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Distribution pattern and ecophysiological characteristics of the European species of the *Lemnaceae*

(*Verbreitungsmuster und ökophysiologische Eigenschaften der europäischen Vertreter der Lemnaceae*)

by

Elias LANDOLT

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1. Introduction

The distribution of a plant species is influenced by climatic and edaphic factors, competition, reproductive systems and a long-distance dispersal potential. The correlations between these factors and the physiological features of the plants are often very complex and our knowledge is frequently insufficient to thoroughly understand the distribution pattern.

In this paper, I shall try to compare ecophysiological features and some distribution patterns occurring in European taxa of the *Lemnaceae*.

Five species of *Lemnaceae* are native of Europe: *Spirodela polyrrhiza* (L.) Schleiden, *Lemna trisulca* L., *L. gibba* L., *L. minor* L. and *Wolffia arrhiza* (L.) Horkel. Furthermore, three taxa are reported to be introduced: *S. punctata* (G.F.W. Meyer) Thompson (PIGNATTI 1957), *L. aequinoctialis* Welwitsch (KOCH 1952) and *L. minuscula* Herter (JOVET and JOVET-AST 1966, KANDELER 1973, LANDOLT 1979); they shall not be discussed in this paper.

2. Distribution of the European *Lemnaceae* in relation to some climatic factors

The distribution of the *Lemnaceae* species can be correlated with some climatic factors. However, these factors are not directy responsible for the presence or absence of given species; numerous complex local factors which are in turn partly influenced by the macroclimatic factors are playing a decisive rôle. If we compare macroclimatic factors with the distribution of a species, it is important to bear in mind the following aspects:

- the knowledge of the climatic factors prevailing in large parts of the world is not very precise;
- the local conditions may be more or less favourable for the existence of a species than it could be expected from the macroclimatic conditions. For instance, locally warmer waters that are fed by warm springs or coming from warmer regions can be colonized by species for which the

general climate would normally be too cold;

- since most species of *Lemnaceae* are easily distributed by birds, there occurs always a possibility of an occasional introduction of duckweeds that can remain only for shorter periods, in particular during favourable years; from herbarium specimens alone it is difficult to decide if the plants result from a short-term introduction or correspond to an established colony;
- competition is an essential factor which limits the occurrence of a species even if the climatic conditions are favourable.

The following limiting climatic factors operating in various combinations seem to determine the distribution of the whole family and the occurrence of each species:

- Number of days with a mean temperature above 10°C (Fig. 1)
- Mean summer temperatures (three warmest months) (Fig. 2)
- Mean winter temperatures (three coolest months) (Fig. 3)
- Aridity factor i of Martonne: coefficient of the mean annual rainfall in cm divided by the mean annual temperature in °C + 10 (Fig. 4)
- For some tropical species which are very sensitive to frosts, it is important to know as well the absolute minimum temperatures (cf. LANDOLT 1981).

The main limiting factors for the *whole family of Lemnaceae* are (Fig. 5):

1. at least 50 days with a mean temperature above 10°C; 2. an aridity factor i between 1 and 8. Some gaps within the distribution area are possibly due to an insufficient collecting.

The limiting factors of each European species are represented in Table 1.

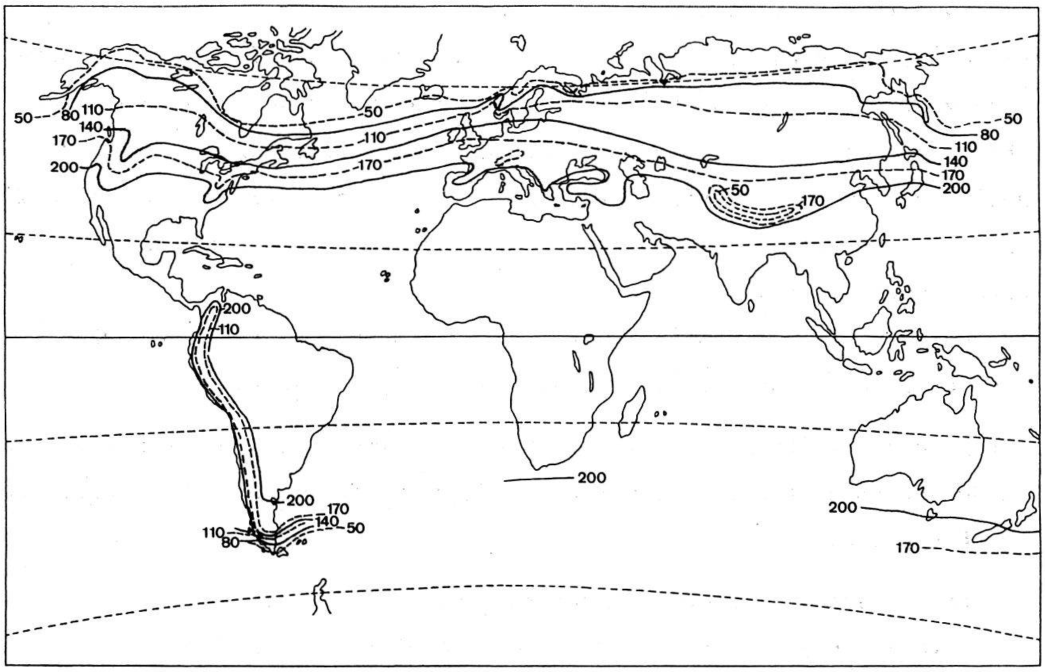


Fig. 1. Number of days with a mean temperature above 10°C

Anzahl Tage mit Mitteltemperaturen über 10°C

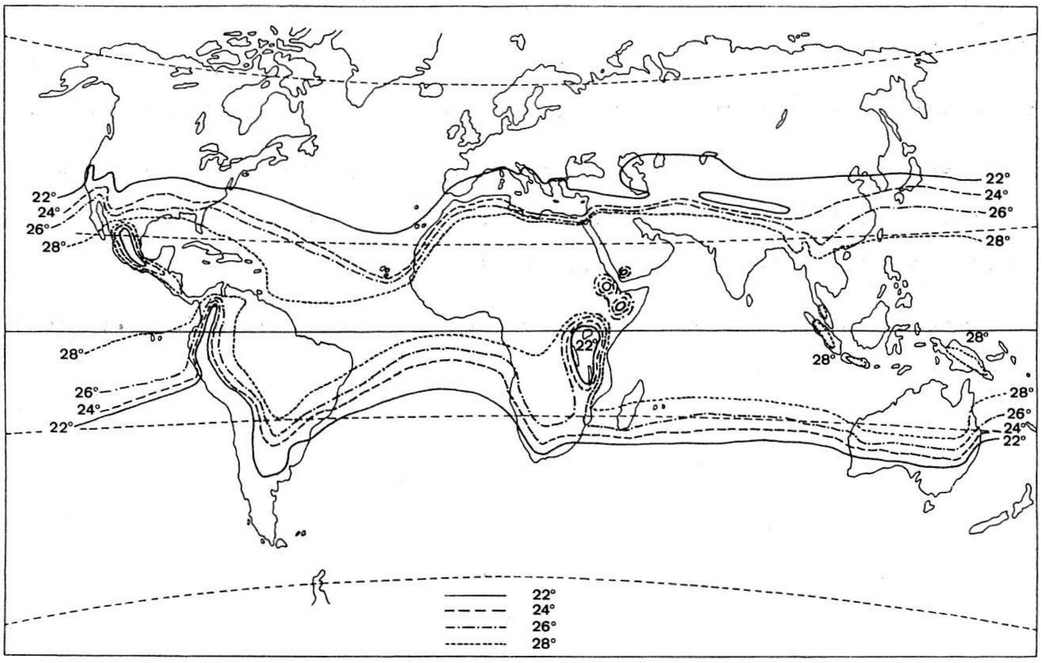


Fig. 2. Mean summer temperatures (three warmest months)

