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4. DISCUSSION: WHAT IS THE LIMITATION OF THE OCCURRENCE OF *LEMNACEAE* IN ARGENTINA ?

4.1 CLIMATIC BOUNDARIES

The relative distribution of the various species within the investigated area shows clearly that at least some of the species have definite climatic preferences (Table 14). The distribution of the species within South America (Fig. 8) indicates several differences in climatic requirements and tolerance. *L. minuta* and *L. gibba* are distributed further south than the other species, in connection with their greater tolerance to lower temperatures (Table 15). The values are purely empiric, from the comparison of climate data with the distribution of the species and from some field work experience. The approximate course of some of the important climatic factors in Argentina is shown in Fig. 9. Unfortunately, the climatic data base is rather incomplete. Southern Argentina is very dry (factor of Martonne <1) and therefore unsuitable for

Table 14. Relative distribution of the species in the three climatic regions.
+++ more than in the average, ++ around the average, + less than average, 0 very rare or not present
BA: *Bonaerense*, MP: *Mesopotamica*, CP: *Correntino-Paraguaya*

species	BA	MP	CP
Azolla filiculoides	+++	++	0
Ricciocarpus natans	+++	++	++
Spirodela intermedia	+++	++	+
Wolffia brasiliensis	+++	++	++
Lemna gibba	+++	+++	+
Lemna minuta	+++	+++	++
Wolffiella oblonga	++	+++	++
Wolffia columbiana	++	+++	++
Salvinia minima	+	+++	++
Salvinia herzogii	+	+++	++
Limnobium laevigatum	+	++	++
Azolla caroliniana	+	++	+++
Wolffiella lingulata	+	++	+++
Pistia stratiotes	+	++	+++
Lemna valdiviana	+	++	+++
Lemna aequinoctialis	0	0	+++
Utricularia gibba	0	0	+++

