

Zeitschrift: Berichte des Geobotanischen Institutes der Eidg. Techn. Hochschule, Stiftung Rübel
Herausgeber: Geobotanisches Institut der Eidg. Techn. Hochschule, Stiftung Rübel
Band: 60 (1994)

Artikel: Benützerfreundliche Computerprogramme zum Bearbeiten von Vegetationstabellen und Auswertungen von Zeigerwerten
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DOI: <https://doi.org/10.5169/seals-377788>

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Benutzerfreundliche Computerprogramme zum Bearbeiten von Vegetationstabellen und Auswerten von Zeigerwerten

Peter BOLLIGER und Hans MÄRKI

1. EINLEITUNG

Die hier beschriebenen Programme sind von Hans Märki für die Ausbildung von Landschaftsarchitektinnen und -architekten an der Ingenieurschule ITR in Rapperswil entwickelt worden. Sie wurden bewusst einfach und bedienerfreundlich gestaltet. Vielleicht gerade darum werden die Programme in vielen Büros heute auch professionell eingesetzt. Das einfache Vegetationstabellenprogramm VEG ergänzt sich vorzüglich mit dem leistungsfähigen Auswertungsprogramm MULVA-4 (WILDI/ORLOCI). Bei der Entwicklung der Programme wurden Schnittstellen zu andern Vegetationsprogrammen, resp. Datenbanken und Exportmöglichkeiten in verbreitete Tabellenprogramme (Excel) vorgesehen und verwirklicht. Der letzte Programmausbau wurde durch das Büro Burger und Stocker in Lenzburg ermöglicht. Um die Programme einem weiten interessierten Kreis zur Verfügung zu stellen und um ihre Weiterentwicklung zu ermöglichen, sind sie seit 1993 public domain.

VEG und AUS sind Jahrringe-Programme: Unter der jüngsten Macintosh-Rinde sind die UNIX-, und MSDOS-Jahrringe früherer Versionen von 1984 und 1987 erkennbar. Die Jahrringe sind entstanden, da bei jeder Portierung jeweils nur ein kleiner Teil des Programmcodes neu geschrieben werden musste.



Fig. 1. Das Zusammenspiel der Programme. Das Programm VEG eignet sich zur Eingabe und manuellen Auswertung von Vegetationstabellen. Die Tabelle kann zur automatisierten Auswertung in das leistungsfähige Programm MULVA-4 eingelesen werden, nachdem sie als origda-Datei gespeichert wurde. Zur geordneten Tabelle berechnet das Programm AUS die gemittelten Zeigerwerte.

2. VEGETATIONSTABELLEN BEARBEITEN, DAS PROGRAMM "VEG"

2.1. DER ANWENDER SIEHT IMMER DIE VEGETATIONSTABELLE VOR SICH

Das Programm VEG ist ebenso bedienungsfreundlich wie Macintosh-Programme: Gleichzeitig lassen sich verschiedene Vegetationstabellen, Stetigkeitstabellen und Schlüssel auf dem Bildschirm darstellen. Für jede Tabelle kann zudem die Schriftgrösse gewählt werden. Dies ist für Das Programm VEG ist ebenso bedienungsfreundlich wie Macintosh-den Bearbeiter sehr angenehm, weil das Editieren in einer grossen Schrift möglich ist und für das Umordnen, bei dem ein möglichst grosser Tabellenausschnitt gewünscht wird, auf eine kleinere Schrift umgeschaltet werden kann. So ist es möglich, auf einem A3-Schirm einen Tabellenausschnitt von max. 120 Arten und 220 Aufnahmen darzustellen.

VEGETATIONSTABELLE		Arten-	1111	33222	2222	2211	2211	1111
Tabelle.veg		zahl	8755	050724	9745	0397	2563	0521 986
27.9.91 08:56		Auf-	145322118	3668	46793544966	2	77237	
SR Art (68)		(36)	2608	123132	8915	3021	8712	7562 941
. A								
10	Plantago media		+++					
10	Silaum silaus		1++					
13	Festuca pratensis		+++		+			
13	Trifolium montanum		1++1					
10	Galium verum		+++					
13	Primula veris		+ ++					
13	Ajuga reptans		+r + +					
20	Brachypodium pinnatum		++++22					
17	Daucus carota		+++ +					
20	Orchis morio		++++ +	+				
. B								
27	Polygala amarella		r+++ + + ++					
31	Briza media		++++ ++++					
31	Linum catharticum		+ +++ ++++		r			
. C								
31	Euphrasia rostkoviana		++ ++ 12 + 12					
31	Chrysanthemum leucantheu		++++ 1 r ++					
27	Lotus corniculatus		++++ 11+ +					

Fig. 2. Die relative Stetigkeit SR (A) der Art *Orchis morio* (B) ist 20. Die Gesellschaft 2 (C) beinhaltet sechs Aufnahmen, die Gesellschaft 3 (D) deren vier. Für die Aufnahme Nummer 70 wurde die Artenzahl 23 berechnet.

2.2. EINGEBEN UND KORRIGIEREN: EINFACH WIE IN DER TEXTVERARBEITUNG

Durch Anklicken der entsprechenden Werkzeuge wird die Tabelle neu eingegeben oder korrigiert. Es genügt dabei, die Arten abgekürzt einzugeben, das Programm ergänzt sie durch den vollständigen Artnamen gemäss BINZ/HEITZ (1990). Die Abkürzung ist frei wählbar, z. B. für *Plantago media* PM oder PL MED. Wenn die Abkürzung eindeutig ist, wird der volle Artnamen eingesetzt, sind mehrere Arten möglich, werden diese zur Auswahl vorgeschlagen. Dieser Programmteil ermöglicht es zudem, Schreibfehler in der Artenliste zu korrigieren.

2.3. UMORDNEN: FÜR DIE HÄUFIGSTEN PROBLEMSTELLUNGEN IST GESORGT

Markierte Zeilen oder Kolonnen lassen sich verschieben resp. umordnen. Dies kann einerseits für das bewusste manuelle Bearbeiten von kleinen Vegetationstabellen für didaktische Zwecke eingesetzt werden. Andererseits kann eine mittels MULVA-4 automatisch geordnete Tabelle manuell weiter umgeordnet werden, um sie in eine dem Bearbeiter entsprechende Form zu bringen.

Es kann aber auch automatisch sortiert werden und zwar nach Artenzahl oder Stetigkeit resp. nach Aufnahme oder Arten alphabetisch aufsteigend. Diese Sortierfunktionen dienen einerseits dem Aufbau einer systematisch aufgebauten Ursprungstabelle. Andererseits können damit beispielsweise aus einer Vegetationstabelle heraus alphabetisch geordnete Aufnahmelisten für die Pflanzenarten mit einer bestimmten Stetigkeit erstellt werden.

Um zwei Vegetationstabellen miteinander zu vergleichen, übernimmt die aktuelle Tabelle die Ordnung einer bestehenden Tabelle.

2.4. ZWEI TABELLEN ZUSAMMENFÜGEN

Durch das Zusammenfügen von Tabellen ist es möglich, aus lokalen Einzeltabellen automatisch regionale Gesamttabellen aufzubauen und diese zu bearbeiten, z. B. zu einem für ein grösseres Gebiet gültigen Kartierschlüssel. Das Zusammenführen zweier Tabellen ermöglicht ferner bei Pflanzensoziologie-Übungen den einzelnen Studenten oder Arbeitsgruppen ihre eigenen Aufnahmen als kleine Tabellen einzugeben und diese Teiltabellen dann zu einer Klassen- oder Semestertabelle zusammenzufügen.

A B

STETIGKEITSTABELLE							
Tabelle.ste 12.1.92 20:46							
	Gesellschaft	1	2	3	4	5	6 7
Art	Anzahl Aufnahmen	4	6	4	4	4	3
: A							
0 Plantago media			3.+				
0 Silaum silaus			3.+				
0 Festuca pratensis s.l.			3.+	2.+			
0 Trifolium montanum			4.+				
0 Galium verum			3.+				
0 Primula veris s.l.			4.+				
0 Ajuga reptans			4.+				
0 Brachypodium pinnatum			5.+				
0 Daucus carota			5.+				
0 <u>Orchis morio</u>			5.+	2.+			
: B							
0 Polygala amarella			5.+	4.+			
0 Briza media			5.+	5.+			
0 Linum catharticum			4.+	5.+	2.r		
: C							
0 Euphrasia rostkoviana			4.+	4.1	3.1		
0 Chrysanthemum leucanthem			4.+	4.+	3.+		
0 Lotus corniculatus s.l.			4.+	4.1	2.+		

C D

Fig. 3. Die Stetigkeitstabelle wird automatisch aufgrund der Vegetationstabelle erstellt. Die Gesellschaft 3 (A) besteht aus 4 (B) Aufnahmen. Die Art *Orchis morio* (C) hat bezüglich der Gesellschaft 3 die Stetigkeitsklasse 2 (D) und den Dominanzwert + (D).

SCHLUESSEL							
Tabelle.sch 12.1.92 20:46							
	Gesellschaft	1	2	3	4	5	6 7
Artengruppe							
: A							
: B							
: C							
: D							
: E							
: F							
: G							
: H							
: I							

Fig. 4. Der Schlüssel m ist die durchschnittliche Präsenz von Arten pro Differentialarten-Gruppe und Pflanzengesellschaft. O bedeutet: m > 75 %, x bedeutet m 35 - 75 %, . bedeutet m 15 - 35 %

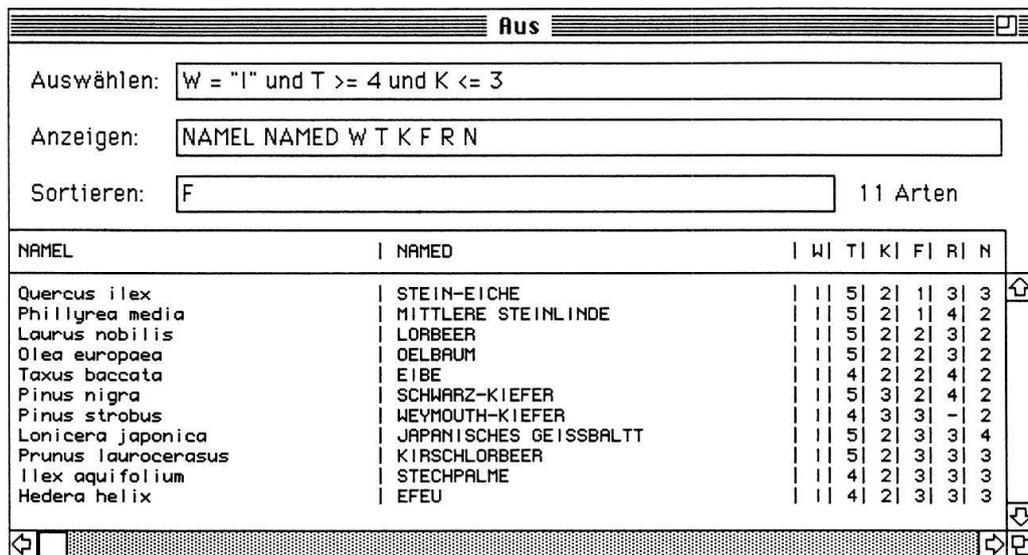
3. AUSWERTEN VON ZEIGERWERTEN: DAS PROGRAMM "AUS"

3.1 DIE ARTENLISTE DER UNI BERN ALS GRUNDLAGE

Diese Artenliste mit den Zeigerwerten nach LANDOLT (1977) wurde von der Universität Bern (W. DÄHLER) erstellt. Das Programm AUS selber kann Arten nur abrufen, aber nicht ergänzen.

3.2 MENGENLEHRE MIT ZEIGERWERTEN

Die Artenliste wird nach den Regeln der Mengenlehre zusammengestellt. UND bedeutet in Fig. 5. die Schnittmenge, resp. alle Arten die der Bedingung $W="I"$ und gleichzeitig der Bedingung $T \geq 4$ entsprechen. Mit den Operatoren UND, ODER, ABER NICHT und der Klammer () können auch komplexe Fragestellungen beantwortet werden.



The screenshot shows the AUS program interface. At the top, the title bar reads "Aus". Below it, there are three input fields: "Auswählen:" with the text "W = 'I' und T >= 4 und K <= 3", "Anzeigen:" with "NAMEL NAMED W T K F R N", and "Sortieren:" with "F". To the right of the "Sortieren:" field, it says "11 Arten". Below these fields is a table with the following columns: NAMEL, NAMED, W, T, K, F, R, N. The table lists 11 species with their corresponding values for each column. The species listed are: Quercus ilex, Phillyrea media, Laurus nobilis, Olea europaea, Taxus baccata, Pinus nigra, Pinus strobus, Lonicera japonica, Prunus laurocerasus, Ilex aquifolium, and Hedera helix. The values for W, T, K, F, R, N are: (5, 2, 1, 3, 3), (5, 2, 1, 4, 2), (5, 2, 2, 3, 2), (5, 2, 2, 3, 2), (4, 2, 2, 4, 2), (5, 3, 2, 4, 2), (4, 3, 3, 1, 2), (5, 2, 3, 3, 4), (5, 2, 3, 3, 3), (4, 2, 3, 3, 3), and (4, 2, 3, 3, 3) respectively.

NAMEL	NAMED	W	T	K	F	R	N
Quercus ilex	STEIN-EICHE	5	2	1	3	3	
Phillyrea media	MITTLERE STEINLINDE	5	2	1	4	2	
Laurus nobilis	LORBEER	5	2	2	3	2	
Olea europaea	OELBAUM	5	2	2	3	2	
Taxus baccata	EIBE	4	2	2	4	2	
Pinus nigra	SCHWARZ-KIEFER	5	3	2	4	2	
Pinus strobus	WEYMOUTH-KIEFER	4	3	3	1	2	
Lonicera japonica	JAPANISCHES GEISSBALTT	5	2	3	3	4	
Prunus laurocerasus	KIRSCHLORBEER	5	2	3	3	3	
Ilex aquifolium	STECHPALME	4	2	3	3	3	
Hedera helix	EFEU	4	2	3	3	3	

Fig. 5. Gesucht sind in einem einfachen Beispiel immergrüne Gehölze ($W="I"$) in warmen Lagen ($T \geq 4$) und im subozeanischen Klima wie z. B. Tessin ($K \leq 3$) vorkommend. Das Programm AUS findet elf Arten.

Auswählen: (NUMMER>=160 und NUMMER<=560 und f>=4 und R>=4) aber nicht f1>="i"

Fig. 6. *Poaceae* und *Cyperaceae* basenreicher Flachmoore, aber nicht an dauernd überfluteten Stellen.

Vegetationstabellen sind auch Artenlisten und können als Auswahlkriterien miteinbezogen werden.

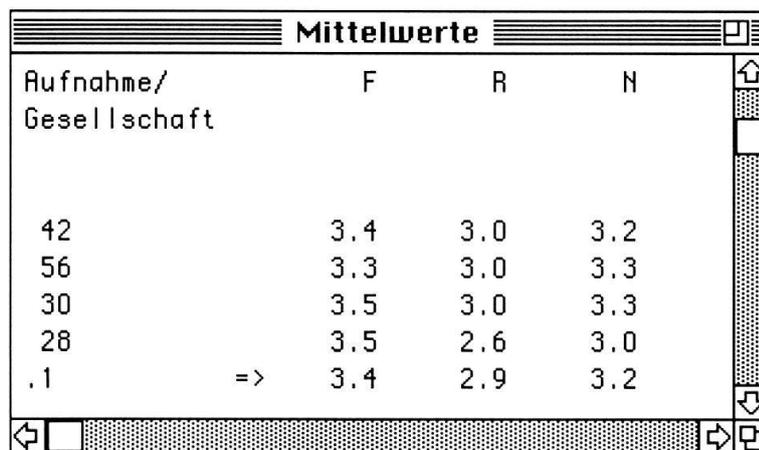
Auswählen: f>=4 und DATEI "riet.veg"

Fig. 7. Alle Feuchtezeiger (F>=4) in der Tabelle *riet.veg*.

