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Distribution pattern of the family *Lemnaceae* in North Carolina

by

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Contents

1. Introduction

The distribution of a plant species is dependent on climatic and edaphic factors, competition, reproductive systems and long-distance dispersal potential. Very often the correlations between these factors and the physiological features of the plants are very complex, and our knowledge is often not adequate to thoroughly understand the distribution pattern.

For several years I have been investigating morphology and ecology of the duckweeds. It was therefore tempting to check whether present knowledge of physiological and ecological characters is adequate to explain the occurrence or absence of the species of *Lemnaceae* in a comparatively area.

The family of *Lemnaceae* consists of the smallest flowering plants of the world. The plants grow on or below the surface of the water and very often form dense floating covers on small quiet or slowly flowing water bodies. There are 18 species of *Lemnaceae* native to the United States following the classification of LANDOLT (1980a), ten of which grow in North Carolina. HARRISON and BEAL (1964) investigated the distribution of *Lemnaceae* in North Carolina; the treatment of the *Lemnaceae* in RADFORD et al. (1978) is based on this paper. Out of the three mentioned species of *Lemna*, *L. perpusilla*, in my opinion, is comprised of four different taxa: *L. perpusilla* s.str., *L. aequinoctialis*, *L. obscura* and *L. minor*, the name *L. gibba* being used for inflated specimens of *L. obscura*.

During the 16th IPE and on a fieldtrip following the IPE I had the opportunity to collect samples of *Lemnaceae* in North Carolina and other neighbouring States. I also collected water samples to analyse the different nutrient content of waters with and without members of the family. Finally I looked through Herbarium specimens to check the distribution area of each species occurring in North Carolina.

I am much indebted to the directors and curators of the many herbaria I consulted who sent their material to Zürich. Ms. A. Lüönd analysed the water samples for which I am most grateful. My thanks are also due to Ms. E. Wohlmann for the drawings and Ms. C.D. Brown for the correction of the English language. The advice of Dr. A. Schwabe-Braun on plantsociological aspects and most valuable suggestions of Dr. R.K. Peet are much appreciated.

2. Materials and methods

The following North American Herbaria were checked for specimens from North Carolina: Amherst (MASS), Ann Arbor (MICH), Athens (GA), Austin (TEX, LL), Baton Rouge (LSU), Berkeley (UC), Bloomington (IND), Burlington (VT), Cambridge (A, GH), Chapel Hill (NCU), Chicago (F), Claremont (POM), Columbus (OS), Cullowhee (WCUH), Durham (DUKE), East Lansing (MSC), Fargo (NCU), Fort Collins (USFS), Gainesville (FLAS), Ithaca (BH), Lafayette (LAF), Laramie (RM), Lawrence (KANU), Lexington (KY), Los Angeles (LA), Madison (WIS), Milwaukee (MIL), Missoula (MONTU), Moscow (ID), Murray (MUR), New Orleans (NO), Oxford (MU), Philadelphia (PH, PENN), Pittsburg (CM), Pullman (WS), Raleigh (NCSC), Saint Louis (MO), Saint Paul (MIN), Salt Lake City (UT), San Francisco (CAS, DS), Stillwater (OKLA), Tallahassee (FSU), Tampa (USF), Tucson (ARIZ), University (UNA), Urbana (ILL), Valdosta (VSC), Washington (US). Beside the own collections most material was found in the three main Herbaria of North Carolina: Chapel Hill (NCU), Durham (DUKE), and Raleigh (NCSC).

Locations mapped by HARRISON and BEAL (1964) which could not be found in the Herbaria consulted were incorporated into the distribution map of the whole family. Locations for *Spirodela, Wolffiella and Wolffia* species also show up in the resp. distribution maps. The identification of the *Lemna* species was not possible due to the different species concept.

The methods used for analysis of water samples were the same as those described by LANDOLT and WILDI (1977). The following factors were measured: specific conductance, pH, Ca^{++}, Mg^{++}, K^{+}, Na^{+}, NO_3^{-} - N, NH_4^{+} - N, PO_4^{--} - P.

The water samples were mainly taken in the Coastal Plains of North and South Carolina, and Southern Virginia, a few samples were also taken around Durham and Raleigh.

3. Results

3.1. *The distribution of the Lemnaceae species in North Carolinas*

There are ten species of *Lemnaceae* occurring in North Carlina: *Spirodela polyrrhiza* (L.) Schleiden, *S. punctata* (G.F.W. Meyer) Thompson (= *S. oligorrhiza* Hegelm.), *Lemna perpusilla* Torrey, *L. aequinoctialis* Welwitsch (= *L. paucicostata* Hegelm., *L. perpusilla* auct. amer. p.p.), *L. obscura*

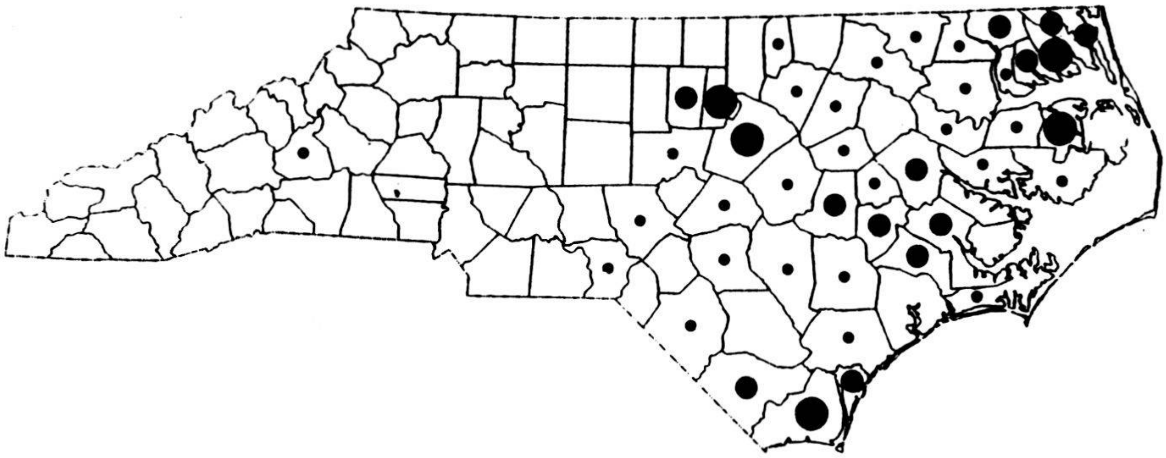


Fig. 1. Distribution map of *Lemnaceae* in North Carolina

- • 1-2 collections
- ● 3-6 collections
- ⬤ >6 collections

(these markings are the same for the figs 1-11)