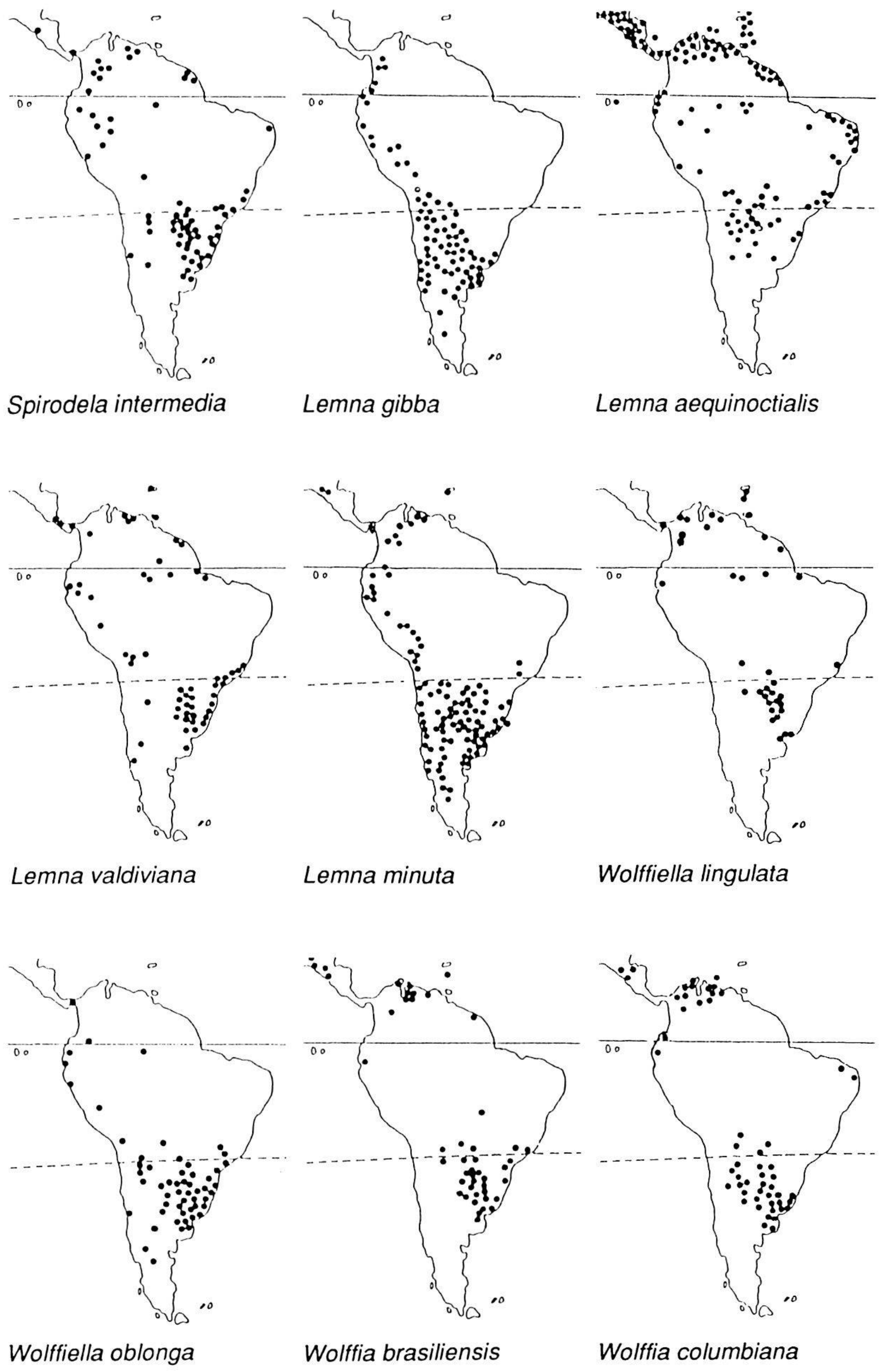

Fig. 8. Distribution of nine *Lemnaceae* species within South America (LANDOLT 1986).

Lemnaceae growth (very few waters with overly high mineral concentrations). The southern limit of *L. gibba* and *L. minuta* is caused by this factor and not by temperatures. *L. valdiviana* is especially intolerant to dry conditions and therefore restricted to the most eastern part of Argentina, withits higher humidity, or to some locally wetter places along the foothills of the Andes. Also in the inundation area of the Paraná, the water coming from moist regions may be suitable for *L. valdiviana.* The southern limitation of all the other species is temperature. *Wolffiella lingulata* and *W. oblonga* are

