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The *Lemnaceae* of Zimbabwe and Botswana

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1. INTRODUCTION

Southern Africa is one of the regions with the highest number of *Lemnaceae* species. Only South America, with 14 species 4 of which are endemic, has a higher diversity. Of the 13 species occurring south of the line Angola - Malawi - Mozambique in Africa 3 are endemic in this region: *Wolffiella denticulata*, *W. repanda* and *W. rotunda*. *W. denticulata* is a species of coastal regions from the Cape to southern Mozambique, *W. repanda* has been found at only two places in central and southern Angola and from one place in northern Botswana. The single known herbarium sample of *W. rotunda* originates from the Kariba Gorge in northern Zimbabwe which is now flooded by the Kariba Lake (LANDOLT 1986). In our collection of living *Lemnaceae, W. repanda* and *W. rotunda* clones were missing and could not

be compared with other species. The ecology and life cycles of the two species were also unknown. It therefore seemed desirable to study the two species in their natural environment and to analyze water samples of their habitat. In April 1992, northern Zimbabwe and Botswana was visited and checked for *Lemnaceae*.

Acknowledgements

Theodor Müller, head of the National Herbarium and Botanical Garden of Harare, Zimbabwe, was so kind to organize our stay in Harare, to put all the facilities of the Garden to our disposal and to help us in every way. Robert B. Drummond, curator of the Herbarium, accompanied us through northern Zimbabwe. His competent knowledge of plants and vegetation, the country and people enabled us to visit regions and localities to which we otherwise would have had no access. In Makuti, N.J. Coetzee, a local authority of the region joined our expedition, drove us around Urungwe Safari Area and through Mana Pool National Park and showed us places with duckweeds. In Kariba we met Peter Clemence who is a profound expert on the Chiara Safari Area and guided us through interesting localities in that area. Ms. J. Faranhar of the Insuza Forest Station lodged us in her beautiful Ngamo Safaris Hotel and showed us around in the river plain of Insuza. In Botswana we were kindly accompanied by Peter Smith of Maun, a scientific expert of the Okavango delta area and its vegetation. He drove us around interesting places in difficult regions with no roads. We are deeply grateful to all these people for there generous help which was a great contribution to the success of our whole trip. We would also like to thank the authorities of Zimbabwe and Botswana for arranging permission for us to visit National Parks and to do research work in them. The water samples were analyzed in the chemical laboratory of the Geobotanical Institute in Zürich by Miguel Baldoma and Kathrin Rentsch Brassel. The newly collected samples of *Lemnaceae* were put in the trustworthy hands of Anita Hegi. The statistical evaluation was performed by Dr. Hansruedi Binz. I. Gödickemeier and R. Venzin fed the computer with the analytical data. To all these persons I am very thankfull. My special thanks go to my attendant and friend Walter Lämmler, Zürich, who assisted me in every way during the trip.

2. INVESTIGATION AREA, MATERIAL AND METHODS

Northern Zimbawe and Botswana was visited (Fig. 1) from March 30 to May 1, 1992. The vegetation in northern Zimbabwe is mainly dry Savanna with Miombo forest (deciduous forest with *Brachystegia* and *Julbernardia*) in the higher altitudes and Mopane (*Colophospermum mopane*) forest in the Zambesi Valley. In the Northwest of Zimbabwe the climate is dryer and the savanna woodland more open. Northern Botswana is also covered by Savanna (Fig. 2).

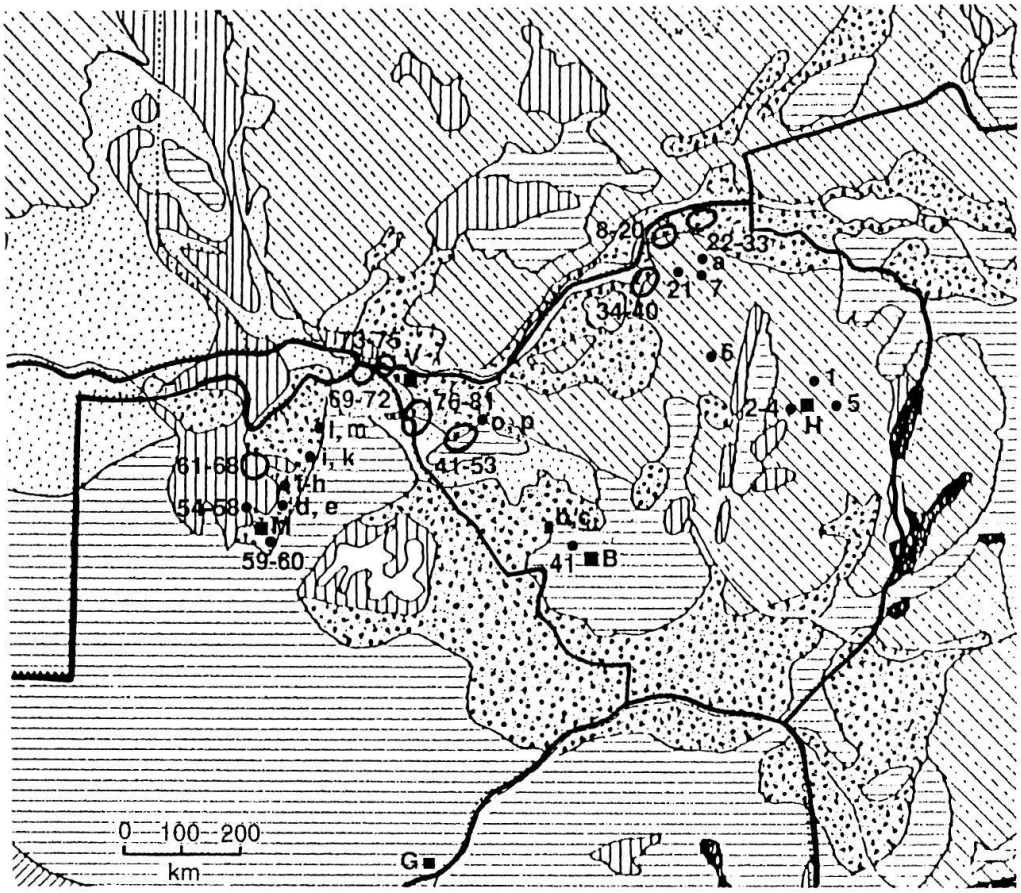


Fig. 1. Locations of the samples on a vegetation map of WERGER and COETZEE (1978).
No. 1 to 81: samples with water; a to p: soil samples
B = Bulawayo; G = Gaborone; H = Harare; M = Maun; V = Victoria Falls
(For explanation of the vegetation types see Fig. 2.)

The region belongs climatically to the subtropical zone with mean summer temperatures between 20° C (southern and higher parts of the area) and 26° (northern and lower parts of the area) and mean winter temperatures between 14° and 20°. Frosts are possible in the dry and higher regions (Fig. 3). In the Okavango Delta and in the Zambesi Valley, the main collecting sites of our field trip, they are very rare or unknown. Mean annual precipitations mount to about 500-1000 mm with a pronounced dry season from May to September (Figs. 4 d, e, f). The climate of a few other stations in southern Africa is shown in Figs. 4 a, b, c, g, h.

The soils of the area are mostly very old ferrisialitic clay or sands, though a detailed soil map for the investigated localities was not accessable. The soils

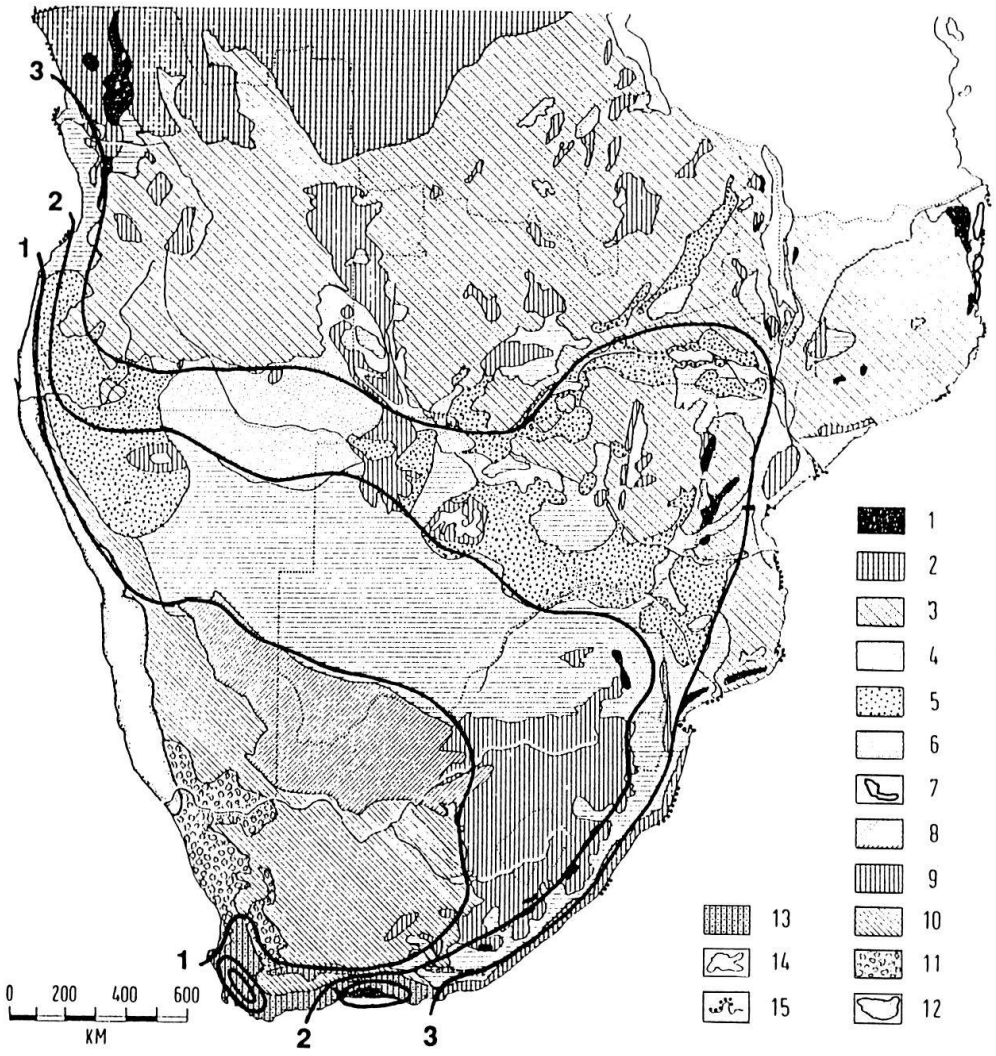


Fig. 2. Vegetation map of southern Africa (from WERGER and COETZEE 1978.)

