRAVO (1930) and SCHWABE-BRAUN and TUEXEN (1981b) forms some kind of transition between the associations 1.5.5. and 1.4.1. (1.4.2.).

1.5.7. **Association of L. gibba and W. hyalina**

Characteristic species: W. hyalina

Additional species: L. gibba, (L. aequinoctialis)

Distribution: Eastern Africa (Egypt to Malawi); in frost-free regions with warm summers.

The association grows in eutrophic waters with high content of Ca and Mg.

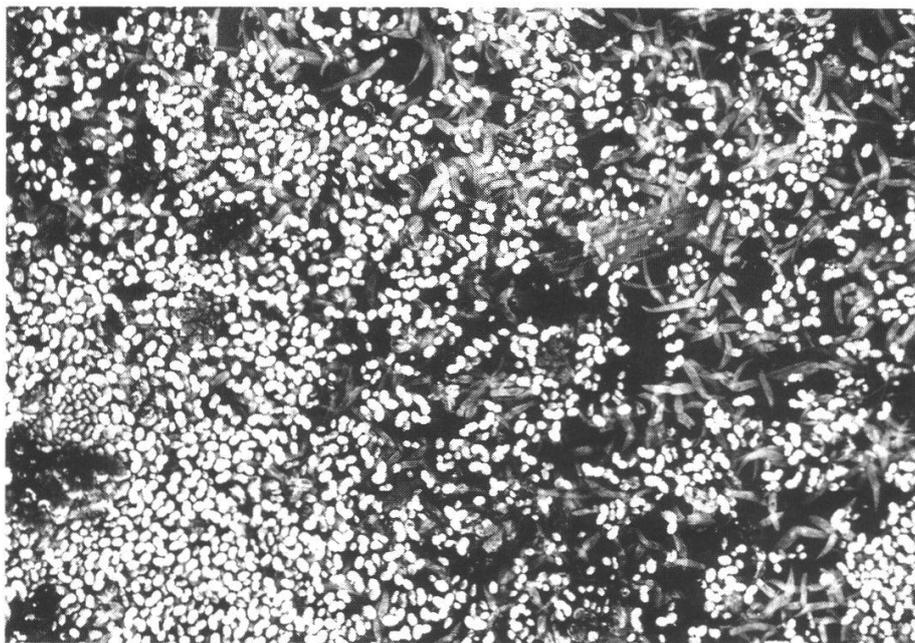


Fig. 5.4. Association of Lemna gibba and Wolffiella oblonga, in the final stage with L. minuscula, L. gibba (few), Wolffia brasiliensis, W. columbiana (few), Azolla filiculoides (few) on the surface of the water, and much Wolffiella oblonga in the "understory" below the water surface. Laguna del Monte, Prov. Buenos Aires, Argentina (photo E.L.).

1.6. Alliance of L. disperma

Characteristic species of the alliance: L. disperma, W. australiana

Distribution: Southern Australia, New Zealand.

The alliance replaces Lemnion gibbae in Australia and New Zealand.

1.6.1. Association of L. disperma and S. punctata

Characteristic species: S. punctata, W. angusta, Azolla filiculoides

Additional species: L. disperma, W. australiana, Ceratophyllum demersum, (S. polyrrhiza, L. aequinoctialis, Ricciocarpus natans)

Distribution: Southern Australia, New Zealand.

The association grows in eutrophic waters.

1.6.2. Association of L. disperma and L. trisulca

Characteristic species: L. trisulca

Additional species: L. disperma, W. australiana, (S. punctata)

Distribution: Southeastern Australia (incl. Tasmania).

The association grows in cooler and less eutrophic waters than that required by association 1.6.1. The waters have a rather high content of Ca and Mg.

2. Order of Lemnetalia aequinoctialis Schwabe-Braun et R.Tx. 1981 (sub nomen Lemnetalia paucicostatae nomen nudum)

Characteristic species of the order: L. aequinoctialis, Azolla pinnata s.l., Azolla caroliniana (Pistia stratiotes)

Distribution: Warm temperate, subtropical and tropical regions of the world.