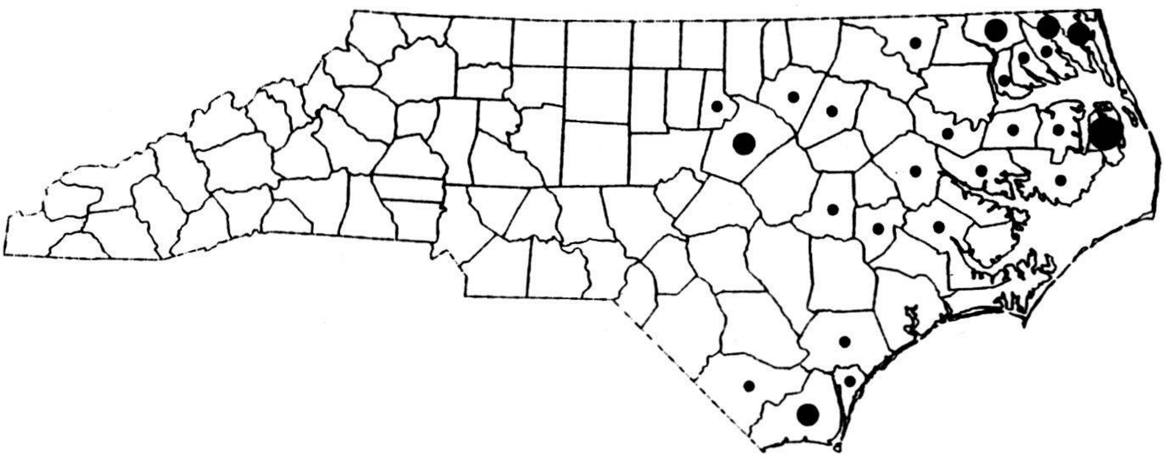


Fig. 2. Distribution map of *Spirodela polyrrhiza*

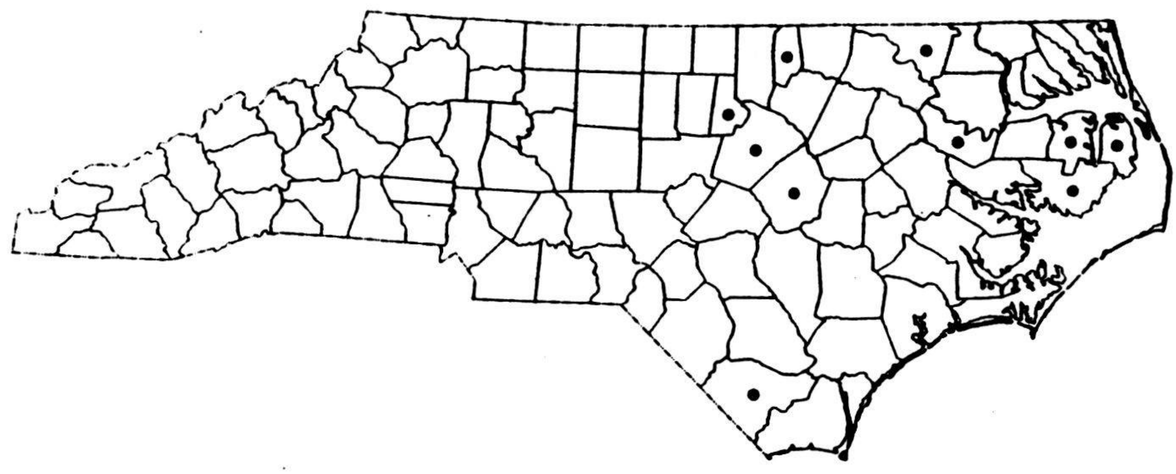


Fig. 3. Distribution map of *Spirodela punctata* in North Carolina

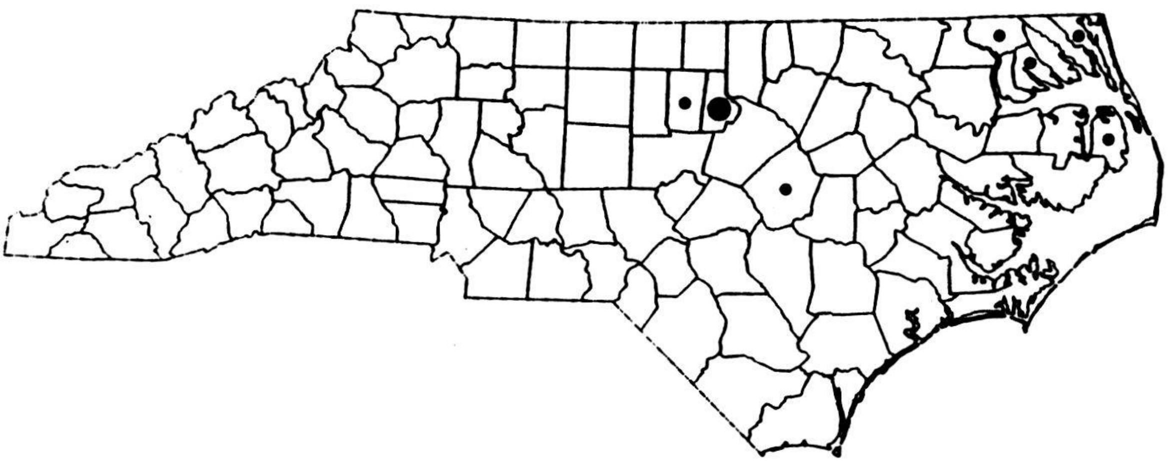


Fig. 4. Distribution map of *Lemna perpusilla* in North Carolina

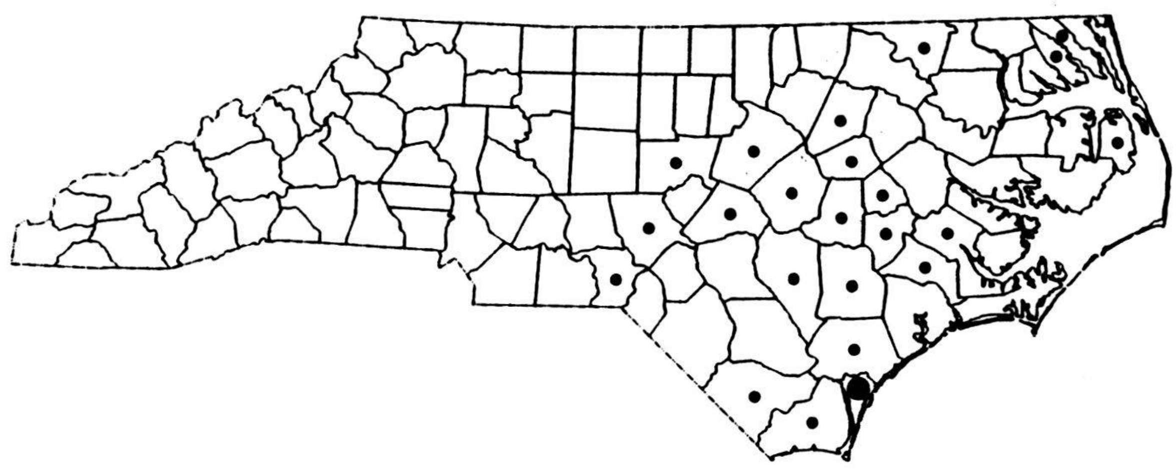


Fig. 5. Distribution map of *Lemna aequinoctialis* in North Carolina

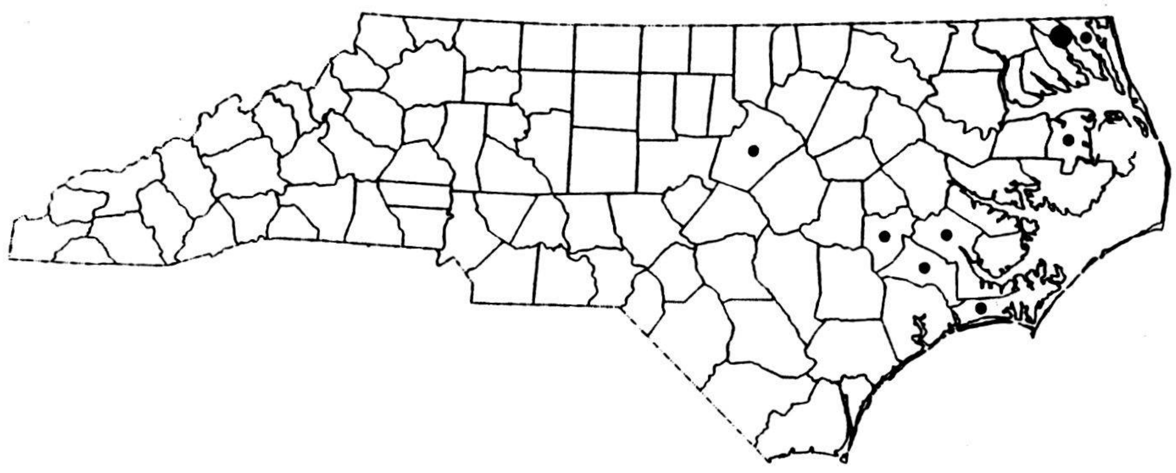


Fig. 6. Distribution map of *Lemna obscura* in North Carolina

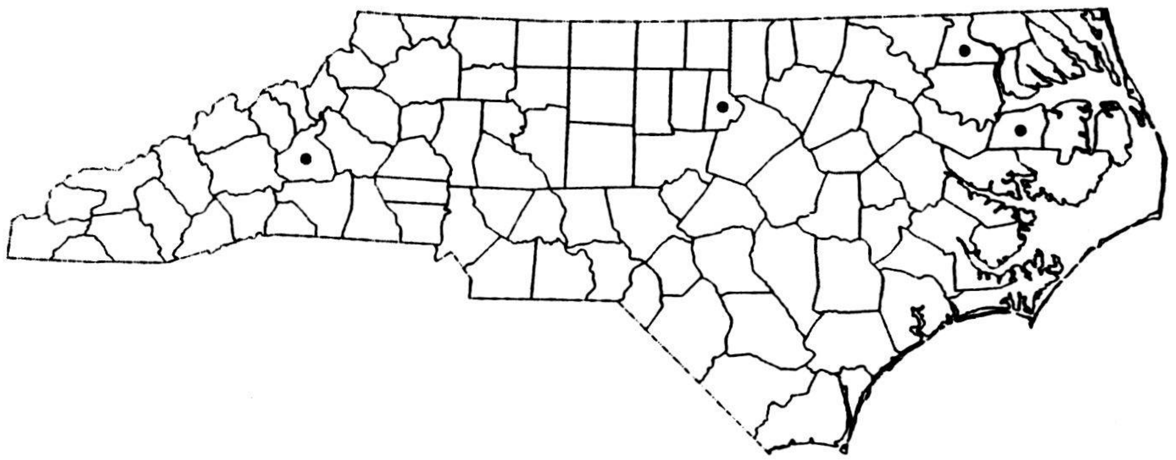


Fig. 7. Distribution map of *Lemna minor* in North Carolina

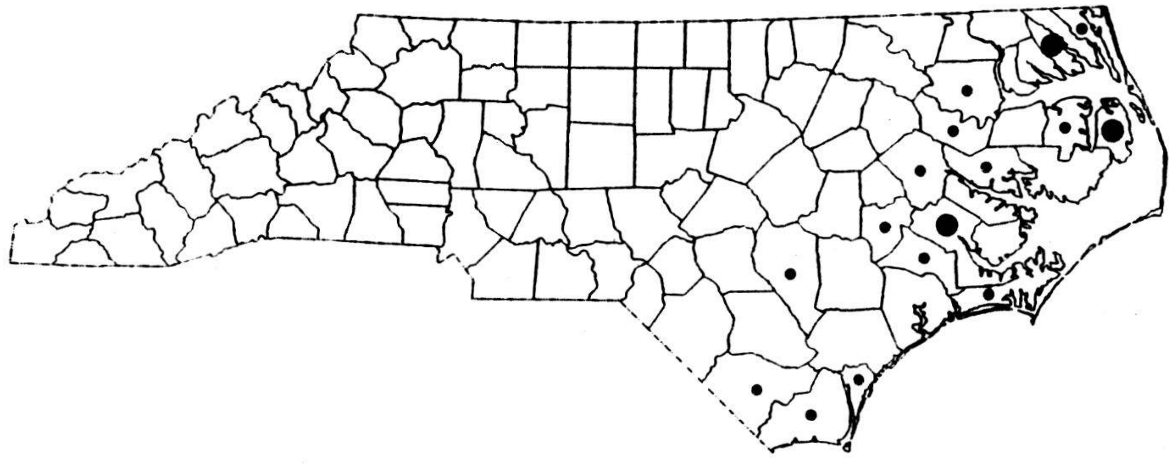


Fig. 8. Distribution map of *Lemna valdiviana* in North Carolina

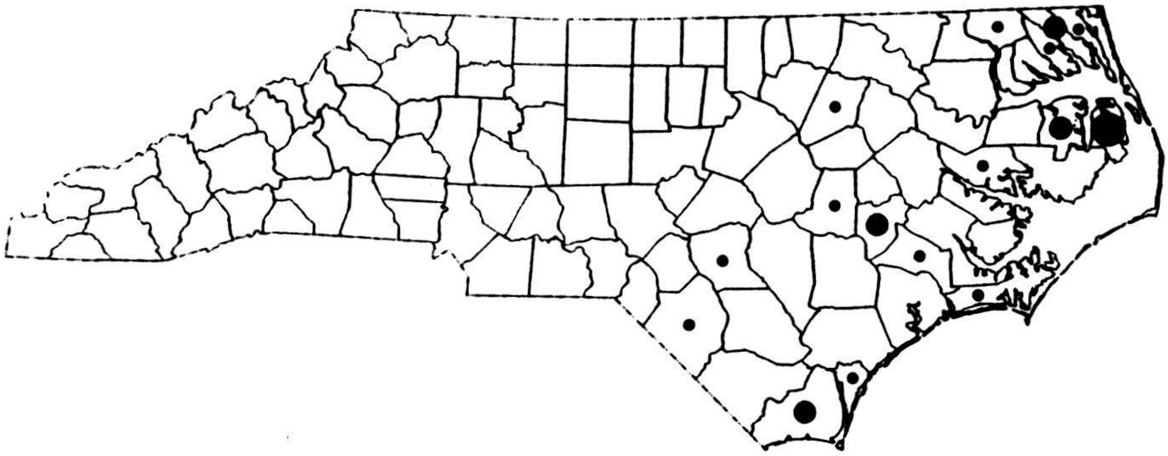


Fig. 9. Distribution map of *Wolffiella gladiata* in North Carolina

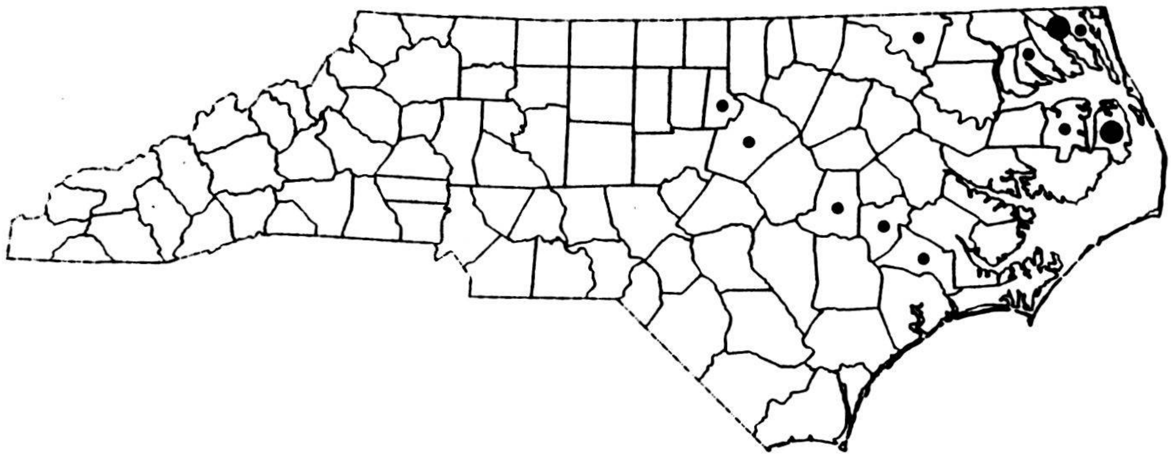


Fig. 10. Distribution map of *Wolffia brasiliensis* in North Carolina

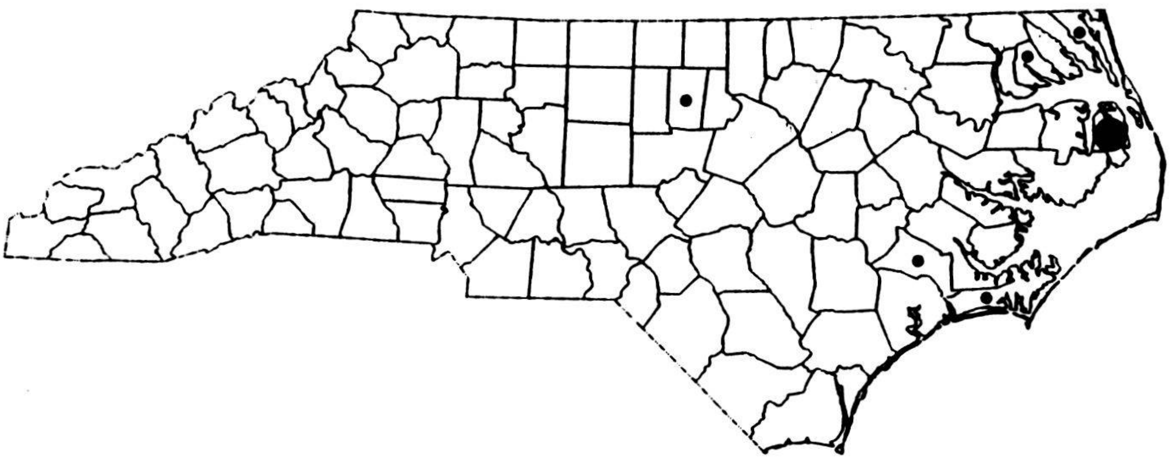


Fig. 11. Distribution map of *Wolffia columbiana* in North Carolina

(Austin) Daubs, *L. minor* L., *L. valdiviana* Phil. (= *L. Torreyi* Austin), *Wolffiella gladiata* Hegelm. (= *W. floridana* [J.D. Smith] Thompson), *Wolffia brasiliensis* Weddell (= *W. papulifera* Thompson), *W. columbiana* Karsten. The first figure shows the distribution of the family. The distribution of the different species is presented in Figs 1 to 11. It can easily be seen that the main distribution of the family within North Carolina is in the Coastal Plain. In the Piedmont *Lemnaceae* are only present in the eastern part. One single sample from the Mountains collected in a fish hatchery is represented in the investigated Herbaria.