1	Forest (lowland and montane)	9	Grassland and herbaceous vegetation
2	Forest-Savanna mosaic	10	Karroid dwarf shrub vegetation
3	Miombo vegetation, thorny savannas	11	Succulent dwarf shrub vegetation
4	Baikiaea vegetation	12	Desert vegetation
5	Mopane vegetation	13	Fynbos vegetation
6	Other woodland, savanna, thicket	14	Bare pan or lake
7	Coastal thicket	15	Mangrove
8	Open *Acacia* savanna		

The aridity factor lines of Martonne (i = 1, 2 and 3) are superimposed on the map.

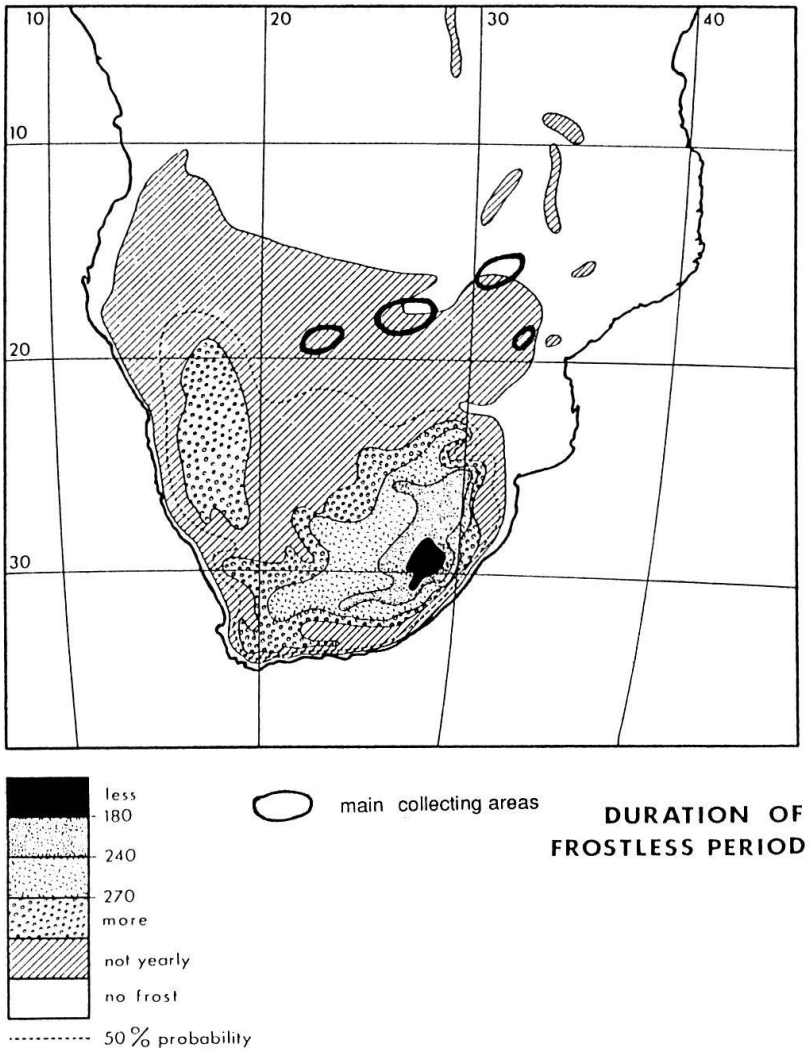


Fig. 3. Duration of frostless period in days per year (from WERGER and COETZEE 1978).

in the Okavango Delta and along the Chobe and Zambesi River are alluvial and therefore richer in most minerals (WERGER and COETZEE 1978).

All waters with pleustophytes along the route were sampled (two bottles of each sample) along with a voucher of the plants (71 samples). Some of the more interesting *Lemnaceae* species were transported live to Zürich and cultivated at the Institute. Soil samples were collected from dried out pans and watered in Zürich to check for a possible content of living diaspores. In addition, 10 samples from waters with no pleustophytes were collected.

Unfortunately, 22 samples (No. 59-81) were totally or partially lost on the way from Harare to Zürich.

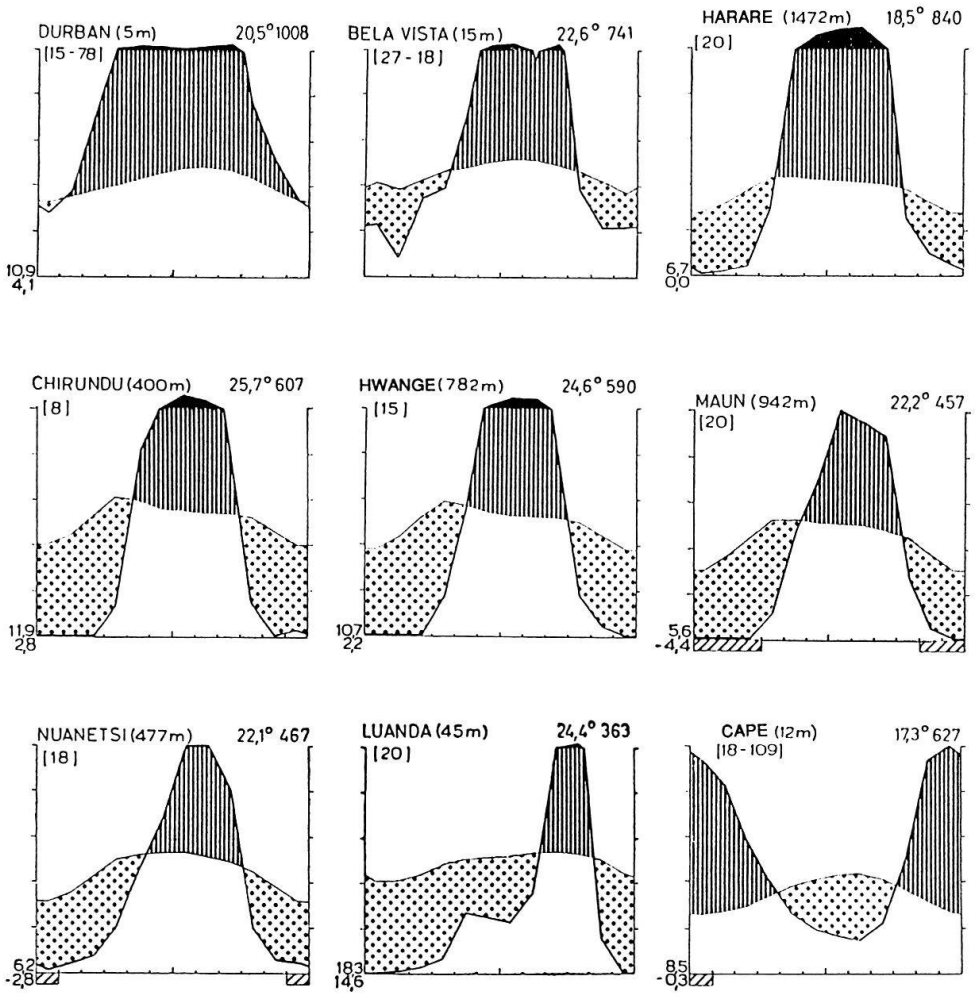


Fig. 4. Climate diagrams of 9 stations in southern Africa (from WALTER and LIETH, 1967). The location of the stations is shown on the map in Fig. 5.

The water samples were analyzed in Zürich for NH_4, NO_3, N_{tot}, PO_{4tot}, Cl, SO_4, Ca, Mg, Na, K, Fe, Mn, pH and conductivity. The methods are listed in LANDOLT and ZARZYCKI (1994). pH and conductivity, as well as water temperature were measured already in the field.

Data aquisition for the common occurrence of *Lemnaceae* in each body of water and chemical distribution was performed in the same manner as in LANDOLT and ZARZYCKI (1994).

For the geographic distribution herbarium specimens were checked (mostly SRGH and PRE)). The collections of the present trip are deposited in ZT and SRGH.