3.3 DIE ZWISCHENABLAGE VERBINDET PROGRAMME

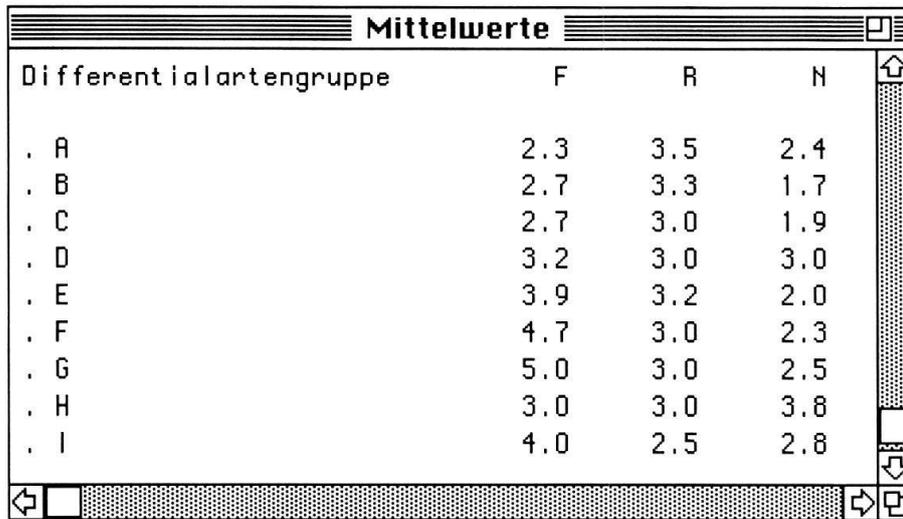
Die Artenliste kann ausgedruckt, oder zur Weiterverarbeitung über die Zwischenablage in eine Tabelle oder einen Text kopiert werden. Die so kopierten Daten sind tabulatorgetrennt. Die Tabellenkalkulation Excel z. B. reserviert für jeden Zeigerwert eine Spalte, so dass diese für weitere Berechnungen verwendbar sind. Excel eignet sich aber auch bestens für die graphische Überarbeitung der Zeigerliste.

3.4 GEMITTELTE ZEIGERWERTE



Aufnahme/ Gesellschaft	F	R	N
42	3.4	3.0	3.2
56	3.3	3.0	3.3
30	3.5	3.0	3.3
28	3.5	2.6	3.0
.1 =>	3.4	2.9	3.2

Fig. 8. Die gemittelten Zeigerwerte der Aufnahmen und Gesellschaften.



Differentialartengruppe	F	R	N
. A	2.3	3.5	2.4
. B	2.7	3.3	1.7
. C	2.7	3.0	1.9
. D	3.2	3.0	3.0
. E	3.9	3.2	2.0
. F	4.7	3.0	2.3
. G	5.0	3.0	2.5
. H	3.0	3.0	3.8
. I	4.0	2.5	2.8

Fig. 9. Die gemittelten Zeigerwerte der Differentialartengruppen.

4. BEZUGSQUELLE DER PROGRAMME

Die Programme VEG, AUS und MULVA-4 können beim Ingenieurbüro Märki bezogen werden. Es wird ein Unkostenbeitrag von Fr. 100.-- berechnet. Das Programm selbst ist public domain. Eine Gewähr für das korrekte Funktionieren kann nicht übernommen werden.

LITERATUR

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LANDOLT E., 1977: Ökologische Zeigerwerte zur Schweizer Flora. Veröff.Geobot.Inst. ETH, Stiftung Rübel, Zürich 64, 208 S.

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Ecological Field Investigations of Duckweed (*Lemnaceae*) in Argentina

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1. INTRODUCTION, AIM OF THE INVESTIGATIONS

Lemnaceae are excellent subjects for physiological and ecological investigations. The results of many studies have been synthesized and published in detailed papers and were revised in LANDOLT (1986) and in LANDOLT and KANDELER (1987). The distribution and habitats of duckweed in North America

were elaborated by LANDOLT and collaborators (LANDOLT 1957, LANDOLT and WILDI 1977, LANDOLT 1981, LANDOLT not publ.). LANDOLT and WILDI (1977) analyzed water samples, with and without *Lemnaceae* species, originating from the southwestern States of the U.S. The results lead to the main conclusion that, beside the climate, the nitrogen and the magnesium content of the water appear to be relevant in explaining the different distribution patterns of various *Lemnaceae* species. Other studies relating water quality and occurrence of *Lemnaceae* species have been carried out in northern Australia (LANDOLT 1992). Some of these field results were confirmed under laboratory conditions (ZIMMERMANN 1981, LÜÖND 1983). However, the requirements and tolerances for different nutrient concentrations are not sufficiently known in order to understand the distribution of the species in nature. Though the aquatic system with a *Lemnaceae* cover is not as complex as a terrestrial one, it still contains so many factors difficult to measure and mutual relationships that it is by no means comprehensible. Therefore it seemed appropriate to investigate more examples to detect correlations between water quality and duckweed occurrence. The aim was not only to observe the ecological properties of the *Lemnaceae* species, closer and in more detail, but also to learn more about the ecological differentiation within a family of related genera and species.

After the 17th International Phytogeographic Excursion (IPE) 1983 through northern Argentina the authors had the opportunity to collect water samples and to note the water plants growing at each sample site. The investigations concentrated on the following questions:

- 1) What is the floristic composition of pleustonic plant communities in northern Argentina ?
- 2) What is the geographical distribution of the various *Lemnaceae* species in Argentina ?
- 3) Are there any water and climatic factors influencing the distribution of the *Lemnaceae*; is the distribution pattern similar to the pattern in other parts of the world?

Acknowledgements

Special thanks are due to Dr. U. Eskuche and his wife L. Zulema Ahumada de Eskuche, Corrientes, Argentina. They guided the 17th International Phytogeographic excursion in a scientifically competent manner. They proved to be superb organizers and lectured to us on the vegetation and environmental conditions of Argentina. Dr. U. Eskuche accompanied us on several field trips in the surroundings of Corrientes and let us take part in his rich experience with aquatic vegetation communities. In Buenos Aires we got very valuable infor-

mation on aquatic habitats from Prof. Dr. R. Leon. We are also grateful for the friendly help of the INAL (Dir. Prof. Clarice Pignalberi, Ing. H. M. Cabral), especially for the boat trip within the inundation areas of Rio Paraná. Prof. Dr. L. Romero Fonseca, Corrientes, kindly filtered our water samples. The analysis of these samples was performed in Zürich by E. Schäffer of our Institute in collaboration with Dr. E. Szabo of the EAWAG. The detailed evaluation of the data was performed by Dr. M. Gasser and Dr. H.R. Binz. I. Gödickemeier and R. Venzin fed the data into the computer. April Siegwolf corrected the English language. We warmly thank all contributors for their very valuable support.

2. INVESTIGATION AREA, MATERIAL AND METHODS

2.1. INVESTIGATION AREA

The area in which the investigations were held extends in Argentina from 24° SL to 41° SL and from 55° WL to 71° WL. The sampling sites (1 to 180) are shown in Fig. 1. Most sampling was done in a transect from Southern Buenos Aires (36° SL) to northeastern Formosa (24° SL) within 57° and 61° WL. The climate data of this transect are presented in Fig. 2. The mean annual temperature decreases from North to South from 23° to 14° C and the annual amount of precipitation from 1400 to 600 mm. Days without frost vary from 350 days in the North to 150 days in the South. The absolute minima are relatively high: -8° C in the South and -4° C in the North. Roughly the transect can be divided into three parts:

- 1) The southernmost part (*Bonareense*) includes the visited parts of the provinces of Buenos Aires and Cordoba, the vegetation consists of prairies (Pampa).
- 2) The central part (*Mesopotamica*) comprises the province Entre Rios and the southern part of the province, Santa Fé (northwards to Depto. San Justo); the vegetation is prairie with forest islands and open forest called Savanna (mainly *Prosopis alba* and *P. nigra* shrub with *Stipa* meadows); gallery forest grows along the rivers.
- 3) The third part (*Correntino-Paraguaya*) covers the north of the province Santa Fé (from Depto. Vera northwards), the east of the provinces Chaco and Formosa and the north of Corrientes; the vegetation is similar to the one in the Mesopotamica, but the rain- green forests are often closer (mainly *Schinopsis balansae*-*Astronium balansae* forest).

There is no physical border between these regions. Consequently the climate and the vegetation transitions are flowing.

Table 1. Coordinates of the sample localities. Reference point: 24° SL / 54° EL, map of Argentina 1:500'000.

1	4.5/1.1	50	19.8/9.6	116-118	10.0/10.3
2-3	7.5/9.2	51-54	19.6/10.1	119	9.5/10.2
4	9.3/8.0	55	19.5/10.0	120	8.8/10.1
5	9.1/9.0	56-57	19.1/11.0	121	8.7/10.1
6	8.0/9.2	58	18.9/11.2	122-123	8.3/10.2
7	6.4/11.5	59-60	18.6/11.5	124-125	8.0/9.6
8	1.5/20.8	61-62	18.1/11.9	126	5.9/9.1
9	1.6/20.8	63	17.7/12.0	127-128	8.3/10.2
10	2.5/22.8	64	16.6/12.2	129	5.2/8.8
11	2.1/22.8	65	16.6/12.4	130-132	5.0/8.7
12	1.7/22.6	66-67	16.5/12.5	133	4.6/8.3
13	14.0/19.7	68-69	16.5/12.6	134	4.4/8.3
14-15	16.1/19.0	70	16.6/12.2	135-136	4.0/8.1
16	15.8/20.1	71-73	16.4/12.7	137-138	3.8/8.0
17	18.9/27.4	74-75	16.2/12.8	139	3.2/7.6
18-19	37.5/29.1	76-78	16.0/12.8	140-143	2.9/7.6
20	37.4/28.0	79-80	15.8/12.7	144	2.8/7.6
21-22	25.0/8.2	81-86	15.3/12.7	145-146	2.7/7.9
23	26.7/6.7	87/88	14.1/12.0	147-148	2.5/8.5
24-25	26.5/6.8	89	13.9/11.9	149-151	2.4/8.7
26	25.2/6.0	90	13.6/11.9	152-156	2.5/8.4
27-30	25.1/7.4	91-92	13.1/11.9	157-160	6.1/9.2
31-36	25.2/7.3	93	13.0/11.9	161-162	6.6/9.6
37-38	22.5/8.8	94-95	12.3/11.8	163-167	7.5/9.2
39	22.4/8.9	96-97	12.3/11.9	168-169	7.4/9.6
40	22.2/9.1	98-101	12.2/12.1	170-171	7.8/9.1
41-42	22.0/9.1	102	12.1/11.7	172	7.6/9.1
43-45	21.9/9.1	103-104	11.7/11.6	173	7.6/9.0
46	21.3/9.2	105-106	11.4/11.1	174	7.6/8.9
47	21.1/9.2	107-111	11.1/10.7	175-181	7.3/8.9
48	20.5/9.4	112-114	11.0/11.3	182	7.5/8.6
49	20.3/9.5	115	10.6/10.6		

2.2. FIELD MEASUREMENTS

At each water sample site, a plant sociological relevé of the pleustophytes was performed (method of Braun-Blanquet), and the water depth was measured. The sampling consisted of 2 x 250 cm³ water and a herbarium sample. The pH was measured colorimetrically as well as with an electric pH meter. Furthermore, conductivity and carbonate hardness data were registered. Most samples could be filtered through bacterial filters right in the field. A few samples, clouded by very fine clay particles, had to be filtered by pressure at the end of the trip in Corrientes.

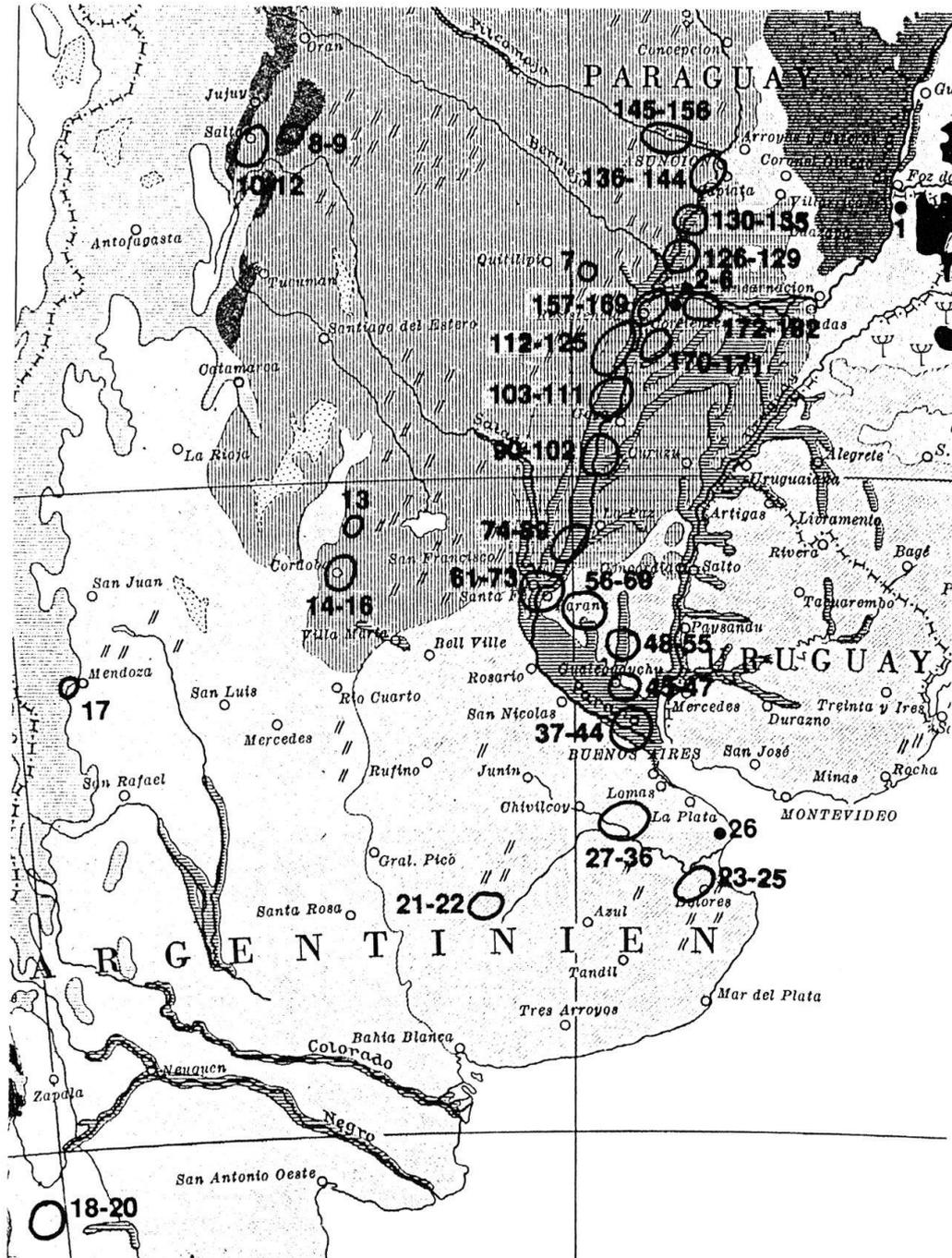


Fig. 1. Vegetation map of northern and central Argentina with location of the samples (map from TORUNSKI 1962). The exact coordinates of the locations are put together in Table 1.