The most equally distributed species within the family area is *Spirodela polyrrhiza*, *Lemna minor* and *L. perpusilla* are restricted to the northern part of the State, *Wolffiella gladiata*, *Lemna obscura* and *L. valdiviana* are only known in the Coastal Plain. The other species are scattered around the area within which the family is found. LEONARD (1972) reports *Lemna minor* from Durham Co. The collection (Leonard No. 5089 in Herb. NCSC) consists essentially of flowering and fruiting *L. perpusilla*. *L. minor* grows in the same region, but flowering and fruiting is extremely rare.

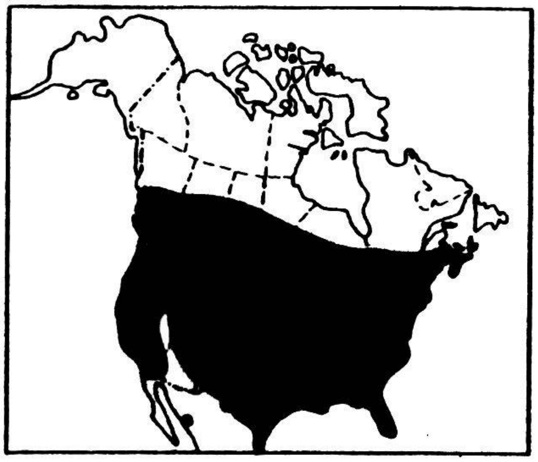
3.2. *The distribution of the North American species of the Lemnaceae in relation to some climatic factors*

3.2.1. *The distribution in North America*

A survey of the distribution of *Lemnaceae* species has been made on a world-wide basis (LANDOLT in prep.). The approximate distribution of the species within North America is shown in the Figs 12 to 29. There are eight additional species occurring in the USA but not in North Carolina: *Lemna trisulca* L., *L. turionifera* Landolt, *L. gibba* L., *L. minuscula* Herter (= *L. minima* Phil. nec Thuill.), *Wolffiella lingulata* Hegelm., *W. oblonga* (Phil.) Hegelm., *Wolffia borealis* (Engelm.) Landolt (= *W. punctata* auct. nec Griseb.), *W. globosa* (Roxb.) Hart. & Plas.

3.2.2. *Climatic factors which are correlated with distribution area*

The different species show a distribution pattern which can be correlated



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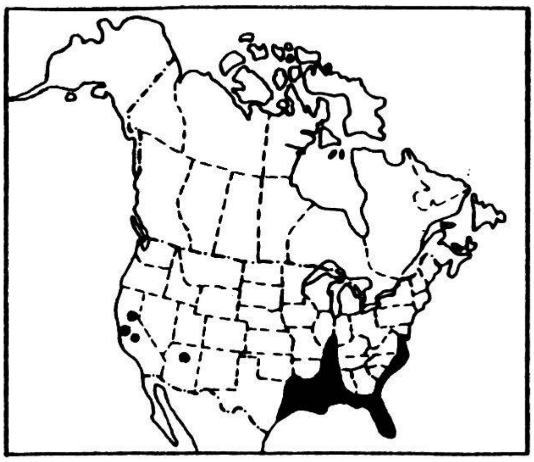

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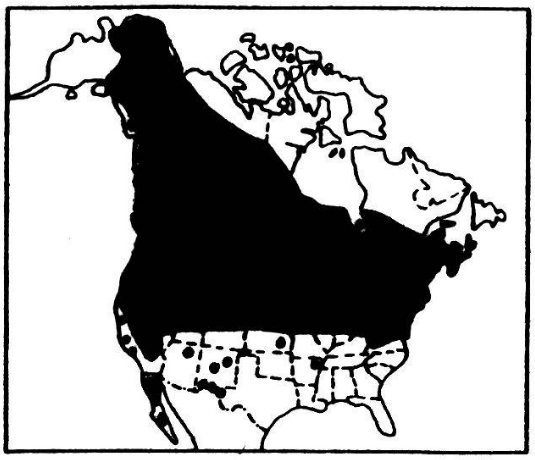

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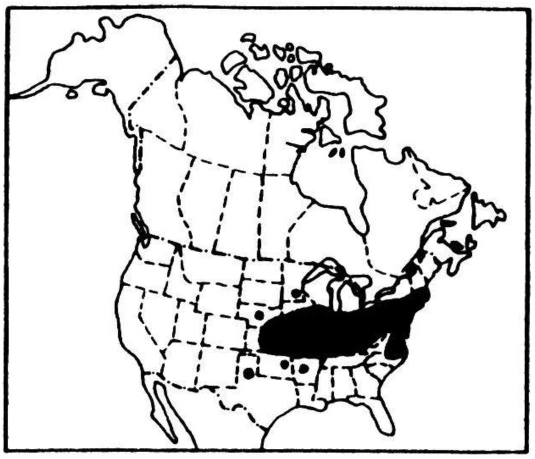

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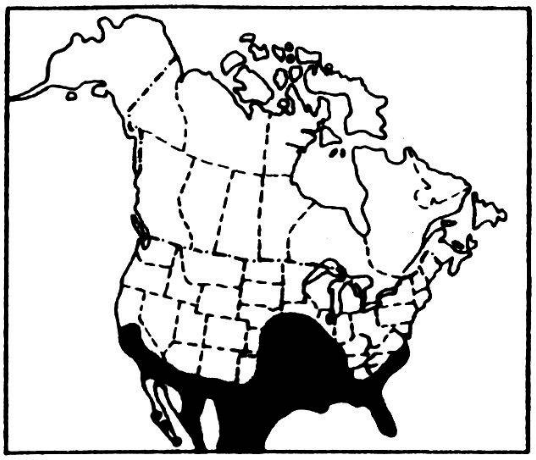
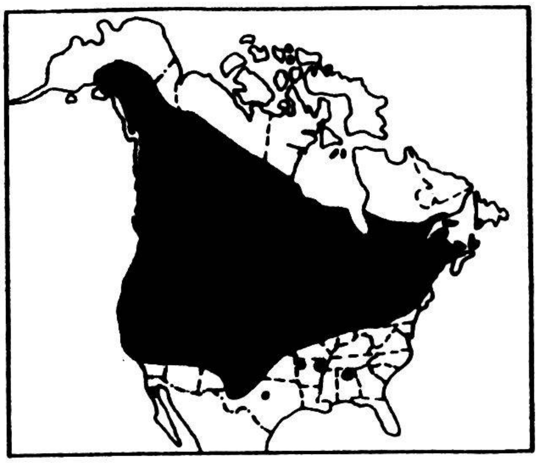