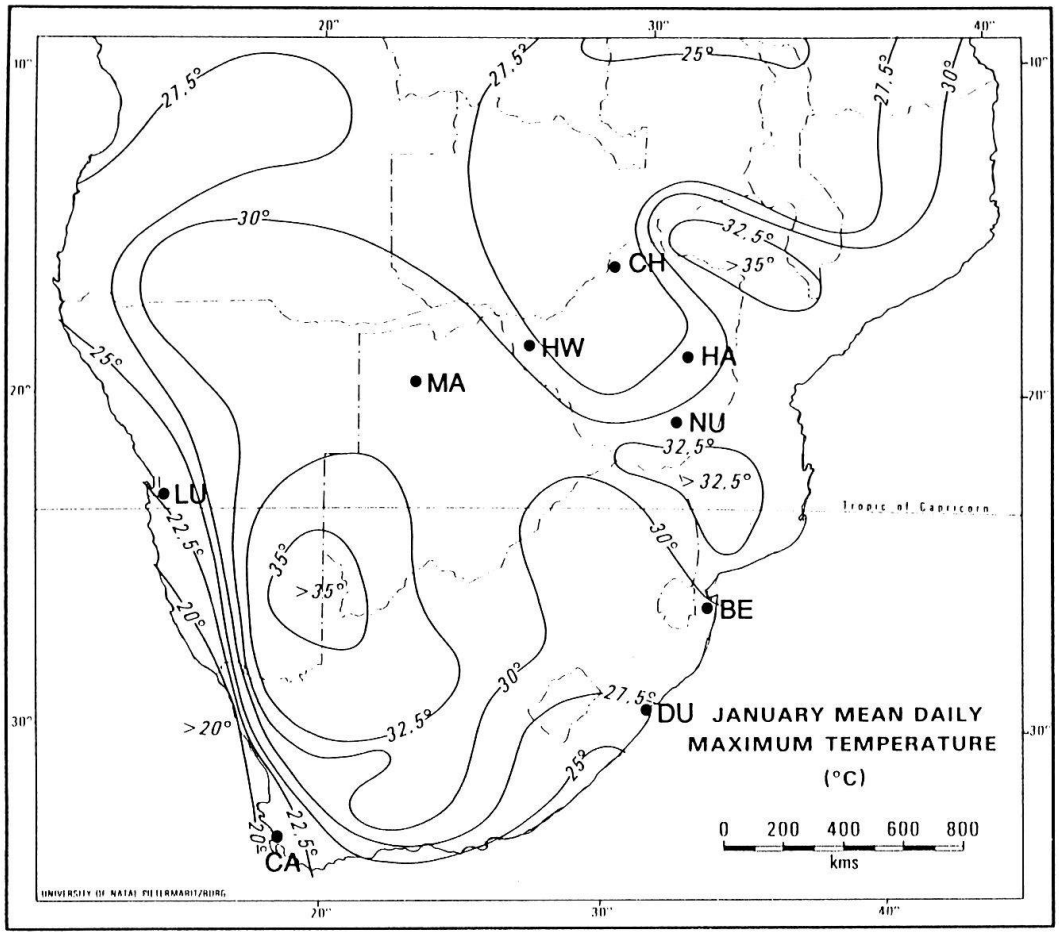


Fig. 5. January mean daily maximum temperature (from SCHULZE and MCGEE, 1978).
The letters show the climate station of Fig. 4:

BE	Bela Vista	CA	Cape Town	CH	Chirundu
DU	Durban	HA	Harare	HW	Hwange
LU	Luanda	MA	Maun	NU	Nuanetsi

3. RESULTS

3.1. DISTRIBUTION AND ECOLOGY OF THE VARIOUS SPECIES

Considering the results of the field work and herbarium samples, the various species have the following distribution in Zimbabwe and Botswana.

Spirodela punctata (Fig. 6a)

S. punctata was collected from the surroundings of Harare at Green Grove Nature Reserve and Ewanrigg Botanical Garden and from the region of Chinhoyi at Sinoia Caves. The following herbarium material has been checked: Harare region, Mahabuti River (MOLL 1963), Goromonzi, Ruva River (BIEGEL 1970), Lake McIlwaine (ELLIS 1956, FAULKENER 1971, PHIPPS 1958); Bulawayo region, Hillside, lower dam (BIEGEL 1972). The species is unknown in Botswana.

The species grows in permanent waters, often together with *Azolla pinnata,* at higher altitudes (above 1200m). It probably cannot survive in predominantly very dry regions (Martonne factor i < 3) or through very hot summers. Of the three collected samples none were flowering.

In southern Africa the species is also growing at the Cape, in Natal, and Transvaal. It is probably native only in Australia and southeastern Asia and introduced elsewhere.

Lemna aequinoctialis (Fig. 6b)

L. aequinoctialis is the most frequent *Lemnaceae* species in Zimbabwe and Botswana just as everywhere else in the tropics and subtropics. It was found in every region passed through on this expedition. It grows throughout the whole area except for the driest regions in the southwest of Botswana and the most humid regions of the mountains in eastern Zimbabwe.

It can be found in permanent as well as in seasonal waters. Of the 50 collected samples, 20 exhibited flowers and/or fruits (40%).

The pantropic species, which normally avoids regions with winter temperatures below 8°, is distributed throughout the whole of southern Africa except for the very dry areas of the west. In the extreme south it is rare.

Wolffiella rotunda (Figs. 6c, 7 c, d)

W. rotunda has been found previously only once in the Urungwe Distr., Kariba Gorge (WILD 1953) mixed with *L. aequinoctialis* (type collection). This place is now under water. Fortunately we found it in several other places in the region between Charara Safari Area and Mana Pools National Park on the plain of the Zambesi River. We collected it from 16 small pans either alone (2 times) or more often mixed with *L. aequinoctialis* (14 times), *W. repanda* (6 times), *W. globosa* (4 times) or *Pistia* (2 times).

At the beginning of April, many of the small pans which are seasonally filled with water and usually measure 2 to 20 m in diameter are covered with *Lem-*

naceae but void of other water plants (Fig. 7a). Buffalo, elefant and other animal tracts indicated that these pans were not only used as drinking places but also for wallowing. The water was accordingly murky brown and muddy. Of the 16 samples, 9 (56%) were flowering and/or fruiting in the field.
According to the present stand of knowledge, *W. rotunda* is restricted to the described area of Zimbabwe.

Wolffiella repanda (Fig. 6d, 7 e, f)
W. repanda was found for the first time in Zimbabwe by the members of this expedition. Until 1976, it was known only in Angola: two collections from the provinces of Luanda (WELWITSCH 1854, type colletion) and Mossamedes (Kers 1968). It was recently detected by P. Smith in northern Botswana (Nqamaga Island, SMITH 1976). In the investigated area of Zimbabwe it was similarly but more rarely distributed as *W. rotunda*. Of 7 localities it grew in association with *L. aequinoctialis* (7 times), with *W. rotunda* (6 times) and with *W. globosa* (3 times). In Botswana the investigated pans were already dried out. However, soil was incidentally collected from 10 pans 4 of which contained living *W. repanda* seeds. The known sites of *W. repanda* are located between Shorobe and Mababe Game Scout Camp: 79 km and 82.7 km NNE of Maun on the way to the south gate of Moremi Wild Life Reserve; 50 km and 85 km NNE of Shorobe along the road to Savuti South Camp.
The ecology of the species is very similar to that of *W. rotunda.* It grows within the Mopane forest belt in seasonal waters and cannot exist in regions with frosts. Of 7 localities 3 (43%) were flowering and/or fruiting.
According to present knowledge *W. repanda* is restricted to the western lowland of Angola, to the eastern border of Ngamiland and the lowland of the Zambesi River.

Wolffiella welwitschii (Fig. 6e)
W. welwitschii is probably wide-spread in the Okavango Delta. Herbarium vouchers are known from Nyamiland, Sepopa (MÜLLER 1975); Duba Island, Xesabe (SMITH 1974), Moanachira River (SMITH 1973); Ngoha Island (SMITH 1974). It was found by the members of this expedition around Daonara; Xio; Nqamaga. Outside this area it is known from Linyanti River area, Shaile (GIBBS RUSSEL 1972). In addition we found it 25 km SE of Maun at Boteti River and along Chobe River near Kubu Lodge. In Zimbabwe a single station is known from Hwange Distr., Ngamo Pan (GARLEY 1950). This place was searched for the species, but it could not be found.