Mitteltemperaturen der drei wärmsten Monate

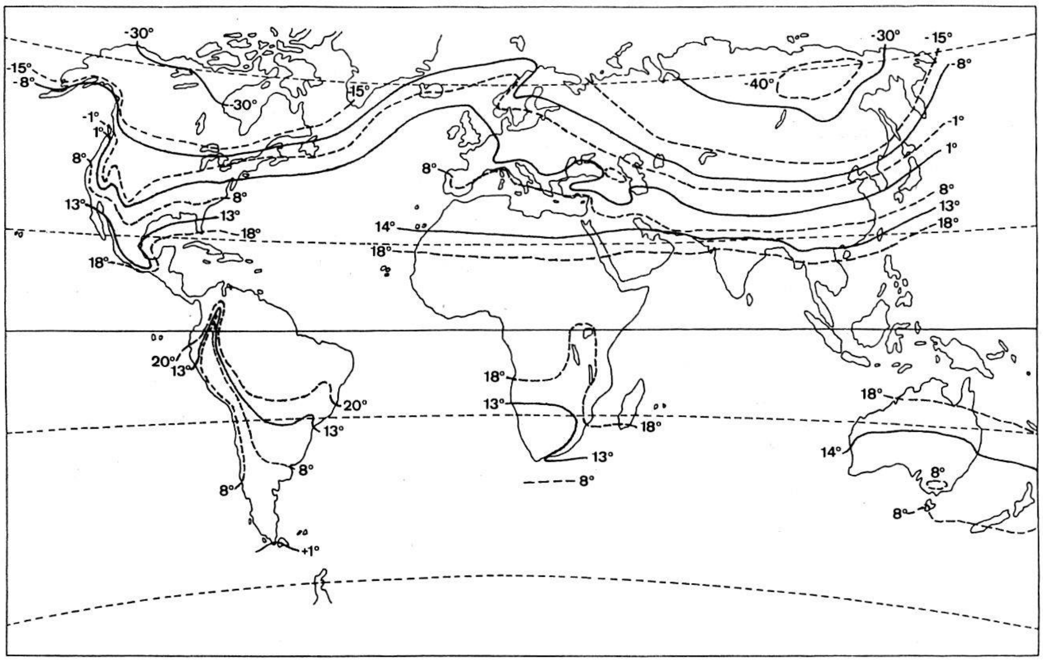


Fig. 3. Mean winter temperatures (three coolest months)

Mitteltemperaturen der drei kältesten Monate

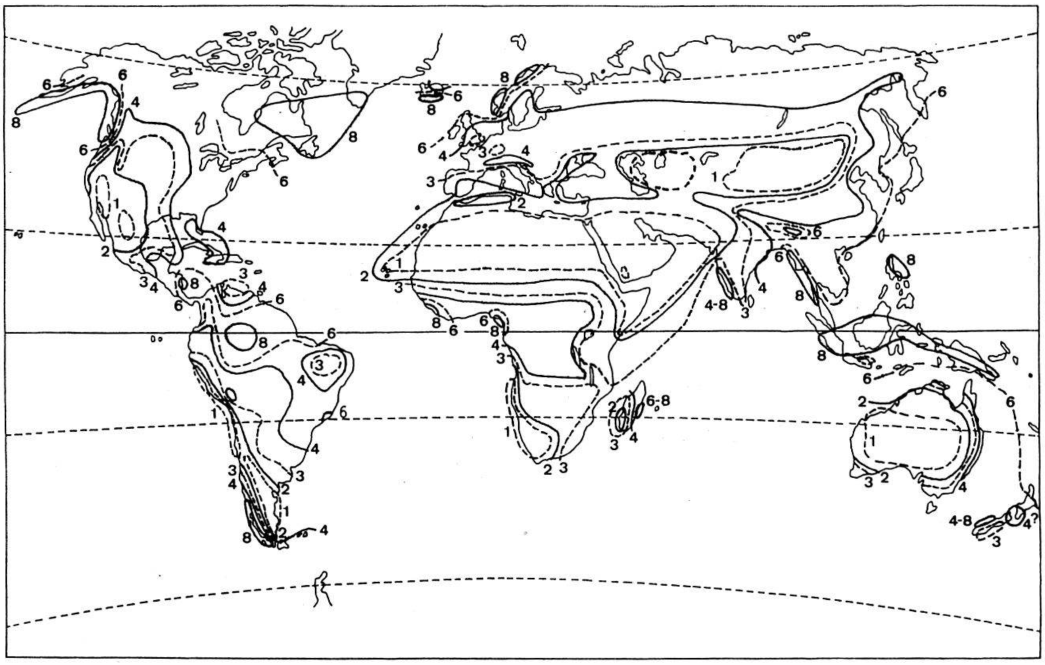


Fig. 4. Aridity factor of Martonne i: Coefficient of the mean annual rainfall in cm divided by the mean annual temperature in ^{O}C + 10.

Martonn'scher Ariditätsfaktor i: Koeffizient der mittleren Jahresniederschläge in cm dividiert durch die mittlere Jahrestemperatur in ^{O}C *+ 10.*

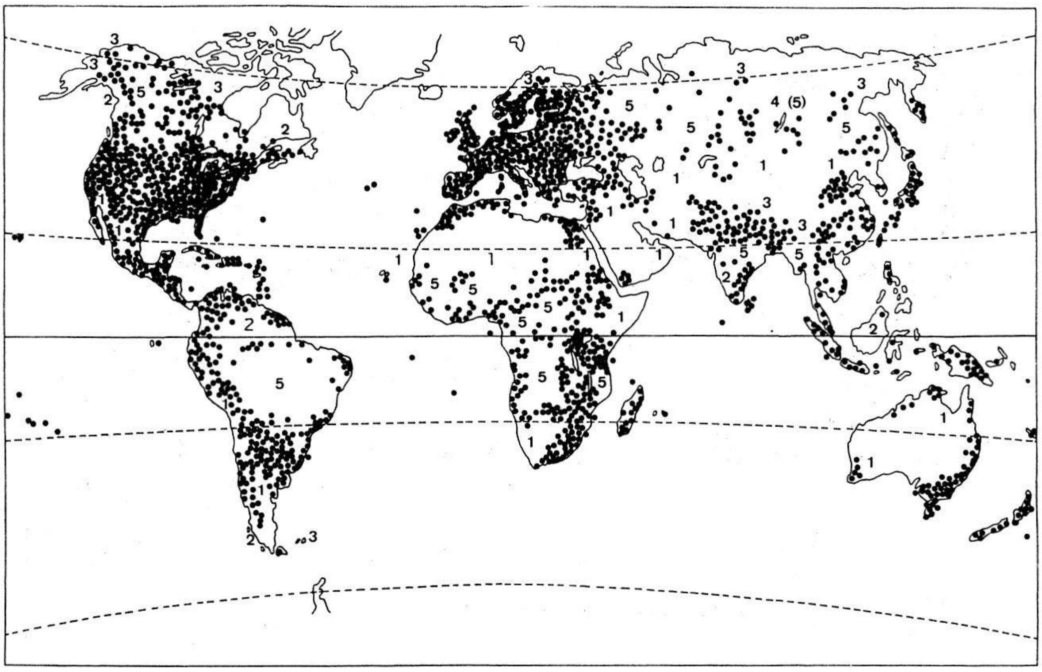


Fig. 5. Distribution of the family of the *Lemnaceae*
1 = too dry, 2 = too wet, 3 = not warm enough in summer, 4 = too cold in winter, 5 = reasons of gaps unknown (e.g. not adequate sampling)