-  Tropical and subtropical rain forest
-  Mountain rain forest
-  *Araucaria* forest (partly destroyed)
-  Chaco forest (quebracho and algarrobo)
-  Galery forest
-  Devastated and open forest (fields and pastures)
-  Shrub steppe, brier (caatinga, chaparal, espinal)
-  Prairies with forest islands
-  Prairies (llanos, pampa)
-  Patagonian steppe
-  Alpine steppe, region of the high mountains without trees (puna, paramo, rocks)
-  Semidesert
-  Sporadic occurrence of *Araucaria*
-  periodically inundated region
-  Salt pan

2.3 ANALYSIS OF THE WATERS

The water analyses were performed in the chemical laboratory of the Institute in Zürich. Conductivity and pH measurements were repeated and the following elements measured (Table 2).

Some of the water samples showed sedimentation on arrival at Zürich. The sediments were also analyzed and the ion balance checked. They contained mostly sulfate, Fe, Zn and Mn. Therefore, it must be concluded that these ions are under-represented in some of the samples. The values of Mn were so fragmentary that we did not evaluate the results.

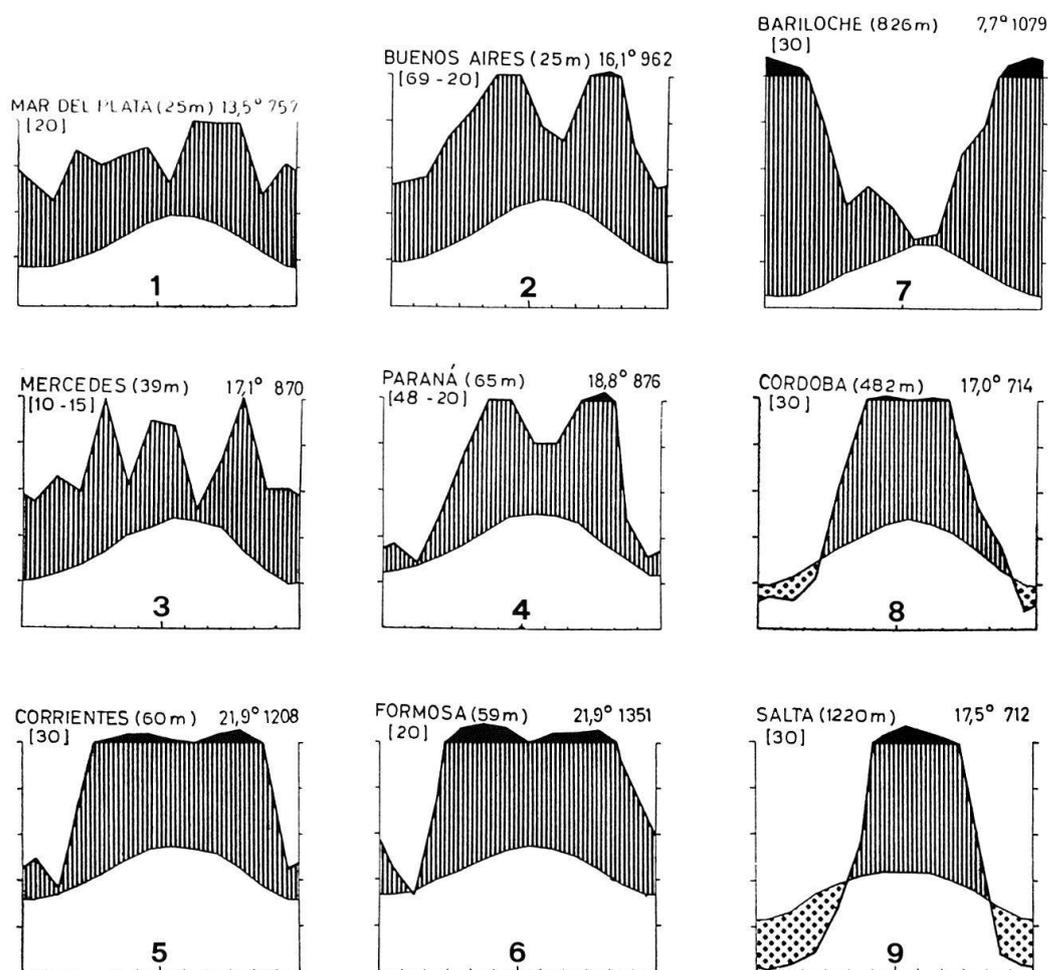


Fig. 2. Climate diagrams of the visited areas in the :

- 1 and 2: *Bonaerense* region (samples No. 21 to 44)
- 3 and 4: *Mesopotamica* region (samples No. 45 to 111)
- 5 and 6: *Correntino-Paraguaya* region (samples No. 1 to 11 and No. 112 to 182)
- 7: *Valdiviano-Neuquena* region (samples No. 18 to 20)
- 8: *Centrale* region (samples No. 13 to 17)
- 9: *Tucumano-Boliviana* region (sample No. 12)

The diagrams 7, 8 and 9 represent three regions with only scarce sampling. The region of Bariloche (Patagonica) (7) is relatively cool and rather dry in summer. *Lemna minuta* was the only lemnid found in that region. The regions of Cordoba (Centrale) (8) and Salta (Tucumano-Boliviana) (9) are climatically similar to the region of Mesopotamica but have much drier winters. The few relevés of this regions were incorporated into group Two (Mesopotamica).

Table 2. Factors and ions measured.

factors and ions	methods
NO ₃ -N	colorimetric with nitro salicylic acid
NH ₄ -N	colorimetric with indophenol
PO ₄ -P	colorimetric with molybdene blue
Cl ⁻	colorimetric with ferrothio-cyanate
SO ₄ ⁻⁻	spectral photometric
Ca ⁺⁺	photometric by flame
Mg ⁺⁺	photometric by flame
Na ⁺	photometric by flame
K ⁺	photometric by flame
Mn ⁺⁺	photometric by flame
Zn ⁺⁺	photometric by flame
Fe ^{++,+++}	photometric with bathophenanthroline-disulfonic acid
carbonate hardness	titration with HCl

2.4. EVALUATION METHODS

2.4.1. Common occurrence of pleustonic species in the same waters

The evaluation of the common occurrence of different species was tested by means of a χ^2 test in a contingency table. The zero hypothesis was checked; the difference between observed and expected frequency of common occurrence indicates a positive or a negative correlation.

2.4.2. Species versus data of environmental factors

The transformed values for the factors (see 2.4.3) were divided into 15 classes with the program GRAP. The number of relevés (N) in each class was determined. In the histogram the percentage of occurrence of each pleustonic species in every class is presented.

The occurrence of a species has not been weighted. The results present only the presence/absence data.

2.4.3. Distribution of the data

The data of the measured values of water parameters are distributed asymmetrically for Na, K, Ca, Mg, N_{tot}, SO₄, Cl, P_{tot}, conductivity in the field and in the laboratory, total and carbonate hardness. A logarithmic (ln) transformation

shows a more or less normal distribution of the values. The transformed values are ready to use for evaluation. The pH values from the field and laboratory did not have to be transformed. For the Zn values, which were only slightly asymmetrically distributed, a root transformation was suitable. On the other hand, the values for NH_4 and less so for NO_3 were extremely asymmetrically distributed and could not be reasonably transformed. The Fe values were often too low to be determined accurately. An evaluation, therefore, made no sense.

2.4.4. Main component analysis

The transformed data of Na, K, Ca, Mg, Zn, SO_4 , Cl, N_{tot} , P_{tot} , total and carbonate hardness, conductivity in the field and in the laboratory were calculated by main component analysis with the aid of the program package of WILDI and ORLOCCI (1983). To estimate the similarities of the relevés, the covariance according to the Rese program was used. The detailed methods are described in WILDI and ORLOCCI (1983) and in WILDI (1986). The graphic presentation of the first two factors proved to be appropriate enough. Therefore the ordination was restricted to these first two dimensions.

2.4.5. Ordination of vegetation relevés

The ordination according to the package of Wildi did not reveal very convincing results, although some of the relevés with *Lemna gibba* and *Azolla filiculoides* could be separated. Therefore typical relevés of the southern part of the transect and of the northern part (except relevés with *Lemna aequinoctialis*) as well as the relevés with *Lemna aequinoctialis* were separately grouped by hand in the sequence of the most frequent species within the group.

3. RESULTS

3.1 CLIMATE AND DISTRIBUTION

The distribution of the different *Lemnaceae* species occurring in Argentina was mapped world-wide by LANDOLT (1986). The localities found during the

reported trip have already been taken into account. Much more collecting is required to facilitate more detailed maps of Argentina. Table 3 shows the occurrence frequency of the species within the shaded area. Apparently, *Lemnaceae* are unequally distributed throughout the visited transect of Argentina. There is a gradient from South to North (BA to CP). *Lemna gibba* and *Azolla filiculoides* (very distinctly), *Spirodela intermedia*, *Wolffia brasiliensis* and *Lemna minuta* (only slightly) are become rarer to the North whereas *Azolla caroliniana*, *Lemna aequinoctialis*, *Pistia stratioides*, *Wolffiella lingulata*, *Lemna valdiviana* and *Utricularia gibba* are more frequent in the North.

In the coolest region, Bonaerense, the following species are represented by a higher frequency than expected: *Azolla filiculoides*, *Lemna gibba*, *Wolffia*

Table 3. The frequency of occurrence of *pleustophyte* species in the different parts of the field trip (only species which occur in more than 20 % of the localities of one region are mentioned). Two localities of Barriloche with a different climate and consisting of only *Lemna minuta* were not considered. The numbers in brackets show the percentage of occurrence for the single species in the region. The relative frequency in a region compared with the whole area is demonstrated by the number in italics.

- Localities with *Lemnaceae*: 166 (100%)
- Localities in Bonaerense (BA): 23 (14%)
- Localities in Mesopotamica (including 5 samples of the region Centrale and one sample of the region Tucumano-Boliviana (MP): 41(25%)
- Localities in Correntino-Paraguay (CP): 102 (61%)

Species	whole area	BA	MP	CP
<i>Lemna minuta</i>	115 (67%)	20 (87%) <i>1.2</i>	34 (83%) <i>1.2</i>	61 (60%) <i>0.9</i>
<i>Azolla caroliniana</i>	93 (55%)	4 (17%) <i>0.2</i>	23 (56%) <i>1.0</i>	67 (66%) <i>1.2</i>
<i>Wolffiella lingulata</i>	84 (51%)	1 (4%) <i>0.1</i>	20 (48%) <i>1.0</i>	63 (62%) <i>1.2</i>
<i>Pistia stratioides</i>	81 (48%)	3 (13%) <i>0.3</i>	18 (44%) <i>0.9</i>	60 (59%) <i>1.2</i>
<i>Salvinia minima</i>	77 (46%)	4 (17%) <i>0.4</i>	23 (56%) <i>1.2</i>	50 (49%) <i>1.1</i>
<i>Wolffiella oblonga</i>	70 (42%)	9 (39%) <i>0.9</i>	20 (48%) <i>1.1</i>	41 (39%) <i>1.0</i>
<i>Limnobium laevigatum</i>	65 (39%)	7 (30%) <i>0.8</i>	17 (41%) <i>1.0</i>	41 (40%) <i>1.0</i>
<i>Wolffia columbiana</i>	61 (36%)	8 (35%) <i>0.9</i>	19 (53%) <i>1.2</i>	34 (33%) <i>0.9</i>
<i>Spirodela intermedia</i>	58 (35%)	13 (57%) <i>1.6</i>	16 (39%) <i>1.1</i>	29 (28%) <i>0.8</i>
<i>Ricciocarpus natans</i>	57 (34%)	15 (65%) <i>1.9</i>	9 (23%) <i>0.6</i>	33 (32%) <i>0.9</i>
<i>Azolla filiculoides</i>	56 (34%)	21 (91%) <i>2.7</i>	31 (76%) <i>2.2</i>	4 (4%) <i>0.1</i>
<i>Lemna gibba</i>	56 (34%)	18 (78%) <i>2.3</i>	27 (66%) <i>1.9</i>	11 (11%) <i>0.3</i>
<i>Lemna valdiviana</i>	44 (26%)	2 (9%) <i>0.3</i>	7 (17%) <i>0.6</i>	35 (34%) <i>1.3</i>
<i>Salvinia herzogii</i>	42 (25%)	2 (9%) <i>0.3</i>	13 (32%) <i>1.2</i>	27 (26%) <i>1.0</i>
<i>Wolffia brasiliensis</i>	32 (19%)	10 (43%) <i>2.3</i>	8 (20%) <i>1.1</i>	14 (14%) <i>0.7</i>
<i>Utricularia gibba</i>	22 (13%)	1 (4%) <i>0.3</i>	1 (2%) <i>0.2</i>	20 (20%) <i>1.5</i>
<i>Lemna aequinoctialis</i>	21 (12%)	0 (0%) <i>0.0</i>	1 (2%) <i>0.2</i>	20 (20%) <i>1.7</i>

brasiliensis, *Ricciocarpus natans*, *Spirodela intermedia*. Species with lower frequencies in this region are: *Lemna aequinoctialis*, *Wolffiella lingulata*, *Azolla caroliniana*, *Pistia stratioides*, *Lemna valdiviana*, *Salvinia herzogii*, *Utricularia gibba*, *Salvinia minima*.

Species with a higher frequency than expected in the Mesopotamica region are: *Azolla filiculoides*, *Lemna gibba*. Of lower frequency are: *Lemna aequinoctialis*, *Utricularia gibba*, *Lemna valdiviana*, *Ricciocarpus natans*.

In the region Correntino-Paraguaya, the following species grow with a relatively high frequency: *Lemna aequinoctialis*, *Utricularia gibba*, *Azolla caroliniana*, *Wolffiella lingulata*, *Pistia stratioides*. With low frequency occur: *Azolla filiculoides*, *Lemna gibba*, *Spirodela intermedia*, *Wolffia brasiliensis*.

From the reported results it can be shown that the distribution of some lemnid species (pleustophytes) is directly or indirectly dependent on the climate (for climatic data see chapters 2.1 and 4.1).

3.2. VEGETATION STUDIES

The various relevés contain between one and 12 lemnid species (fig. 3). In addition, *Scirpus cubensis*, a species rooting in the soil, was included in the relevés when it was growing on floating mats of organic detritus and/or pleustophytes within the water. It must be remembered that the selection of the investigated waters was not purely accidental. Waters with no lemnids were

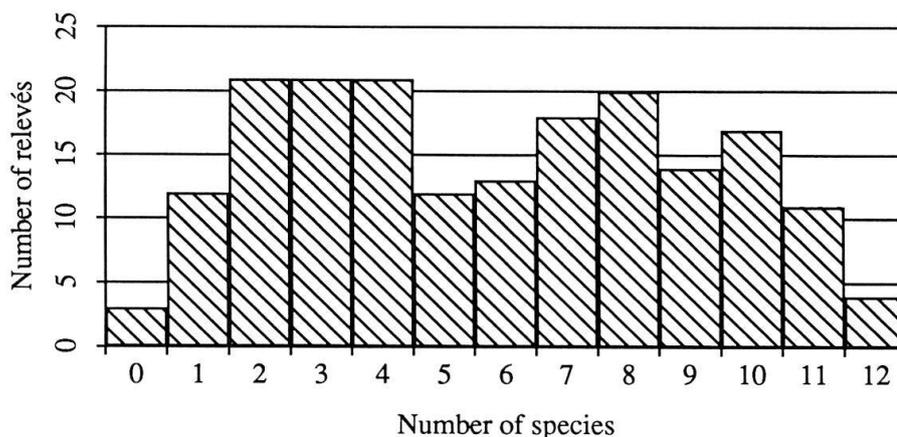


Fig. 3. Distribution of pleustophyte species numbers within the relevés.

sampled only very specifically. In regions with many lakes, ponds and pools, not all waters could be examined, waters with a closed cover (containing more than one or two species) were preferred. Therefore the classes with 1 (and 2) species in Fig. 3 are underrepresented. Two peaks are obvious, one from 2 to 4 species and one from 7 to 10 species. The diversity of up to 12 lemnid species per relevé is quite remarkable. In Europe relevés with more than 7 species are very rare.