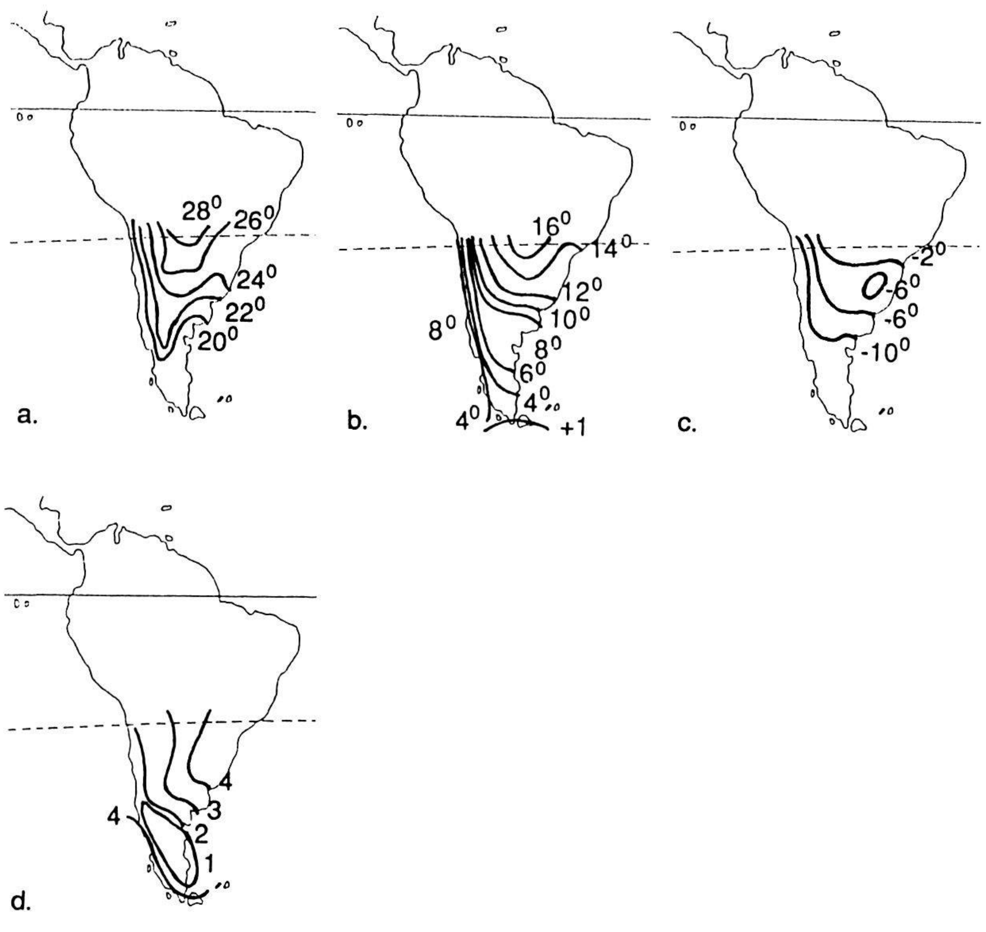

Fig. 9. Climatic factors in Argentina (data put together from climate diagrams of WALTER and LIETH 1967).
a) mean summer temperatures
b) mean winter temperatures
c) absolute minima temperatures
d) factor of Martonne

Table 15. Limiting climatic parameters for the distribution of *Lemnaceae* (LANDOLT 1986).
1 Lowest mean temperature of the three coolest months in C°
2 Lowest absolute minimum temperature in C°
3 Highest mean temperature of the three warmest months in C°
4 Lowest mean temperature of the three warmest months in C°
5 Aridity factor of Martonne: annual precipitation in cm divided through the mean annual temperature in C° + 10

species	1	2	3	4	5
Spirodela intermedia	+8	-10	> 28	20	3-8
Lemna gibba	-1	-20	26	10	1-4
Lemna aequinoctialis	+8	-20	> 28	20	1-8
Lemna valdiviana	-1	-20	> 28	12	4-8
Lemna minuta	-1	-20	26	16	2-6
Wolffiella lingulata	+8	-8	> 28	20	2-8
Wolffiella oblonga	+8	-10	28	18	2-6
Wolffia brasiliensis	-1	-20	28	22	2-5
Wolffia columbiana	-12	-20	28	18	2-5

limited by the winter minima, *Spirodela intermedia* and *Lemna aequinoctialis* by low winter temperatures, and*Wolffia brasiliensis* and *W. columbiana* by low summer temperatures. To the North the limitation for some species is caused by the high summer temperatures (26° for *L. gibba* and *L. minuta*). For *L. gibba* there is also an eastern limit (areas with a Martonne factor >4).

4.2. NUTRIENT CONCENTRATION

The measurement of a few inorganic elements in the water during a single field trip is just a fixation of the momentary situation. We know that the nutrient content of the water can change considerably during the year. The collecting time fell in the rainy and still cool season. Mineral contents were therefore below the average concentrations. The presented values are consequently only indications. In addition, two waters with the same nutrient content but with differing biomass might offer quite different conditions to duckweed. In a water with a dense cover of *Lemnaceae,* there is always some nutrient flux from the dying biomass to the water, and the fronds are able to take up some nutrients, even if the free nutrient content in the water is minimal and would be insufficient in a water free of water plants. Especially in

Table 16. Minimum and maximum nutrient requirements (in mg/l) of *Spirodela polyrrhiza* (according to EYSTER 1966).