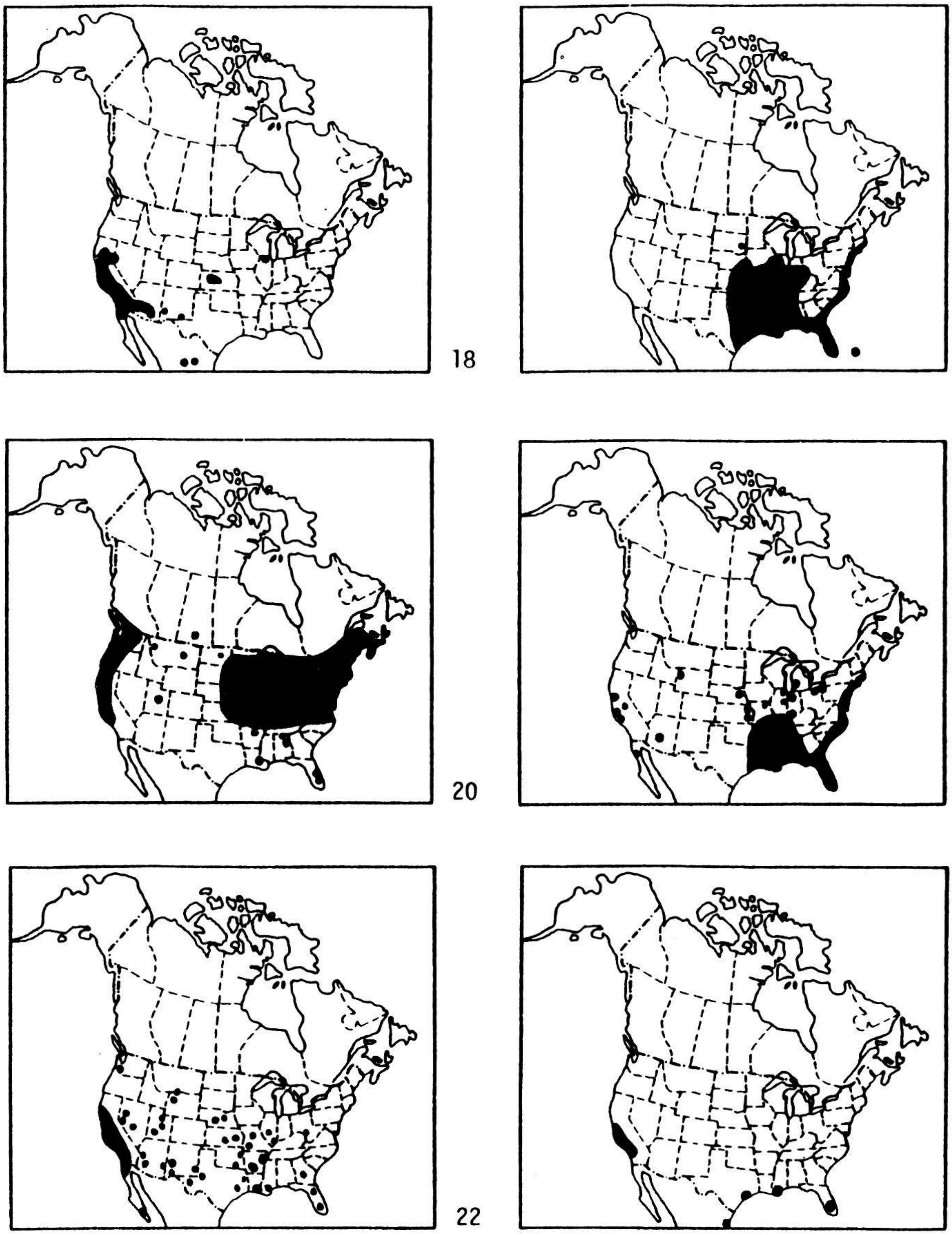
16



17

Figs 12-17. Distribution maps of *Lemnaceae* in North America

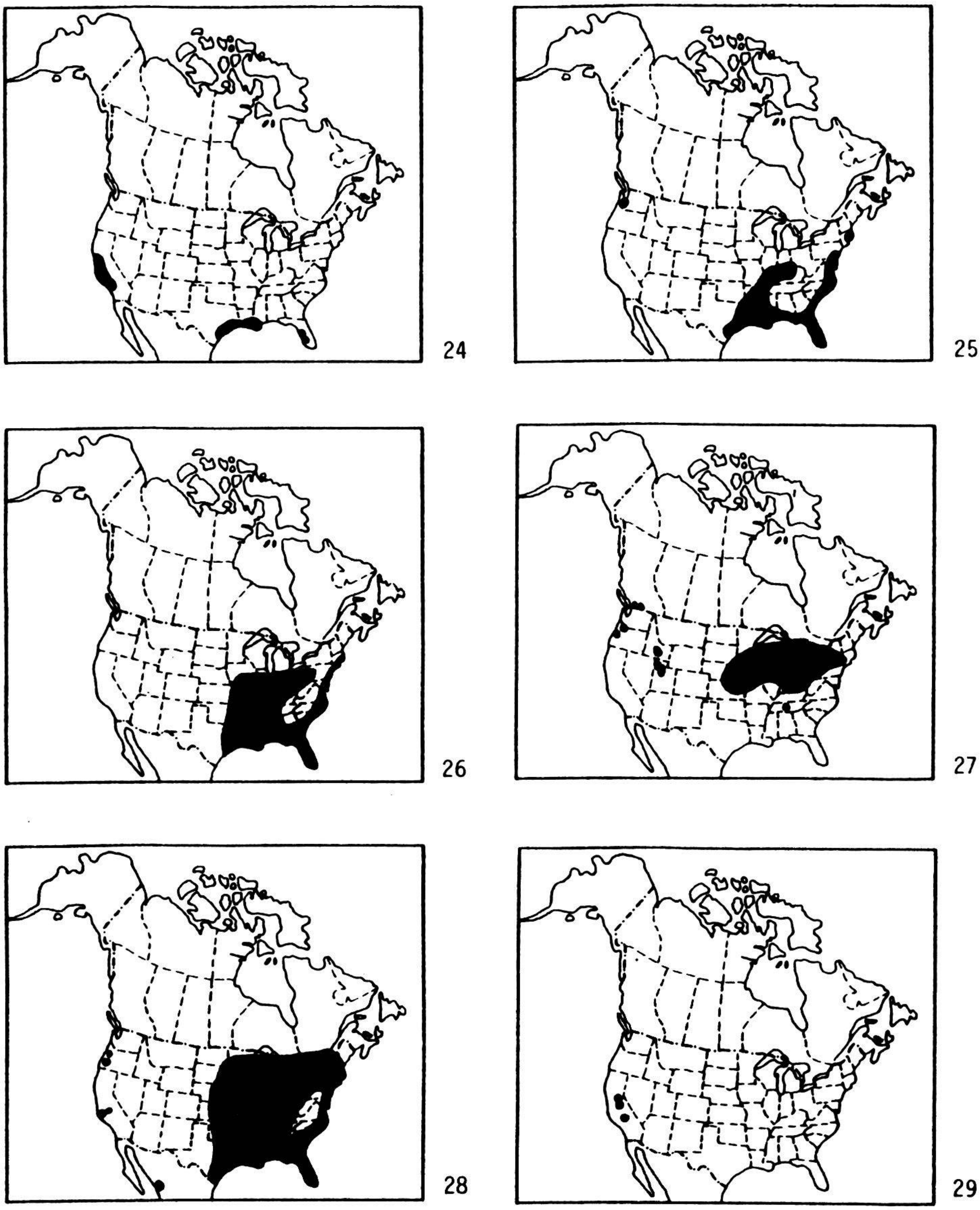
12. *Spirodela polyrrhiza*, 13. *S. punctata*, 14. *Lemna trisulca*, 15. *L. perpusilla*, 16. *L. aequinoctialis*, 17. *L. turionifera*



18 19 20 21 22 23

Figs 18-23. Distribution maps of *Lemnaceae* in North America

18. *Lemna gibba*, 19. *L. obscura*, 20. *L. minor*, 21. *L. valdiviana*, 22 *L. minuscula*, 23. *Wolffiella lingulata*



Figs 24-29. Distribution maps of *Lemnaceae* in North America

24. *Wolffiella oblonga*, 25. *W. gladiata*, 26. *Wolffia brasiliensis*, 27. *W. borealis*, 28. *W. columbiana*, 29. *W. globosa*

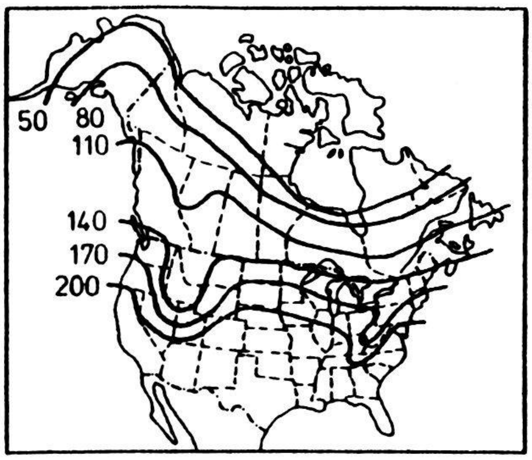
with some climatic factors. However, these factors are not directly responsible for the presence or absence of given species. The species are dependent on many complex local factors which are partly influenced by the macroclimatic factors. If we compare macroclimatic factors with the distribution of a species, it is important to bear in mind the following aspects:

- the knowledge of the climatic factors prevailing in large parts of the world is not very precise
- the local conditions may be more or less favourable for the existence of a species than it could be expected from the macroclimatic conditions. For instance, locally warmer waters fed by warm springs or coming from warmer regions can be colonized by species for which the climate would normally be too cold.
- since most species of *Lemnaceae* are easily distributed by birds there is always the possibility of the occasional introduction of *Lemnaceae* species which can only remain for shorter periods (in particular during favourable years); from Herbarium specimens it is difficult to decide if the plants result from a short-term introduction or correspond to an established colony.
- competition is an essential factor which limits the occurrence of a species even if the climatic conditions are favourable.

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

1. *Number of days with a mean temperature above 10°C* (Fig. 30).

This factor is used as a measure of the growing season of the plants. The temperature of water will very often be higher than the mean air temperature, especially during periods of sunshine. Species with a low minimum growth temperature may grow in areas where for short periods of time the mean temperature rises above 10°C, species with a high minimum growth temperature require much longer periods during which the mean temperature rises above 10°C. Possible local deviations may be because warm springs have a longer, and cool springs a shorter vegetation period than that expected from the general climate.



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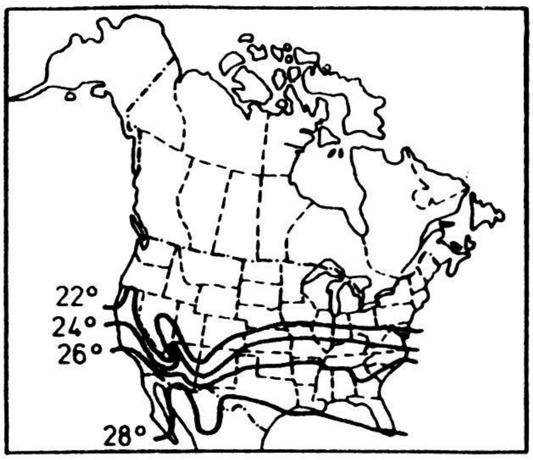

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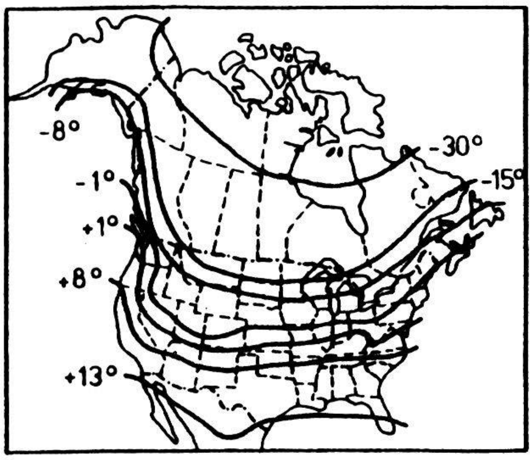

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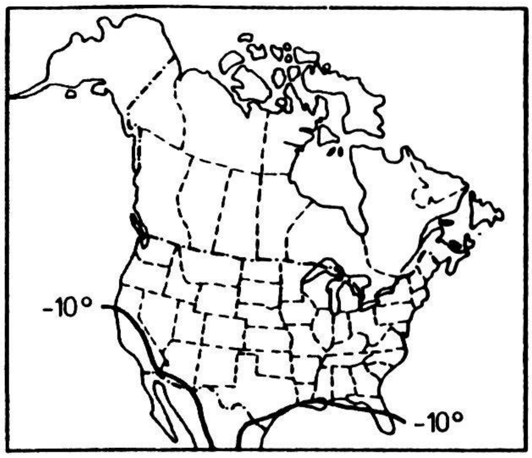

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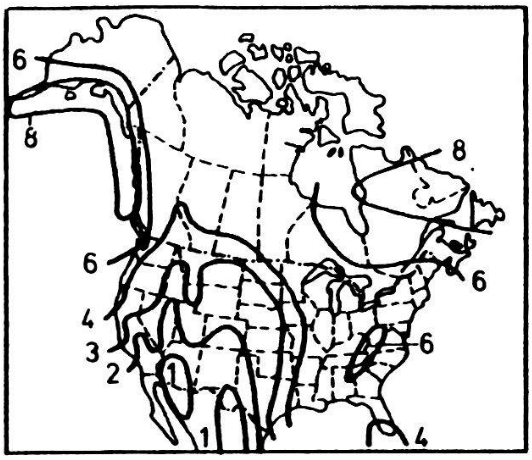

34

Figs 30-34. Maps of climatic factors of North America

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

31. Mean summer temperatures. 32. Mean winter temperatures.

33. Absolute minimum temperatures (-10°C). 34. Aridity factor of Martonne.

2. *Mean summer temperatures* (Fig. 31).

Water temperatures are generally found to be higher in regions with high mean summer (June, July, August) air temperatures. Most *Lemnaceae* species can survive temperatures of up to 50°C for a short time. For longer periods temperature limiting the growth of *Lemnaceae* is much lower ranging from 26° to 38°C depending upon the species or the clones (LANDOLT 1957). A mean summer temperature of 22°C corresponds approximately to a limiting water temperature of 26° to 30°C. Local deviations from this pattern may be found in cool springs, in shaded areas, and in waters originating from cooler mountainous regions where the water temperature allows growth of species with a lower temperature limit.

3. *Mean winter temperatures* (Fig. 32).

Mean temperatures during winter time (December, January, February) determine the water temperature, and are correlated with the frequency with which freezing temperatures occur, the thickness of the ice cover and the length of the growing season. Those species which are not very frost resistent or which do not have the ability to sink to the bottom of the water and thus avoid low temperatures grow only in regions with mild winter temperatures. There may be found the following local deviation: locally warmer waters may allow species to grow further north.

4. *Absolute minimum temperatures* (Fig. 33).

Some species with tropical and subtropical distribution are very sensitive to frost. Even if the mean winter temperatures are relatively high they are not found growing in regions where severe frosts occur every few years. Absolute minimum temperatures are a measure of frost intensity and frequency.

5. *Aridity factor of Martonne*: $i = \frac{\text{annual precipitation in cm}}{\text{mean annual temperature in } ^{o}\text{C} + 10}$
(Fig. 34)

The aridity factor (i) is the coefficient of the annual precipitation in cm divided by the mean annual temperature in °C + 10. This factor is generally related to the concentration of minerals in the water. Very dry areas (with a low aridity factor) may have toxic concentrations of minerals (e.g. magnesium); furthermore the waters may dry out periodically. In wet regions the ion content of the water and, correspondingly, the nutrient content is generally very low: duckweeds floating on the surface of the water are not able to take up their nutrients by roots from the soil and are therefore dependent upon higher concentrations of nutrients in the water. There are many deviations from this pattern: If the waters originate from a more humid or more arid region various species may be able to grow in a region which is generally too dry or too humid for the species. In regions with soils poor in minerals (e.g. sandy soils, fens, soils on acidic silicate rocks such as granite, gneiss) the waters compare with those found in a more humid climate. Waters surrounded by fields which are intensely fertilized or which have inlets of waste water generally have a higher nutrient content than that expected from the aridity factor.

The distribution of each species may be explained by a combination of limiting factors (Table 1).

3.2.3. *The climatic limitations of the different North American species of Lemnaceae.*

1. *Spirodela polyrrhiza*

S. polyrrhiza has an almost world-wide distribution. It occurs in all states of the contiguous United States. It reaches its northern limit far north of the Canadian border. The northern limit is the isoline of 110 days with a mean temperature above 10°C. To overwinter it forms turions which sink to the bottom of the water; thus it can stand very cold winter temperatures. The turions require temperatures between 12° and 15°C to germinate (JACOBS 1947, LANDOLT 1957) and therefore a relatively long period with temperatures above 10°C. *S. polyrrhiza* avoids only the very humid regions ($i>8$) of the Appalachian Mountains and of the north-eastern and north-western part of North America and the driest regions ($i<2$) of the South-west. In the higher regions of the Rocky Mountains the vegetation period is too short for *S. polyrrhiza*.