Since the statistical evaluation did not reveal an ordination useful for sociological units, the ordination was made by hand after having divided the samples in three groups according to predominance of the following three *Lemna* species: *L. gibba*, *L. minuta*, *L. aequinoctialis*. In the tables 4 to 6, relevés with only one or two species are excluded.

The three distinct pleustonic communities can be characterized by the following combinations:

***Lemna gibba* - *Azolla filiculoides* community:** *Azolla filiculoides*, *Lemna gibba*, *Lemna minuta*, *Wolffiella oblonga*

***Lemna minuta* - *Salvinia minima* community:** *Salvinia minima*, *Lemna minuta*, *Wolffiella lingulata*, *Azolla caroliniana*, *Limnobium laevigatum*, *Pistia stratioides*

***Lemna aequinoctialis* - *Azolla caroliniana* community:** *Lemna aequinoctialis*, *Azolla caroliniana*, *Pistia stratioides*.

The three communities are connected by many transitions. The main factor for the development of these communities seems to be the climate since the first community is mainly distributed in the South (and West) i.e. in the cooler and drier regions. Whereas, the third community with *Lemna aequinoctialis* prefers the northern (and eastern) region which is warmer and receives more precipitation. Whether the three communities can be divided into subunits is difficult to decide. The qualitative feature of a body of water may determine the abundance of a species at a certain place. The abundance is also dependent on a few other factors like seasonal drying, possibility of colonizing the water, temperature conditions, birds, fish and other herbivores. Some plant sociologists may divide the community into many lower units. However, it would be difficult to clearly distinguish defined associations because the stands change their species composition throughout the year, and the presence of one species or another might well be incidental and temporary.

The first community belongs to the *Lemnion gibbae* R. Tx. et Schwabe 1974 and is not yet documented by many relevés. A typical relevé of this

Table 4. 35 relevés of the *Lemma gibba*-*Azolla filiculoides*-community. The number of the relevé can be localized on the map in fig. 1. (Fr = frequency)

relevé number	27	29	21	32	22	23	54	77	75	30	82	48	24	49	76	28	33	26	53	36	39	37	34	25	13	59	60	55	79	62	57	58	31	78	56	Fr	
species number	10	10	8	8	8	8	7	7	10	7	6	11	9	10	6	5	4	4	4	3	3	3	3	3	3	4	4	4	3	4	3	4	3	4	7	4	
<i>Azolla filiculoides</i>	2	1	2	3	2	4	5	5	5	5	5	3	4	1	3	5	+ 3	5	5	4	5	3	1	5	3	1	5	1	4	3	1	1	4			V	
<i>Lemma gibba</i>	1	1	2	1	+	1	1	2	1	2	2	+	+	+	1	1	+	+	1	1	+	3	+	5	1	3	3	5	4	1	2	1			4	2	V
<i>Lemma minuta</i>	3	2	4	2	+	3	2	2	3	2	1	1	1	2	+	2	+	+	1	2	2	1	+	1	+									2	1	IV	
<i>Wolffia oblonga</i>	2	1	2	2	+	3	1	2	3	3	2	+	2	+																				4		III	
<i>Wolffia columbiana</i>	2	1	+	+	2	+	2	1	2	+	3							3							2	1	1	2	2	1	2			2		III	
<i>Wolffia brasiliensis</i>	1	1	2	+	2	3	+	1	+		1	2	+												2	1	2									III	
<i>Ricciocarpus natans</i>	1	+	2	5	3	+			1	2	1	1		2	+	+																	1			III	
<i>Spirodela intermedia</i>	4	4	1	+					1	+	+	1		+	+	1																		+		II	
<i>Ceratophyllum dem.</i>	5	3		3	+			3																												I	
<i>Limnobium laevig.</i>	+	+										+	+	+																				2		I	
<i>Lemma valdiviana</i>							+		1		2	+	1																								I
<i>Azolla caroliniana</i>									3	3	4																3								1		I
<i>Wolffia lingulata</i>							1	+																											+		I
<i>Sabina minima</i>											+		5																					2			I
<i>Sabina herzogii</i>								2																											3		I
<i>Pistia stratiotes</i>																																			+		I

community is No. 21. OBERDORFER (1960) describes a fragment of this community from Chile under the name of *Lemno-Azolletum chilense*. Further relevés can be found in SCHWAAR (1986; there *L. gibba* is named *L. parodiana*; only fragments), in RAMIREZ and BECK (1981) (from the region of La Paz, Bolivia with only fragments reduced to stands of *L. gibba* and *Azolla filiculoides*) and in LIBERMANN CRUZ et al. (1988,1991) (from Lake Titicaca and Lake Uru-Uru, Bolivia). These authors classify the relevés as an association *Lemno minutae (minusculae)-Lemnetum gibbae*. However, these relevés have only up to 4 species. *L. gibba* and *Azolla filiculoides* are frequent, *L. minuta* relatively rare. In addition, *L. valdiviana* occurs in several relevés. The fragmentary formation of all these *Lemna gibba* communities demonstrates that the climatic conditions (above all the cold temperatures) are more extreme in those places.

ESKUCHE and ROMERO-FONSECA (1982) and ESKUCHE (1986) published relevés of associations with *Lemnaceae* from the region of Corrientes, part of which can well be compared with the relevés of **the second community**. Differing from ESKUCHE et al., but in agreement with SCHWABE-BRAUN and TÜXEN (1981), only pleustophytes (plants swimming on the surface of the water or floating in the water, but not rooting in the ground) were taken into account by the present authors. Furthermore, plants which protrude more than 10 cm above the water surface (e.g. *Eichhornia*, *Hydrocotyle*) were left out, even if the plants had no connection with the bottom of the water. If this is taken into account, many of their relevés can be integrated in table 5. A typical relevé of the second community is No. 165. The community belongs to its own alliance which is characterized by *L. minuta*, *Limnobium laevigatum* and *Salvinia minima* (and *S. herzogii*).

The third community is poorly represented in the investigated area. The stands are mostly fragments. A typical relevé is No. 129b. Additional relevés are needed. This community belongs to a different order (*Lemnetalia aequinoctialis* Schwabe-Braun and R.Tx. 1981) which is mainly wide-spread in tropical regions throughout the whole world.

If vegetation of the *Lemnetea* are to be seriously studied, it must be kept in mind that:

- 1) occurrence and frequency of the species change often during the year
- 2) propagules of the species are transported by birds from one water to the other
- 3) the ecosystem may perform a succession over years or decades, from an original pioneer stage with only one or very few species to a well developed final stage of many organisms.

Table 6. 10 relevés of the *Lemna aequinoctialis* - *Azolla caroliniana* community. The number of the relevé can be localized on the map in fig. 1. (Fr = frequency)

relevé number	129a	129b	99	132	123	27	149	131	4	25	Fr
species number	10	10	9	3	4	3	5	4	3	5	
<i>Lemna aequinoctialis</i>	2	3	+	4	2	5	4	5	5	+	V
<i>Azolla caroliniana</i>	1	+	3	4	4	1	1				IV
<i>Pistia stratioides</i>	3	2	+	2	3			1	2		IV
<i>Ricciocarpus natans</i>	1	2	+			2				+	III
<i>Limnobium laevigatum</i>	+	+	1					2			III
<i>Spirodela intermedia</i>	2	2						1	+		III
<i>Wolffiella lingulata</i>	1	1								+	II
<i>Wolffia columbiana</i>	3	3					3				II
<i>Lemna minuta</i>	1	1								+	II
<i>Salvinia minima</i>	5		4								II
<i>Utricularia gibba</i>			1		2					2	II
<i>Ceratopteris pteridoides</i>		+									I
<i>Lemna gibba</i>			+								I
<i>Wolffiella oblonga</i>			1								I
<i>Lemna valdiviana</i>							3				I

Table 7. Frequency of the *Lemnetea* species in the three communities. V >80%; IV 60-79%; III 40-59%; II 20-39%; I 1-19 %.

species	communities		
	1	2	3
<i>Azolla filiculoides</i>	V	I	-
<i>Lemna gibba</i>	V	I	I
<i>Wolffia brasiliensis</i>	III	II	-
<i>Wolffiella oblonga</i>	III	III	I
<i>Lemna minuta</i>	IV	V	II
<i>Wolffiella lingulata</i>	I	V	II
<i>Salvinia minima</i>	I	IV	II
<i>Limnobium laevigatum</i>	I	IV	III
<i>Azolla caroliniana</i>	I	V	IV
<i>Pistia stratiotes</i>	I	IV	IV
<i>Lemna aequinoctialis</i>	-	I	V
<i>Spirodela intermedia</i>	II	III	III
<i>Ricciocarpus natans</i>	III	III	III
<i>Wolffia columbiana</i>	III	III	II
<i>Lemna valdiviana</i>	I	II	I
<i>Salvinia herzogii</i>	I	II	-
<i>Ceratophyllum demersum</i>	I	I	-
<i>Salvinia auriculata</i>	-	II	-
<i>Utricularia gibba</i>	-	I	II

Whereas pioneer stages often differ distinctly from each other in their nutrient and other mineral content characteristics, the final stages are more similar in mineral composition of the water, most of the minerals being fixed in the biomass. Therefore pioneer stages can begin with various species whereas the final stages differ only slightly in species composition. Sometimes it is difficult to decide if a community of one or two species corresponds to a pioneer stage or if it is a very reduced variant of the final stage caused by some extreme factors like temperature, competition of other organisms, presence of herbivores etc. For a classification of the *Lemnetea* communities, it is best not to regard these stands as independent associations but to try to understand them either as pioneer stages or fragments of well developed end stages.

In the southeastern and western part of the investigated area (i.e. in the provinces of Buenos Aires, Rio Negro, Cordoba and Salta) the succession begins with either *L. gibba* on waters rich in minerals (especially magnesium and nitrogen) or with *Azolla filiculoides* (or sometimes *Lemna minuta*) on waters poor in nitrogen and phosphorus. The succession proceeds to a two-storied cover of *Lemnaceae* consisting of a surface cover of *Lemna minuta*, *L. gibba*, *Azolla filiculoides*, *Wolffia brasiliensis* and *W. columbiana*, and in the lower story of submerged floating *Wolffiella oblonga*. The ecosystem does not develop further under the regular climatic conditions. In the drier and cooler regions of the South, *Wolffiella oblonga* cannot exist.

In the more northern regions of Argentina (Entre Rios, Santa Fé, Corrientes, Formosa) the succession begins with a layer of one or very few of the following species: *Lemna minuta*, *Spirodela intermedia*, *Wolffia brasiliensis*, *Azolla caroliniana*, *Pistia stratiotes*, *Salvinia minima*. It is not quite sure which species occurs first under which conditions. However, *Pistia*, *Salvinia* and *Azolla* are able to colonize waters which are too poor in nutrients (especially phosphorus and nitrogen) for the growth of *Lemnaceae*. The stands of *Azolla caroliniana* from Uruguay described by SCHWAAR (1983) also belong to these pioneer stages. In the course of succession the nutrient cycle of the ecosystem increases, eventually giving growth possibilities for *Lemnaceae*. The further succession leads to a many-layered cover of pleustophytes and finally to a carpet of floating vegetation which enables amphibious plants like *Scirpus cubensis* to root. The mentioned succession was described by SCHULZ (1961), JUNK (1970), TUR (1972), NEIFF (1982), ESKUCHE (1986), WOLF (1990) and is demonstrated in Fig. 4.

The final stage of the tropic-subtropic pleustonic vegetation in northern Argentina, beginning with *Lemna aequinoctialis* or *Azolla caroliniana*

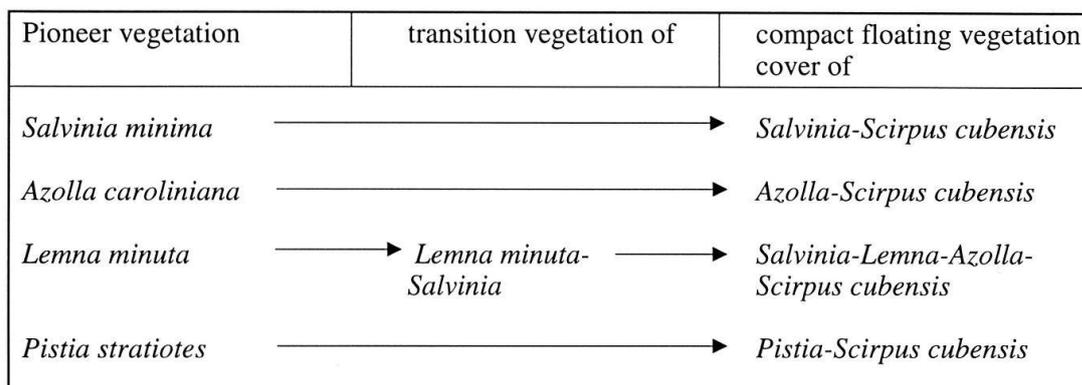


Fig. 4. Successions of pleustonic vegetation in Northern Argentina.

seems to be similar as in Fig. 4. Since the typical vegetation with *L. aequinoctialis* is very rare in Argentina, the succession has to be studied in northern South America where there additional species exist (e.g. *Wolffiella neotropica*, *Wolffiella welwitschii*, *Wolffiella caudata*).

3.3. COMMON OCCURRENCE OF VARIOUS SPECIES IN THE SAME WATER

Table 8 shows the results of the test of independent appearance of the *Lemnaceae* species collected on the trip and table 9 summarizes the situation within the whole southern part of South America. For this purpose, herbarium specimens from Argentina, Chile, Uruguay, Paraguay and the extratropical parts of Brazil, Bolivia and Peru were considered in addition to the notes of the field trip. This should give rise to higher statistical significance.

All together, 700 localities (duplicates carefully excluded) have been considered. Consulted herbariums include BA, BAA, BAB, BAF, CORD, CTES, LIL, LP, MCNS, MERL, SI, SP, VALD, Herb. G. Beck, La Paz and most of the larger herbaria of North America and Europe (see LANDOLT 1986). Unfortunately, lemnids other than *Lemnaceae* were not always determined and therefore not included in the present study. Between 7 % and 48 % of the samples of the various species consist of pure stands. The typical pioneer species like *L. gibba*, *L. aequinoctialis* and to a lesser extent *L. minuta* and *S. intermedia* are frequently found without other species of *Lemnaceae*, whereas species indicating stable situations usually grow along with other species (*Wolffiella lingulata*, *W. oblonga*, *W. columbiana*).

