How do Lemnaceae (duckweed family) survive dry conditions?

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Summary

1 According to literature and own observations, seeds of all Lemnaceae investigated so far tolerate drying out for at least a few months to several years. By contrast, vegetative fronds are not able to withstand desiccation for more than half an hour or a few hours. To survive dry periods most species occurring in such habitats form seeds (e.g. *Lemna aequinoctialis* Welw., *L. disperma* Hegelm., *L. gibba* L., *Wolffiella repanda* [Hegelm.] Monod, *W. rotunda* Landolt). However, some species are known to grow in seasonal waters producing seeds only rarely or not at all.

2 The objective of this study is to learn if and how these species survive desiccation. Normal fronds and turions (if present) of ten species were stored at 40–60% air humidity and 20–25 °C and the survival was measured subsequently (*Lemna aequinoctialis, L. minor* L., *Spirodela polyrrhiza* [L.] Schleid., *Wolffia angusta* Landolt, *W. arrhiza* [L.] Horkel, *W. australiana* [Benth.] den Hartog & van der Plas, *W. cylindracea* Hegelm., *W. globosa* [Roxb.] den Hartog & van der Plas, *W. neglecta* Landolt, *Wolffiella neotropica* Landolt).

3 Vegetative fronds and turions, if embedded tightly in fine-grained soil, were able to survive dry conditions for a short time. After two months, soil water content dropped below 20 g per 100 g dry soil, and the fronds of most species died subsequently.

4 Only turions of *Wolffia cylindracea* were able to survive dry periods for at least 16 months. The soil water content reached *c.* 12 g per 100 g dry soil after four months; it did not change distinctly after longer periods. *Wolffia cylindracea* is a species occurring in pans with seasonal waters in Africa south of the equator. It could not be detected whether the species is provided with special physiological or biochemical properties, or if the possibility of long survival under dry conditions is due to the smallness of the turions which are better suited for a tight embedding in the soil than bigger ones or normal fronds.

Keywords: drought resistance, seasonal waters, turions, *Wolffia cylindracea*

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Introduction

Plants of the Lemnaceae family dry quickly if taken out of the water. Fronds of *Spirodela polyrrhiza, Lemna gibba* and *Lemna minor* die after a 2.5 h exposure to 21–26 °C and a relative air humidity of 60–70%, those of *L. trisulca* after 1.2 h and those of *Wolffia arrhiza* after 20–30 min (Wolek 1981). Keddy (1976) observed for *L. minor* completely dead fronds after 2 h and for *L. trisulca* after 1.2 h (25 °C; 70% humidity). Many authors working with Lemnaceae report similar observations. Turions as well as other resting fronds also die within a few hours (Jacobs 1947 and Das & Gopal 1969 for *S. polyrrhiza;* Landolt 1986 for *L. turionifera;* Godziemba-Czyz 1970 for *W. arrhiza*). The time until the fronds dry out irreversibly depends on the air temperature and humidity. Under special conditions such as low temperature, high humidity, and within relatively thick layers of fronds, Lemnaceae remain alive for a longer time. Godziemba-Czyz (1970) detected *W. arrhiza* fronds still living after having been removed from the water for 6 h; Ridley (1930) found living *L. minor* fronds 12–22 h after removal from the water. This would certainly not be sufficient time to survive natural dry periods in the vegetative stage.

The notion of McCann (1942) that "resting buds (of *S. polyrrhiza)* vegetated readily when placed in water after being kept dry under normal conditions for two years" must be erroneous. However, Gopal (pers. comm. 1984) detected in India that turions completely covered by mud or silt could survive in ponds that dry out for a short time.

From several species it is known that they can live in seasonal waters and survive by forming seeds which are resistant to desiccation. In northern Zimbabwe, there are pans which dry out for about five months a year and are covered by *Lemna aequinoctialis, Wolffiella rotunda, W. repanda* and *Wolffia cylindracea.* No fronds of *Spirodela polyrrhiza, Wolffiella welwitschii* and *Wolffia arrhiza* were seen in the pans although these species occur in permanent waters of the same region (Landolt 1994). Contrary to the other species of Lemnaceae in the pans, *W. cylindracea* produced only turions and no seeds. Before the pans dry out they usually get visited by elephants, buffels and other large herbivores who stamp in the mud and thus firmly embed vegetative fronds, seeds and turions of Lemnaceae into the clayey and humus soil.

