

# Drought resistance in water plants in rock pools of Southern Africa

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## ABSTRACT

Water plants growing in ephemeral pools on rock outcrops in arid areas of southern Africa exemplify contrasting adaptation to drought. Some possess leaves or rhizomes that can tolerate dehydration. *Aponogeton desertorum* dies back to perennating organs which resist excessive water loss. The former group experience extreme fluctuations of temperature and aridity; they have evolved tolerance of complete desiccation.

## INTRODUCTION

Early botanists classified plants according to habitats into xerophytes, mesophytes and hydrophytes (adapted to arid, well-watered, or aquatic habitats respectively). Xerophytes frequently possess anatomical features which were thought to restrict water loss. The difficulties of such classifications are exemplified by the water-plants which grow in hollows in granitic rock outcrops (Giess 1969, 1970; Mauve 1966) in the arid regions of southern Africa adjoining the Atlantic Ocean. These grow as typical hydrophytes with aerenchymatous tissue in floating or submerged leaves when the rock-hollows are temporarily filled with rain water, but they are extremely drought resistant when the pools are dry (Heil 1925; Hickel 1967).

Drought resistance has been subcategorized into the ability of tissue to recover from reduced water content (i.e. drought tolerance) and the ability to minimize reduction in water content when external conditions are adverse (i.e. drought avoidance; see Levitt 1980).

This paper examines the protoplasmic drought tolerance of the drought resistant water plants of South Africa, as part of a search for 'resurrection plants', i.e. plants whose protoplasm survives air-dryness. As this involved continual travel, ecological data were of necessity, restricted.

## METHODS

Plants were collected by the authors (in August and September) during the dry season in southern Africa. With the exception of rhizomes of *Aponogeton desertorum*, all plants were dry, shrivelled and discoloured either brown or purple-black. Speci-

mens were sealed in air-tight glass containers for periods of one to fourteen days before physiological examination could be commenced.

The following species were collected:

*Aponogeton desertorum* Zeyher ex Sprengel f.; family Aponogetonaceae; = W. Giess 9191, (Plate 1, 2, 3), perennating as brown tuber-like rhizomes with moist white flesh during the dry season. These sprout during the wet season to produce long-petiolate leaves with elliptical leaf blades (5 x 15cm) floating on the water surface, and yellow inflorescences up to 7cm long rising above the water surface. Rhizomes were collected in September 1970 from large pools on bare granite hills at Okombahe Reserve OM 139, 34 km east of Uis Mine on road to Omaruru (21°30'S, 15°59'E).

*Limosella grandiflora* Benth.; family Scrophulariaceae; = Giess, Volk & Bleissner 6273. (Plate 4, 5) Thin perennating corms about 1cm long, 1 to 2mm wide, covered with black-brown scale-like projections, possibly remnants of old leaf-petioles. Sprouting in the wet season to give oval leaf blades, 1.5 x 0.8cm, floating on the water surface with petioles 15cm long. Flowers are 7mm in diameter and light violet in colour. Air-dry rhizomes were collected from shallow pools on bare granite rock outcrops in the Okombahe Reserve 16 km from Uis on the road to Omaruru.

*Lindernia intrepidus* (Dinter) Oberm., Syn *Chamaegigas intrepidus* Dinter; family Scrophulariaceae; = W. Giess 9614, (Plate 6, 7, 8). Plants are minute, consisting of a short rhizome close to the soil surface, see Hickel (1967), threadlike adventitious roots and leaves of two kinds: (a) a vertical tuft of bifurcate leaves with linear-subulate lobes about 1cm tall, which grow submerged when pools are water-filled; and (b) a rosette of 4 sessile oval leaves (3 x 5mm) floating on the surface of the water and attached to the rhizome by a thin flexible petiole. Flowers are produced in the rosette of floating leaves. A fuller description is provided by Smook (1969).

Air-dry plants were collected from dry shallow depressions with 1cm of silty soil on granite hills in the Fritz Gaerdes Nature Park, NE of Okahandja (18°45'S, 15°29'E).

*Craterostigma monroi* S. Moore, family Scrophulariaceae. (Plate 9). Basal 'submerged' leaves are purple-black and very similar to linear-subulate leaf lobes of *L. intrepidus*, but the inflorescence is supported by a stiff vertical stem (3cm) with opposite decussate linear subulate leaves (7 x 2mm), which subtend small axillary flowers.

Air-dry plants were collected from dry pools, similar to those for *L. intrepidus*, in bare granite hills at Rusapi (18°31'S, 32°10'E).

Although it was not possible to make continuous observations of the drying and refilling of pools, estimates were made for two dissimilar *L. intrepidus* pools at Fritz Gaerdes Nature Park, Okahandja. Estimates were based on rainfall records from the nearest weather station at Okaundua (22°07'S 16°50'E, 1350m), on observations of the rate of decrease in height of water in filled pools due to surface evaporation (14mm d<sup>-1</sup>), on measurement of the average depth of the pools when full (4.5 and 18cm respectively for pool 'A' and 'B', pool A being the more typical), on the surface area of the pools (2.0 and 2.4m<sup>2</sup> respectively), and on the catchment area of rock sur-

face draining into each pool (14.9 and 9.6m<sup>2</sup> respectively). An arbitrary correction of 1mm rain was allowed for evaporation of water from the catchment after each shower. Five mm was allowed for the water capacity of the 1cm layer of soil. Estimates of pool filling and drying were made for two consecutive wet seasons, 1969/70 and 70/71, and the intervening dry season.