The following species have positive connections (statistically significant) (Table 8):

- ***Spirodela intermedia*** with *Lemna minuta*, *Salvinia minima*, *S. herzogii*, *Ricciocarpus natans*, *Limnobium laevigatum*, *Pistia stratiotes*, *Azolla caroliniana* and *Eichhornia crassipes*
- ***Lemna gibba*** with *Azolla filiculoides*, *Ceratophyllum demersum*, *Wolffia columbiana*, *Wolffia brasiliensis*
- ***Lemna valdiviana*** with *Wolffiella oblonga*, *Salvinia minima*, *Limnobium laevigatum*, *Utricularia gibba*, *Wolffiella lingulata*, *Salvinia herzogii*, *Ricciocarpus natans*
- ***Lemna minuta*** with *Spirodela intermedia*, *Ricciocarpus natans*, *Limnobium laevigatum*, *Salvinia minima*, *S. herzogii*, *Wolffiella lingulata*, *W. oblonga*, *Wolffia columbiana*, *Pistia stratiotes*
- ***Wolffiella lingulata*** with *Wolffiella oblonga*, *Salvinia minima*, *S. auriculata*, *Limnobium laevigatum*, *Pistia stratiotes*, *Azolla caroliniana*, *Salvinia herzogii*, *Lemna valdiviana*, *L. minuta*, *Wolffia columbiana*, *Ricciocarpus natans*, *Scirpus cubensis*
- ***Wolffiella oblonga*** with *Lemna valdiviana*, *Wolffiella lingulata*, *Wolffia brasiliensis*, *Salvinia minima*, *Limnobium laevigatum*, *Lemna minuta*, *Salvinia herzogii*, *Ricciocarpus natans*, *Utricularia gibba*, *Ceratophyllum demersum*, *Pistia stratiotes*
- ***Wolffia brasiliensis*** with *Wolffiella oblonga*, *Ricciocarpus natans*, *Lemna gibba*, *Wolffia columbiana*
- ***Wolffia columbiana*** with *Lemna gibba*, *Lemna minuta*, *Ceratophyllum demersum*, *Wolffiella lingulata*, *Wolffia brasiliensis*, *Pistia stratiotes*

Especially remarkable is the close connection between *L. gibba* and *W. oblonga* which also reflects the phytosociological distinctiveness of stands with these three species. *Azolla filiculoides*, which belongs to the same vegetation communities, was only considered for the samples collected on the field trip (without samples from the herbaria) and demonstrates the same close connection to *L. gibba*.

On the other hand, the following species grow much more seldom together than expected (statistically significant) (Table 8):

- ***Spirodela intermedia*** with *Lemna gibba*, *Azolla filiculoides*, *Utricularia gibba*
- ***Lemna gibba*** with *Wolffiella lingulata*, *Azolla caroliniana*, *Salvia minima*, *Pistia stratiotes*, *Eichhornia crassipes*, *Salvinia herzogii*, *Limnobium*

- laevigatum*, *Utricularia gibba*, *Lemna aequinoctialis*, *Salvinia auriculata*
- *Lemna aequinoctialis* with *Azolla filiculoides*, *Lemna gibba*, *L. minuta*
 - *Lemna valdiviana* with *Azolla filiculoides*
 - *Wolffiella lingulata* with *Lemna gibba*, *Azolla filiculoides*
 - *Wolffia brasiliensis* with *Pistia stratiotes*
 - *Wolffia columbiana* with *Utricularia gibba*

Azolla filiculoides and *A. caroliniana* avoid each other to a high degree. The rare common occurrence of *Lemna aequinoctialis* with *L. gibba*, *L. minuta*, *Wolffiella oblonga* and *Azolla filiculoides* reflects the different climatic requirements of the species (see chapter 4.1). *L. aequinoctialis* has stronger connections to tropical species which are not considered here. Under tropical conditions, *L. aequinoctialis* is by far the most frequent species of *Lemna-ceae*. In the Rio de Janeiro (Brazil) region, *L. aequinoctialis* was found in two out of three waters with pleustonic plant species. The connection between *L. gibba* and *L. minuta* is negative though *L. minuta* is strongly connected to the *Lemna gibba* - *Azolla filiculoides* community. However, *L. minuta* is also distributed in warmer climates where *L. gibba* does not occur.

Table 9. Common occurrence of lemnid species in extratropical South America (652 herbarium samples).

Significance levels: ***, --- p< .001; **, -- p< .01; *, - p< .05

* : positive correlation, - : negative correlation

	<i>Spirodela intermedia</i>	<i>Lemna aequinoctialis</i>	<i>Lemna gibba</i>	<i>Lemna minuta</i>	<i>Lemna valdiviana</i>	<i>Wolffiella lingulata</i>	<i>Wolffiella oblonga</i>	<i>Wolffia brasiliensis</i>	<i>Wolffia columbiana</i>
<i>Spirodela intermedia</i>			---						
<i>Lemna aequinoctialis</i>			---	---			---		
<i>Lemna gibba</i>				---	---	---	***	-	--
<i>Lemna minuta</i>					---				
<i>Lemna valdiviana</i>						***	***		
<i>Wolffiella lingulata</i>							*		*
<i>Wolffiella oblonga</i>								*	
<i>Wolffia brasiliensis</i>									***
<i>Wolffia columbiana</i>									
number of samples	144	61	248	318	93	91	174	53	97

Table 10. Flowering *Lemnaceae* species in the field.

species	flowering samples	total samples	percent of flowering in Argentina	percent of flowering world-wide
<i>Lemna gibba</i>	16	56	29	14
<i>Lemna aequinoctialis</i>	4	21	19	19
<i>Lemna minuta</i>	9	115	0.8	5
<i>Wolffia columbiana</i>	4	61	0.7	1.5
<i>Wolffia brasiliensis</i>	2	32	0.6	2
<i>Wolffiella oblonga</i>	3	70	0.4	4
<i>Spirodela intermedia</i>	2	58	0.3	3
<i>Lemna valdiviana</i>	0	44	<0.2	3
<i>Wolffiella lingulata</i>	0	84	<0.1	13

3.4. FLOWERING

In some of the collected samples flowering was observed (Table 10). The world-wide flowering percentage is taken from LANDOLT (1986). In this publication, some 10'000 *Lemnaceae* samples have been tested for flowering. Some of the species show the same flowering percentage in Argentina as world-wide (*L. aequinoctialis*, *W. oblonga* and *S. intermedia*). This probably means that the environmental conditions in October and November 1983 represented the average flowering conditions for the species. However, the conditions for flowering of *L. gibba*, *L. minuta*, *W. columbiana* and *W. brasiliensis* apparently were more favourable than the average conditions throughout the collecting season. *L. valdiviana* and *Wolffiella lingulata* were not found flowering at all.

3.5. WATER QUALITY AND SPECIES OCCURRENCE

3.5.1. Ecological characterization of the sites

The water analysis values are distributed asymmetrically for Na, K, Ca, Mg, N_{tot}, SO₄, Cl, P_{tot}, conductivity in field and in laboratory, total and carbonate hardness. A logarithmic (ln) transformation leads to a more or less normal distribution of the values. In this way the transformed values can be used for

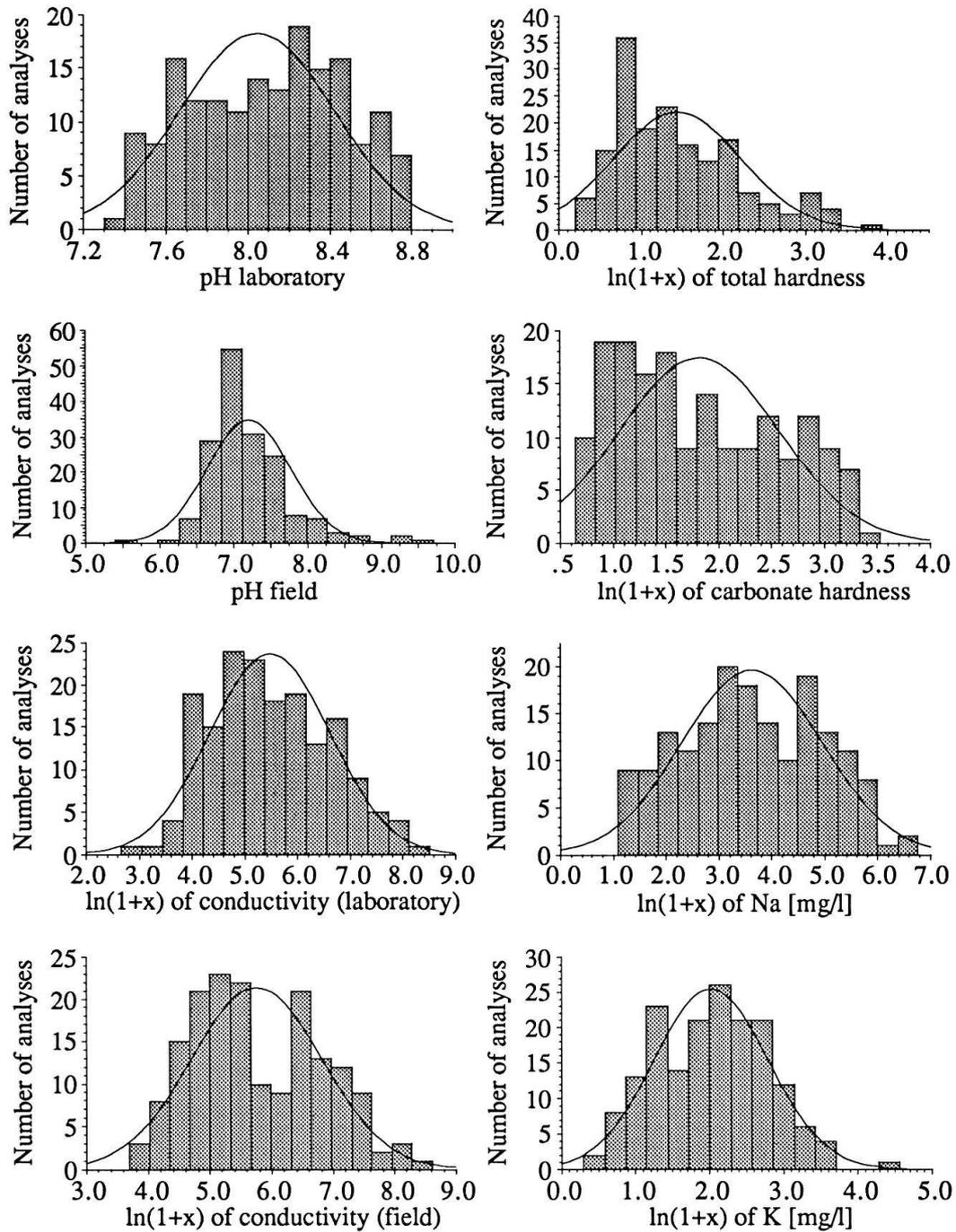


Fig. 5. Data of water analysis.

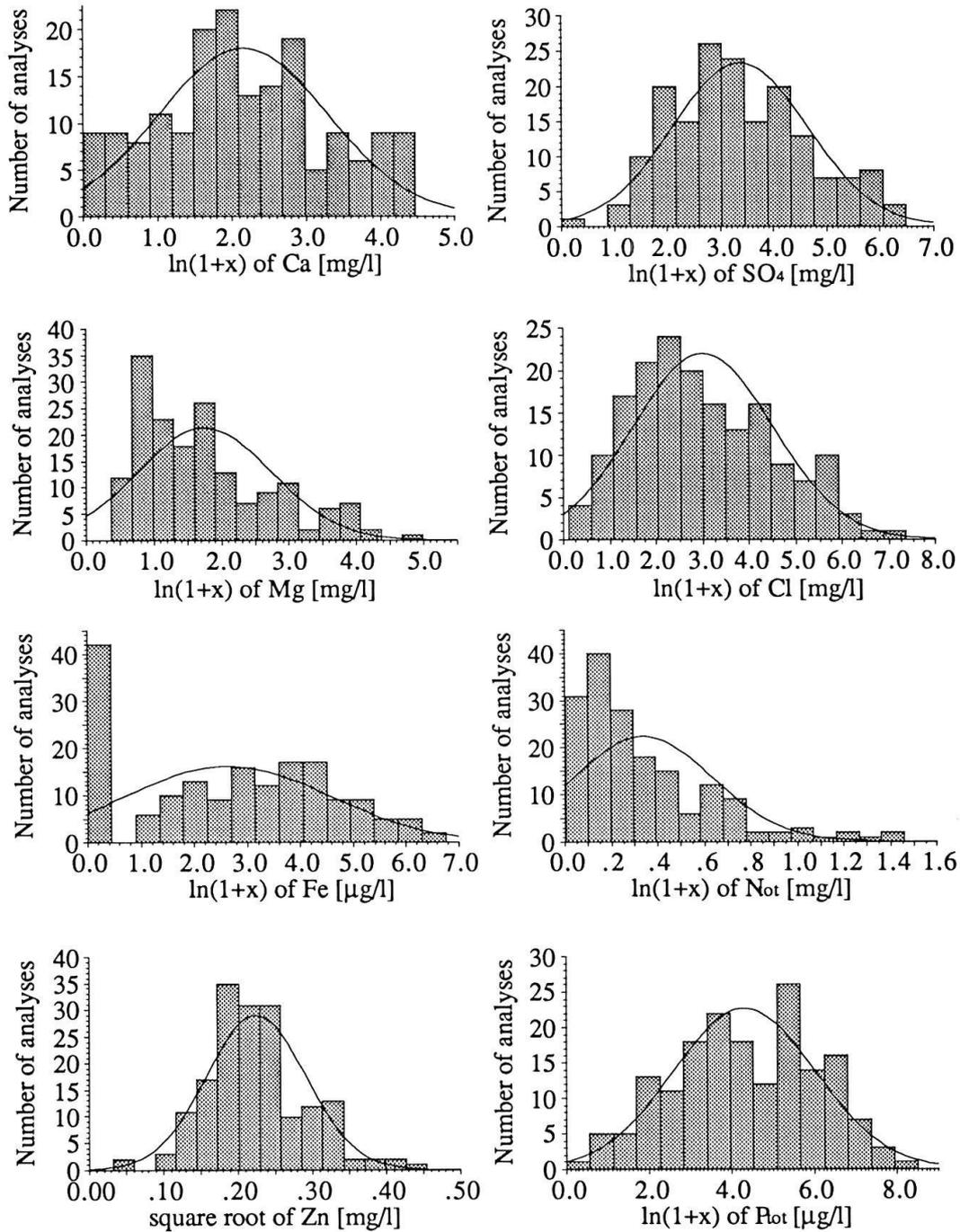


Fig. 5. (contin.) Data of water analysis.

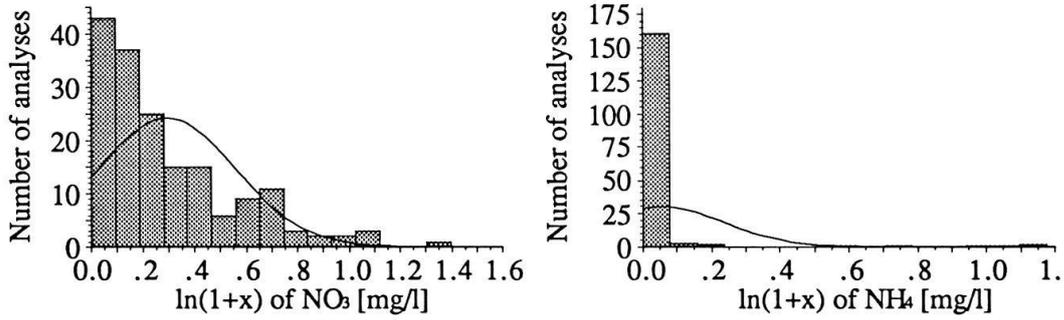


Fig. 5. (contin.) Data of water analysis.

5) pH is independent of all other factors. The pH in the field and in the laboratory is not correlated (see Fig. 6c). The pH range in the field was higher than in the laboratory (between 5.5 and 9.5 versus 7.3 and 8.8 in the laboratory), and the average pH was lower as well. Since the pH in the field is dependent not only on the base content of the water but also on the intensity of biological reactions going on. The measured pH reflects only a momentary stage and is subject to changes throughout the day and year.