elements	minimal amount	maximal amount
N	0.09	2500
P	0.014	3100
S	0.032	1600
K	0.197	5400
Na	< 0.0002	>1380
Ca	4.00	2000
Mg	0.24	1200
Cl	0.0035	> 350
Fe	0.028	56
Zn	0.13	320

shallow waters there is a considerable amount of nutrients per liter fixed in the biomass. If the water is 10 cm deep and just covered with *Lemnaceae* (ca. 0.2 g dry weight per dm^2) the nutrient amount corresponds to the following values (mg /l): N 10, P 3, K 3, Ca 2, Mg 0.5, Na 0.3, Fe 0.1, Zn 0.04, S 3.
The values may be higher if the cover is very dense. It is correspondingly lower if the *Lemnaceae* cover only part of the area or if the water is deeper. In addition, the nutrient conditions are better for duckweed floating in waters where nutrients taken out by the plants are always replaced.
The minimum and maximum content of nutrients in artificial solutions for growth of various *Lemnaceae* species was tested by different authors (LANDOLT and KANDELER 1987). The results are not always comparable due to

Table 17. Minimum and maximum need of nitrogen and phosphorus (in mg /l) for some *Lemnaceae* species (from LANDOLT and KANDELER 1987).

species \ elements	N		P	
	min.	max.	min.	max.
Spirodela polyrrhiza	0.09	2500	0.014	3100
Lemna gibba	0.14	2500	0.017	2700
Lemna aequinoctialis		6300		< 2480
Lemna minuta	0.02	700	0.003	540
Wolffia columbiana	0.04		0.046	

different nutrient compositions. However a general trend can be recognized (Table 16, 17). Though *S. polyrrhiza* does not occur in Argentina and different species vary in their demand. Table 16 shows the approximate dimensions of the nutrient requirements of *Lemnaceae*. Unfortunately, known values are restricted to only certain minerals and species.

When the minimal nutrient content from physiological experiments is compared with the minimal nutrient content in the analyzed waters of the field, it becomes evident that the maximal content of all nutirents in the field samples of all nutrients is far below the maximal tolerance in Table 16. This means that it is well below a damaging value in all investigated samples. In none of the collected samples are Na, K, Mg and Cl too low for good growth of duckweed. The lowest contents in the field are 2.0, 0.35, 0.46 and 0.13 mg, respectively. These nutrients are probably not minimum factors for *Lemnaceae* growth in the waters of Argentina. Only in one sample (from Foz do Iguazu) is the content of S below the minimal amount. Interestingly no *Lemnaceae* were growing in this water. All the other samples have much more S. Also for N only one sample with 0.015 mg/l is slightly below the minimum content for *L. minuta* (0.02 mg/l). However, the content of P in 27 field samples (16%) is at least more than 10% lower than 0.014 mg which shows that phosphorus is an important minimum factor for the occurrence of *Lemnaceae* in Argentina.

Of these 27 samples only 3 contain no *Lemnaceae*. Table 17 demonstrates that some species occur under much lower P content , e.g. *L. minuta* at 0.003 mg/l. Only 6 samples have significantly less P in the water. The reason why *Lemnaceae* can be found in waters with less nutrient content than the minimum nutrient need might be the following:

- There is the possibility that the phosphorus precipitated either in the field or during the transportation of the water before analysis. It is known that *Lemnaceae* can excrete phosphatases in case of P deficiency, thereby covering part of the phosphorus requirement in the field (LANDOLT and KANDELER 1987).
- The P content of the water varies during the year, it is higher during other seasons.
- In all the waters with a low phosphorus content, a dense cover of pleusto phytes was present. It is possible that phosphorus is stored in the biomass and transported immediately from mother to daughter frond.

In a similar way, the calcium content of 47 samples was significantly lower than the minimal requirement of 4 mg in cultures of *S. polyrrhiza* (Table 16). In investigations of other authors, the minimal need of Ca was lower in *Lemnaceae* (e.g. 0.8 mg for *S. polyrrhiza* according to BEYER in LANDOLT and KANDELER 1987) if the Mg content was kept low. If this value is considered the lower limit, 16 samples have even lower values. And 10 of them have a content of less than two thirds of it. Of these 10 samples only one did not contain *Lemnaceae*. The reason for *Lemnaceae* surviving in waters with a Ca content well below the minimal requirement may be as follows:

- The Ca content varies during the year, it is higher in other seasons.
- All the waters with a low Ca content looked "milky" indicating a suspension with clay particles. Since the clay particles on which Ca ions can be fixed were filtered out before analysis, Ca might have been filtered out with it.