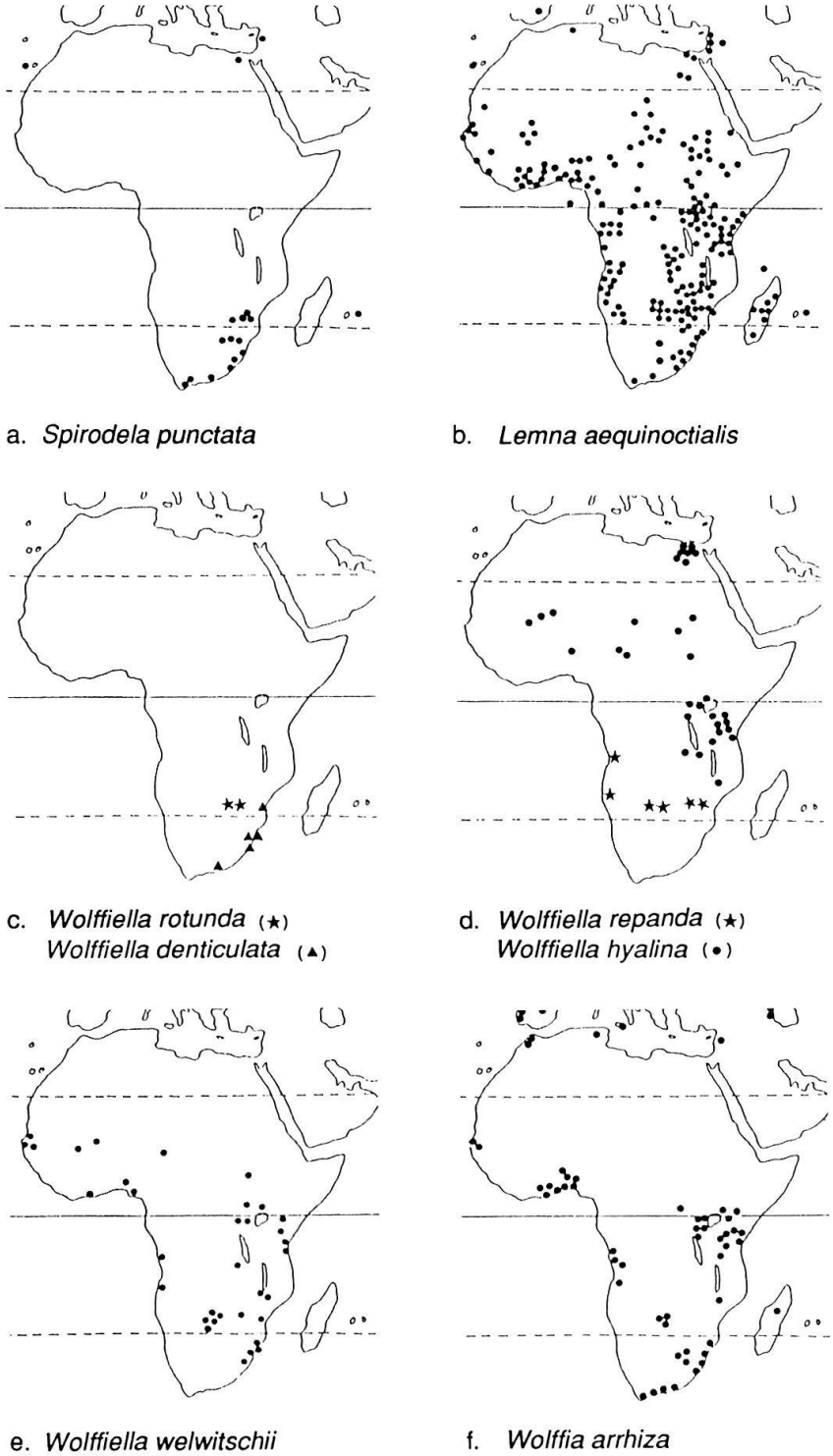
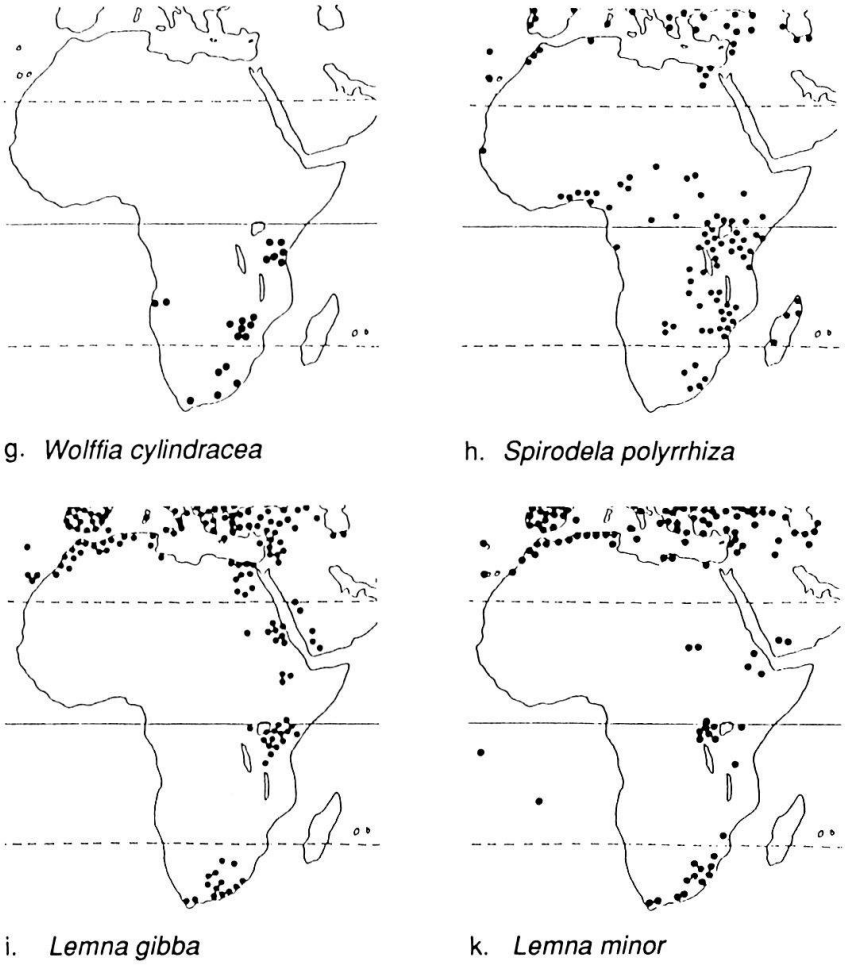


Fig. 6. Distribution area of *Lemnaceae* in southern Africa.



g. *Wolffia cylindracea*

h. *Spirodela polyrrhiza*

i. *Lemna gibba*

k. *Lemna minor*

Fig. 6. (contin.) Distribution area of *Lemnaceae* in southern Africa.

W. welwitschii grows in the investigated area only in permanent waters between stands of *Phragmites*, *Furena* or other reed grasses (Fig. 7b). At the time of the visit (end of rainy season) it was not well developed. In some places the fronds were hidden in the top soil and appeared only when the ground was stirred up. No flowering or fruiting was observed in the field collection.

W. welwitschii is distributed in tropical-subtropical areas of South America and Africa. It does not grow in regions with frost and in very dry regions (aridity factor of Martonne above 2). In southern Africa it is known outside of Zimbabwe and Botswana in Angola (Luanda and Benguela Prov.), Malawi (Southern Prov.), Zambia (Mporokoso Distr.) and from the coastal areas of Mozambique (Inhaca) and Natal; in the latter two areas it grows in association with *Wolffiella denticulata, Wolffia arrhiza* and *Lemna minor.*

Wolffia arrhiza (Fig. 6f)

W. arrhiza is known only in northern Botswana, but not from Zimbabwe. Its distribution there is similar to *W. welwitschii:* Okavango swamps, Ngoha Island (Smith 1974), Thaoge River (SMITH 1975); Savuti (WAGER 1972); Chobe, Shaile (EDWARDS 1975). This expedition found it only in one place in Nqamaga Island.

W. arrhiza seems to be restricted in southern Africa to permanent waters in regions with an aridity factor of Martonne above 2. No flowering or fruiting was observed.

W. arrhiza has its main distribution in Africa, Europe and western Asia. In southern Africa, it grows outside of Botswana in Angola (Prov. Huila and Luanda), Mozambique (Sul do Save) and South Africa (Cape, Natal, Transvaal).

Wolffia cylindracea (Fig. 6g)

W. cylindracea is frequent in Zimbabwe but unknown until now in Botswana. Herbarium samples seen from : Nuanetsi Distr., Manjinji Pan (TAYLOR 1971), Malipate (DRUMMOND et al. 1961), Merrivale Ranch (WEST 1967); Hwange Distr., Ngwashla Rd. Inpan (WILD 1956); Hartley Distr., Gokwe, Sessami Mission (collector unknown , living material at the Botanical Garden in Harare 1992). On this trip the species was observed in the following localities: Urungwe Distr., 9 localities between Charara Safari Area and Mana Pools National Park; Hwange Distr., Ngamo Windpump.

In Zimbabwe, *W. cylindracea* seems to be restricted to seasonal waters of relatively dry regions (aridity factor of Martonne between 1 and 3), contrary to the situation in Asia and North America where *W. globosa* usually grows in permanent waters of regions with an aridity factor above 3. The African plants which have been included in *W. globosa* by many authors (see LANDOLT 1986) are separated here again. There are also some morphological and enzymatical features which justify the separation. This will be shown in a separate publication (LANDOLT 1994). Only one sample of 10 had a few fruits. However, all samples showed plenty of turions. It is supposed that the species survives the dry season in the soil as turions (see chapter 3.4.).

W. cylindracea occurs in central and southern Africa from southern Kenya and southern Angola to South Africa. In southern Africa it is known outside of Zimbabwe in Angola (Mocamedes, Libongo) and South Africa (Cape, Natal, Transvaal).

Further species of southern Africa not observed on this trip:

Spirodela polyrrhiza (Fig. 6h) is represented in herbarium samples from Malawi (not rare), Zambia (Mpika Distr., Luanswa Valley, Zambesi Valley), Zimbabwe (Zambesi Valley, Nuanetsi Distr.), Botswana (Okavango Delta, Linyanti River), Mozambique (Zambesi Distr., Manica e Sofala Distr., Maputo Distr.), South Africa (frequent in Natal, rare in Orange Free State: Vredefort). It is supposed that the species is mostly restricted to permanent waters.