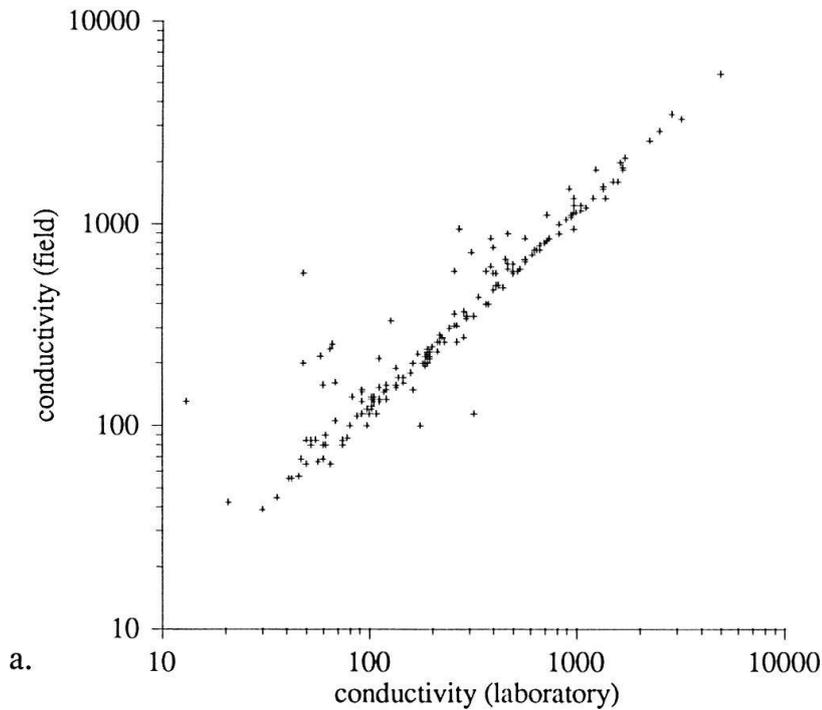


Fig. 6. Correlations between different water parameters.

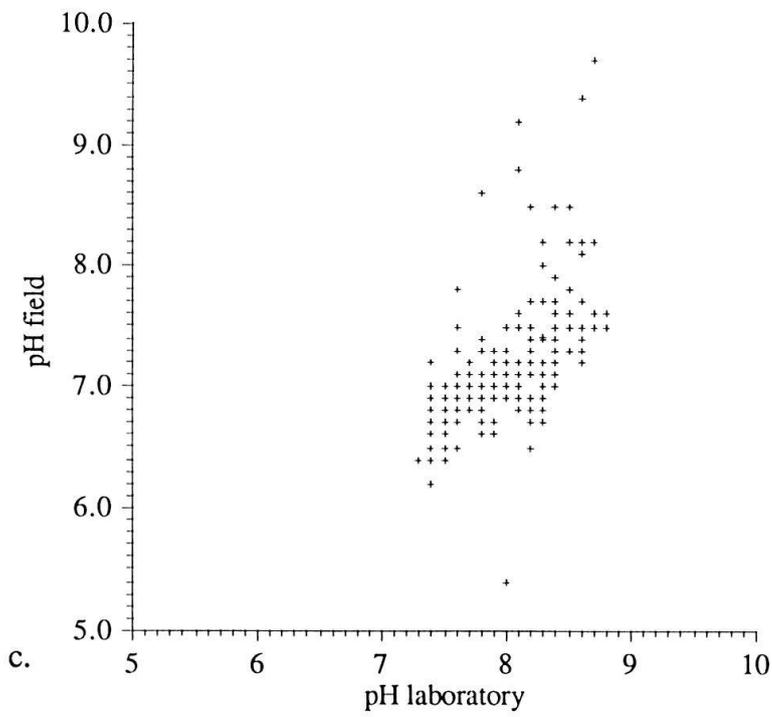
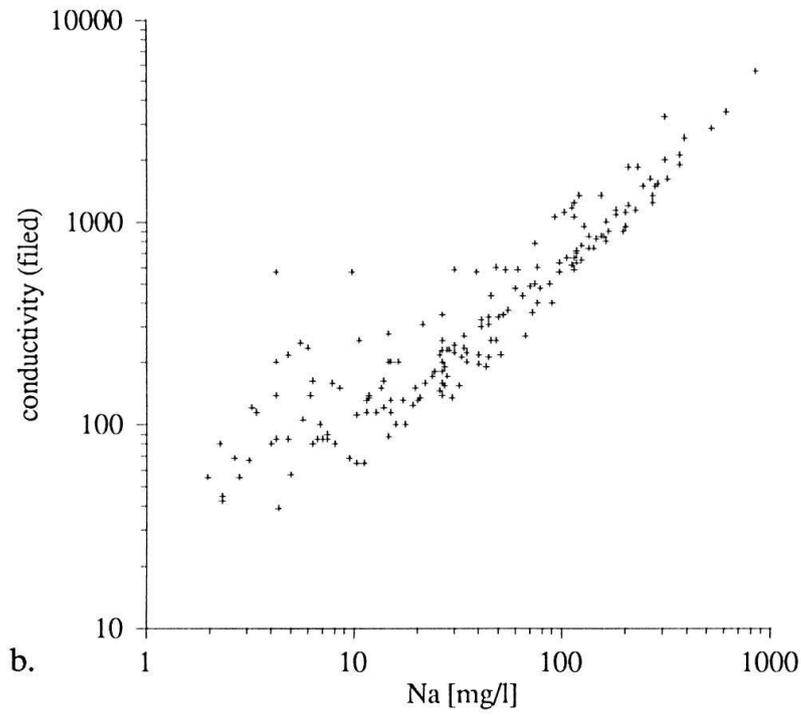


Fig. 6. (contin.) Correlations between different water parameters.

Table 12. Mean values of various nutrient factors in the water for each species of lemnids. n = number of samples.

	Na	K	Ca	Mg	Zn	SO ₄	Cl	N _{tot}	P _{tot}	carb. hard.	pH	cond.	n
<i>Spirodela intermedia</i>	66	6.1	10.7	6.7	0.050	49	47	0.59	0.16	5.6	7.2	459	53
<i>Lemna gibba</i>	157	14.8	24.2	16.1	0.053	16	126	0.70	0.22	13.4	7.6	973	53
<i>Lemna aequinoctialis</i>	77	8.5	20.2	12.2	0.048	77	58	1.07	0.58	6.7	7.1	546	18
<i>Lemna valdiviana</i>	83	9.4	21.1	14.7	0.053	99	87	0.40	0.37	6.5	7.9	509	42
<i>Lemna minuta</i>	85	8.1	13.5	8.9	0.056	66	71	0.42	0.19	6.8	7.2	563	110
<i>Wolffiella lingulata</i>	74	7.2	14.9	9.6	0.054	71	70	0.36	0.24	5.1	7.1	530	69
<i>Wolffiella oblonga</i>	81	8.5	13.5	9.5	0.060	73	71	0.34	0.24	6.2	7.2	538	66
<i>Wolffia brasiliensis</i>	92	12.5	14.6	9.9	0.068	88	66	0.53	0.15	8.1	7.3	600	32
<i>Wolffia columbiana</i>	128	9.1	19.6	13.5	0.048	104	104	0.46	0.30	9.9	7.4	822	56
<i>Salvinia auriculata</i>	27	4.0	5.7	3.0	0.052	15	21	0.12	0.10	2.8	6.9	173	12
<i>Salvinia herzogii</i>	50	6.0	10.1	5.7	0.051	42	48	0.32	0.12	4.0	7.0	369	38
<i>Salvinia minima</i>	58	6.1	11.9	7.2	0.058	47	53	0.35	0.26	4.5	7.1	346	67
<i>Azolla caroliniana</i>	41	6.1	10.3	6.1	0.057	50	32	0.36	0.19	4.0	7.0	321	91
<i>Azolla filiculoides</i>	146	13.5	18.3	11.7	0.058	87	120	0.63	0.21	12.0	7.6	859	52
<i>Ricciocarpus natans</i>	68	7.8	9.3	7.5	0.064	46	67	0.35	0.11	5.2	7.1	444	55
<i>Limnobium laevigatum</i>	46	5.4	9.1	4.8	0.060	40	38	0.30	0.12	3.9	7.0	325	63
<i>Pistia stratiotes</i>	71	6.8	14.8	9.4	0.050	70	63	0.57	0.30	5.4	7.1	510	80
<i>Ceratophyllum dem.</i>	171	9.3	16.1	12.6	0.051	114	140	0.32	0.16	10.8	7.7	1070	13
<i>Utricularia gibba</i>	30	6.3	8.0	3.4	0.070	29	25	0.27	0.09	3.6	6.8	228	22

3.5.2. Distribution of species and water quality

The mean values of nutrient content of all waters in which the various species occur are shown in Table 12 and the variation is put together in Fig. 7. Species with distinct deviations from the mean are listed in Table 13. The NO₃ and the NH₄ contents were so varied that there is no sense in correlating these factors with the occurrence of different species. *Lemna gibba*, *Ceratophyllum demersum*, *Azolla filiculoides* and, to a lesser extent, *Wolffia columbiana* and *W. brasiliensis*, occur usually in water with more Na, K, Ca and Mg than the other species. On the other hand *Salvinia auriculata* and *Utricularia gibba* generally grow in waters with a below average content of these ions.

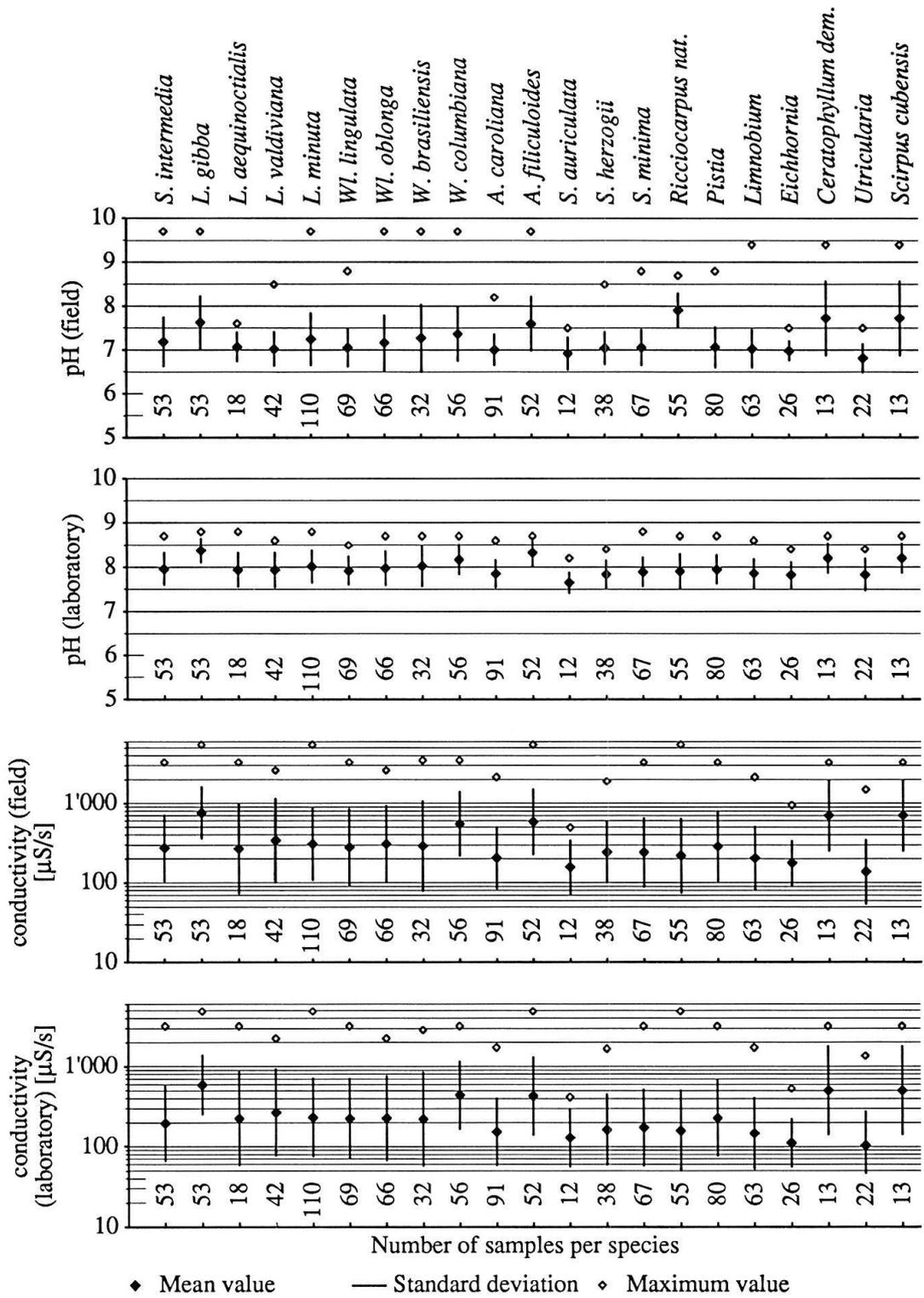


Fig. 7. Parameters of the water samples with the various species of lemnids.

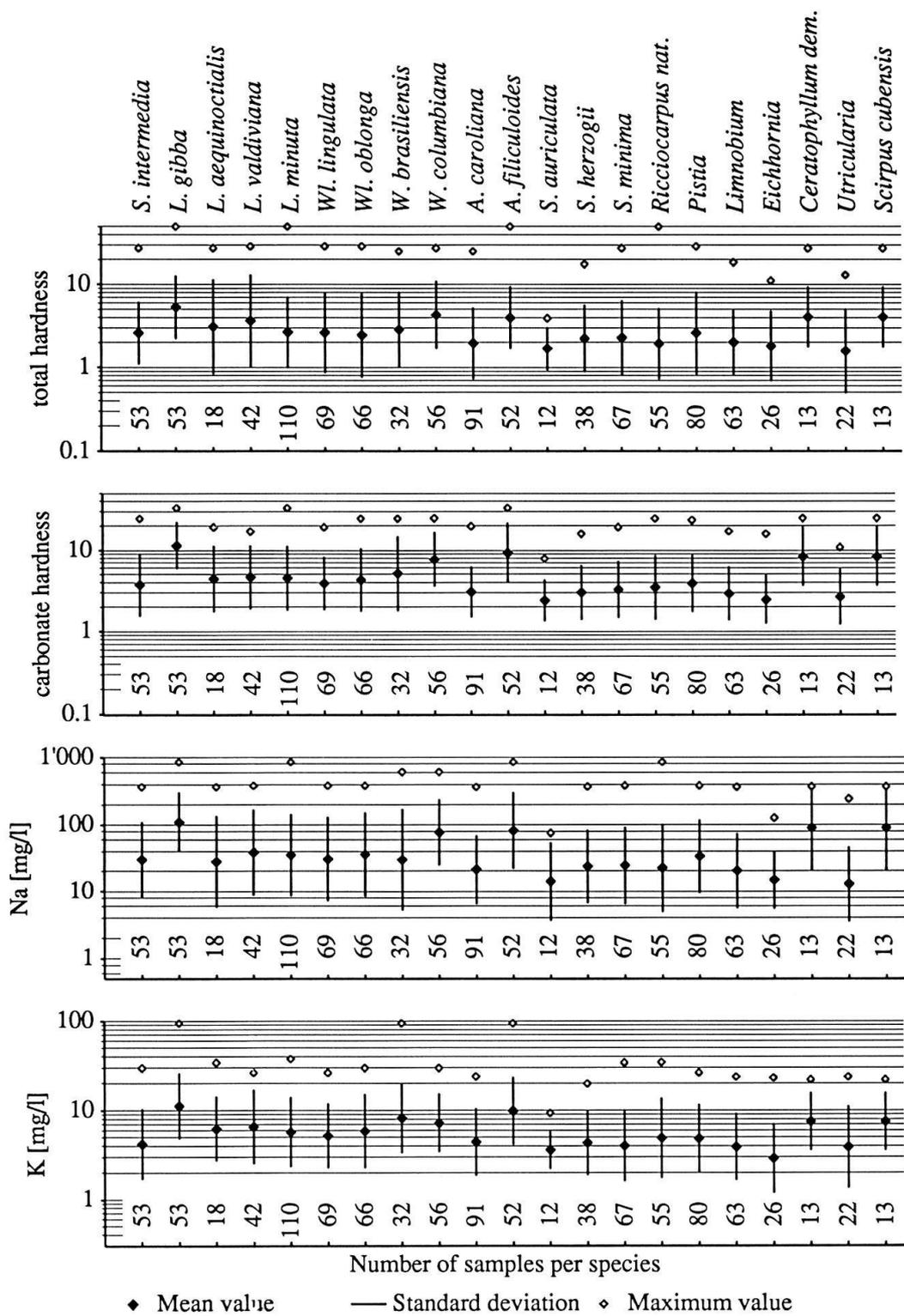


Fig. 7 (contin.) Parameters of the water samples with the various species of Lemnids.