Also the Fe and the Zn content was much lower than the minimal requirement for *S. polyrrhiza* in more than half of the samples. The reason for these differences may be the same as for Ca. Some of the *Lemnaceae* species probably need much less Fe and Zn than *S. polyrrhiza*. There is also a possibility that they precipitated in the water during transportation. Actually, there was some precipitation in most of these samples. A few precipitations samples were analyzed and showed a considerable amount of Fe and Zn.

4.3. IMPORTANT FACTORS REGULATING THE DISTRIBUTION OF *LEMNACEAE;* COMPETITION

To find out which factors especially control the distribution of *Lemnaceae* in Argentina, several statistical evaluations were performed. Only two of them will be discussed, a direct ordination with Mg and N total as parameters (Fig. 10). This Fig. demonstrates that *Lemna gibba* and *Spirodela intermedia* exclude each other to a certain degree for these two factors, *L. gibba* growing preferably in waters with higher Mg and N content. There is probably a strong competitive effect. At lower concentrations of one or both of the factors *L. gibba* is less competitive or can not grow at all and is replaced by *S. intermedia*. At higher concentrations of Mg or N, *L. gibba* is so competitive that *S. intermedia* has nearly no chance anymore. Interestingly, *S. intermedia* can become gibbous under certain conditions, similarly to *L. gibba,* but in contrast to *S. polyrrhiza* which is gibbous only in extremely rare cases. This