2. *Spirodela punctata*

S. punctata with its mainly tropical-subtropical distribution is found in all continents. In North America it is considered to have been introduced; it was

Table 1. Limiting climatic factors of North American *Lemnaceae*

	minimum number of days with a mean temperature above 10°C	highest mean summer temperatures in °C	lowest mean winter temperatures in °C	absolute minimum temperatures in °C	aridity factor of Martonne (minimum - maximum)
Lemnaceae	50	>30	-40	<-40	1-8
Spirodela polyrrhiza	110	>30	-40	<-40	2-8
S. punctata	200	28	+ 1	<-20	3-8
Lemna trisulca	50	22	-40	<-40	1-8
L. perpusilla	140	24	- 8	<-20	3-6
L. aequinoctialis	170	>30	(+ 8)	<-20	1-8
L. turionifera	80	26	-40	<-40	1-6
L. gibba	50	26	- 1	<-20	1-4
L. obscura	170	28	+ 1	<-20	3-6
L. minor	50	24	-15	<-20	3-8
L. valdiviana	170	30	+ 1	<-20	4-8
L. minuscula	170	26	+ 1	<-20	1-5
Wolffiella lingulata	260	30	+ 8	>- 8	2-8
W. oblonga	260	28	+ 8	>-10	2-6
W. gladiata	170	28	+ 1	<-20	4-6
Wolffia brasiliensis	170	30	- 1	<-20	3-6
W. borealis	140	22	- 8	<-20	2-5
W. columbiana	140	30	- 8	<-20	3-6
W. globosa	200	>30	+ 1	<-20	3-8

observed for the first time in 1930 in Kansas City, Missouri (SAEGER 1934). Today the species has a wide distribution area in North America and possibly occupies most of its potential climatic growing area. The northern limit of the species is the $+1^{\circ}C$ winter isotherm. *S. punctata* is unlike *S. polyrrhiza*, *Lemna turionifera* or the *Wolffia* spp. unable to form abundant turions which sink to the bottom of the water during cold temperatures; on the other hand, it is more sensitive to long cold temperatures than *Lemna minor* and *L. gibba*. Therefore it is absent from most of the northern and continental states. It is absent or only found in local areas in the drier regions of the South-west ($i<3$).

3. *Lemna trisulca*

L. trisulca is found growing further north than any other species of *Lemnaceae* but it is rare in the Southern hemisphere (East Africa, New Guinea, Australia). The northern limit is the isoline of 50 days of mean temperature above $10^{\circ}C$ in Northern Canada and Alaska. In the mountains it nearly reaches the timber-line. The southern limit coincides with the $22^{\circ}C$ isotherm of mean summer temperatures. Therefore it grows only on the mountains in the southern part of the United States. It is absent or only present locally in humid or dry regions ($i > 8$ and <1).

4. *Lemna perpusilla*

L. perpusilla is an endemic species in the north-eastern part of the US, extending from north-western Texas and North Carolina to southern Minnesota and southern Quebec. The isoline of 140 days with a mean temperature above $10^{\circ}C$ (or $-8^{\circ}C$ isotherm of mean winter temperatures) forms the northern limit, the $24^{\circ}C$ isotherm of mean summer temperatures is correlated with the southern limit. The species is able to overwinter in the seed stage which is not very sensitive to cold temperatures. It is absent from the drier western half of the US ($i<3$).

5. *Lemna aequinoctialis*

The pantropic *L. aequinoctialis* is very widespread in the southern US. The species readily forms seeds and is able to withstand dry periods and cold temperatures in this form. Since the seeds are only formed during warm periods and germinate immediately in warm water the only way in which the seeds can survive cold periods is to dry out after ripening. *L. aequinoctialis* needs relatively high temperatures (at least 13°C to 16°C, cf. LANDOLT 1957) for its growth. The northern limit is therefore formed by the 8°C isotherm of mean winter temperatures. Exceptionally they can reach the isoline of 170 days with a mean temperature above 10°C where the waters dry out during winter time (e.g. in rice fields, fish ponds). In the US *L. aequinoctialis* is absent from the southern States only in high mountain areas and true deserts ($i<1$).

6. *Lemna turionifera*

L. turionifera is distributed in North America and in Central and North Asia. It reaches its northern limit at the isoline of 80 days with a mean temperature above 10°C. The southern limit is formed by the 26°C isotherm of mean summer temperatures. *L. turionifera* is able to overwinter in the turion stage on the bottom of the water. It avoids humid and very dry regions ($i>6$ and <1). The absence or rarity of *L. turionifera* in many of the eastern States is probably due to the competition of the morphologically similar species *L. obscura* and *L. minor*.

7. *Lemna gibba*

L. gibba essentially has a mediterranean distribution in North and South America, Europe, South-western Asia and Africa. In the US it is mainly found in California. The northern limit is the -1°C isotherm of mean winter temperatures, the southern limit is the 26°C isotherm of mean summer temperatures. It needs relatively high concentrations of Ca^{++}, Mg^{++} and other nutrients, therefore it is absent from humid and subhumid regions ($i>4$). East of the Rocky mountains it only grows in small areas of central Nebraska and southern Illinois. The rarity of this species east of the Rocky Mountains may be partly due to the competition of *L. turionifera* and *L. obscura*.

8. *Lemna obscura*

L. obscura is an endemic species of southern North America. Outside of the continental US it grows in the mountainous regions of Mexico (rare) and in Hawaii (possibly introduced). The northern limit is formed by the +1°C isotherm of mean winter temperatures, the southern limit by the 28°C isotherm of mean summer temperatures. The western limit is reached at the 3 isoline of the aridity factor.

9. *Lemna minor*

L. minor outside of the tropics has an almost worldwide distribution. It is absent from South America, West Africa, most of Australia, and Eastern Asia. This species has its main distribution in cool temperate regions of rather oceanic character. The northern limit is formed by the $-15^{o}C$ isotherm of mean winter temperatures, the southern limit by the $24^{o}C$ isotherm of mean summer temperatures. It is absent or very rare in drier regions ($i<3$).

10. *Lemna valdiviana*

L. valdiviana shows little distinction either morphologically or ecologically from *L. minuscula*. It is also an American species, has the same northern limit as *L. minuscula* but almost no limit within warm regions. Whereas *L. minuscula* has its main distribution in rather arid warm temperate regions *L. valdiviana* grows mainly in tropical, subtropical and temperate humid regions (i between 4 and 8). In North America it has the centre of its distribution in the South-eastern States.

11. *Lemna minuscula*

L. minuscula is an American species. It has its main distribution in the mediterranean climate. The northern limit is the $+1^{o}C$ isotherm of mean winter temperatures, the southern limit the $26^{o}C$ isotherm of mean summer temperatures. *L. minuscula* is absent from humid and very dry regions ($i >5$ and <1). In North America *L. minuscula* grows mainly in the South-west.

12. *Wolffiella lingulata*

W. lingulata is an American species with a mainly tropical-subtropical distribution. The northern limit is formed by the $8^{o}C$ isotherm of mean winter temperatures and superimposed by the $-8^{o}C$ isoline of absolute minimum temperatures. This species is sensitive to frost. It is absent only from the driest and the most humid regions ($i <2$ and >8). In the US it is restricted to the most southern part (California, southern Florida, southern Louisiana and south-eastern Texas).

13. *Wolffiella oblonga*

W. oblonga is an American species and shows little distinction when compared with *W. lingulata*. It is ecologically related to *W. lingulata* in a similar manner to the relationship of *L. minuscula* to *L. valdiviana*. *W. oblonga* is a little less sensitive to frost (-10°C isoline of absolute minimum temperatures) and does not grow in very warm regions (28°C isotherm of mean summer temperatures forms its limit within warm regions). The centre of its distribution lies in more arid regions (i between 2 and 5). In North America it has almost nearly the same distribution as *W. lingulata* but also grows a little further north.

14. *Wolffiella gladiata*

W. gladiata is an endemic species of the south-eastern part of North America. The only locality where it is found outside of the US lies in Mexico D.F. It is the only species of *Wolffiella* in the world which grows outside of tropical-subtropical regions due to the ability to sink to lower layers of the water when temperature conditions become unfavourable. The northern limit is formed by the isoline of 170 days with a mean temperature above 10°C (or by the +1°C isotherm of mean winter temperatures), the southern limit by the 28°C isotherm of mean summer temperatures. It is rather narrowly restricted to subhumid conditions (i between 4 and 6).

15. *Wolffia brasiliensis*

W. brasiliensis is an American species which has its northern limit at the isoline of 170 days with a mean temperature above 10°C. The species is able to overwinter in the turion stage on the bottom of the water. It grows only in a subarid to subhumid climate (i between 3 and 6). In North America it is mainly distributed in the south-eastern part.

16. *Wollfia borealis*

W. borealis is morphologically related to *W. brasiliensis*. It grows further north, its northern limit being the isoline of 140 days with a mean temperature above 10°C. The southern limit is formed by the 22°C isotherm of mean summer temperatures. It also grows in slightly drier areas than *W. brasiliensis* (i between 2 and 5). In North America the species is restricted to southern British Columbia, southern Ontario and the northern states of the US being absent in the extreme North-east where it is too humid and very rare in the north-eastern states.

17. *Wolffia columbiana*

W. columbiana, an endemic American species, has its northern limit at the isoline of 140 days with a mean temperature above 10°C and grows southwards to the warm tropics. Like the other *Wolffia* spp. it overwinters in cool regions in the form of turions, on the bottom of the water. It grows in almost the same subarid to subhumid climate as *W. brasiliensis* and has a similar distribution (i between 3 and 6). In North America it grows as far north as *W. borealis*. It is absent from most of the Rocky Mountains and the West.

18. *Wolffia globosa*

W. globosa has its main distribution in south-eastern Asia and in southern Africa. It is not completely sure if the species is indigenous to North America where it is restricted to California. The isoline of 200 days with a mean temperature above 10°C is the northern limit. The species is able to form turions and overwinters in cold regions on the bottom of the water. It is absent from very humid and dry regions (i >8 and <3).

3.3. *Water analysis from North Carolina*

HARRSION and BEAL (1964) analysed 748 samples of waters from North Carolina with respect to pH, chloride content and organic matter content. 534 of these samples came from waters containing *Lemnaceae*. In the "Aquatic Flora of North Carolina" BEAL (1977) gives the results of analysis of the same factors from 3000 water samples; additionally he measured the specific conductance.

The author obtained the results of 39 samples from North and South Carolina and of 33 samples from surrounding states for the following factors: pH, specific conductance, Na^+, K^+, Ca^{++}, Mg^{++}, NO_3^- - N, NH_4^+ - N, PO_4^{--} - P content. The results are summarized here only very briefly (Table 2). For a detailed study one should know the course of the nutrient content of the waters during the whole season. Since these waters were collected after several weeks of rain they are probably more diluted than the average for the season. This may also explain the generally lower limiting values in 1978 compared with the results of LANDOLT and WILDI (1977) who collected the water samples after a dry period. Table 3 shows the results of all American species.

3.3.1. *pH*

We know from other investigations (e.g. LANDOLT and WILDI 1977) that the pH of the water only limits the growth of *Lemnaceae* in rare cases. *Lemnaceae* are able to grow from pH 4 to over pH 8. Several species can survive at pH 3.5 and up to pH 10. HARRISON and BEAL (1964) found *Lemnaceae* in waters with a pH between 4.5 and 8.1. In waters containing no *Lemnaceae* they measured a pH between 3.5 and 10.4. Personal measurements revealed pH values only between 6.6 and 7.5 in North Carolina. In the western states in waters containing *Lemnaceae* we measured the pH to be between 3.5 and 10.4 (LANDOLT 1957, LANDOLT and WILDI 1977).

The lack of *Lemnaceae* in waters with a pH below 4.5 as measured by HARRISON and BEAL (1964) is probably due to the low mineral content very often associated with a low pH. Waters of high pH are very often void of *Lemnaceae* because they have toxic concentrations of some minerals.

3.3.2. *Specific conductance*

The specific conductance is proportional to the ion content of the water. In natural waters it is positively correlated with the concentrations of Na^+, K^+, Ca^{++} and Mg^{++}. BEAL (1977) found *Lemnaceae* only in waters with specific conductance between 20 µS/cm and 2000 µS/cm ($20 \cdot 10^{-6}$ and $2000 \cdot 10^{-6}$ mhos/cm). In North Carolina I found no *Lemnaceae* species in waters below 40 µS/cm. Only 10 per cent of the hitherto investigated 119 *Lemnaceae* samples of North America were collected in waters with a specific conductance below 100 µS/cm. LANDOLT unpubl.). *Lemnaceae* are generally not able to grow in waters with a low nutrient content (cf. LÜÖND 1980, ZIMMERMANN 1981). Low specific conductance therefore expresses a limiting nutrient supply for *Lemnaceae*.