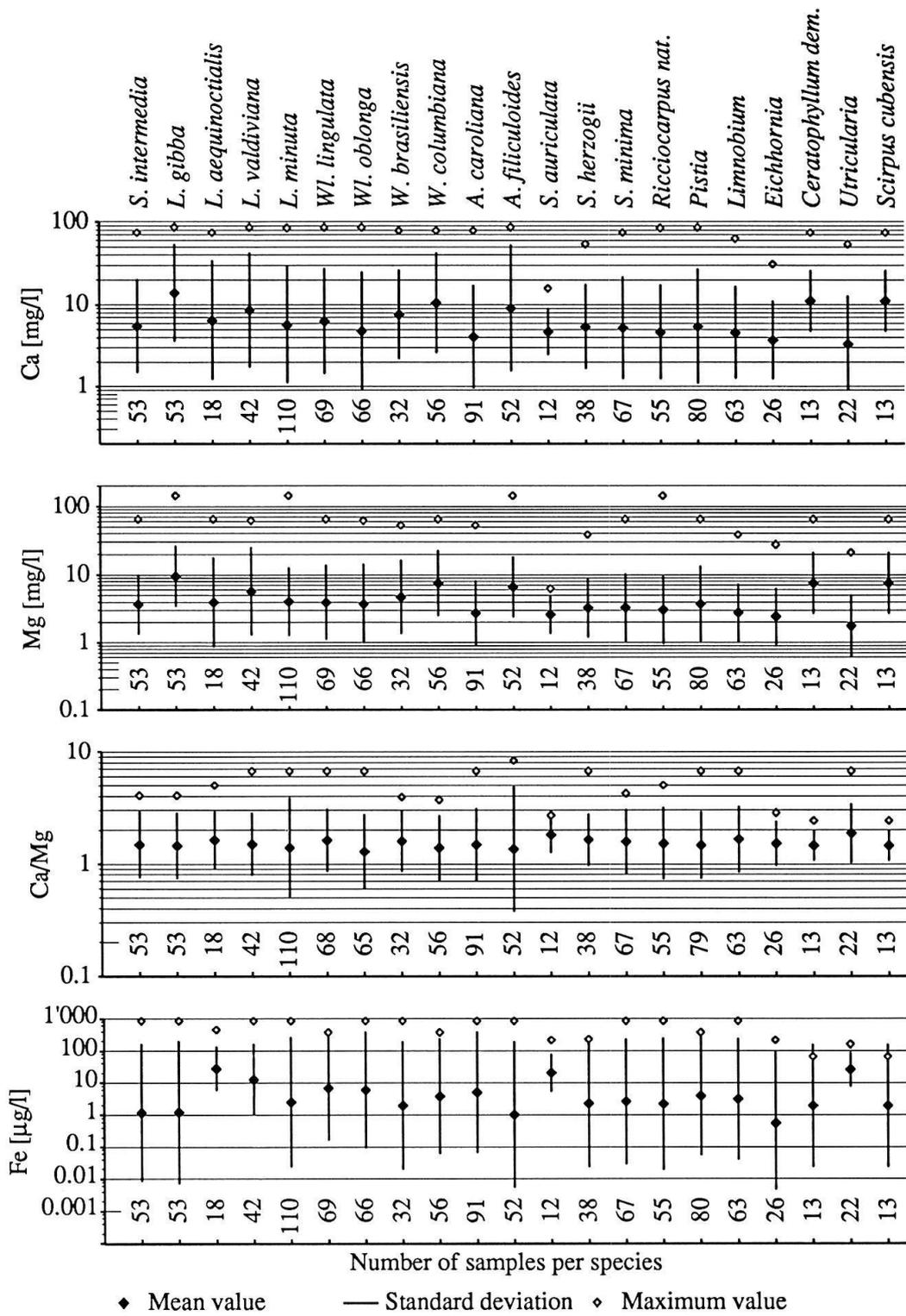


Fig.7. (contin.) Parameters of the water samples with the various species of lemnids.

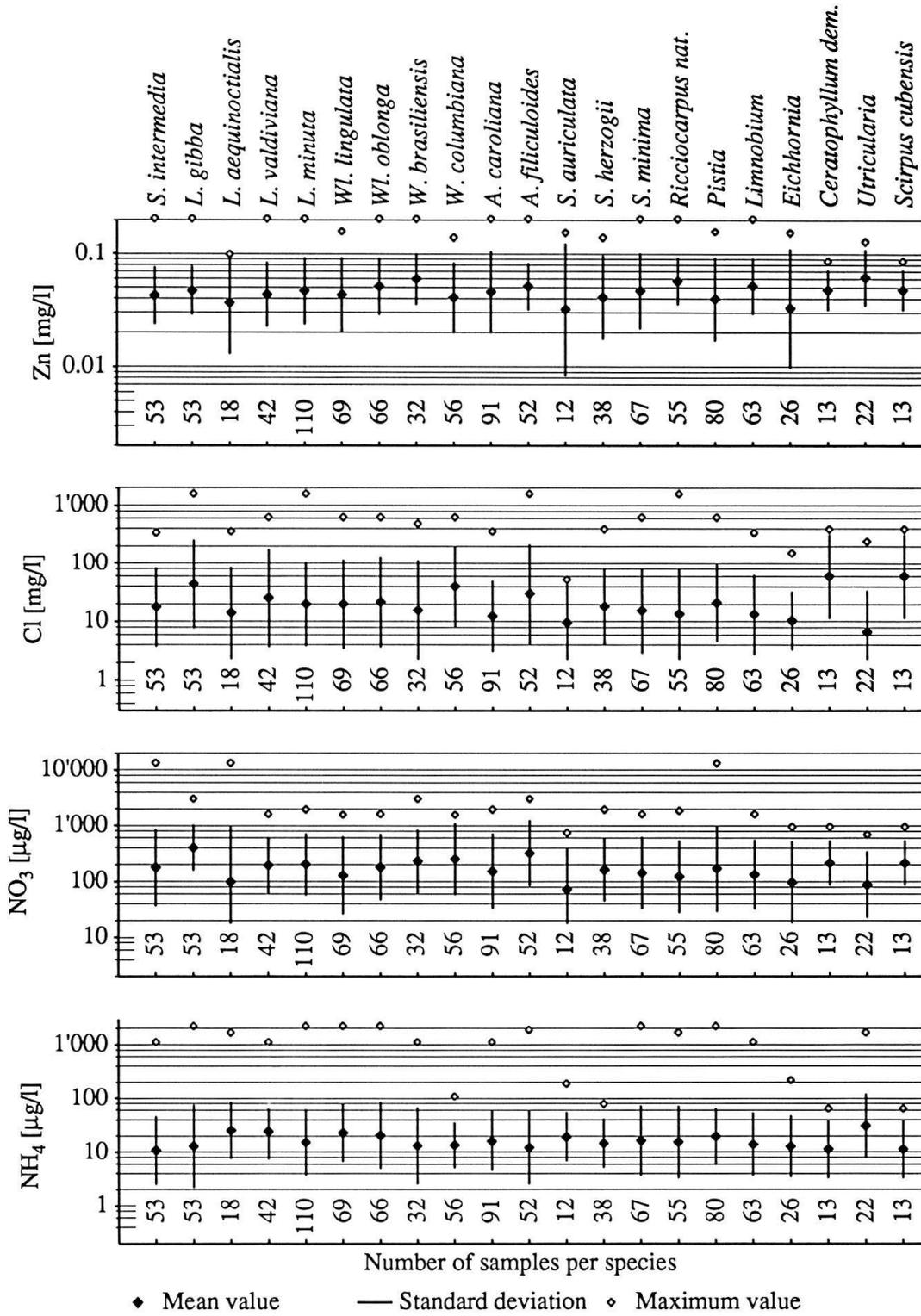


Fig.7. (contin.) Parameters of the water samples with the various species of lemnids.

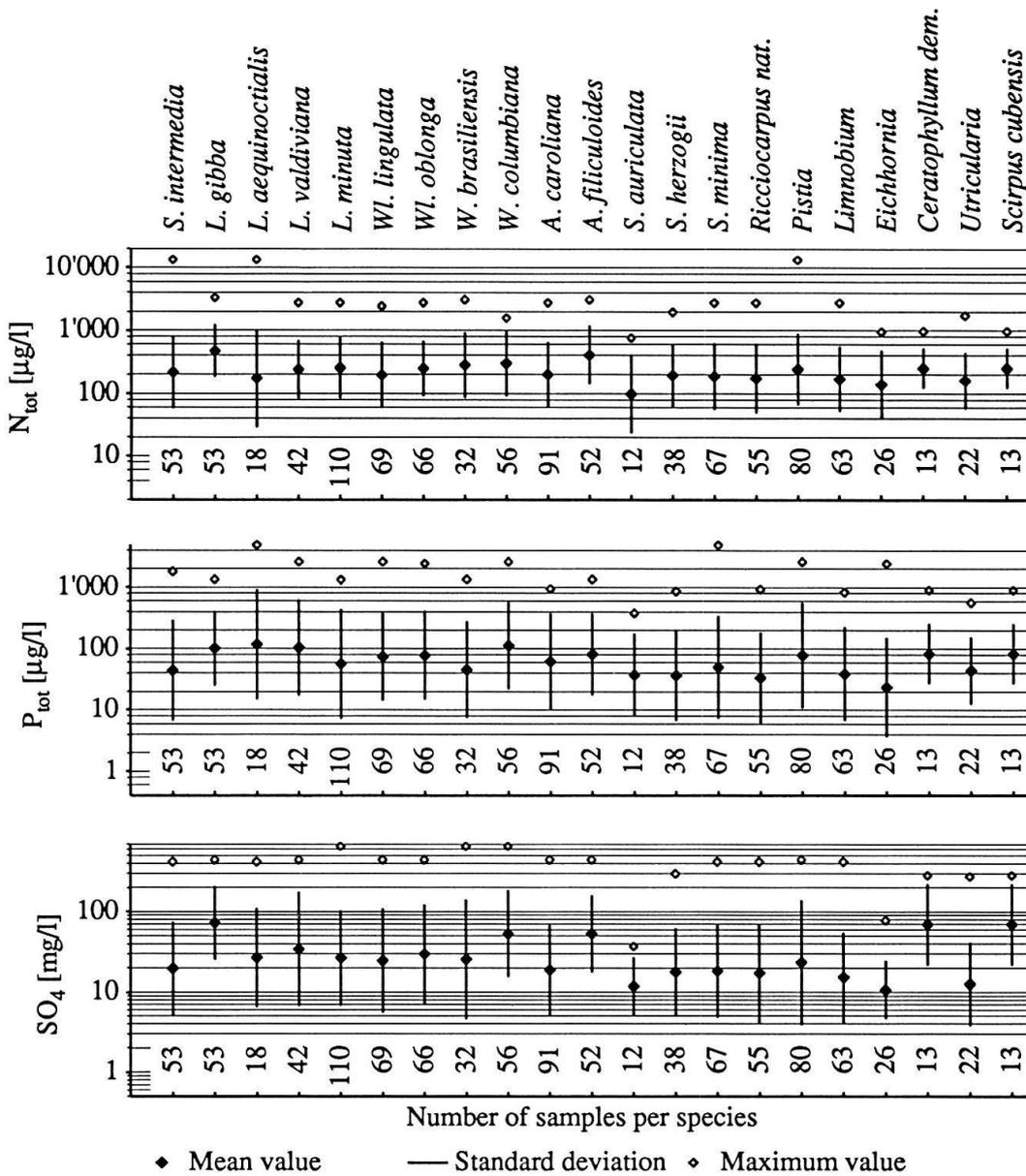


Fig.7. (contin.) Parameters of the water samples with the various species of lemniids.

Table 13. Deviation of the various species from the mean of various water characteristic values.

ions	higher than mean	lower than mean
Na	<i>Lemna gibba</i> <i>Azolla filiculoides</i> <i>Wolffia columbiana</i> <i>Ceratophyllum demersum</i>	<i>Salvinia auriculata</i> <i>Utricularia gibba</i> <i>Eichhornia crassipes</i>
K	<i>Lemna gibba</i> <i>Azolla filiculoides</i>	<i>Salvinia auriculata</i> <i>Eichhornia crassipes</i>
Ca	<i>Lemna gibba</i>	<i>Utricularia gibba</i>
Mg	<i>Lemna gibba</i> <i>Azolla filiculoides</i> <i>Wolffia columbiana</i>	<i>Utricularia gibba</i> <i>Eichhornia crassipes</i>
Fe	<i>Lemna aequinoctialis</i> <i>Salvinia auriculata</i> <i>Utricularia gibba</i>	<i>Eichhornia crassipes</i>
Zn	<i>Utricularia gibba</i> <i>Wolffia brasiliensis</i>	
SO ₄	<i>Lemna gibba</i> <i>Ceratophyllum demersum</i> <i>Wolffia columbiana</i>	<i>Salvinia auriculata</i> <i>Utricularia gibba</i> <i>Eichhornia crassipes</i>
Cl	<i>Lemna gibba</i> <i>Ceratophyllum demersum</i>	<i>Utricularia gibba</i>
N _{total}	<i>Lemna gibba</i> <i>Azolla filiculoides</i>	<i>Salvinia auriculata</i>
P _{total}	<i>Lemna aequinoctialis</i> <i>Lemna valdiviana</i> <i>Wolffia columbiana</i>	<i>Eichhornia crassipes</i> <i>Lemna gibba</i>
total hardness	<i>Lemna gibba</i> <i>Wolffia columbiana</i> <i>Azolla filiculoides</i>	<i>Salvinia auriculata</i> <i>Utricularia gibba</i> <i>Ceratophyllum demersum</i>
carbonate hardness	<i>Lemna gibba</i> <i>Wolffia columbiana</i> <i>Azolla filiculoides</i> <i>Ceratophyllum demersum</i>	<i>Salvinia auriculata</i> <i>Utricularia gibba</i> <i>Eichhornia crassipes</i>
conductivity in the field	<i>Ceratophyllum demersum</i> <i>Lemna gibba</i> <i>Wolffia columbiana</i> <i>Azolla filiculoides</i>	<i>Utricularia gibba</i> <i>Salvinia auriculata</i> <i>Eichhornia crassipes</i> <i>Azolla caroliniana</i>