Lemna gibba (Fig. 6k) is a species with distribution center in mediterranean areas. In Africa it occurs in the north, in the mountain areas of the east and in the south. The area shows a gap between southern Tanzania and Transvaal, where the summers are probably too hot. In South Africa it is frequent at the Cape, in Natal, Orange Free State and southern Transvaal. It grows in permanent as well as in seasonal waters.

Lemna minor (Fig. 6i) is a species of temperate zones growing throughout almost the whole world. In Africa it grows in the north, east (only higher mountains) and south. There is a distribution gap between Rwanda - Kenya and South Africa - southern Mozambique (only in Sul do Save, Inhanombe). The species is still more sensitive to high temperatures than *L. gibba.* It is absent in very dry places (with an aridity factor below 3). In South Africa it is quite frequent at the Cape, in Natal and southern Transvaal. The species lives in permanent waters.

Lemna trisulca is a species of the northern hemisphere often growing together with *Lemna minor.* In Africa it grows in the North and in the higher elevations of East Africa. It reaches southwards the region of Kilimanscharo and northern Lake Tanganyika. In the lowlands of South Africa the summer temperatures are too warm for successful growth of *L. trisulca.*

Wolffiella hyalina (Fig. 6d) is restricted to the tropical-subtropical zones of Africa. As far as known, the southern limit of the species is in Malawi (Southern Prov.) and Zambia (Northern Prov.) The species probably lives in permanent as well as in seasonal waters and is sensitive to frost.

Wolffiella denticulata (Fig. 6c) is an endemic species of southern Africa where it grows along the southern and eastern coast from the Cape (Tsitsi-

kama) to Natal and further north to southern Mozambique (Sul do Save, Inhanombe). The species lives in permanent waters of frost-free areas with an aridity factor above 3.

3.2. VEGETATION STUDIES

Of the 81 collected water samples, 10 contained no pleustophytes and 15 contained pleustophytes without *Lemnaceae.*
The 71 samples with pleustophytes consist of the following species number:

1: 24 times (10 *Lemna aequinoctialis,* 7 *Utricularia gibba*, 2 *Wolffiella rotunda*, 2 *Azolla pinnata*, 1 *Spirodela punctata*, 1 *Wolffiella welwitschii*, 1 *Salvia molesta*)
2: 23 times
3: 16 times
4: 8 times

In 15 soil samples the following pleustophyte species germinated in Zürich:
no pleustophyte species: 8
L. aequinoctialis: 2
W. repanda: 3
L. aequinoctialis and *W. repanda*: 1
L. aequinoctialis, W. repanda, W. rotunda: 1

Of the ca. 400 investigated herbarium samples (including the new collections) a little more than half contained only one pleustophyte species. The probability of the common occurrence of two species is shown in Table 1. The values were taken from herbarium specimens and field trip observations.
Table 1 shows positive correlations between *Lemna aequinoctialis, Wolffiella rotunda, W. repanda* and *Wolffia cylindracea.* A second group of positively correlated species consists of *Lemna minor* and *Wolffiella denticulata* as well as *W. denticulata* and *W. welwitschii.* Negatively correlated are: *L. aequinoctialis* with *Spirodela polyrrhiza, S. punctata, L. gibba, L. minor, L. trisulca, W. denticulata* and *W. arrhiza.* This rare common occurrence has probably climatic reasons (except for *S. polyrrhiza*). *L. aequinoctialis* is distributed subtropical to tropical regions whereas the other species prefer warm temperate to cool subtropical regions. *S. polyrrhiza* which is wide-spread in cool as well as in warm regions avoids seasonal waters. In the

Table 1. Common occurrence of *Lemnaceae* species in southern Africa (439 samples).

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

	Spirodela polyrrhiza	*Spirodela punctata*	*Lemna gibba*	*Lemna minor*	*Lemna trisulca*	*Lemna aequinoctialis*	*Wolffiella rotunda*	*Wolffiella hyalina*	*Wolffiella repanda*	*Wolffiella welwitschii*	*Wolffiella denticulata*	*Wolffia arrhiza*	*Wolffia cylindracea*
Spirodela polyrrhiza			-			---							
Spirodela punctata						---							
Lemna gibba						---							
Lemna minor						---					***		
Lemna trisulca						---							
Lemna aequinoctialis							***		*		--	---	*
Wolffiella rotunda									***				***
Wolffiella hyalina													
Wolffiella repanda													
Wolffiella welwitschii											**		
Wolffiella denticulata													
Wolffa arrhiza													
Wolffia cylindracea													
number of samples	57	20	59	42	28	203	19	24	11	34	10	52	27

humid tropics which are not considered in this work it often grows together with *L. aequinoctialis* . However, in southern Africa permanent waters are situated in cooler regions where it is to cool for *L. aequinoctialis*. In the northern part where it is warm enough for *L. aequinoctialis* permanent waters are rare. A few species are too rare to show definite correlations.

The relevés taken on the field trip (see Fig. 1) are combined in Tables 2 and 3. According to the habitat (seasonal or permanent water), two vegetation units could be demonstrated. Both units are characterized by *Lemna aequinoctialis*. The first one is additionally marked by *Wolffiella welwitschii* and *Azolla pinnata*, and the second by *Wolffiella rotunda* and *Wolffia cylindracea* (plus *Wolffiella repanda* and *Pistia*). There is an indication that *S. punctata* might form a separate unit (together with *Azolla*).

It is interesting to note that the number of pleustophyte species in an African relevé is much lower than in North or South America. In these African relevés, the highest species number was 4, whereas in Argentina relevés consist of up to 12 pleustophytes (LANDOLT and ZARZYCKI 1994). Also in North Carolina relevés with 6 to 9 species could be observed (LANDOLT 1981).

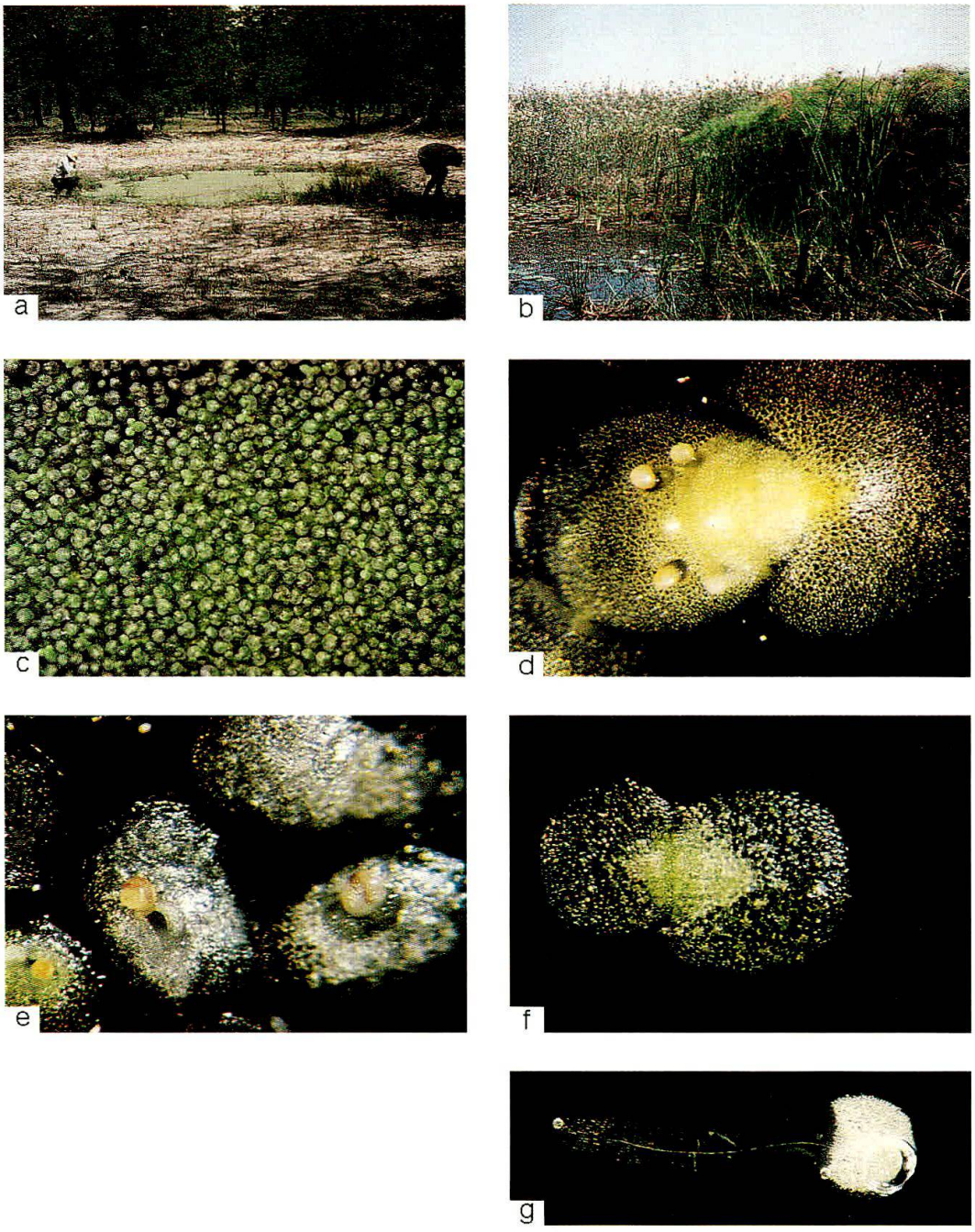


Fig. 7. Sites and appearence of African *Lemnaceae*.
a. Site of *W. rotunda* and *W. repanda* (near Chirundu, Zimbabwe)
b. Site of *W. welwitschii* (Boteti River, near Maun, Botswana)
c., d. *W. rotunda*: c. water covered with fronds from above (2/3 nat. size); d. flowering frond (16 x)
e., f., g.*W. repanda*: e. vegetative fronds from above 16 x); f. flowering fronds from above 16 x); g. vegetative frond from below (16 x)