Verbreitung der Familie der Lemnaceen.
1 = zu trocken, 2 = zu feucht, 3 = zu wenig warm im Sommer, 4 = zu kalt im Winter, 5 = unbekannte Ursachen (z.B. nicht durchforscht)

Table 1. Limiting climatic factors for European species of *Lemnaceae*

Begrenzende Klimafaktoren für europäische Lemnaceae-Arten

	days with average temperature above 10^{o}	average winter temperature	average summer temperature	aridity factor of Martonne*
Spirodela polyrrhiza	> 110	> -40^{o}	> 30^{o}	2-8
Lemna trisulca	> 50	> -40^{o}	< 22^{o}	1-8
Lemna gibba	> 50	> -1^{o}	< 26^{o}	1-4
Lemna minor	> 50	> -15^{o}	< 24^{o}	3-8
Wolffia arrhiza	> 150	> -8^{o}	< 28^{o}	2-5

* Aridity factor of Martonne: $i = \frac{\text{annual precipitation in cm}}{\text{average temperature in } ^{o}C+10}$

Martonn'scher Ariditätsfaktor: $i = \frac{\textit{mittlere Jahresniederschläge in cm}}{\textit{mittlere Jahrestemperatur in } ^{o}C+10}$

Spirodela polyrrhiza (Fig. 6) has an almost world-wide distribution. It reaches its northern limit at the isoline of 110 days with a mean temperature above $10^{o}C$. The species avoids the very humid regions ($i > 8$) and the driest regions ($i < 2$). It is rather rare in mediterranean regions for the vegetation period (with mean monthly temperatures above $10^{o}C$) is too dry, and in the wet winter season it is too cold for *S. polyrrhiza*. *S. polyrrhiza* grows essentially everywhere within the mentioned climatic limits except in South America where its distribution is probably limited by the competition from the closely related species *S. intermedia* W. Koch and *S. biperforata* W. Koch (Fig. 7).

Lemna trisulca (Fig. 8) is found growing further north than any other species of the *Lemnaceae* family. It is rare in the Southern Hemisphere: East Africa, New Guinea, Southern Australia. The northern limit is the isoline of 50 days mean temperature above $10^{o}C$. In the mountains it almost reaches the timberline. The southern limit coincides with the $22^{o}C$ isotherm of mean summer temperatures. In warmer regions it is found only in the mountains. It is absent in the driest ($i < 1$) and in the most humid ($i > 8$) regions. *L. trisulca* occurs almost in all regions of the world where the conditions are favourable except for some more distant areas in the Southern Hemisphere (South America, Southern tip of Africa, New Zealand).

Lemna gibba (Fig. 9) essentially has a "mediterranean" distribution throughout the world except Australia where it is replaced by the very similar *L. disperma* Hegelm., in Japan it is introduced. The northern limit is the $-1^{o}C$ isotherm of the mean winter temperatures, the southern limit is the $26^{o}C$ isotherm of mean summer temperatures. It does not occur within very dry ($i < 1$), humid and subhumid regions ($i > 5$).

Lemna minor (Fig. 10) has an almost worldwide distribution within cool temperate climatic regions of rather oceanic character. The northern limit is formed by the $-15^{o}C$ isotherm of mean winter temperatures, the southern limit by the $24^{o}C$ isotherm of mean summer temperatures. It is absent or very rare in drier regions ($i < 3$) and in most humid regions ($i > 8$). *L. minor* is found almost in every place where the conditions are suitable except in South America where there are only small areas favour-

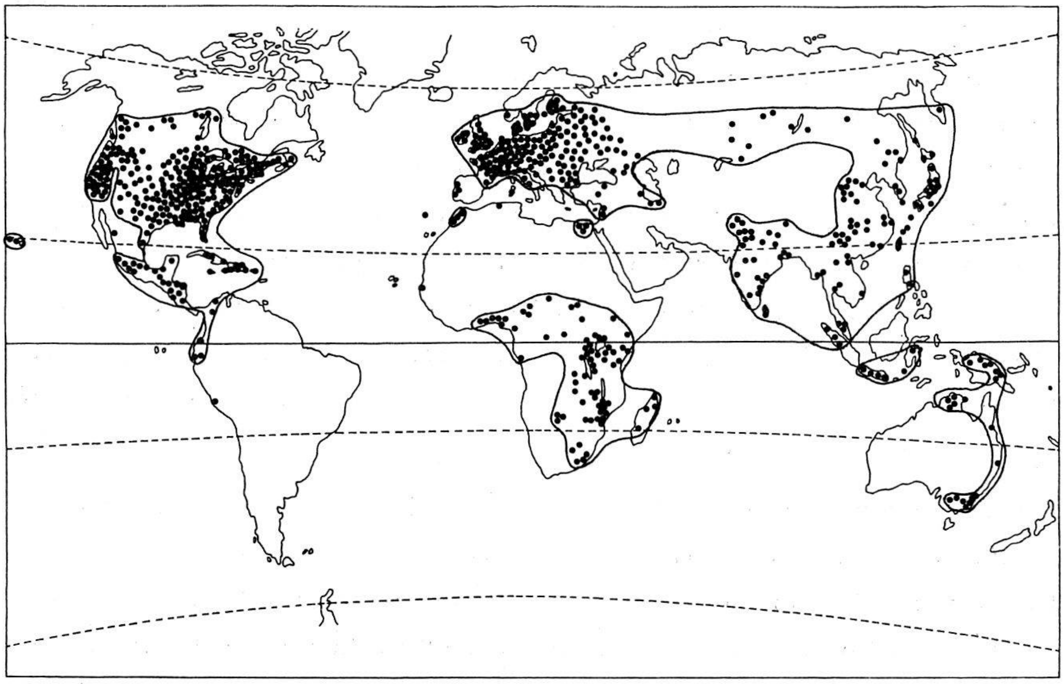


Fig. 6. Distribution of *Spirodela polyrrhiza*

Verbreitung von Spirodela polyrrhiza

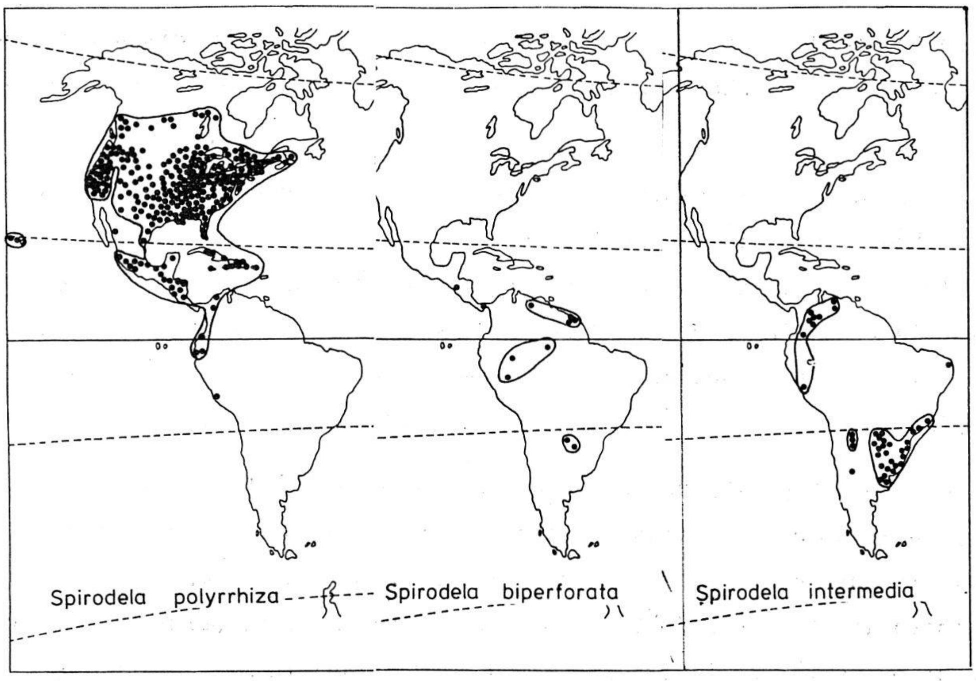


Fig. 7. Distribution of *Spirodela polyrrhiza, S. intermedia* and *S. biperforata* in South America.