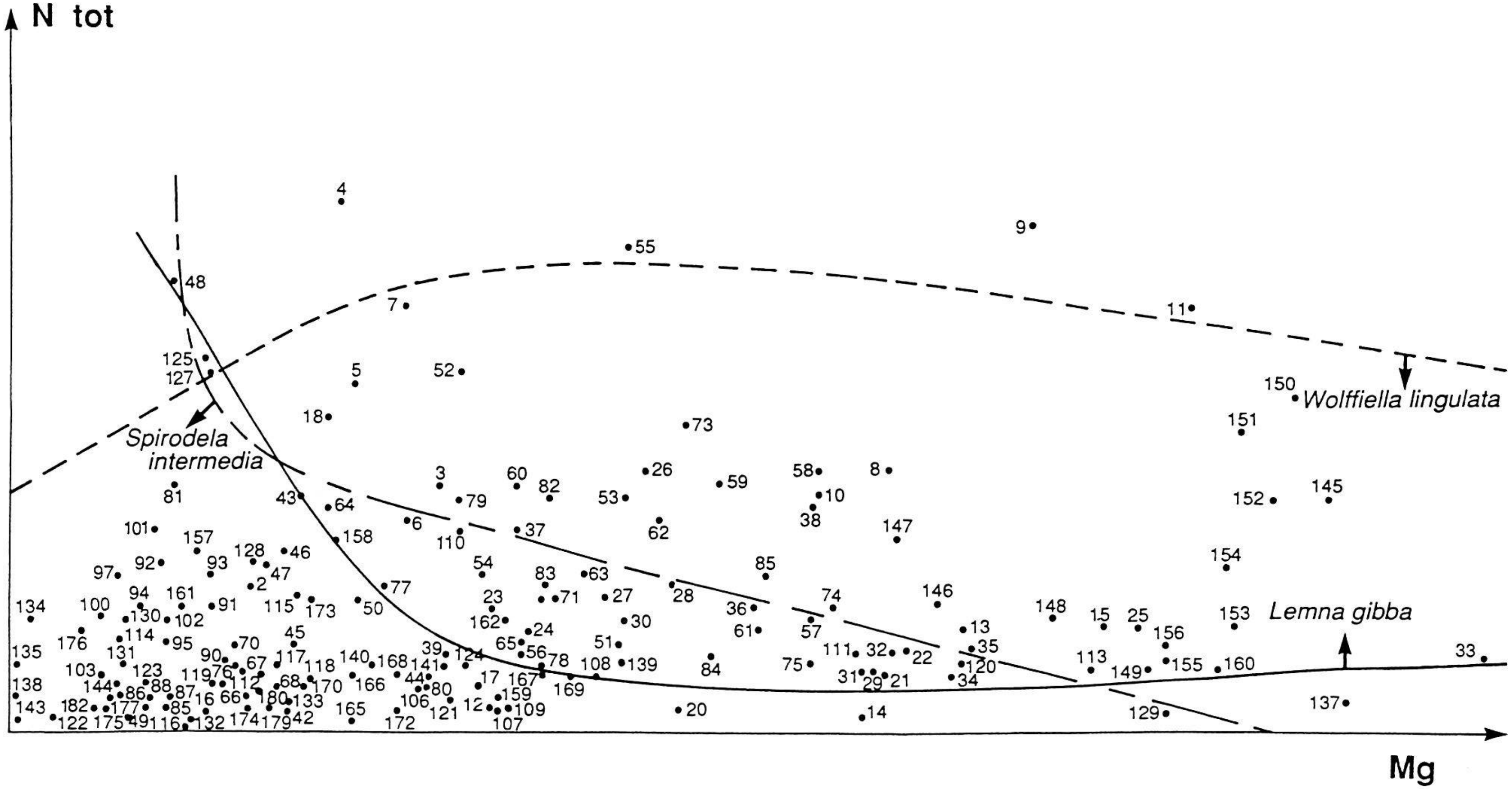

Fig. 10. Direct ordination of Mg content and N content.

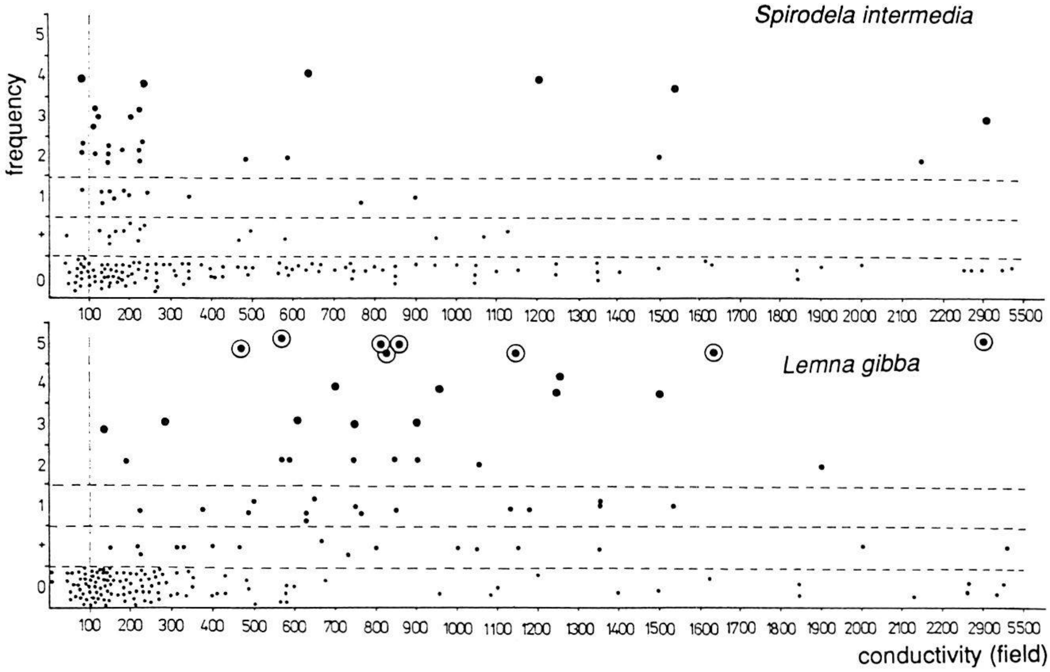

Fig. 11. Distribution of *Lemna gibba* and *Spirodela intermedia* in waters of different conductivity, according to the density of their cover (scale of Braun-Blanquet).