Due to the very few species of most of these associations, it is very difficult to distinguish different alliances. Most Lemnaceae stands consist only of 1 to 4 species. Stands of L. aequinoctialis alone, Pistia alone, or both species mixed together are especially frequent (Lemno - Pistietum Lebrun 1947, according to MIYAWAKI and TUEXEN 1960). Possibly, a classification of the order in alliances can be made by taking geographically limited species as W. arrhiza, W. globosa, and W. columbiana as characteristic species. Also Azolla and the group of S. polyrrhiza might be considered. A special difficulty arises with the classification of the association-group with L. minuscula (2.1.17) in which L. aequinoctialis is very rarely present. The association-group forms some kind of transition between this order and the Lemnion gibbae but mostly lacks L. gibba as well as L. aequinoctialis. Instead, L. minuscula is very frequent which is characteristic for the Lemnion gibbae. On the other hand, Azolla caroliniana, W. lingulata, Pistia, and Salvinia auriculata are much more typical for the order of L. aequinoctialis. Possibly this group can be characterized as order of its own by Salvinia minima, S. hercogii, and some other species.

2.1.1. Association of L. aequinoctialis and L. gibba: Lemnetum aequinoctialis Pignatti 1957 (sub nomine Lemnetum paucicostatae)

Characteristic species: L. gibba, L. minor

Additional species: L. aequinoctialis, S. polyrrhiza

Distribution: Southern Europe; southwestern Asia; northern Africa; California.

The association grows in the area of the Lemnion gibbae association mostly in rice fields.

2.1.2. Association of L. aequinoctialis and Salvinia natans: Lemno aequinoctialis - Salvinietum natantis Miy. et J.Tx. 1960 (sub nomine Lemno paucicostatae - Salvinietum)

Characteristic species: Salvinia natans

Additional species: L. aequinoctialis, S. polyrrhiza (Ricciocarpus natans, L. japonica)

Distribution: Eastern Asia.

The association grows mainly in rice fields.

2.1.3. Association of L. aequinoctialis and W. globosa

Characteristic species: W. globosa

Additional species: L. aequinoctialis, S. polyrrhiza, Azolla pinnata, A. nilotica, S. punctata, (W. arrhiza)

Distribution: Eastern Asia; Africa.

In eastern Asia, the association is widespread in rice fields and in shallow waters. The Lemna paucicostata - Azolla imbricata (= A. pinnata) association of MIYAWAKI (SCHWABE-BRAUN and TUEXEN 1981b) may be a variant of this association reduced in species. Stands without Wolffia are found within the whole area of Azolla pinnata s.l. but are probably not an independent association. Relevés of MIRASHI (1954, 1957), VYAS (1964) and MAHESHWARI (1960) belong to this association. The indications of L. minor and W. arrhiza are erroneously (instead of L. aequinoctialis and W. globosa).

2.1.4. Association of L. aequinoctialis and W. angusta

Characteristic species: W. angusta

Additional species: L. aequinoctialis, S. polyrrhiza, S. punctata, Azolla pinnata, Ceratophyllum demersum, (Ricciocarpus natans)

Distribution: Australia, southeastern Asia.

2.1.5. Association of L. aequinoctialis, W. brasiliensis and W. gladiata

Characteristic species: W. brasiliensis, Azolla caroliniana, (Salvinia auriculata, W. gladiata)

Additional species: L. aequinoctialis, S. polyrrhiza, L. valdiviana, (L. minuscula, L. obscura, W. columbiana)

Distribution: Southeastern North America.

2.1.6. **Association of L. aequinoctialis and S. punctata: Spirodeletum punctatae Okuda 1978 (sub nomine Spirodeletum oligorrhizae)**

Characteristic species: S. punctata

Additional species: L. aequinoctialis, S. polyrrhiza, (Azolla pinnata)

Distribution: Eastern Asia; Australia; southeastern Africa.

This association is not very well documented. It is characterized by good development of S. punctata. Perhaps it is only a variant of association 2.1.3. or 2.1.4. reduced in species. Similar reduced stands with S. punctata, L. aequinoctialis and S. polyrrhiza occur in the eastern states of USA (which, in addition, sometimes contain L. valdiviana and W. gladiata), also in eastern Brazil.

2.1.7. **Association of L. aequinoctialis and W. elongata**

Characteristic species: W. elongata

Additional species: L. aequinoctialis (not well developed), W. columbiana

Distribution: Northern Columbia; Curaçao; very localized.