Verbreitung von Spirodela polyrrhiza, S. intermedia und S. biperforata in Südamerika

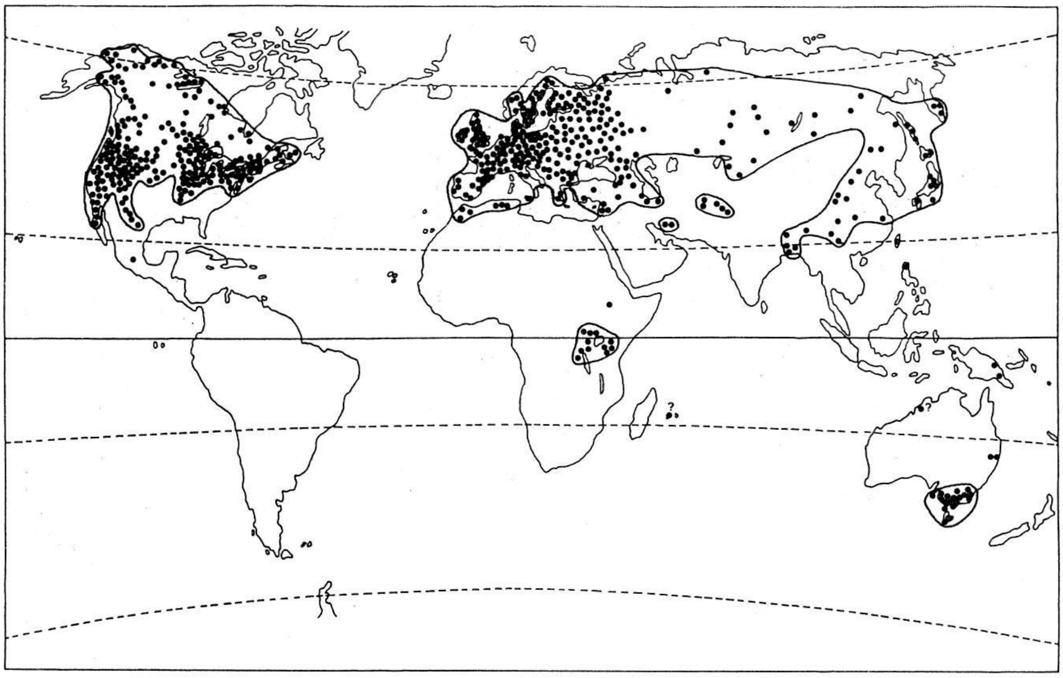


Fig. 8. Distribution of *Lemna trisulca*
Verbreitung von L. trisulca

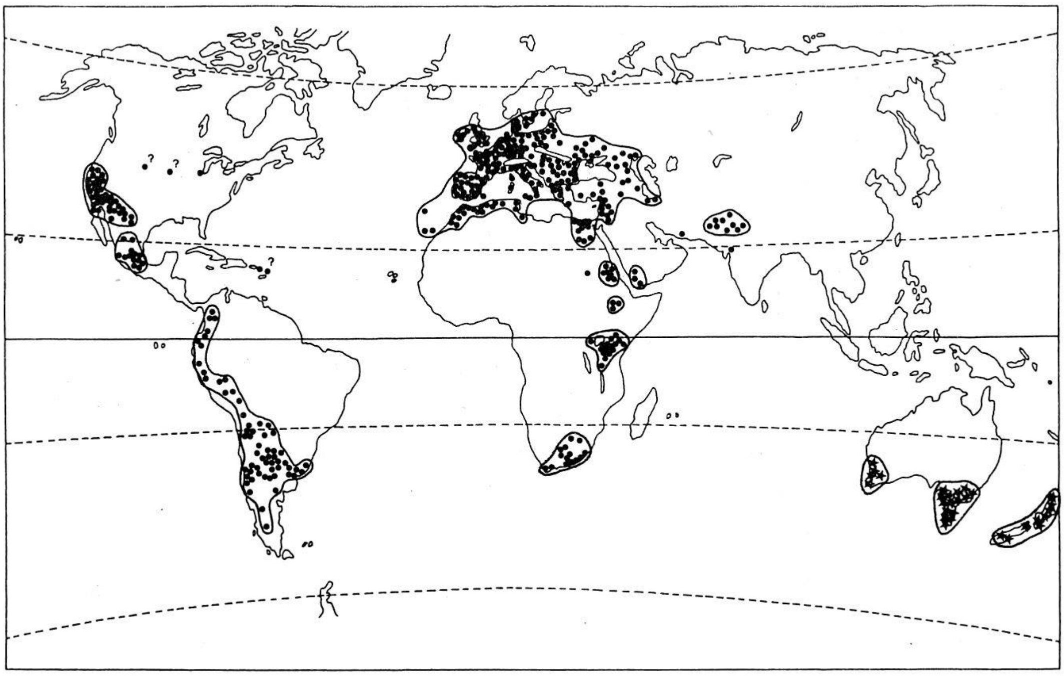


Fig. 9. Distribution of *Lemna gibba* (and *L. disperma**)
Verbreitung von Lemna gibba (und L. disperma)*

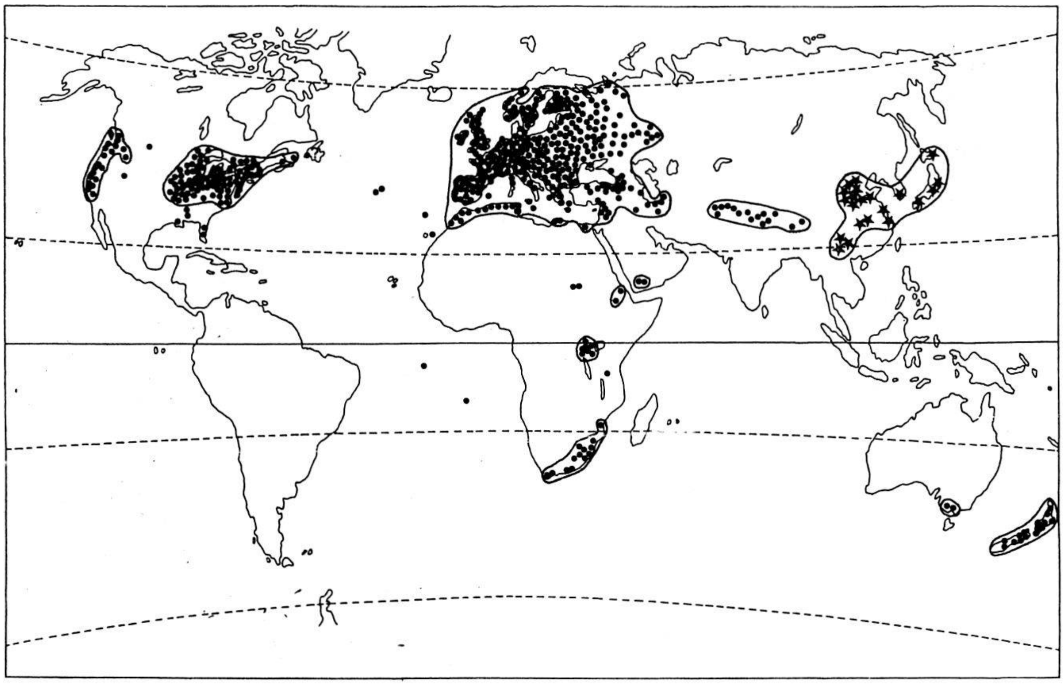


Fig. 10. Distribution of *Lemna minor* (und *L. japonica**)