The question arised whether *W. cylindracea* is able to stand dryness in form of turions, or whether, at the end of every season, there was a recolonization of the ephemeral pond with fronds from a permanent site. Since no *W. cylindracea* occurred in permanent waters of the surroundings, this last possibility seemed unlikely.

The aim of this study is to answer the following questions: (1) Are turions of *W. cylindracea* able to survive dry soil conditions? (2) Do turions of *W. cylindracea* react differently to desiccation than other Lemnaceae?

Material and methods

Ten species of Lemnaceae (Table 1) were grown in Erlenmeyer flasks in 1/5 Hutner solution for four weeks. The light intensity was *c.* 15000 Lux white fluorescent light for 16 h daily. This corresponds to a photon flux density of nearly 1 mmol $m^{-2} s^{-1}$. The temperature was 25 °C. The fronds (turions included) were embedded in a mixture of wet peat and clayey soil (1:1). The firmly stamped, wet soil was put in jars and stored in darkness at 20–24 °C and 40–60% humidity. Each jar contained several hundred fronds. For *Spirodela polyrrhiza* and *Wolffia cylindracea* (clone no. 9080) jars were also stored in the refrigerator at a temperature of *c.* 5 °C and in the deep freezer at *c.* -25 °C.

Two series of desiccation experiments with different species were performed, the first series from December 1993 to August 1994, the second series from December 1994 to April 1996. Thirteen clones of ten species were investigated (cf. Table 1).

Table 1. Species and clones investigated in the desiccation experiments

First series (12.1993 – 8.1994) Species	Clone no.	Origin
Spirodela polyrrhiza	7551	Australia, N.T.
Lemna minor	6578	Switzerland
Lemna aequinoctialis	6746	USA, California
Wolffiella neotropica	7225	Brazil, Guanabara
Wolffia cylindrica	9080	Zimbabwe
Second series (12.1994 – 4.1996) Species	**Clone no.**	**Origin**
Spirodela polyrrhiza	7551	Australia, N.T.
Wolffia australiana	7267	Australia, Tasmania
Wolffia angusta	7274	Australia, NSW
Wolffia neglecta	9150	Pakistan, Karachi
Wolffia cylindracea	9080	Zimbabwe
Wolffia cylindracea	8378	Tanzania
Wolffia globosa	6592	USA, California
Wolffia globosa	8341	China, Nanking
Wolffia arrhiza	7014	Germany
Wolffia arrhiza	7347	South Africa

The following treatment was applied after 2, 4 and 6 months on the first series, and after 2, 4, 8, and 16 months on the second series: two jars of each species were mixed with water, stirred up thoroughly and exposed to the same light and temperature conditions as at the beginning of the experiment. The soil water content of the first series was measured once after four months in four jars, that of the second series every time the treatment was applied (in three jars). To measure the soil water content the soil samples were weighed after drying for 24 h at 105 °C.

Results

Some fronds of all species and clones survived the dryness for at least two months if embedded in clayey and peaty soil (Table 2). Several dozens of germinating fronds or turions of *Lemna minor, Spirodela polyrrhiza, Wolffia cylindracea* and *Wolffiella neotropica* were detected. The other six species showed only few surviving fronds or turions, but the latter had better chances to survive. However, normal vegetative fronds also germinated.

After 4, 6, 8, and 16 months of desiccation, only *Wolffia cylindracea* was able to develop new living fronds, in both series and both clones. Some turions still rose to the water surface after 5–12 d and produced living daughter fronds. I estimate that about 2–8% of the originally embedded turions were able to produce new fronds after having been stored in dry mud for four months. This did not change until the experiment was stopped (after 16 months). However, the percentage was significantly higher after two months (*c.* 20%). All other species did not show any sign of life after more than two months, except *Lemna aequinoctialis,* which germinated from seeds formed in the original culture.

Storing of *Spirodela polyrrhiza* and *Wolffia cylindracea* for four months in the refrigerator or in the deep freezer revealed the same results as storing under 20–25 °C., i.e. only *W. cylindracea* showed some green germs.