Table 2. Distribution of *Lemnaceae* species in North and South Carolina in relation to some water factors (No. = number of samples)

	No.	pH	specific conductance µS/cm	Na mg/l	K mg/l	Ca mg/l	Mg mg/l	N mg/l	P mg/l
all samples	39	6.5-7.4	17-1060	1.1-67	0.3-34	3.7-66	0.2-35	0.09-3.7	0.002-0.12
Lemnaceae	33	6.6-7.4	41-1060	2.9-67	0.6-34	4.8-66	0.8-35	0.17-3.7	0.003-0.12
S. polyrrhiza	17	6.6-7.4	41-1060	2.9-66	0.6-13	4.8-66	0.8-25	0.44-1.8	0.003-0.07
S. punctata	6	6.7-7.0	41- 331	2.9-66	0.6-34	4.8-41	0.8-35	0.43-1.70	0.003-0.006
L. perpusilla	5	6.8-7.4	116- 199	7.5-29	3.1-6.0	12-27	3.2-6.2	0.66-2.81	0.005-0.012
L. aequinoctialis	14	6.7-7.2	41- 224	2.9-38	0.6-5.5	4.8-33	0.8-7.8	0.43-3.7	0.003-0.068
L. obscura	8	6.8-7.2	99-1060	9.0-66	2.4-30	11-28	2.7-25	0.17-0.95	0.004-0.062
L. minor	4	6.8-7.4	116- 538	9.6-63	3.8-12	14-64	3.5-15	1.50-2.8	0.004-0.12
W. gladiata	11	6.6-7.2	41- 199	2.9-26	0.6-5.6	4.8-26	0.8-7.8	0.43-3.7	0.003-0.009
W. brasiliensis	9	6.7-7.4	91- 538	3.8-18	1.0-4.0	5.7-26	2.1-5.5	0.17-3.7	0.002-0.009
W. columbiana	3	6.8-7.0	124- 135	11-19	2.4-5.6	11-26	3.1-4.1	0.60-1.8	0.006-0.067

Table 3. Distribution of *Lemnaceae* species in North America in relation to some water factors. (Data from LANDOLT and WILDI 1977 and unpublished data from 1975 and 1978).

NO. = number of samples

	No.	pH	specific conductance µS/cm	Na mg/l	K mg/l	Ca mg/l	Mg mg/l	N mg/l	P mg/l
all samples	134	6.4-10.4	17-4400	1.1-1000	0.3-100	1.0-168	0.2-230	0.09-11.2	0.000-0.99
Lemnaceae	119	6.4-10.4	41-4400	2.9-1000	0.6-100	1.0-145	0.7-230	0.15-11.2	0.000-0.99
S. polyrrhiza	53	6.6-10.4	41-4400	2.9-1000	0.6- 33	4.8-145	0.8- 85	0.2 - 4.8	0.003-0.06
S. punctata	8	6.7- 7.3	41- 331	2.9- 66	0.6- 34	3.0- 41	0.8- 35	0.4 - 1.7	0.003-0.06
L. trisulca	2	7.4- 7.5	286- 352	7.2- 25	5.2- 12	45- 70	10- 93	0.2 - 0.5	0.001-0.005
L. perpusilla	9	6.8- 7.4	116- 199	7.5- 29	3.1- 6	12- 27	3.2-6.2	0.7 - 2.9	0.005-0.12
L. aequinoctialis	41	6.6- 9.4	41-2100	2.9- 500	0.6- 36	2.4- 64	0.8- 75	0.2 - 3.7	0.003-0.10
L. turionifera	12	7.1-10.4	85-1300	7- 290	3.3- 18	4.6- 73	3.9- 95	0.2 - 2.9	0.000-0.04
L. gibba	14	7.4- 9.8	200-2600	28- 850	4.7- 30	6.5-115	7.5-145	0.2 -10.6	0.002-0.99
L. obscura	19	6.6- 7.9	99-1060	9- 800	1.7- 35	4.8- 68	2.7-100	0.2 -11.2	0.004-0.06
L. minor	39	6.8- 7.7	55-1657	5.4- 115	1.0- 53	2.5-168	2.6- 85	0.1 - 2.8	0.003-0.27
L. valdiviana	16	6.7- 7.6	41- 199	2.9- 47	0.6-13.5	4.8- 31	0.8- 17	0.4 - 3.6	0.003-0.09
L. minuscula	11	6.6- 9.1	55-2100	8.5- 500	1.6- 22	1.0- 79	0.7-110	0.2 - 2.8	0.000-0.13
W. lingulata	4	6.6- 7.7	345-1150	47- 224	4.9- 23	5.3- 24	12- 59	0.2 - 0.6	0.000-0.05
W. oblonga	6	6.6- 7.4	120- 425	9- 95	1.7- 20	4.8- 68	4.8- 23	0.3 - 0.6	0.011-0.05
W. gladiata	12	6.6- 7.2	41- 199	2.9- 26	0.6-7.0	4.8- 26	0.8- 11	0.3 - 3.7	0.003-0.02
W. brasiliensis	24	6.7- 7.9	41- 740	3.8- 135	1.0- 45	4.5-110	2.1- 30	0.2 - 3.7	0.002-0.03
W. borealis	9	7.2- 7.9	182- 538	13- 63	1.0- 11	43-124	0.7- 13	0.2 - 2.3	0.001-0.094
W. columbiana	24	6.7- 9.8	124-1300	8.9- 225	1.0- 45	5.3-124	3.1- 95	0.1 - 2.3	0.001-0.094
W. globosa	2	6.8- 7.2	55- 250	13- 34	2.2- 16	3.0-6.5	2.6- 11	0.8 - 2.7	0.062-0.74

The measurements of BEAL (1977) show that most of the waters of North Carolina have a very low specific conductance, waters with a higher conductance being found only in the eastern part of the State (Figs 35 and 36).

3.3.3. *Chloride and sodium content*

The chloride and sodium content of natural waters show a strong correlation at higher concentrations. HARRISON and BEAL (1964) observed *Lemnaceae* in waters from 0.1 to 780 mg Cl^-/l. Very few of the waters measured had a lower content of Cl. The upper limit corresponds to a 1.3 o/oo NaCl solution. In our investigation we found no *Lemnaceae* in waters with less than 3 mg Na^+/l. The waters containing *Lemnaceae* with the highest Na^+ content had 68 mg Na^+/l. In earlier investigations we found up to 1000 mg Na^+/l (LANDOLT and WILDI 1977), corresponding to a 5.2 o/oo NaCl solution. Other publications show similar results. LUTHER (1951) found *Lemna trisulca* in waters of up to 4 o/oo, salinity and for a short time even in waters of over 6 o/oo salinity, DE LANGE and SEGAL (1968) observed *L. gibba* in waters up to 4.7 o/oo salinity. Though it is known that chlorine as well as sodium is an essential element for *Lemnaceae* (HALLER et al. 1974, STRAUSS 1976) it is probably rare to find that the concentration of these elements in natural waters will limit the growth of *Lemnaceae*. Martin (1963) showed that there are differences in minimum content of Cl^- needed for different species (for *S. polyrrhiza* 0.5 mg, for *L. minor* 0.027 mg and for *L. aequinoctialis* 0.009 mg).

3.3.4. *Potassium content*

The lowest potassium content observed in waters containing *Lemnaceae* was 0.6 mg K^+/l. In the results of LANDOLT and WILDI (1977) no *Lemnaceae* were found in waters containing less than 2 mg K^+/l.

3.3.5. *Calcium and magnesium content*

The lowest concentration of Ca^{++} and Mg^{++} found in the waters of North Carolina containing *Lemnaceae* was 4.8 mg Ca^{++} and 0.8 mg Mg^{++}/l. No *Lemnaceae* were found in three samples with lower concentrations of both minerals. LANDOLT and WILDI (1977) collected *Lemnaceae* only in waters containing at least 3 mg Ca^{++} and 3 mg Mg^{++}/l.

From these findings it seems very probable that calcium and magnesium might be limiting factors for *Lemnaceae* especially in humid regions. ZIMMERMANN (1981) showed that the investigated *Lemnaceae* (*S. polyrrhiza, L. gibba, L. minor, L. minuscula*) slowed down their growth rate with a Ca^{++} and Mg^{++} content between 0.1 - 0.5 mg/l and even died. *L. gibba* needs a higher Mg content (0.35 mg/l) than the other investigated species (0.04 mg/l) if the Ca content is relatively high (12 mg/l). If the Mg^{++} content is high (8.7 mg/l) the multiplication rates of the species except *L. gibba* were much slower with a Ca^{++} content of 2.4 mg/l. In a balanced nutrient solution *Lemnaceae* still grow with concentrations of 600 mg Ca^{++}/l and 435 mg Mg^{++}/l (ZIMMERMANN 1981). Toxic concentrations of Ca^{++} and Mg^{++} are never reached in North Carolina.

3.3.6. *Nitrogen content*

Since we could not observe any difference between nitrogen being present as nitrate or as ammonium here we will discuss only the total inorganic nitrogen content. The lowest nitrogen concentration in waters with *Lemnaceae* was found to be 0.17 mg N/l. In two waters of lower nitrogen content we did not detect any *Lemnaceae*. The highest concentration found in our measurements in a water containing *Lemnaceae* was 3.5 mg N/l. LANDOLT and WILDI (1977) measured up to 10 mg N/l in waters containing *Lemnaceae* which is much lower than the toxic limit. LÜÖND (1980) found no toxic effect with N concentrations of 350 mg N/l; only the next higher concentration of 1750 mg N/l was toxic. The lowest concentration for nearly optimal growth was between 0.02 and 2.8 mg N/l depending on the species. It is probable that the low nitrogen concentration of natural waters is a limiting growth factor for at least some *Lemnaceae* species.

3.3.7. *Phosphorus content*

The lowest P content of waters in North Carolina containing *Lemnaceae* was 0.003 mg P/l, the highest 0.27 mg P/l. In one sampling place with 0.002 mg P/l there were no *Lemnaceae* present. LANDOLT and WILDI (1977) found *Lemnaceae* in waters with up to 0.99 mg P/l (the numbers quoted there for P are erroneously ten times too high). LÜÖND (1980) found no toxic effects in concentrations of 10.8 mg P/l. The next higher investigated level of 6790 mg P/l was toxic. The lowest concentration which permitted optimal growth rates was 0.434 mg P/l. Some species grow very well with concentrations of 0.002 mg P/l. A low concentration of phosphorus seems to be one of the limiting factors for the occurrence of *Lemnaceae*.

3.3.8. *Organic matter content*

No personal measurements were made in this respect. HARRISON and BEAL (1964) showed that only waters with at least 0.09 % organic matter content contained *Lemnaceae*. Organic matter may act as

- energy supplier for fronds not receiving enough light
- chelating agents to supply the plants with heavy minerals which might otherwise be unavailable
- growing substance to promote plants which are inhibited by certain conditions.

But the high content of organic mater in waters containing *Lemnaceae* may be at least partly a consequence and not necessarily a condition for the growth of *Lemnaceae*. Waters containing a closed cover of *Lemnaceae* are poor in oxygen. The conversion of dead fronds and other organic matter to CO_2 and minerals is incomplete, and consequently the organic matter content will rise.

3.4. *Associations of Lemnaceae in North Carolina*

Water plants and animals as competitors and commensals are very important factors determining the occurrence of *Lemnaceae* in a region. Ducks, fish and many small animals (e.g. snails, insects, crustacea) feed on the *Lemnaceae*. In waters with fish, *Lemnaceae* can only survive if there are some niches inaccessible to fish.

Running water and big lakes can only be colonized by *Lemnaceae* if the fronds become fixed between water plants. Otherwise they are removed or washed onto the shore and die due to dehydration. Thick covers of algae either prevent *Lemnaceae* from obtaining adequate light or sufficient nutrients. On the other hand a cover of *Lemnaceae* excludes the development of algae.