Verbreitung von Lemna minor (und L. japonica)*

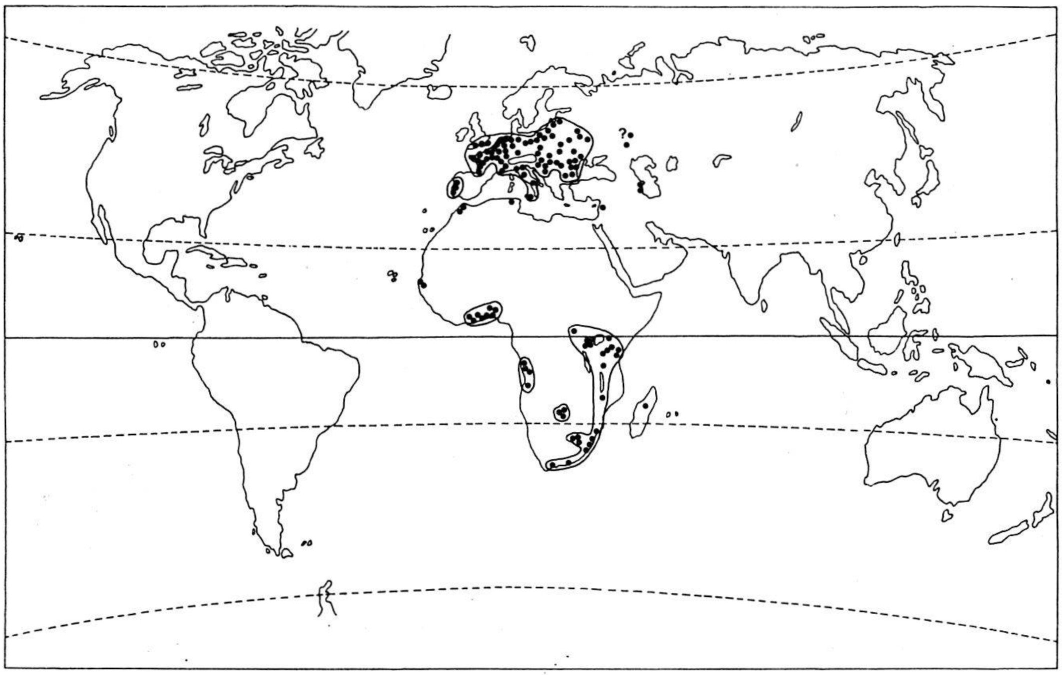


Fig. 11. Distribution of *Wolffia arrhiza*

Verbreitung von Wolffia arrhiza

able for growth, far distant from each other. In East Asia it is replaced by the related *L. japonica* Landolt. In Australia and New Zealand it is probably introduced.

Wolffia arrhiza (Fig. 11) is found growing in Africa, Southwestern Asia and Europe. It has its nothern limit at the isoline of 150 days of mean temperatures above $10^{o}C$ and reaches the tropics where it avoids the warmest regions (maximum temperature of the warmest three months not more than $28^{o}C$). It apparently does not support very dry ($i < 2$) and humid conditions ($i > 5$). In Eastern Asia, America and Australia it is replaced by other species of the genus.

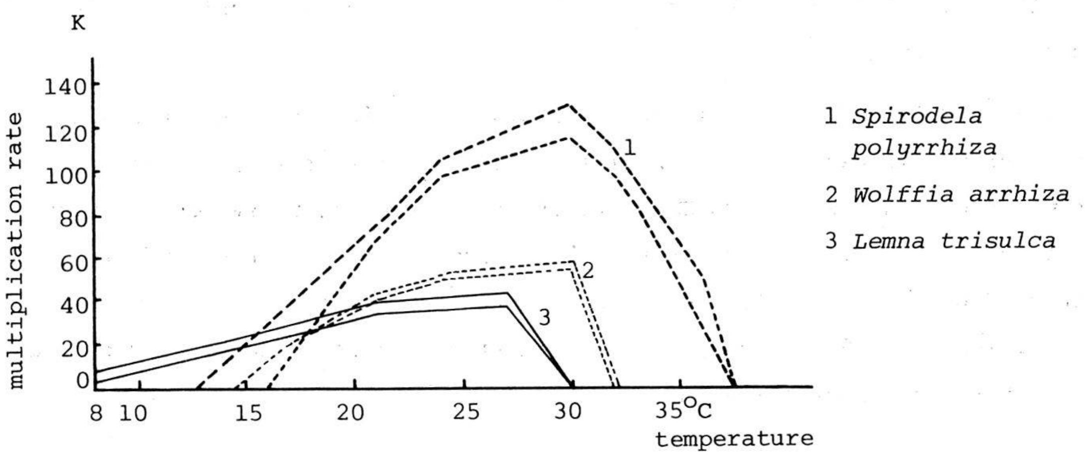
3. Ecophysiological characteristics of the *Lemnaceae* species and their distribution

The distribution of the *Lemnaceae* species is strongly influenced by their ecophysiological characteristics and the relevant climatic factors occurring in a potential distribution area.

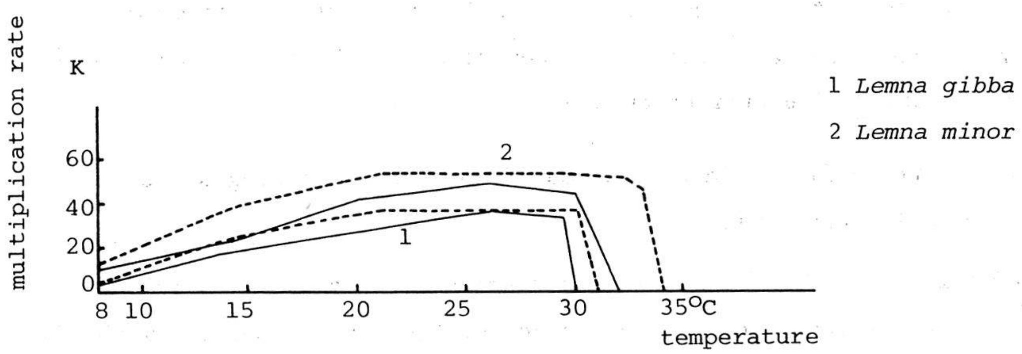
To each of the climatic factors we may find a corresponding set of ecophysiological characteristics:

The minimum number of days with a mean temperature above $10^{o}C$ is a measure for the length of growing season of the plants. Species with high minimum growth temperatures (e.g. *S. polyrrhiza* and *W. arrhiza*) require a long period with relatively high temperatures (110 rsp. 150 days), whereas species with low minimum growth temperatures (e.g. *L. trisulca, L. minor, L. gibba*) perform well within a shorter period (50 days) (Fig. 12).