Table 2. Survival of Lemnaceae clones in the desiccation experiments (T, storage temperature; ++, good survival, > 40 living fronds; +, survival of 1– 20 fronds; –, no survival; (+), survival by seeds)

Species	Clone no.	T	Exposure time to dry air (months)				
		(°C)	2	4	6	8	16
Spirodela polyrrhiza	7551	20	++	–	–	–	–
		5	.‡	–	.	.	.
		-20	.	–	.	.	.
Lemna minor	6578	20	++	–	–	.	.
Lemna aequinoctialis	6746	20	+	(+)	(+)	.	.
Wolffiella neotropica	7225	20	++	–	–	.	.
Wolffia australiana	7267	20	+	–	.	–	–
Wolffia angusta	7274	20	+	–	.	–	–
Wolffia neglecta	9150	20	+	–	.	–	–
Wolffia cylindracea	9080	20	++	+	+	+	+
		5	.	+	.	.	.
		-20	.	+	.	.	.
	8378	20	++	+	.	+	+
Wolffia globosa	6592	20	+	–	.	–	–
	8341	20	+	–	.	–	–
Wolffia arrhiza	7014	20	+	–	.	–	–
	7347	20	+	–	.	–	–

‡ no records

The soil water content of the second series was 19.4 ± 0.9 g per 100 g dry soil (mean ± SD; three samples) after two months, 10.8 ± 0.0 g after four months, 13.2 ± 0.2 g after eight months, and 12.3 ± 0.3 g after 16 months (Fig. 1). In the first series, the soil water content was 11.3 ± 0.6 g (four samples) after four months. The soil water content of the jars from the refrigerator and the deep freezer was 22.2 ± 2.8 g (two samples) and 23.1 ± 1.3 g (two samples) after four months. Since air humidity is higher under cold conditions, the evaporation of the soil water was slower in the cooler kept jars.

Discussion

The experiments show that the survival of the investigated Lemnaceae species during a dry season is possible under the following conditions:

(1) The soil water content of the clayey soil should not drop under *c.* 20 g per 100 g dry soil. This limit is reached after two months at temperatures between 20–25 °C and an air humidity of 40–60%. It corresponds with a negative osmotic pressure of *c.* -1.5 MPa in clayey soil (cf. Jeffrey

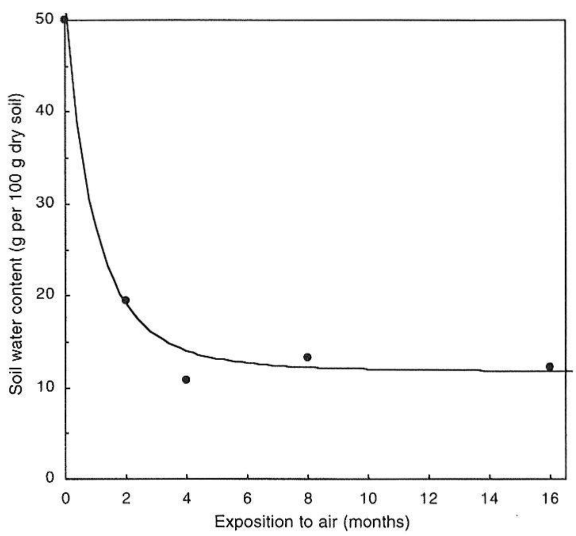

***Fig. 1.** Soil water content in the jars in relation to length of exposure to ambient air.*

1987: 124), from which it is well-known that water is available for plant roots down to this low water content.

(2) The fronds have to be embedded tightly in very fine-grained material (mud, silt, clay, peat) which prevents dry air from reaching the Lemnaceae plant. Therefore, it is assumed that fronds of Lemnaceae stay only alive if they are isolated from the surrounding air by the fine-grained soil.

From the ten species investigated, only *Wolffia cylindracea* was able to survive longer than two months under dry conditions. The estimated survival rate of the turions (2–8%) did not change remarkably between the dry periods of 2–16 months. After four months, the soil water content in the jars had reached the lowest value which amounted roughly to 12 g per 100 g dry soil. Under the experimental conditions the value did not drop any further. The slight variation between the values at different times may be due to varying conditions outside the jar (40–60% air humidity, 20–25 °C). In clayey soil, water content below *c.* 15 g per 100 g dry soil is called non-available capillary water. It is bound to the soil by a tension of -1.5 to -3 MPa. Turions of *W. cylindracea* appear not obviously different from those of other *Wolffia* species except that they are slightly smaller in size (diameter *c.* 0.3 mm). It is conceivable that smaller bodies are better protected from the air by small soil grains than bigger ones. How they can stand conditions of an osmotic potential of -1.5 to -3 MPa for months without drying out irreversibly is not that evident. This value is almost outside the range of tissue osmotic potential, except for halophytes. Therefore, different physiological or biochemical traits of the turions must be considered.