The colonization of waters by *Lemnaceae* is somehow casual and dependant on water birds flying in from neighbouring waters containing duckweeds. The first species arriving in these waters are *Lemna obscura*, *L. aequinoctialis*, *Spirodela polyrrhiza*, and more rarely *Wolffia brasiliensis*. *L. aequinoctialis* is the only native *Lemnaceae* species of North Carolina which is able to grow in periodically dry waters. *L. valdiviana*, *Wolffia columbiana* and especially *Wolffiella gladiata* prefer stable water conditions. They grow in small lakes and water systems with a relatively closed circulation of nutrients. The biomass of the *Lemnaceae* is relatively high and the freely accessible nutrient concentration of the water low. Under these conditions *W. gladiata* is a good competitor growing slowly below the surface of the water and being able to assimilate first nutrients which diffuse from deeper parts of the water. As soon as the nutrient supply becomes more scarce the cover of *Lemna* and *Spirodela* species on the surface of the water breaks up giving better light conditions for the *Wolffiella* species. If the whole system becomes disturbed by water inlets, water movements or human action more nutrients reach the surface of the water and enable the floating *Lemna* and *Spirodela* species to spread and close the cover keeping the *Wolffiella* species from the light.

Table 4 shows some relevés of the typical climactic water association of the Carolinas. The first three relevés are characteristic for more pioneer like conditions. 15 other relevés showed only one or two species of *Lemnaceae* in the Carolinas.

I have named the association with *Wolffiella gladiata* "*Lemno valdivianae - Wolffielletum gladiatae*" in accordance with the methods of BRAUN-BLANQUET (c.f. BRAUN-BLANQUET 1964).

Lemno valdivianae - Wolffielletum gladiatae ass.nov.

The new association is a two layered community of floating water plants belonging to the class of *Lemnetea* which is described in detail by SCHWABE-BRAUN and TÜXEN (1981).

Type relevé: No. 14 of Tab. 4.

Characteristic species: *Wolffiella gladiata* and *L. valdiviana*. The first

Table 4. Relevés of communities containing *Lemnaceae* in the Coastal Plain of the Carolinas

Relevé No.	39	38	13	33	15	14	34	35	31	5	4
Lemna obscura	1	1	1	1	+	2	1				
Spirodela polyrrhiza	1	2	2	3	4	4	2	2	2	1	+
Wolffia brasiliensis			1	4	+	+	+	+			
Utricularia purpurea			1	3	3	1					
Limnobium spongia				2	1	1	1				
Wolffiella gladiata				2	2	5	4	2	4	5	
Lemna valdiviana				+	+	+	4	4	3	1	3
Lemna aequinoctialis				2	+	+			3	2	2
Wolffia columbiana					2	2		4			
Ceratophyllum demersum							2	3	2		
Spirodela punctata										3	2
Azolla caroliniana										+	

Frequencies based on the scale of BRAUN-BLANQUET:

5: 75-100% covering
4: 50- 75% covering
3: 25- 50% covering
2: 5- 25% covering
1: frequent but less than 5% covering
+: few scattered fronds

Localities:

No. 4, 5 : S.C. Jasper Co., highway 119, Savannah River
No. 13, 14, 15: N.C. Dare Co., Nags Head Woods
No. 31, 33, 34: N.C. Camden Co., highway 158
No. 35 : N.C. Currituck Co., highway 158
No. 38, 39 : N.C. Currituck Co., Waterlily

species is mainly restricted to this association, the latter is also associated with other species of *Wolffiella* (e.g. *W. lingulata*) in the tropical and subtropical regions. If one considers the more pioneer like stages of *L. obscura* only as a precursory or degenerating stage of the association and not as an association by its own, *L. obscura* is also a typical species of the association. *S. polyrrhiza, S. punctata, L. aequinoctialis, W. columbia-*

na, W. brasiliensis and the liverwort *Riccia fluitans* are far more widespread and grow in many other associations of *Lemnaceae*. *Utricularia purpurea* and *Ceratophyllum* have their ecological centre in associations of more oligotrophic and eutrophic waters. *Limnobium* may be a typical member of the association although this was not checked.

Distribution: It is known from herbarium samples that the association has approximately the same distribution as *Wolffiella gladiata* (Fig. 25): coastal regions from southern Virginia to Florida and eastern Texas and the Mississippi valley upwards to southern Illinois where it is very rare.

4. Discussion

4.1. *What factors limit the distribution of* Lemnaceae *in North Carolina?*

If we compare the climate of North Carolina with the climatic factors limiting the growth of *Lemnaceae* in North America we recognise that there are apparently no climatic reasons for the absence of *Lemnaceae* in most of the western part of the State except for the higher regions of the Appalachian Mountains which are too humid (i>8). Therefore there must be some special conditions which limit the growth of *Lemnaceae* in North Carolina. We know from the investigations of BEAL (1977) that the specific conductance of most of the waters of North Carolina is very low (cf. Figs 35, 36), lower than in waters generally containing *Lemnaceae*. We know also that the soils of most of the Piedmont belong to the oldest soils known in the world (cf. LIETH 1979); most minerals are washed down to great depths and very few minerals are freshly leached out by the water. The underground rock in the Mountains and the western part of the Piedmont consists mostly of carboniferous, cambrian and precambrian gneisses, schists, quartzites, slates and tuffs which are poor in soluble minerals (Fig. 37). The occurrence of *Lemnaceae* in North Carolina is restricted to areas with quaternary, tertiary, cretaceous and triassic clays marles and shales containing some alkalines. It can also be shown from other areas of the world that the effect of high rainfall is enhanced in regions with poor base underground or soils and leads to oligo-

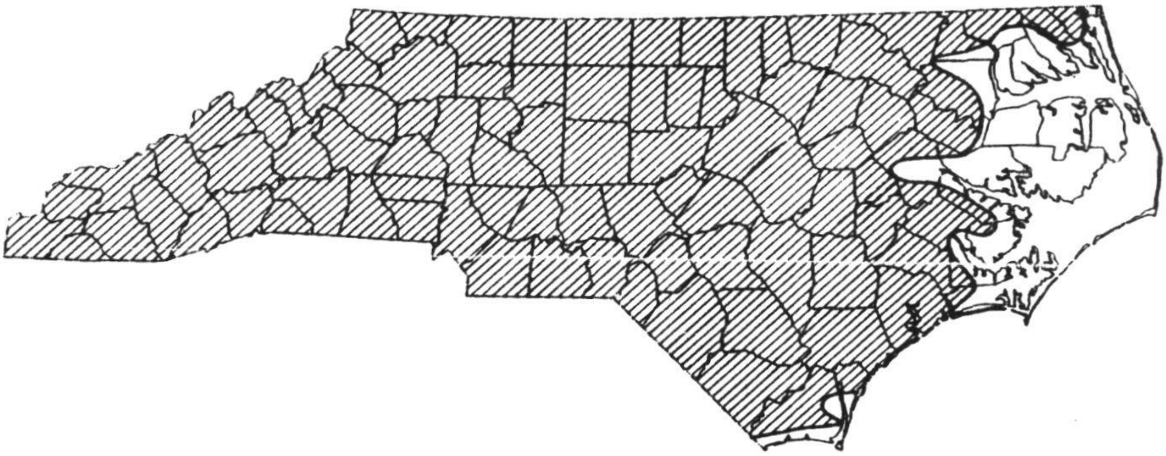

Fig. 35. Specific conductance of waters from North Carolina (from BEAL 1977).
Waters with 86 µS/cm or less

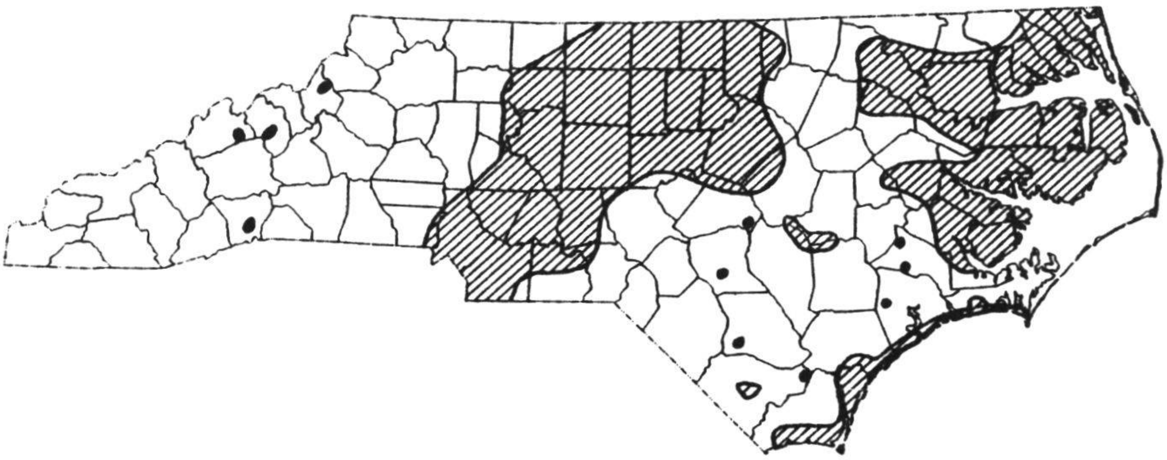

Fig. 36. Specific conductance of waters from North Carolina (from BEAL 1977).
Waters with more than 86 µS/cm

trophic waters. JACOBS (1947) noted that *Spirodela polyrrhiza* is very common in Minnesota (i<6) except in the region just north of Lake Superior where precambrian rocks form the underground.

The eastern part of Piedmont and the Coastal Plains is also in many areas unfavourable for the growth of *Lemnaceae*. Sandy and turfy soils mainly give rise to oligotrophic waters. The best areas for *Lemnaceae* are waters in the regions of alluvial or maritime soils.

4.2. *Distribution pattern of the Lemnaceae species in North Carolina*

The reasons for the absence or limited growth in North Carolina of the different species of *Lemnaceae* are now explained.

Lack of natural waters. - In Western North Carolina there are no natural lakes save for a few beaver ponds, because of the maturity of this very ancient landscape. The absence of standing water would lead to (1) few places for *Lemnaceae* to grow as well as few sources of plants for disseminations, (2) absence of much migratory water fowl to introduce *Lemnaceae*. Most water fowl migrate along either the coast or the Mississippi valley.

Warm summer temperatures (Fig. 38). - The mean summer temperatures of 24°C to 27°C in North Carolina are too high for *Lemna trisulca* and *Wolffia borealis* which are completely absent. *Lemna minor* and *L. perpusilla* reach their southern limit in northern North Carolina. Their limiting temperature being about 24°C they are very rare in North Carolina and prefer shaded and locally cooler waters.

Cold winter temperatures (Fig. 39). - *L. aequinoctialis* has its northern limit in North Carolina requiring an average temperature of 8°C. It may cross this limit only in waters which dry out during the winter time permitting the species to outlast the low temperatures in the seed stage. *Wolffiella lingulata* and *W. oblonga* are excluded from North Carolina by the too low absolute minimum temperatures reached even in the mild climate of Cape Hatteras - 13.3°C.