enables *S. intermedia* also to compete with *L. gibba* in regions with optimal climate for *L. gibba*.Table 4 demonstrates that *S. intermedia* occurs within the *Lemna gibba - Azolla filiculoides* association. However, this is only in the final stage of the succession where *L. gibba* is present with a frequency of not more than two. Fig. 11 shows that throughout its main distribution area, *S. intermedia* inhabits water with lower mineral concentrations. On the other hand, waters with a dense cover of *L. gibba* (4 or 5 of the Braun-Blanquet scale) contain more minerals. Fig. 12 presents the result of a main component analysis. The samples with *L. gibba, S. intermedia* and *W. lingulata* have differing distributions. The main differing factors are Mg and N (see Fig.10). A discriminant analysis confirmed the results stated previously. The two species can be separated quite neatly. The samples containing both species lie somewhere between.

Competition is a very important factor for the occurrence of *Lemnaceae* in various waters. This is not only the case for *L. gibba* and *S. intermedia* but also for *L. gibba* and *L. aequinoctialis*, *L. aequinoctialis* and *L. minuta*,

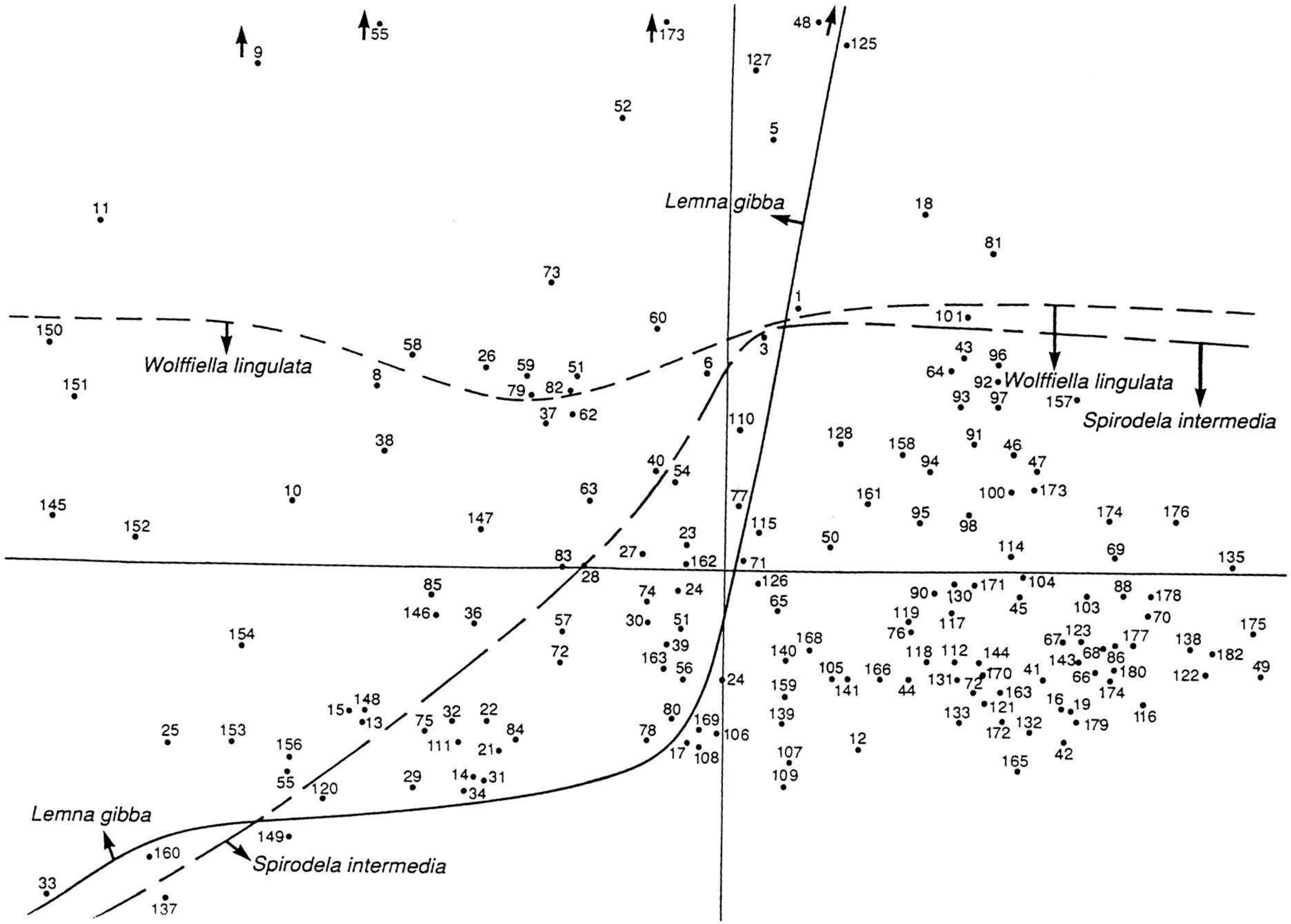

Fig. 12. Results of the main component analysis.

Wolffiella lingulata and *W. oblonga.* However, it must be kept in mind that birds transport fronds easily between waters, thus preventing the long-lasting exclusion of one species by another. It is also known that some species like *Nymphaea, Nuphar* or *Myriophyllum* produce some allelopathic substances, keeping waters in which they grow free from *Lemnaceae* (ELAKOVICH 1989, ELAKOVICH and WOOTEN 1991, SUTTON and PORTIER1989).
Other organisms may also play an important role in controlling the occurrence of *Lemnaceae,* e.g. fish and water fowl feeding on *Lemnaceae,* nitrogen production of the blue-green algae *Anabaena azollae* in symbiotic community with *Azolla.* However, this relationships were not investigated in the present work.

SUMMARY