2.1.8. **Association of L. aequinoctialis and W. microscopica**

Characteristic species: W. microscopica

Additional species: L. aequinoctialis (not well developed), S. polyrrhiza, W. globosa

Distribution: India.

2.1.9. **Association of L. aequinoctialis and W. hyalina**

Characteristic species: W. hyalina

Additional species: L. aequinoctialis (S. polyrrhiza, L. gibba, Ceratophyllum demersum, Utricularia inflexa, U. reflexa, Pistia stratiotes)

Distribution: Africa (except the northern and southern areas and the Congo basin).

HOWARD-WILLIAMS (1979) gives examples of stands with this association from Lake Chilwa with great seasonal changes of vegetation development and nutrient content.

2.1.10. **Association of L. aequinoctialis and W. repanda**

Characteristic species: W. repanda

Additional species: L. aequinoctialis

Distribution: Angola, Botswana.

2.1.11. **Association of L. aequinoctialis and W. rotunda**

Characteristic species: W. rotunda

Additional species: L. aequinoctialis

Distribution: Zimbabwe.

2.1.12. Association of L. aequinoctialis and L. tenera

Characteristic species: L. tenera

Additional species: L. aequinoctialis, (S. polyrrhiza)

Distribution: Malaysia, Burma, previously also Singapore.

2.1.13. Association of L. aequinoctialis and W. Welwitschii

Characteristic species: W. Welwitschii

Additional species: L. aequinoctialis, (S. polyrrhiza)

Distribution: Tropical regions of Africa and America.

2.1.14. Association of L. aequinoctialis, W. Welwitschii, and W. brasiliensis

Characteristic species: W. Welwitschii, W. brasiliensis

Additional species: L. aequinoctialis, W. lingulata, Azolla caroliniana, (S. intermedia, W. columbiana, L. valdiviana)

Distribution: Tropical Central and South America.

2.1.15. Association of L. aequinoctialis, W. lingulata and L. valdiviana

Characteristic species: W. lingulata

Additional species: L. aequinoctialis, L. valdiviana, Limnobium laevigatum, Pistia, Salvinia auriculata, Eichhornia crassipes, Ceratopteris, Utricularia gibba (S. intermedia, S. polyrrhiza)

Distribution: Tropical South and Central America, Caribbean Islands.

2.1.16. Association of L. aequinoctialis and W. neotropica

Characteristic species: W. neotropica

Additional species: S. intermedia, L. aequinoctialis, L. valdiviana, Azolla caroliniana, Salvinia auriculata, (W. lingulata, S. punctata)

Distribution: Humid tropical regions of South America.

2.1.17. Association of L. minuscula

Characteristic species: L. minuscula, Azolla caroliniana, Limnobium laevigatum

Additional species: S. intermedia, W. lingulata, W. oblonga, W. columbiana, Ricciocarpus, Salvinia minima, S. hercogii, S. auriculata, Pistia, Eichhornia, Ceratopteris thalictroides, (W. brasiliensis, L. gibba, L. aequinoctialis, Azolla filiculoides, L. valdiviana, Utricularia gibbosa)

Distribution: Subtropical South America.

ESKUCHE and ROMERO FONSECA (1982), ESKUCHE (1986) and LANDOLT and ZARZYCKI (in prep.) give some relevés which belong to this association group. The relevés are very rich in species (up to 14 floating species). Certainly, the group can be divided in different associations, but the delimitations are not so obvious.

5.5.3. Influence on Lemnaceae communities by human activities

Human activities, especially the inlet of waste water in natural water bodies greatly changes the distribution of Lemnaceae communities. In regions with much rain and very dilute salt concentrations in natural water, the eutrophication of waters by sewage enables duckweed communities to grow which otherwise would not occur in the region. On the other hand, increasing pollution of waters will change the naturally occurring Lemnaceae communities and eventually eliminate them by intoxication. Generally, stable associations with good development of follower species such as Lemnetum trisulcae, Ricciocarpetum natantis, Riccietum fluitantis, and especially associations with Wolffiellas will disappear first and give place to associations with good development of pioneer species. POTT and WITTIG (1985) give instructive examples of this change in Western Europe.