The results confirm that *W. cylindracea* is able to survive the yearly dry period of 5–7 months in form of turions. However, the preceding embedding in mud by trampling animals is necessary. This is probably the reason why similar *Wolffia* species did not develop in other regions where such animals are missing. The drought resistance for at least 16 months is sufficient to make the survival of the species possible even if the rainy season is wanting for one year.

If we assume that 5% of the turions survive desiccation, and that it takes two weeks for germination, two weeks for doubling the frond number and two weeks to form an equal turion number from the number of normal fronds, we can conclude that a growing time of at least 12–15 weeks is necessary to keep the population on the same level and thus viable.

The survival by seeds is more effective because nearly all seeds are protected by an impermeable coat and thus able to germinate in water to nearly 100% after the dry season. However, seed production is much lower than turion production. In the present experiment, the number of germinating seeds of *L. aequinoctialis* corresponded to the number of germinating turions in *W. cylindracea* after four months of desiccation. Similarly to the turions of *W. cylindracea,* seeds resist to drying periods for much more than one year. Seeds of *Lemna gibba* stayed alive for more than five years (Witztum 1977). However, the germination rate drops rapidly with time. Rejmankova (1976) found in the second year a germination rate of only 3–7.6%. The seeds of various Lemnaceae species may react differently in this respect, though. According to Brock & Lane (1983), *Lemna disperma* is only able to live in places which are wet for at least seven months. For *L. aequinoctialis,* the wet time required is shorter. In the Po plaine of northern Italy, the species grows in rice fields, which stay dry for about seven months (pers. observ.).

Storing at cold temperatures (*c.* 5° and -25 °C) for four months is not tolerated by normal fronds or turions of *Spirodela polyrrhiza* even if the fronds are embedded in fine-grained soil and the water content reaches more than 20 g per 100 g dry soil. Under the same conditions, some turions of *Wolffia cylindracea* are able to survive cold temperatures. Interestingly, the effect of cold temperature on turions of *S. polyrrhiza* is probably more severe under dry (soil water content around 20 g) than under wet conditions. Jacobs (1947) reports that turions of *S. polyrrhiza* can stand temperatures of -4 °C for at least three months. At +4 °C, Kronberger (pers. comm. 1985) observed living turions, even after a storage in water for four years.

Conclusions

The experiments show that there are different mechanisms of drought resistance in Lemnaceae.

SURVIVAL BY SEEDS

All seeds so far known are drought resistent. A contrary indication of Rostowzew (1905) who had no success in germinating dry seeds of *Lemna minor* is exceptional. I observed *L. minor* in rice fields of northern Italy in August 1992 forming seeds abundantly. Those seeds germinated after drying and being stored for two months. However, seed production is very rare for most species. Species surviving dry periods regularly by seeds are: *L. gibba* (e.g. Wilson 1830; Hegelmaier 1868; Rejmankova 1976; Witztum 1977), *L. disperma* (Brock & Lane 1983; Landolt, unpubl. observ.), *L. aequinoctialis* (Landolt 1957, 1986, 1994; Beppu & Takimoto 1981), *Wolffiella repanda* and *W. rotunda* (Landolt 1994). It is supposed that *Wolffiella hyalina* and *Wolffia microscopica* are also able to survive dry seasons regularly by seeds. Certainly, some other species which rarely produce seeds are able to stand dryness under special conditions. In Australia, *Spirodela punctata* was observed by farmers to survive dry seasons in ponds that dry out periodically (pers. comm. 1981). *Wolffia brasiliensis* was also observed surviving desiccation in farm ponds of South America (pers. observ.).

SURVIVAL BY NORMAL FRONDS AND TURIONS FOR SHORT PERIODS

All investigated species are able to survive dry periods of up to two months if they are embedded firmly in clayey soil.

SURVIVAL BY TURIONS FOR LONGER PERIODS

Wolffia cylindracea with extremely small turions is the only species which can cope with dry periods for many months and thus survive in seasonal waters without seeds if the turions are imbedded firmly in clayey soil.

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