3.3 WATER ANALYSES (Fig. 8)

The results from the chemical analyses show that water sites without *Lemnaceae* have generally a lower amount of potassium and phosphorus than waters with *Lemnaceae*. This is in accordance with water analyses from other parts of the world (e.g. LANDOLT and ZARZYCKI 1994). *Lemnaceae* need

Table 2. Plant sociological relevés of pleustophytes in Zimbabwe and Botswana. Vegetation from permanent water.
Fr: frequency (according to Braun-Blanquet); I: 1-19%, II: 20-39 %, III: 40-59 %, I: 60-79 %, V: 80-100%.

relevé no. / species	1	5	3	4	26	45	48	50	70	60	59	63	66	64	58	62	69	Fr
Lemna aequinoctialis			1	1	+	+	1	2		1	1	3	+	4	+	1	1	V
Spirodela punctata	1	1																I
Azolla pinnata	2		2	2	4				2			3	1	3				III
Wolffiella welwitschii											+	2	1	+	1	1	1	III
Utricularia stellaris						3	2	1	1	1								II
Salvinia molesta					1				3								2	I
Ceratophyll. demers.		2							3	4	5							II
Wolffia arrhiza														2				I

Table 3. Plant sociological relevés of pleustophytes in Zimbabwe and Botswana. Vegetation from seasonal waters.
Fr: frequency (according to Braun-Blanquet). I: 1-19%, II: 20-39 %, III: 40-59 %, IV 60-79 %, V: 80-100%

relevé no. / species	16	17	19	20	23	33	18	15	22	37	38	40	11	39	30	29	13
Lemna aequinoctialis	4	4	2	2	3	+	4	2	2	2	4	3	2	5	3	+	2
Wolffiella rotunda	1	1	3	3	4	1		1	5	4	1	1	+	1	1	2	+
Wolffiella repanda	3	4	2	+	+	+	2										
Wolffia cylindracea	3	4					2						+	+	+		
Pistia stratiotes															3	+	2

	49	35	31	32	10	14	24	27	Fr
Lemna aequinoctialis	4	2	1	2	2	2	5	3	V
Wolffiella rotunda									IV
Wolffiella repanda									II
Wolffia cylindracea	3	+	3	4					III
Pistia stratiotes			5	5	5	1	+	1	II

a relatively high amount of phosphorus and potassium. The reason for this is most probably the small surface area through which the plants must take up the nutrients. In contrast to *Lemnaceae Salvinia* which has hairs on the lower surface as well as roots and transformed feathery rootlike leaves grows in waters with low phosphorus and potassium content. The waters with *Spirodela punctata* are characterized by a high field pH and a high calcium and magnesium content. Since there are only three sites with *S. punctata* this character could be purely incidental. However, investigations from Australia and Thailand with much more localities gave similar results (LANDOLT, unpubl.). *Wolffiella rotunda, W. repanda* and *Wolffia cylindracea* which often grow together have apparently high requirements for phosphorus, manganese and iron. From all *Lemnaceae Wolffiella welwitschii* is able to grow in the waters with lowest conductivity and lowest amount of potassium, phosphorus and magnesium. However, the small number of samples with *W. welwitschii* (partly two and partly three) relativizes the result. The low nutrient concentration in the waters with *W. welwitschii* can be explained by the fact that this species is able to sink to the bottom of the water during unfavourable condition. There it can receive directly nutrients from soil particles. At the time of the water sample collecting most of the plants of *W. welwitschii* were lying in the mud on the ground and hat to be stirred up. *Lemna aequinoctialis* which is most frequent of all *Lemnaceae* in the region grows nearly throughout the whole range of nutrient concentrations within the water sites with *Lemnaceae*.

3.4. CULTIVATION EXPERIMENTS AND MORPHOLOGICAL OBSERVATIONS

Some of the samples collected in Zimbabwe and Botswana have been cultivated in Zürich. *Wolffiella rotunda , W. repanda* and *L. aequinoctialis* developed flowers and fruits rather regularly in old cultures (12 hours light of about 20000 Lux and 26/24 ° C in 1/5 Hutner solution). All three species have a very high growth rate which corresponds to about a doubling within 24 hours. *W. welwitschii* and *W. cylindracea* did not flower under these conditions.
The characters of *W. rotunda* and *W. repanda* as well as *W. cylindracea,*were studied more closely in culture and compared with the descriptions in LANDOLT 1986). The following modifications must be noted:

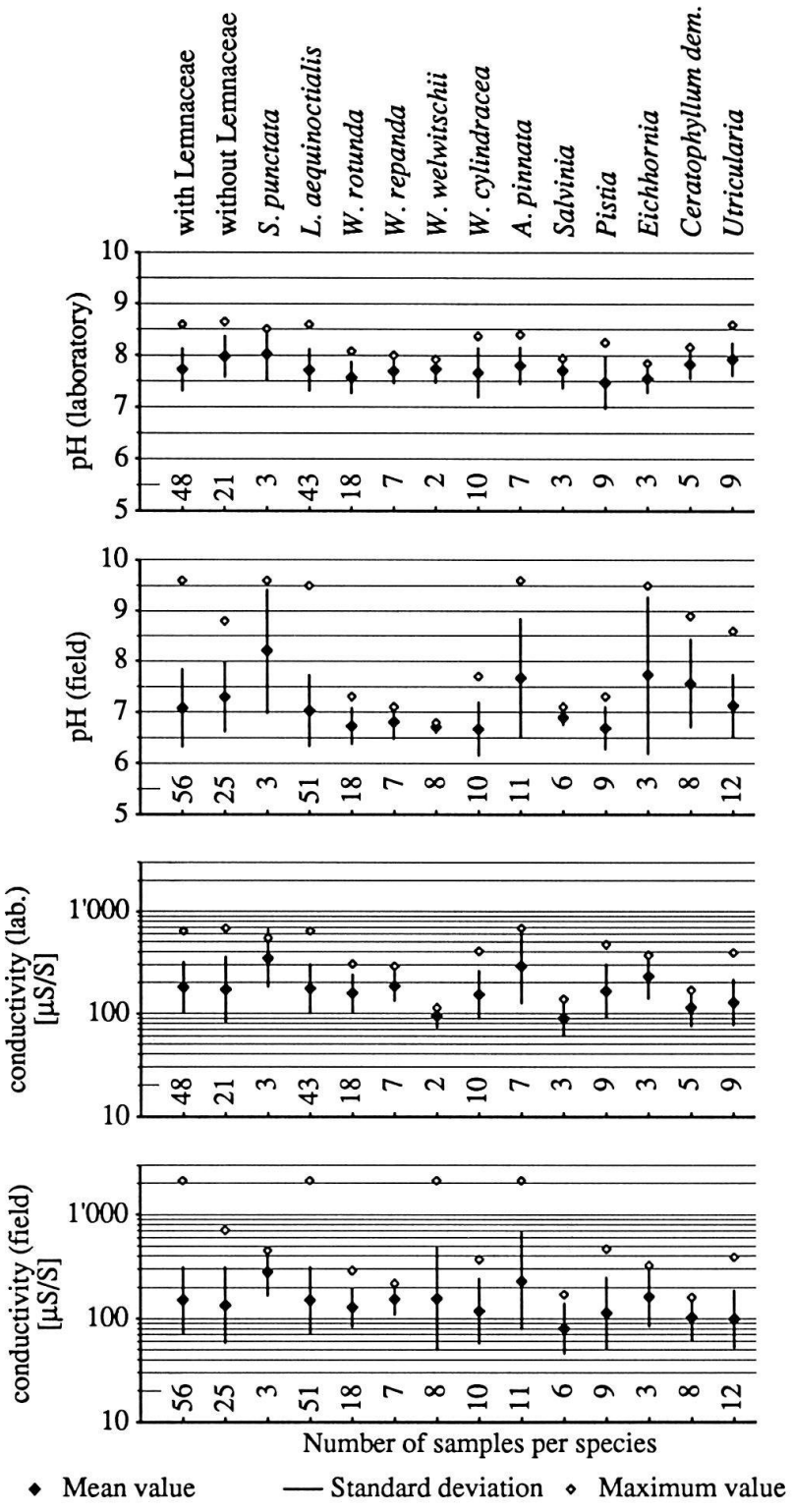


Fig. 8. Parameters of the water samples from *Lemnaceae* sites in Zimbabwe and Botswana.