Maximum mean summer temperatures. The water temperatures are generally found to be higher in regions with high mean summer air temperatures. Most *Lemnaceae* species can endure temperatures up to 40 - $50^{o}C$ for a short time. For a longer time, the temperatures limiting growth of *Lemnaceae* are much lower, ranging from 26^{o} to $38^{o}C$ depending on species or clones (Fig. 12). *L. trisulca, L. minor, L. gibba, W. arrhiza, S. polyrrhiza* form a sequence of tolerance towards higher temperatures corresponding to the climatic limits of 22^{o}, 24^{o}, 26^{o}, 28^{o} and higher than $30^{o}C$, respectively.



a.



b.

Fig. 12. a. Multiplication rate of *S. polyrrhiza* (6581, 6593, 6613, 6627, 6628, 6731, 6862, 7003, 7010), *W. arrhiza* (6862, 7014), and *L. trisulca* (6601, 6624, 7013) at different temperatures grown in darkness (from LANDOLT 1957).

b. Multiplication rate of *L. gibba* (6566, 6583, 6729, 6745, 6751, 6861, 7007), and *L. minor* (6568, 6570, 6579, 6591, 6625, 7004, 7008, 7011) at different temperatures grown in darkness (from LANDOLT 1957).

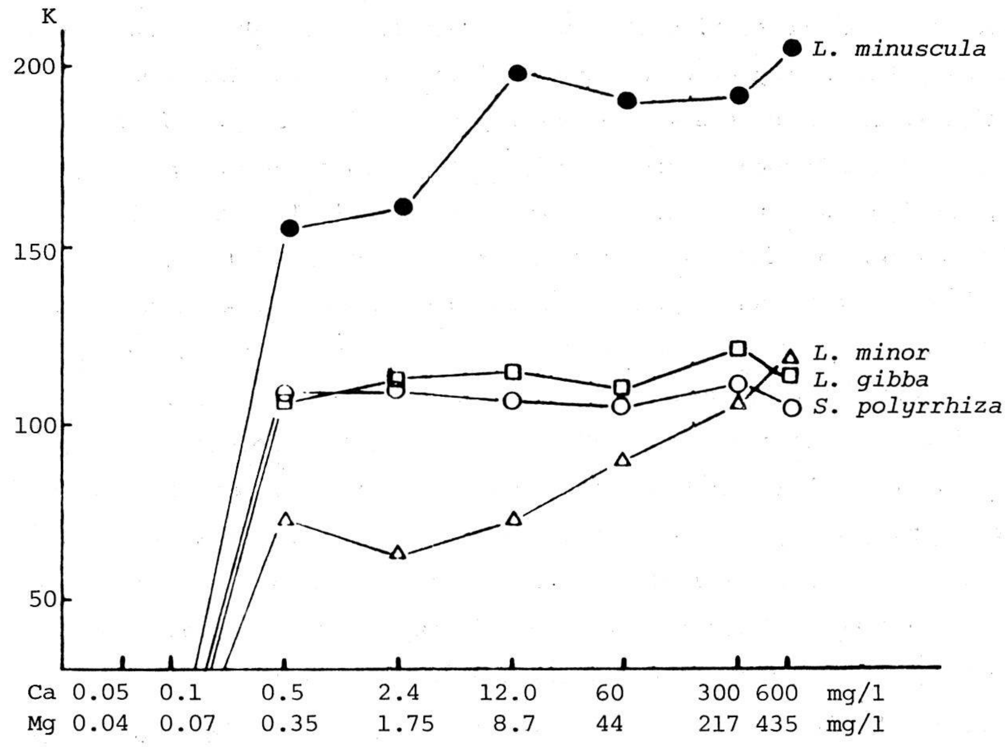
a. Wachstumsraten von S. polyrrhiza, W. arrhiza und L. trisulca bei verschiedenen Temperaturen im Dunkeln (nach LANDOLT 1957).

b. Wachstumsraten von L. gibba und L. minor bei verschiedenen Temperaturen im Dunkeln (nach LANDOLT 1957).

Minimum mean winter temperatures are correlated with the frequence with which freezing temperatures occur, with the thickness of the ice cover and with the length of the growing season. Most duckweed species die after a period of a few days with tenperatures of several degrees centigrades below zero. Species which have not the ability to grow submerged (as *L. trisulca*) or to form turions which sink to the bottom of the water (as *S. polyrrhiza* and *W. arrhiza*) are only found growing in regions with mild winter temperatures (mean winter temperatures above -1^{o}C) as for *L. gibba* (or *L. minuscula*). *L. minor* is an exception in this respect. If the fronds are dying after a period of heavy frost they sink partly to the bottom of the water and may still enclose some small living buds.

Climatic conditions too arid or too humid. The aridity factor is generally related to the concentration of ions in the water. Very dry areas with a low aridity factor may have waters containing toxic concentrations of some minerals; furthermore, the waters may dry out periodically, a factor to which out of the European species only *L. gibba* is adapted. In humid regions, the ion content of the water and correspondingly the nutrient content is very low. *Lemnaceae* floating on the surface of the water are obviously dependent upon higher concentrations of nutrients in the water than many water plants rooting in the bottom. *Lemnaceae* species may behave quite different in relation to the concentration of nutrients. Earlier investigations of our Institute in the field (LANDOLT and WILDI 1977, LANDOLT 1981) and in the laboratory (LÜÖND 1980, ZIMMERMANN 1981) suggested that nitrogen, phosphorus, magnesium, calcium, potassium and, possibly, a few other nutrients are the limiting factors in nature. Figs. 13 and 14 show the multiplication rates of four *Lemnaceae* species for different concentrations of calcium, magnesium, nitrogen and phosporus.