Plant sociological relevés of the pleustophytes (mostly *Lemnaceae*) of 182 water localities in northern Argentina were performed. Water samples were also collected and chemically analyzed. Species composition was checked in more than 700 herbarium samples of *Lemnaceae* from southern South America. The mineral content of the various waters is presented and compared with the occurrence of *Lemnaceae* species by a main component analysis. The following main results and conclusions can be drawn:

1) The distribution pattern of *Lemnaceae* in northern Argentina is similar to patterns shown from North America (LANDOLT and WILDI 1977, LANDOLT 1981, 1994) and other parts of the world (LANDOLT, not published).
2) Climate (mostly temperature and aridity) as well as the content of nitrogen and magnesium in the water are the most important factors which influence *Lemnaceae* distribution.
3) Species in the investigated area which are limited by climatic factors are: *Lemna gibba* and *Azolla filiculoides* avoid regions with high summer temperatures, *Lemna aequinoctialis, Spirodela intermedia, Wolffiella lingulata* and *W. oblonga* do not occur in regions with low winter temperatures.
4) Species best characterized by the mineral content of the water are: *Lemna gibba, Azolla filiculoides, Wolffia columbiana, Ceratophyllum demersum* (relatively high content) and *Salvinia auriculata, Utricularia gibba, Eichhornia crassipes* (relatively low content).
5) Beside these factors, interaction between plant species and between plants and other organisms determine the occurrence of the *Lemnaceae* species. Especially competition between *Lemnaceae* species of similar growth forms is an important factor (e.g. *Lemna gibba* and *Spirodela intermedia, L. gibba* and *L. aequinoctialis, Lemna aequinoctialis* and *L. minuta, Wolffiella lingulata* and *W. oblonga.*
6) Three typical communities of lemnid vegetation could be distinguished:
   a) *Lemna gibba - Azolla filiculoides* vegetation unit (Table 4) characteristic for eutrophic waters in the rather dry warm temperate region of central and western Argentina.
   b) *Lemna minuta - Salvinia minima* vegetation unit (Table 5) characteristic for mostly mesotrophic waters of the Paraná valley.
   c) *Lemna aequinoctialis - Azolla caroliniana* vegetation unit (Table 6) characteristic for meso- to eutrophic waters in the subtropical climate of northern Argentina.

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