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
<i>Azolla filiculoides</i>	+++	++	0
<i>Ricciocarpus natans</i>	+++	++	++
<i>Spirodela intermedia</i>	+++	++	+
<i>Wolffia brasiliensis</i>	+++	++	++
<i>Lemna gibba</i>	+++	+++	+
<i>Lemna minuta</i>	+++	+++	++
<i>Wolffiella oblonga</i>	++	+++	++
<i>Wolffia columbiana</i>	++	+++	++
<i>Salvinia minima</i>	+	+++	++
<i>Salvinia herzogii</i>	+	+++	++
<i>Limnobium laevigatum</i>	+	++	++
<i>Azolla caroliniana</i>	+	++	+++
<i>Wolffiella lingulata</i>	+	++	+++
<i>Pistia stratiotes</i>	+	++	+++
<i>Lemna valdiviana</i>	+	++	+++
<i>Lemna aequinoctialis</i>	0	0	+++
<i>Utricularia gibba</i>	0	0	+++

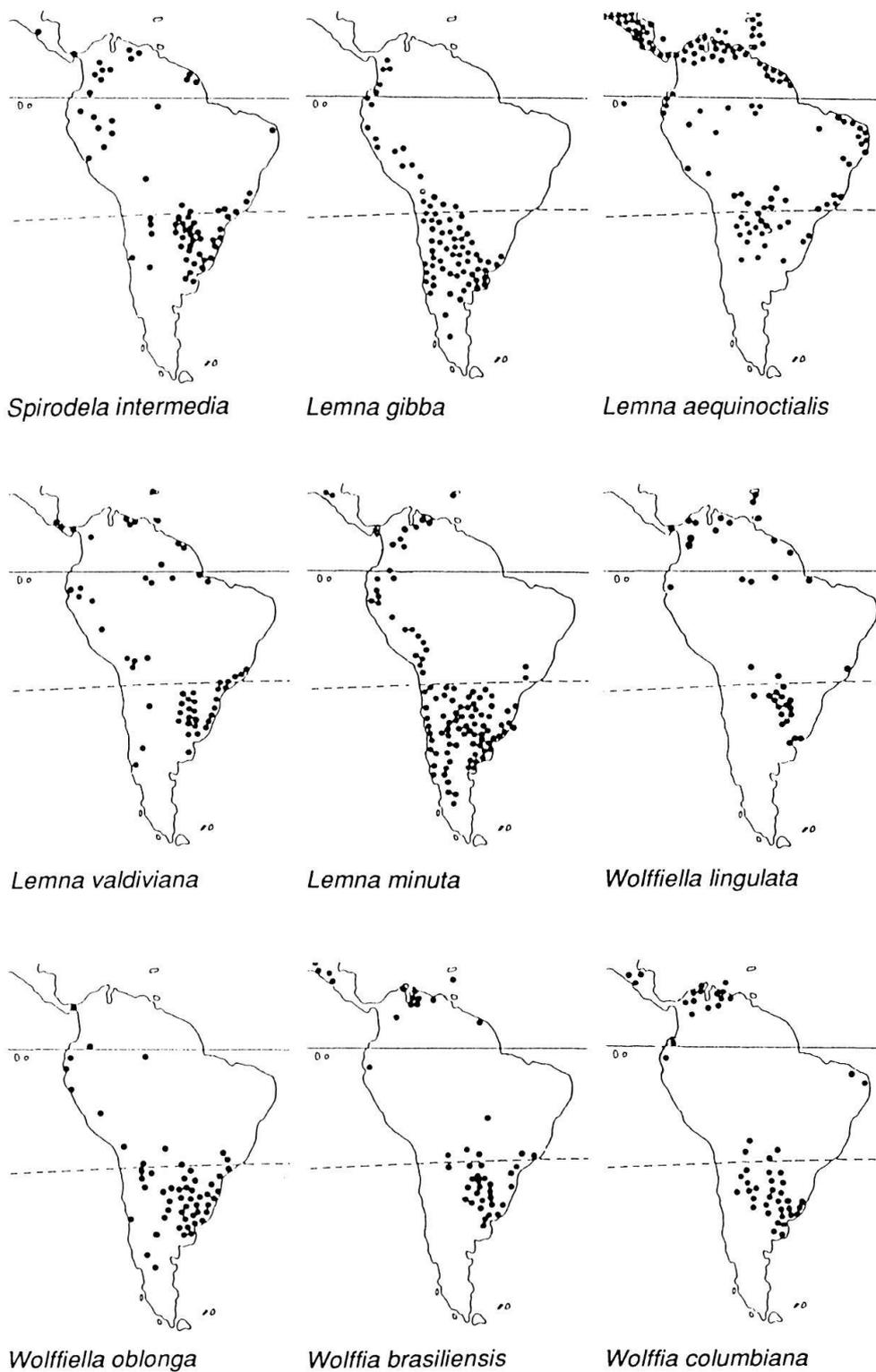


Fig. 8. Distribution of nine *Lemnaceae* species within South America (LANDOLT 1986).

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, with its 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

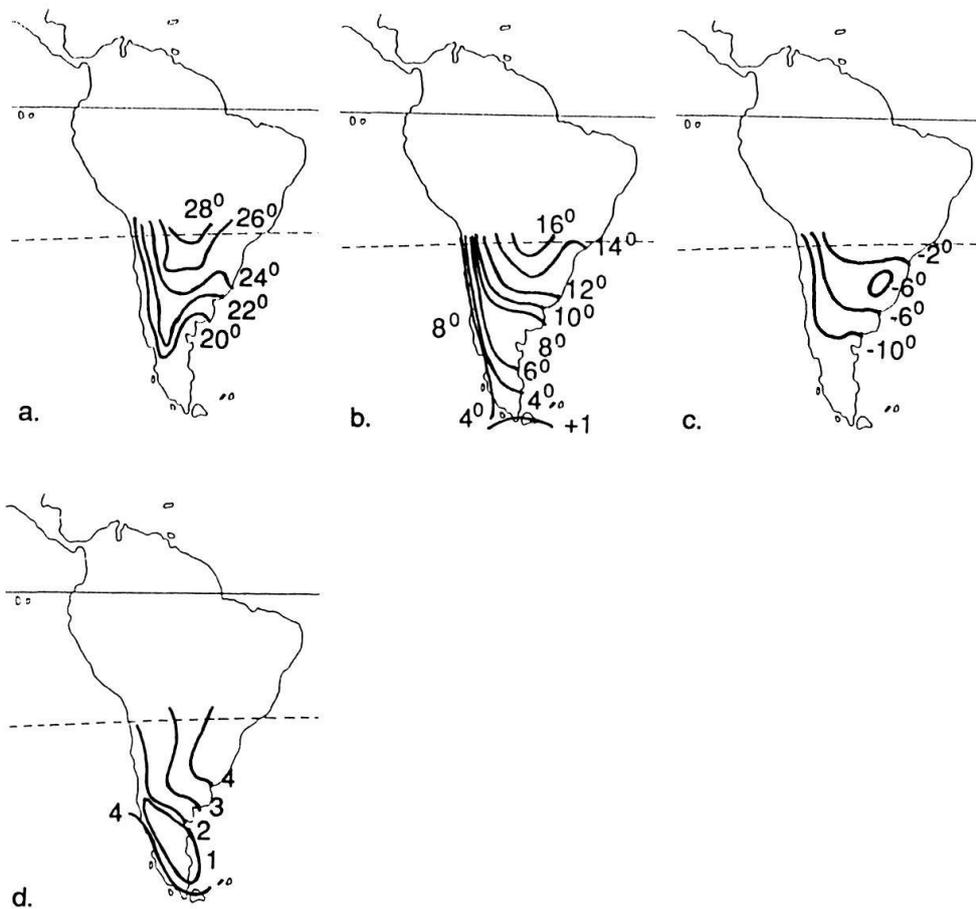


Fig. 9. Climatic factors in Argentina (data put together from climate diagrams of WALTER and LIETH 1967).

a) mean summer temperatures
c) absolute minima temperatures

b) mean winter 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
<i>Spirodela intermedia</i>	+8	-10	> 28	20	3-8
<i>Lemna gibba</i>	-1	-20	26	10	1-4
<i>Lemna aequinoctialis</i>	+8	-20	> 28	20	1-8
<i>Lemna valdiviana</i>	-1	-20	> 28	12	4-8
<i>Lemna minuta</i>	-1	-20	26	16	2-6
<i>Wolffiella lingulata</i>	+8	-8	> 28	20	2-8
<i>Wolffiella oblonga</i>	+8	-10	28	18	2-6
<i>Wolffia brasiliensis</i>	-1	-20	28	22	2-5
<i>Wolffia columbiana</i>	-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 dm²) 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).

elements species	N		P	
	min.	max.	min.	max.
<i>Spirodela polyrrhiza</i>	0.09	2500	0.014	3100
<i>Lemna gibba</i>	0.14	2500	0.017	2700
<i>Lemna aequinoctialis</i>		6300		< 2480
<i>Lemna minuta</i>	0.02	700	0.003	540
<i>Wolffia columbiana</i>	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 nutrients 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 pleustophytes 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

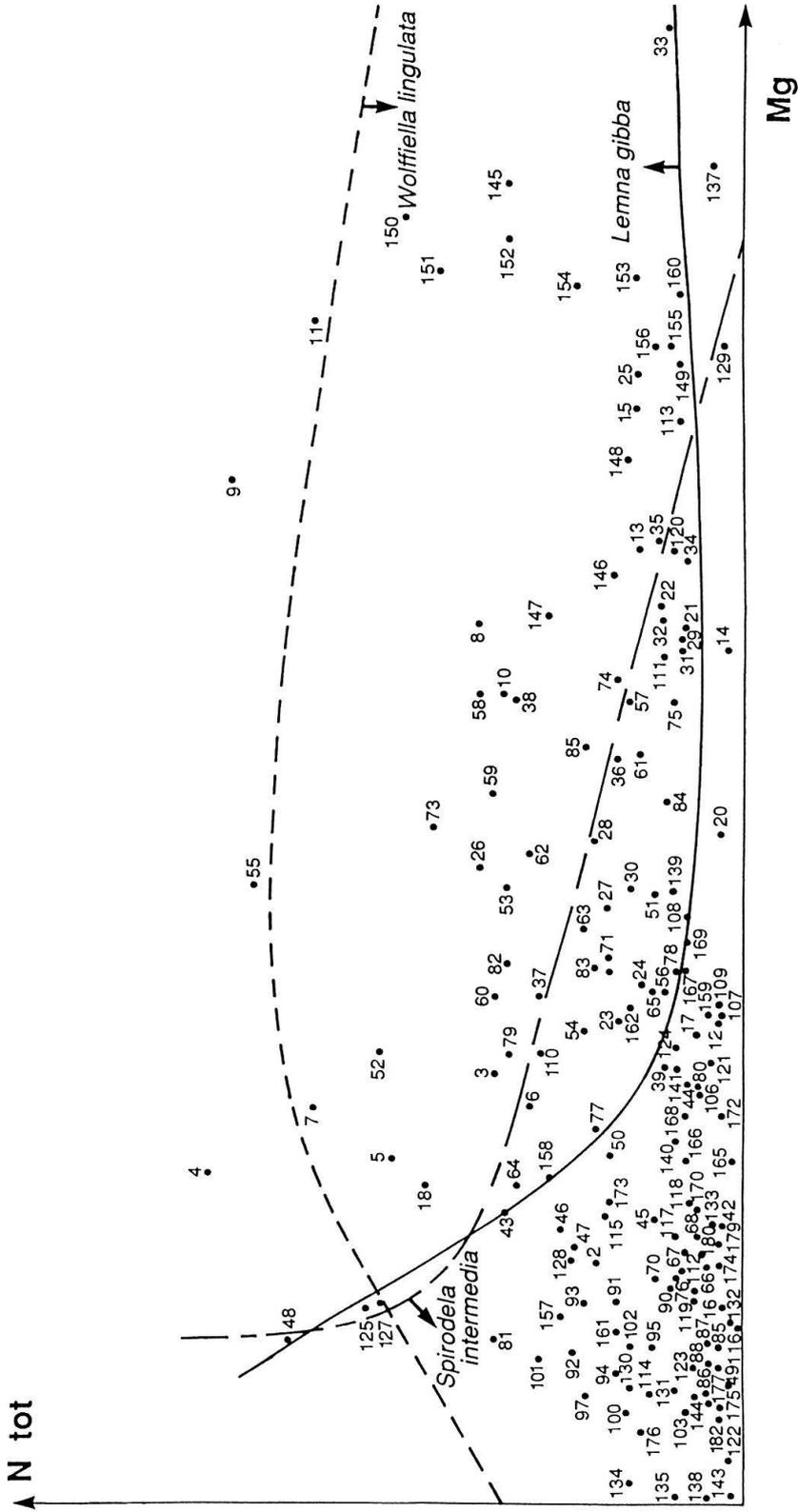


Fig. 10. Direct ordination of Mg content and N content.

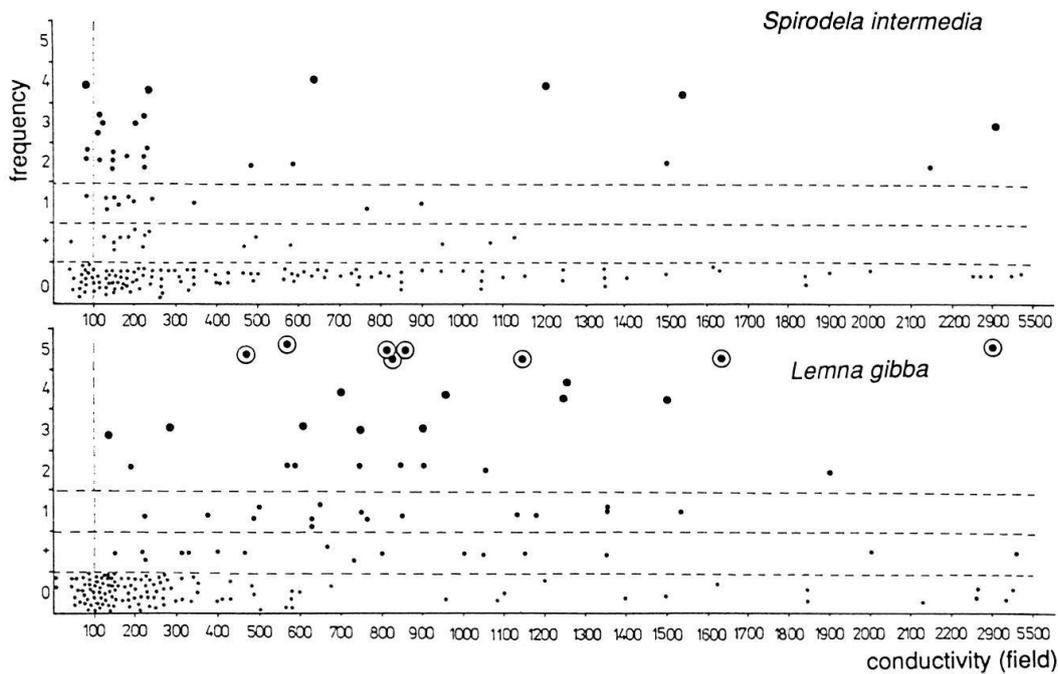


Fig. 11. Distribution of *Lemna gibba* and *Spirodela intermedia* in waters of different conductivity, according to the density of their cover (scale of Braun-Blanquet).

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*,

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 PORTIER 1989).

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 lemniid 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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