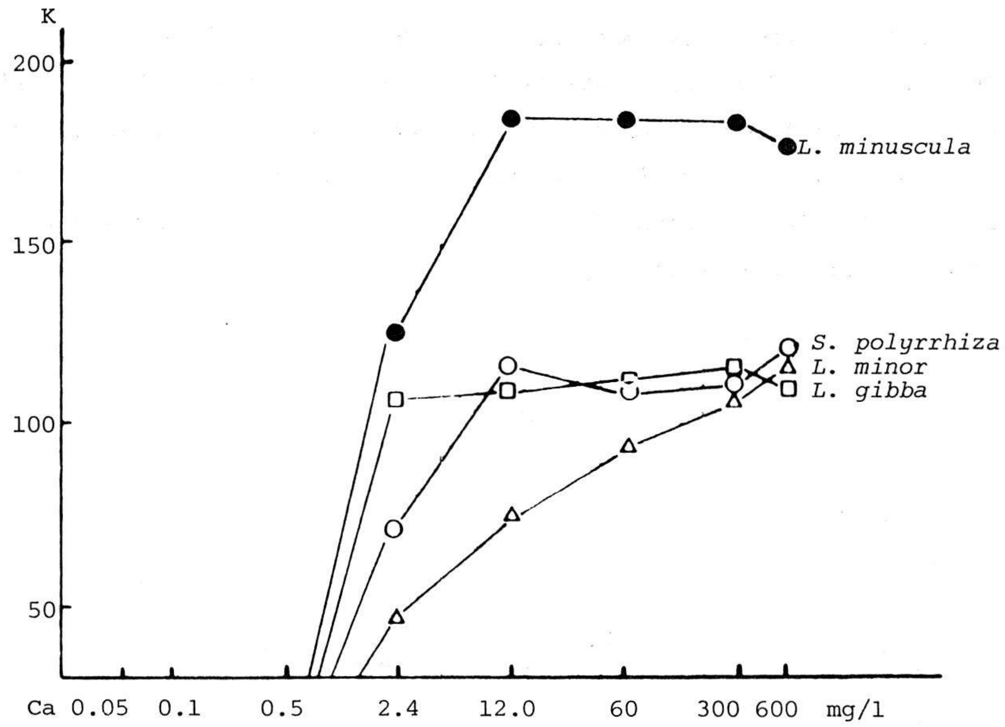
From the results of LÜÖND (1980) we see that a concentration of 0.0007 mg P/1 is still sufficient for *L. minor* but limiting for *S. polyrrhiza* and *L. minuscula*. According to EYSTER (1966) the upper limiting concentration for growth of *S. polyrrhiza* is situated around 1500 mg P/1. A concentration of 14 mg N/1 is necessary for an optimal growth of *S. polyrrhiza*; the corresponding concentration for *L. gibba* and *L. minor* is 2.8 mg N/1 and for *L. minuscula* 0.02 mg/1. The upper limiting concentration lies for all investigated species between 350 and 1750 mg N/1, a concentration which is almost never observed in nature, P and N are probably less responsible for the distribution within large areas than for the occurrence of a species within local waters. The lowest calcium concentration permitting growth of *Lemnaceae* species is between 0.1 and 0.5 mg Ca/1 at a low level of magnesium. The upper limiting concentration is not yet reached even at 600 mg Ca/1, a concentration not found hitherto in our analysis of natural waters. However, the upper limit for magnesium is reached if the Ca concentration is fixed at 12 mg Ca/1. For *S. polyrrhiza* and *L. minor* the limit is 140 mg Mg/1, for *L. gibba* and *L. minuscula*



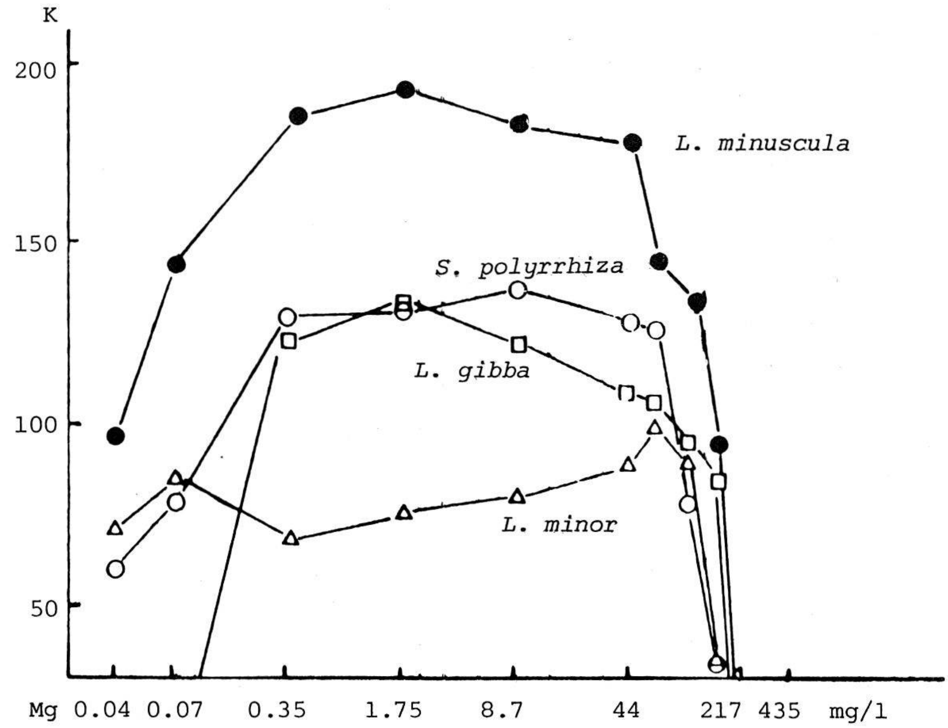
a. Variation of Ca and Mg - *Ca und Mg variieren*

Fig. 13. Multiplication rate of *Lemna minor*, *Lemna minuscula*, *Lemna gibba* and *Spirodela polyrrhiza* in relation to the concentration of calcium and magnesium (from ZIMMERMANN 1981).

Wachstumsraten von Lemna minor, Lemna minuscula, Lemna gibba und Spirodela polyrrhiza in Beziehung zur Konzentration von Kalzium und Magnesium (nach ZIMMERMANN 1981).