Oligotrophic waters. - As we saw in chapter 4.1 the waters in North Carolina are generally lower in mineral content than would normally correspond to the

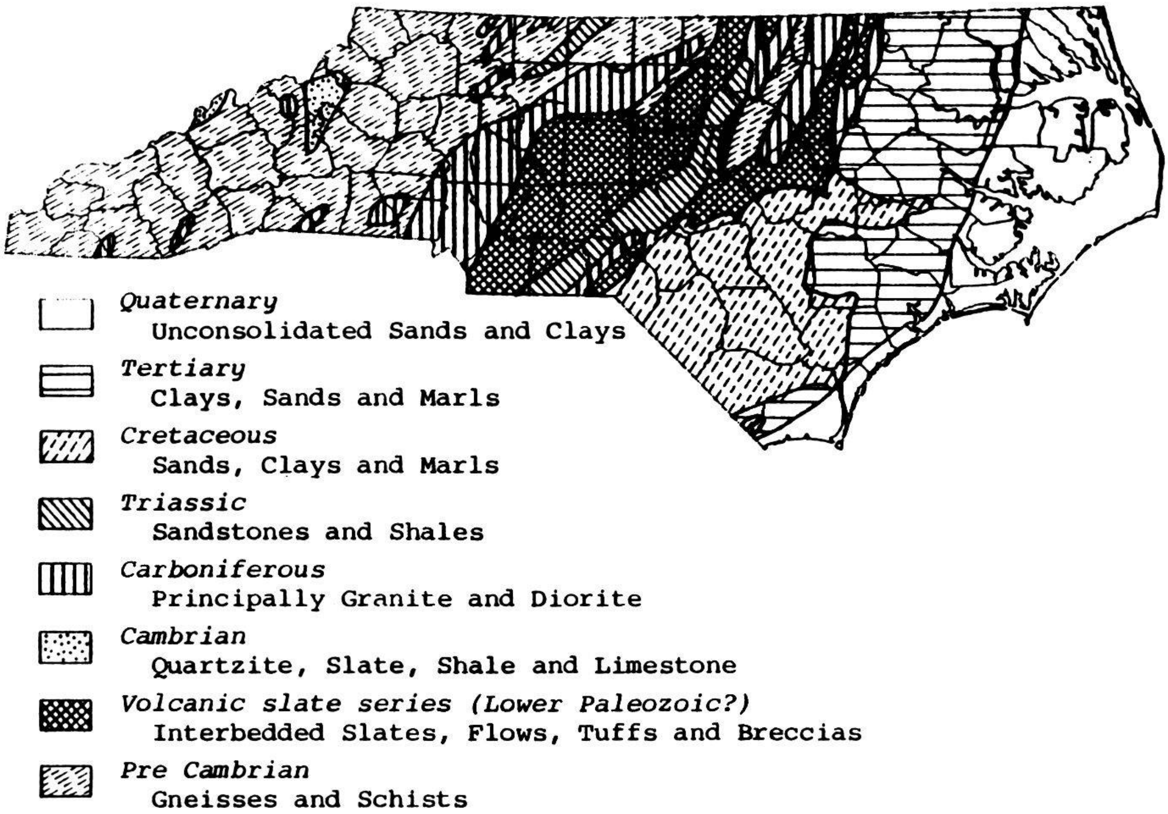

Fig. 37. A generalized geological map of North Carolina (from LEE 1955).

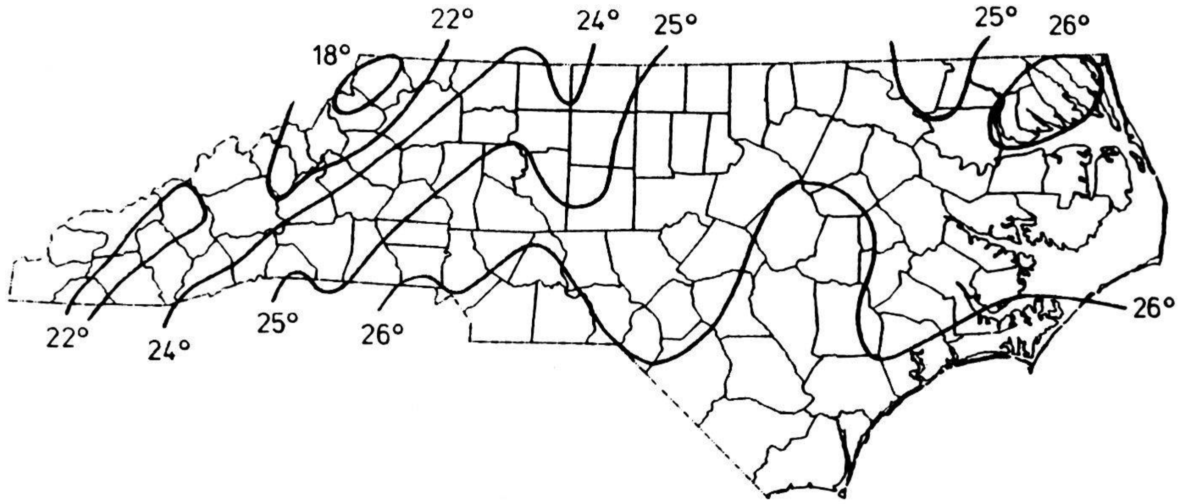

Fig. 38. Mean summer temperatures in North Carolina (transcribed from HARDY and HARDY 1971).

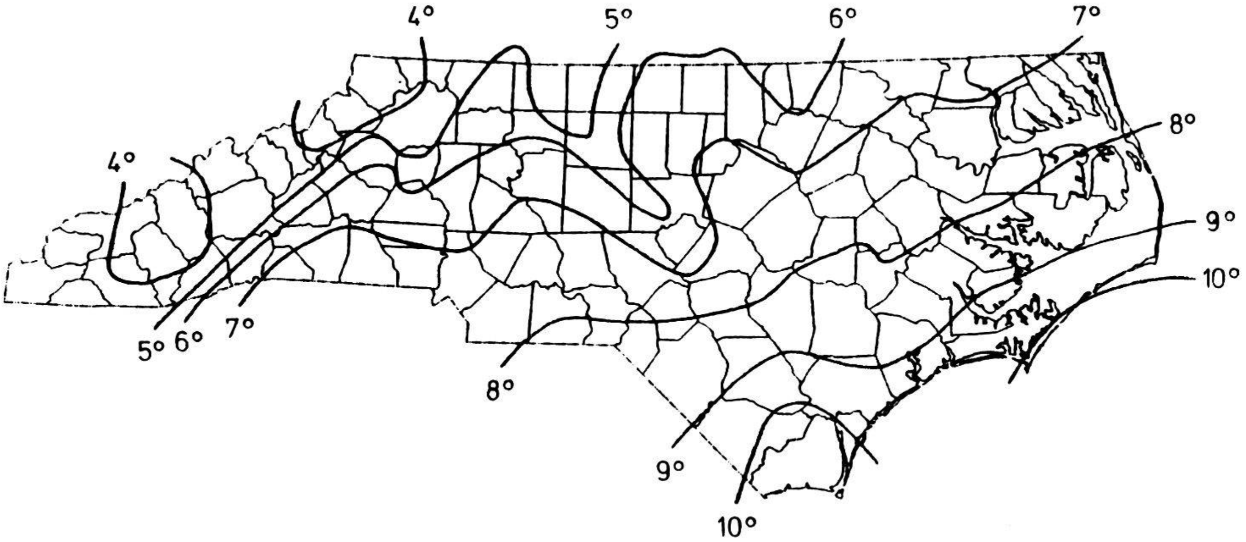

Fig. 39. Mean winter temperatures in North Carolina (transcribed from HARDY and HARDY 1971).

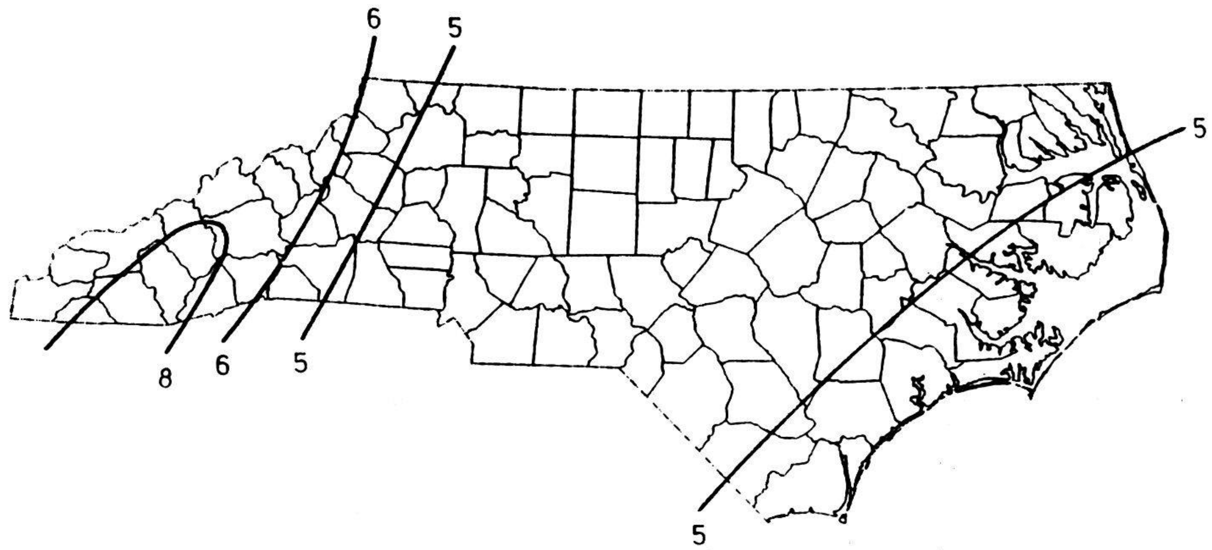

Fig. 40. Aridity factor of Martonne in North Carolina (calculated from the data of HARDY and HARDY 1971).

average amount of rainfall (aridity factor of Martonne for North Carolina predominantly between 4 and 6, Fig. 40). Therefore only species with a high tolerance towards a humid climate are able to grow. Those species with the ability to spread to regions with an aridity factor up to 8 are the most widespread species in North Carolina, within the other climatic limits. These species are *Spirodela polyrrhiza, S. punctata, L. aequinoctialis, L. minor, L. valdiviana. L. perpusilla, L. obscura, Wolffia brasiliensis* and *W. columbiana* which are generally absent in regions with an aridity factor higher than 6 have a more restricted distribution. Species with a lower tolerance ($i<5$) were not observed in North Carolina (*L. gibba, L. minuscula*).

Competition. - The only two species of North American *Lemnaceae* which are absent in North Carolina and the absence of which is not explainable by a single climatic factor are *Lemna turionifera* and *Wolffia globosa*. *L. turionifera* is near its climatic limits in North Carolina with respect to average summer temperatures as well as to the aridity factor ($i<6$). The competition of the morphologically very similar *L. obscura, L. aequinoctialis* and *S. punctata* which are much better fitted for the climate of North Carolina may exclude *L. turionifera*. *W. globosa* has a very isolated occurrence in California. It probably just did not have the opportunity to cross the Rocky Mountains. In addition it would have great competition in the eastern US from the ecologically very similar *W. columbiana*.

Summary

1. The distribution of the ten *Lemnaceae* species in North Carolina is given (Figs 2 to 11).
2. The distribution of the 18 North American species of *Lemnaceae* is shown in relation to some climatic factors: number of days with mean temperatures above $10^{o}C$, mean summer temperatures, mean winter temperatures, absolute minimum temperature and the aridity factor of Martonne ($i = \frac{\text{annual precipitation in cm}}{\text{mean annual temperature in } ^{o}C + 10}$). (Table 1, Figs 12 to 34).
3. Measurements of 39 watersamples from the Carolinas were made for pH, specific conductance, sodium, potassium, calcium, magnesium, nitrogen and phosphorus. The waters of North Carolina in general show a low concentration of minerals (Table 2, Figs 35 and 36).
4. The restriction of the *Lemnaceae* to the eastern part of North Carolina

is explained by the lack of natural lakes in this very old landscape and by the very old soils and the mostly paleozoic acidic rocks of the western part of North Carolina which deliver very few minerals to the waters.

5. The specific distribution pattern of some of the species in North Carolina and the absence of several other North American species in North Carolina is explained.

Zusammenfassung

1. Die Verbreitung von zehn Lemnaceen-Arten in North Carolina wird dargestellt (Abb. 2-11).

2. Die Verbreitung der 18 nordamerikanischen Arten wird in Beziehung zu einigen klimatischen Faktoren gesetzt: Anzahl Tage mit Mitteltemperaturen über $10^{o}C$, mittlere Sommertemperaturen, mittlere Wintertemperaturen, absolute Minimumtemperaturen, Martonne'scher Ariditätsfaktor ($i = \frac{\text{Jahresniederschlag in cm}}{\text{mittlere Jahrestemperatur in } ^{o}C + 10}$). (Tab. 1, Abb. 12-34).

3. An 39 Wasserproben aus den Carolinas wurden die folgenden Faktoren gemessen: pH, Wasserleitfähigkeit, Gehalt an Kalium, Natrium, Calcium, Magnesium, Stickstoff und Phosphor. Der Mineraliengehalt der Gewässer in North Carolina ist im allgemeinen niedrig (Tab. 2, Abb. 35 und 36).

4. Die Beschränkung der Lemnaceen auf den östlichen Teil von North Carolina wird durch den Mangel an natürlichen Seen in der Landschaft des westlichen Teils und durch die dort vorhandenen sehr alten Böden und die palaeozoischen sauren Gesteine erklärt, die nur sehr wenig Mineral-Ionen an die Gewässer abgeben.

5. Das Verbreitungsmuster der einzelnen Arten und das Fehlen bestimmter Arten in North Carolina wird erläutert.

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