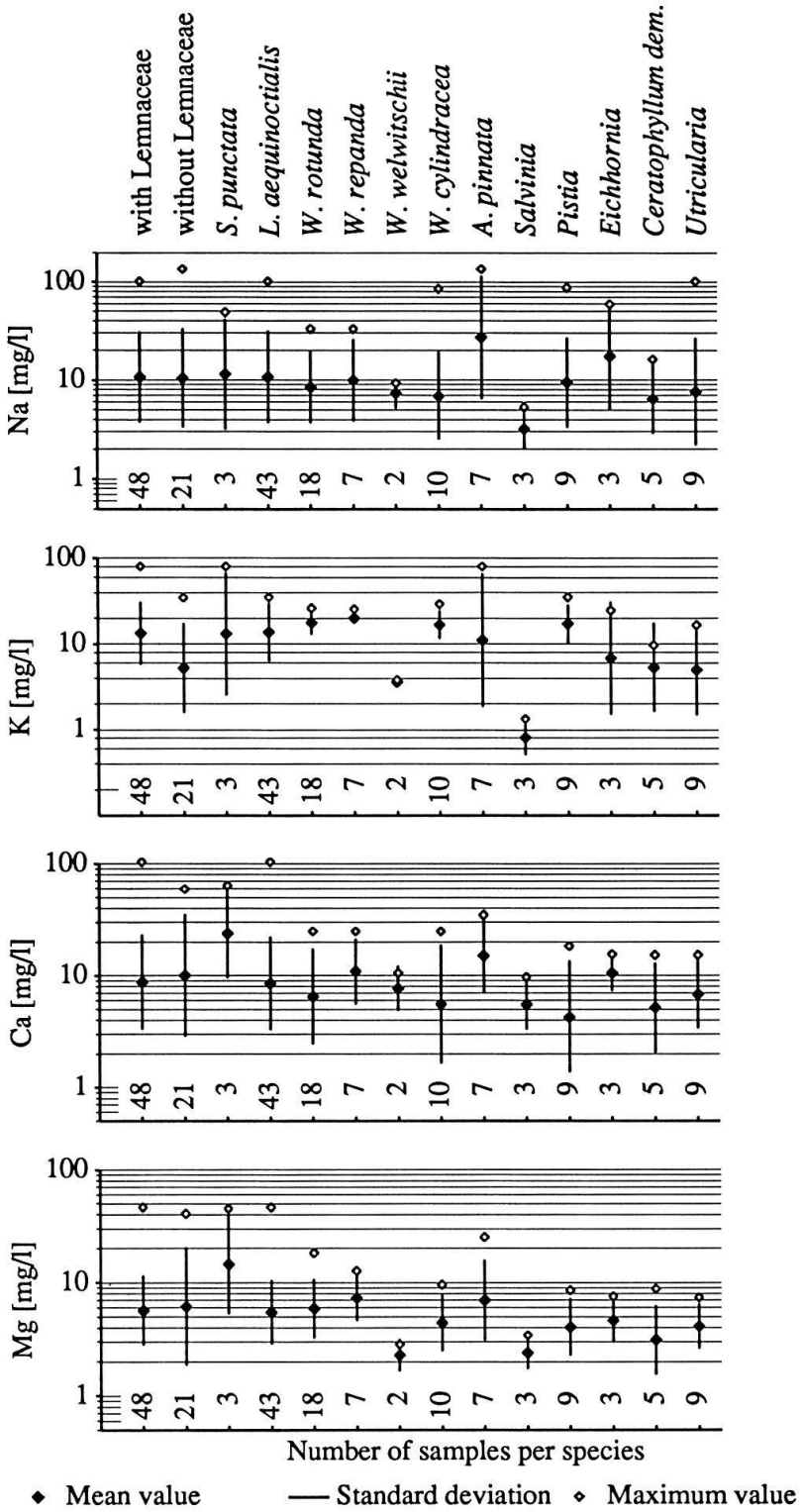


Fig. 8. (contin.) Parameters of the water samples from *Lemnaceae* sites in Zimbabwe and Botswana.

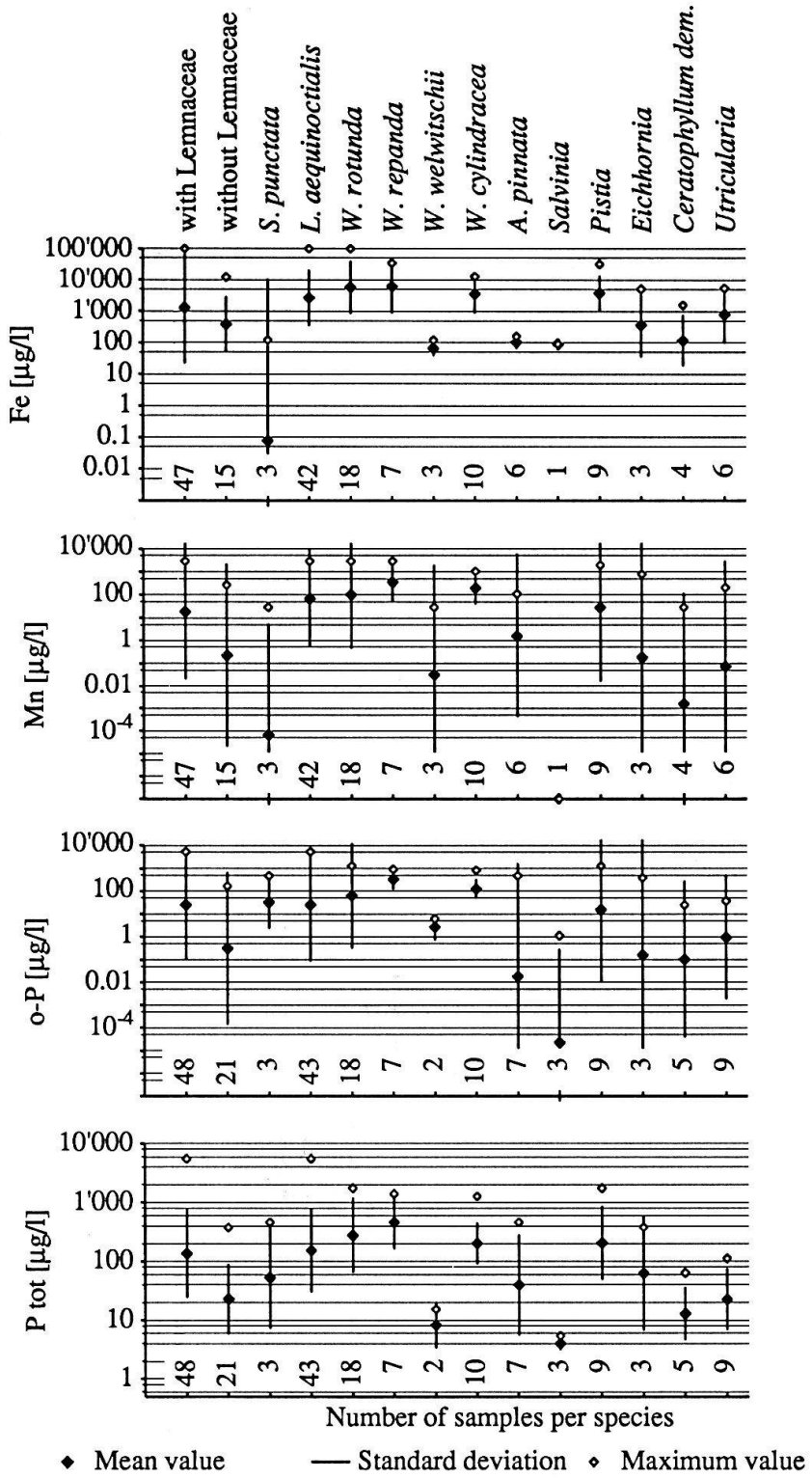


Fig. 8. (contin.) Parameters of the water samples from *Lemnaceae* sites in Zimbabwe and Botswana.

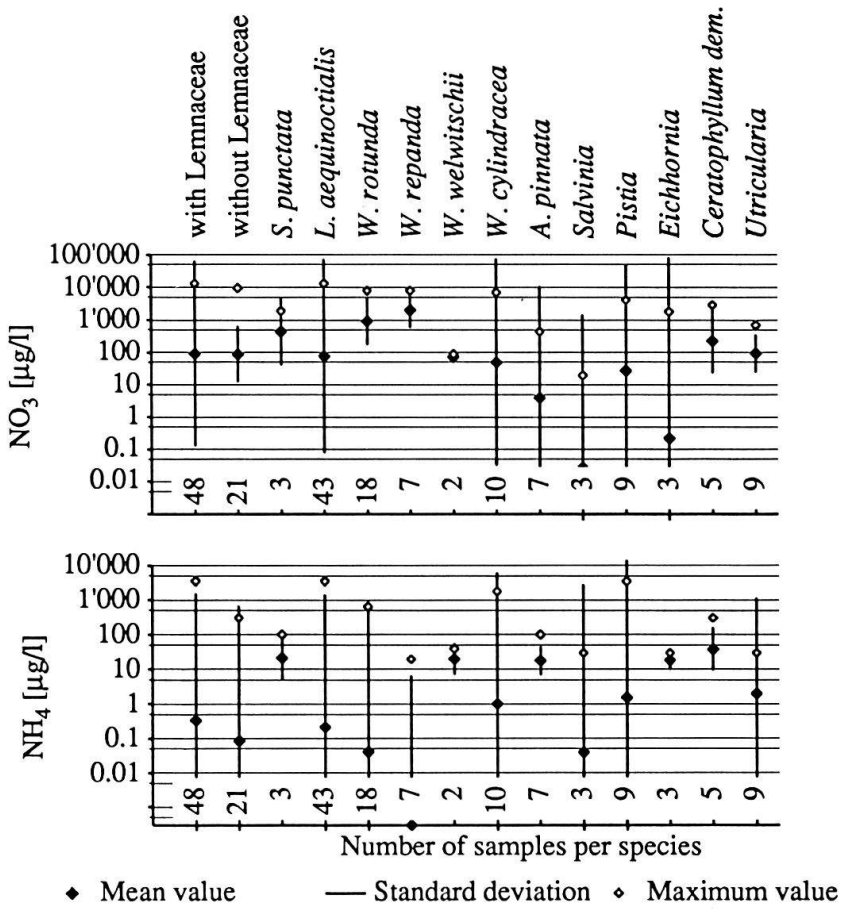


Fig. 8. (contin.) Parameters of the water samples from *Lemnaceae* sites in Zimbabwe and Botswana.