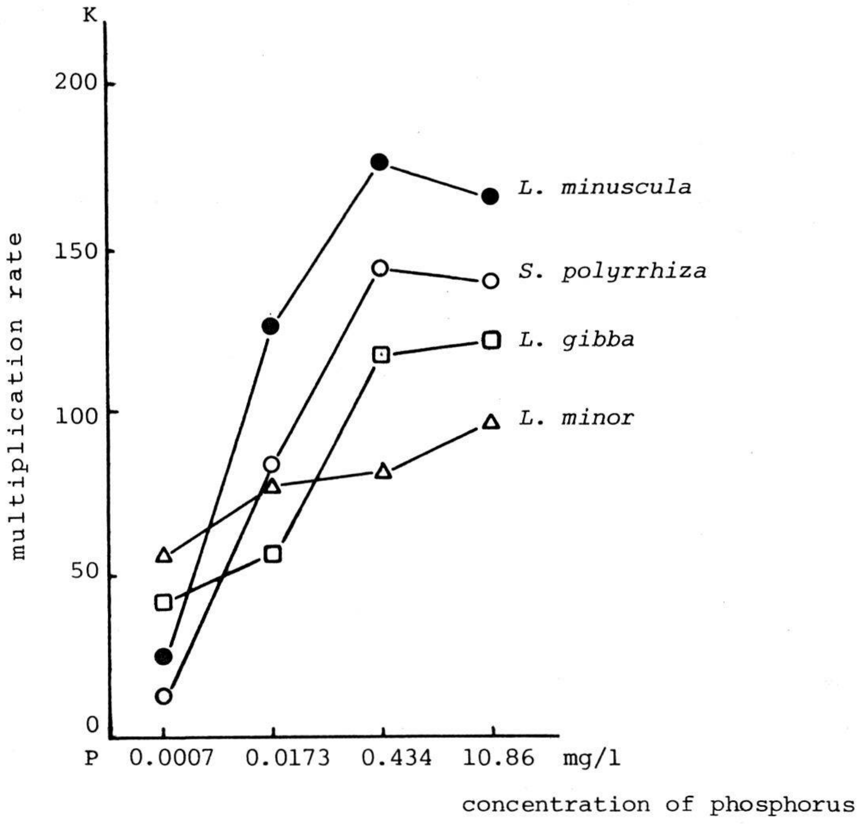


b. Variation of Ca (Mg 8.7 mg/l) - *Ca variiert (Mg 8.7 mg/l)*



c. Variation of Mg (Ca 12 mg/l) - *Mg variiert (Ca 12 mg/l)*

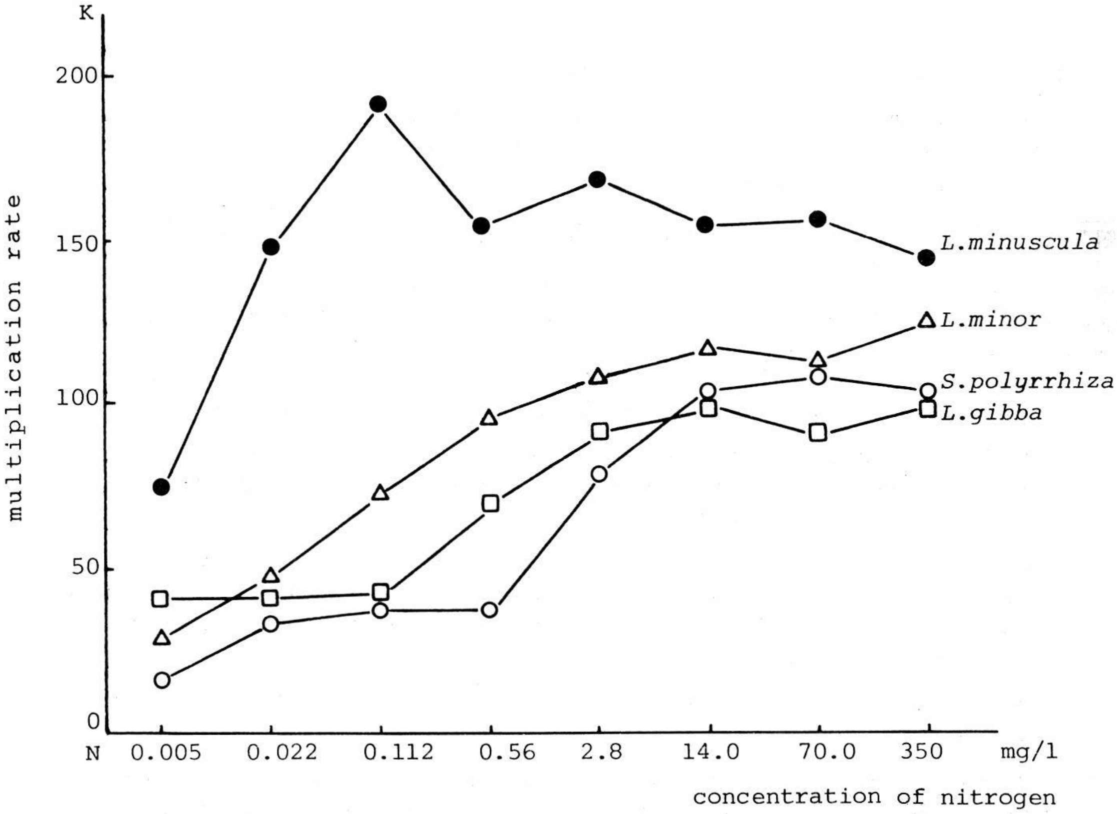
215 mg Mg/1. In nature, high magnesium concentrations are found in waters of dry regions (LANDOLT and WILDI 1977). The higher tolerance of *L. gibba* (and *L. minuscula*) towards high magnesium concentration is in accordance with its main distribution in drier regions. On the other hand, *L. gibba* requires much more magnesium than other *Lemnaceae* species which explain its rare occurrence in humid regions.



a. Variation of phosphorus - *Phosphor variiert*

Fig. 14. Multiplication rate of *Lemna minor, L. minuscula, L. gibba* and *S. polyrrhiza* in relation to the concentration of phosphorus (a) and nitrogen (b) (from LüöND 1980, changed).

Wachstumsraten von Lemna minor, L. minuscula, L. gibba und S. polyrrhiza in Beziehung zur Konzentration von Phosphor (a) und Sticktoff (b) (nach LüöND 1980, abgeändert).



b. Variation of nitrogen - *Stickstoff variiert*

4. Conclusions

From our investigations it is obvious that even the most frequent and wide-spread species of *Lemnaceae* have its clear climate limits corresponding to ecophysiological characteristics of each taxon. Many of these relations and characteristics are not yet known in detail. But we hope that, after having better understood the distribution pattern of each species, we shall be able to tell in which region and under which conditions the different species can be successfully cultivated.

Summary

The distribution area of different species of the *Lemnaceae* shows a pattern which correlates with some climatic factors:

1/ Number of days with mean temperatures of at least 10°C
2/ Mean temperature of the three warmest months
3/ Mean temperature of the three coolest months
4/ Aridity factor of Martonne $\left(i = \frac{\text{annual precipitation in mm}}{\text{annual mean temperature in °C+10}}\right)$

The limiting rôle of these climatic factors is exemplified by distribution trends observed in the European taxa of the *Lemnaceae: Spirodela polyrrhiza* (L.) Schleid., *Lemna trisulca* L., *L. gibba* L., *L. minor* L. and *Wolffia arrhiza* (L.) Horkel. It can be shown that the limiting factors are in relation to some physiological characteristics:

1/ There are relations between the minimum growing temperature and the number of days with mean temperatures of at least 10°C which is needed for a long-term occurrence of the species.

2/ The possibility of the fronds to form turions or to sink to the bottom of the water during unfavourable conditions and the ability to support cold temperatures are decisive for the occurrence of a species in areas with cool winter temperatures.

3/ The maximum growing temperature is limiting the distribution of a species in regions with warm temperatures.

4/ The ability of using nutrients in low concentration and surviving under high concentration of different ions are important for the occurrence of a species under humid or arid climatic conditions. It can be shown that the growth of the species in relation to the content of nitrogen, phosphorus, calcium and magnesium in the medium is specific. Analyses of the nutrient content of waters containing *Lemnaceae* corroborate these findings.

Zusammenfassung

Das Verbreitungsareal der verschiedenen Wasserlinsenarten zeigt deutliche Beziehungen zu einigen Klimafaktoren:

- Anzahl Tage mit Mitteltemperaturen über 10°C
- Mitteltemperatur der drei wärmsten Monate
- Mitteltemperatur der drei kühlsten Monate
- Martonn'scher Ariditätsfaktor $\left(i = \frac{\text{mittlere Jahresniederschläge in mm}}{\text{mittlere Jahrestemperatur in °C+10}}\right)$

Am Beispiel der europäischen Vertreter der *Lemnaceae* (*Spirodela polyrrhiza, Lemna trisulca, L. gibba, L. minor, Wolffia arrhiza*) wird die begrenzende Wirkung dieser Klimafaktoren aufgezeigt. Die begrenzenden Faktoren stehen in Wechselwirkung mit physiologischen Eigenschaften der Arten:

- Es bestehen Beziehungen zwischen der minimalen Wachstumstemperatur und der Anzahl Tage mit Mitteltemperaturen über 10°C, die für ein langfristiges Auftreten einer Art notwendig sind.

- Die Fähigkeit der Arten, Turionen zu bilden oder sonst auf den Boden des Gewässers zu sinken, um ungünstige Bedingungen zu ertragen, und die Toleranz gegenüber kalten Temperaturen sind entscheidend für das Auftreten einer Art in winterkalten Gebieten.
- Die maximale Wachstumstemperatur begrenzt die Verbreitung in sommerwarmen Gebieten.
- Die Fähigkeit Nährstoffe in geringen Konzentrationen zu nutzen und die Toleranz gegenüber hohen Konzentrationen sind wichtig für das Auftreten von Arten in humiden bzw. in ariden Gebieten. Besonders wichtig für das Vorkommen von Lemnaceen sind die Konzentrationen von Stickstoff, Phosphor, Kalzium und Magnesium. Messungen der Nährstoffgehalte in Gewässern mit Lemnaceen bestätigen diese Befunde.

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