Wolffiella rotunda (Fig. 7c, d)

Fronds 1-3 cohering together, 1-3 mm long and about as wide, with a distinctive papule near the tip and above the node (contrary to the indicated indistinctive papules in LANDOLT 1986), with a narrow hyaline rim around the frond, no teeth-like papules along the rim, more than 60 stomata. No appendage present. Flowers, 1-4 per frond with pigment cells along the dehiscent line of the anthers. Fruits as in the whole subfamily of *Wolffioideae*.

The occurrence of 4 flowers (Fig. 7d) within a frond is unique for *Lemnaceae*. However, it demonstrates that the members of this family "show a predominance of irregular (adventitious) organ formation" (KANDELER 1988).

Wolffiella repanda (Fig. 7e, f)
Fronds 1-3 cohering together, 0.5-1.8 mm long and 0.4-1.5 mm wide, with an indistinct papule near the tip and above the node; no hyaline rim, only 20-30 stomata (not > 60 as indicated in LANDOLT 1986), teeth-like papules along the rim; lower wall of the pouch elongated towards the basal section into a ribbon-like appendage; appendage 0.5-8 mm long and 0.2-0.5 mm wide, 1-20 times as long as wide, 1/4-7 times as long as the frond and 1/4 to 1/2 as wide as the frond. Flower, one per frond with pigment cells along the dehiscent line of the anthers. Fruits, as in the whole subfamily.
In the cultures from Zimbabwe and Botswana the ribbon-like appendage was never longer than 3 mm. This might be due to the culture conditions. However, there seems to be a gradient from Angola to Botswana and Zimbabwe. In Luanda (Angola) the appendage is longer and comparatively narrower than at the other places. Further studies of living material from Angola have to confirm this indication.

Wolffia cylindracea
The morphology of this species in comparison to *W. globosa* will be described and illustrated in another publication (LANDOLT 1994). The different ecology between the Asian and the African plants and a few morphological and enzymatic differences suggest the separation of the African plants from *W. globosa* under the name *W. cylindracea* Hegelmaier.
To understand why *W. cylindracea* can survive the dry season without fruits (as in *W. rotunda* and *W. repanda*) turions of this species were checked for their ability to stand dry periods. Whereas normally air dried turions survived for no more than an hour exposed to the air, turions embedded and pressed firmly in a moist soil of clay and turf in an open beaker stayed alive for at least two months. After two weeks in the beaker the soil was quite dry. Also turions from other tested species (*Spirodela polyrrhiza, W. arrhiza, W. australiana, W. brasiliensis, Lemna turionifera* and even normal fronds of *L. minor*) could survive under the same conditions.The experiment must still be repeated. Maximal survival duration of the turions should be investigated.

4. DISCUSSION

Endemic species of *Lemnaceae* are rare. Living conditions in water are mostly similar over wide areas, and *Lemnaceae* are frequently distributed by birds from one body of water to another. Therefore species with world-wide distribution or at least with a distribution area over several continents are common. Man has also introduced *Lemnaceae* species in many places where it could not have reached by means of natural vectors (as is probable for *Spirodela punctata* in Africa). Species with a restricted area must be adapted to a specialized habitat. Such a narrow ecological niche was observed in *Lemna tenera* in northern Australia (LANDOLT 1992). This species grows only in forest swamps covered with *Melaleuca* trees. *Wolffiella rotunda* which may be the species of *Lemnaceae* with the smallest geographical area also has a very special habitat. It grows only in regions without frosts (Fig. 3), of Mopane vegetation, in small seasonal pans (Fig. 7a). Its high growth rate and the ability to produce plenty of seed within a short period gives the species an advantage in such a habitat. However, the nutrient concentration must be high for rapid growth. This high nutrient content can only be achieved in waters where animals fertilize the water with their manure. The animals come to the water to drink and cool off. When they walk through the water, they take many frondsout and uproot plants colonizing the water. Compared to *L. aequinoctialis* and other water plants, *W. rotunda* and *W. repanda* have only little substance and are able to replace lost fronds very fast. In addition they adhere less to the fur of animals since they have no roots or other organs which can become entangled in it.

Preconditions for the occurrence of *W. rotunda* (and *W. repanda*) in a certain place are:

a) A regular change of dry and rainy seasons
b) No or only slight frost
c) Pans which are too small to develop waves and have no fish and not many water fowl
d) A clayey soil rich in minerals (the old soils of the highlands are too poor) where water is stored during the rainy season
e) Animals which disturb and fertilize the water destroying competing plant species and deliver enough phorphorus and nitrogen for rapid growth.

Interestingly, *W. cylindracea,* which survives the dry season as turion, takes advantage of animals not only by utilizing the high nutrient content of the water: the stirring up of the muddy soil by the animals mixes the turions lying on the bottom into the clayey soil where they can sucessfully survive. If they were not imbedded in clay they would die. Since *W. cylindracea* tolerates light frost it has a larger distribution area than the two *Wolffiellas.*

It is not quite clear why *W. rotunda* has a narrower distribution than *W. repanda.* The present known area in northern Zimbabwe is only about 360 square kilometers. Of course it is possible that it was just overlooked in other areas. The small, muddy, seasonal pans with naked shores do not look very inviting to botanists. Especially in the adjacent regions of Zambia and Mozambique with simliar climatic and edaphic conditions, it might very well occur. However, this does not explain why it is absent in Botswana and Angola where the climate diagrams look rather similar and the conditions a) to c) are met with. The only climatic difference known to the author between the region of the Zambesi Valley below Kariba and the region of Maun or Luanda are the higher summer temperatures which in Chirundu reach nearly 30 ° compared with 26° in Maun and Luanda (compare Fig. 3 d with Figs 3f and 3h). Fig. 5 shows that the Zambesi Valley below Kariba has very high January mean daily maximum temperatures (up to more than 35°) whereas in northern Botswana and western Angola these temperatures are lower. Similarly high temperatures are known from the lower Limpopo Valley and in the southern Kalahari. This last region is too dry for *W. rotunda* and *W. repanda.* If *W. rotunda* grows much faster at high water temperatures it might be competitive against *W. repanda* only under very high summer temperatures. Provided that this assumption is true, *W. rotunda* should also be found in most of the lower Zambesi Valley of Zambia and especially of Mozambique as far down as the Mopane forest reaches. The possibility also exists that *W. rotunda* (and *W. repanda*) can be found in the lower Bimpopo Valley. As depicted in Fig. 2, *W. repanda*, like *W. rotunda,* keeps to regions with Mopane forest (except the locality Luanda near Bemposta).

Another specialist is *Wolffiella welwitschii* which grows in permanent waters in regions without frosts. The waters are probably not always provided with enough nutrients. In such a case, the fronds sink to the bottom where nutrient access is more likely. Especially phosphorus can be taken up from the neighboring soil through secretion of phosphatases (KANDELER 1988). From the organic soil they are probably also able to take up some organic substances to maintain their energy balance. As soon as the nutrient content is more favo-

rable, the fronds emerge to the surface. The aridity factor of Martonne (i) of regions with *W. welwitschii* varies generally between 2 and 5. In the Okavango Delta the factor is somewhat lower than 2. But the water of the Okavango River is not autochthonous. It comes from regions in Angola with a much higher rainfall corresponding to a higher aridity factor.
If we look at the other species of *Lemnaceae* in southern Africa *Wolffiella denticulata* is another specialist restricted to a small coastal area of these regions with the highest rainfall (i > 3) and without frosts.

SUMMARY

Eighty-one samples of waters containing pleustophytes (mostly *Lemnaceae*) were collected in northern Zimbabwe and Botswana and analyzed for minerals.
Plant sociological relevés can be arranged into two different units: one in permanent waters with *Wolffiella welwitschii* and *Azolla pinnata* as characteristic species, the other in seasonal pans with *Wolffiella rotunda* and *Wolffia cylindracea* as characteristic species (Tables 2 and 3).
Wolffiella rotunda, hitherto known from only one locality was found in several places in the region between Kariba Lake and Mana Pools .
Wolffiella repanda, which was known from only three collections (two in Angola and one in Botswana) was also deteced in northern Zimbabwe along with *W. rotunda.* In northern Botswana, soil samples of three places contained seeds of *W. repanda.*
W. rotunda and *W. repanda* survive the dry season by seeds which are frequently formed in nature.
W. cylindracea, which also grows in seasonal waters, was separated in the present publication from *W. globosa* on account of the different habitat and slightly different morphology. It survives the dry periods by turions.
Wild animals, such as buffalos play an important role in the occurrence of *Lemnaceae* in the small pans, by fertilizing the pans and destroying competing water plants.
Wolffiella welwitschii is capable of sinking to the bottom of the water, by this means surviving periods with inadequate nutrient supply.
The relation between mineral content in the water and the occurrence of *Lemnaceae* species is described (Table 4, Fig. 8).
The geographic distribution of all *Lemnaceae* species occurring in southern Africa is presented in Fig. 6.

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