On return to Windhoek or Pretoria, samples of each specimen were rehydrated in water in diffuse light at room temperature (25°C) for 24 hours. Live tissue became fully turgid and crisp within this time; dead tissue usually was saturated with water, but flaccid and limp.

Survival of fully turgid tissue was verified by the ability of membranes of living cells to exclude Evan's blue and to contain vacuolar substances which combine chemically with neutral red (Sullivan and Levitt 1959; Gaff and Okong'o-Ogola 1971). In some instances, the ability of live leaves to assimilate carbon dioxide by photosynthesis was also established by cresol red colour changes (Leith and Ashton 1961).

No rhizomes of *Aponogeton* were found in an air-dry condition. Drought tolerance limits were in this case determined by allowing sample slices (1mm thick) of tissue to lose water to a pre-determined proportion of the initial fresh weight; samples were then weighed, rehydrated and tested for survival. The water potential of tissue at the 50% survival point was determined by the vapour exchange gravimetric method (Arcichovskij and Arcichovskaja 1931; Slatyer 1958). A similar procedure was adopted for leaves of *Limosella* and inflorescence leaves of *Lindernia*, which grew from plants rehydrated in the laboratory. Finally, samples were oven dried at 105°C for 2 days. Water contents were expressed as a percentage of the water content of tissue when fully turgid (i.e. Relative Water Content, RWC). On this basis, fully turgid tissue has a RWC of 100% and fully dry tissue a RWC of 0%.

## RESULTS AND DISCUSSION

*Aponogeton desertorum* occurs in relatively deep rock pools (1m deep) in runnels on the lower slopes of granitic rocks. Rhizomes were located under 10cm of coarse sand and quartz fragments. Although the sand was airdry at the time plants were collected, internal tissues of rhizomes were perceptibly moist when cut open and registered a relatively high water content (87% RWC; Table 1). That is, rhizomes had considerable capacity to avoid dehydration; presumably the outermost layer has a high resistance to diffusion of water. In addition, overlying coarse sand would give some protection from the drying effect of the aerial environment. Rhizomes had a water content well in excess of the 50% death point of 38% RWC. The latter value corresponded to a water potential of about 89% RH (at full air-to-tissue equilibrium), a drought tolerance equivalent to very hardy crop plants (Levitt, Sullivan and Krull 1960; Iljin 1930), but in no way comparable to resurrection plants where protoplasm can survive complete dehydration (equilibrium with 0% RH; Gaff 1977). No leaves were found: presumably remnants had been swept away by wind or water. Rhizomes sprouted rapidly in water in the laboratory. Leaves were thin and soft; lack of fibre is reflected in the low content of dry matter (Table 2). Although the RWC at 50%

death (19% RWC) is half that for rhizomes: this corresponded to a higher water potential (97% RH), — a reflection presumably of the very different nature of the tissues, one being a dense reserve-storage tissue, the other a soft hydrophytic leaf.

*Limosella grandiflora* was found in much shallower pools near the top of granitic rock outcrops. The thin shrunken corms, embedded in the surface soil of the dry pools had a very low water content (11.7% RWC) and water potential (11% RH; Table 1). Even so, their ability to sprout leaves and adventitious roots rapidly after rehydration indicated clearly that they were alive. When equilibrated from this air-dry state to lower relative humidities for 12 weeks, 44% of rhizomes survived 0% RH.

Leaves of *Limosella* did not share the desiccation tolerance of corms. Brown, shrivelled leaves were found attached to the short vertical corms, which were embedded in the surface of the shallow soil of the dry pools. The leaves proved to be dead on rehydration. Drought tolerance tests on leaves grown from rehydrated corms gave values (94% RH water potential; 18% RWC) of a similar order to those for *Aponogeton* leaves (Table 1).

*Lindernia intrepidus* occurs in the shallowest ephemeral pools. Soil (only about 1cm deep) is held firmly by a dense mat of intertwined fine roots arising from a very short horizontal rhizome, near the apex of which the foliage arises (see Hickel 1967).

All parts of the plant become air-dry when the shallow pools dry out. Basal ('submerged') leaves then become shrivelled and purple to brown in colour; mature ('floating') inflorescence leaves become light purple and equally dry and shrivelled. Plant rehydrated fully in 2 hours when soaked in water (Hickel 1967), — by far the most rapid recovery of any resurrection angiosperm, 12 to 24 hours is usual (Gaff 1977).

Air-dry leaves had a water potential equivalent to 30% RH, nevertheless, all viability tests clearly showed that the basal leaves were alive, and plants rapidly resumed growth (Table 1). Mature air-dry inflorescence leaves failed to revive. *Lindernia* then is extraordinary in exhibiting such a dramatic distinction in the drought tolerance of two types of leaf on the same plant. Fifty percent of basal leaves withstood complete loss of all their diffusible water (i.e. water potential equilibrated to 0% RH), whereas mature inflorescence leaves, from plants grown on after rehydration, did not survive 96% (Table 1). No other species has been recorded with such a dramatic contrast in the drought tolerance of distinct forms of mature leaves on the same plant. The contrast however, is much less for immature inflorescence leaves. In plants collected air-dry in the field, these had a drought tolerance between 0 and 5% RH, i.e. very close to the tolerance of mature basal leaves (Table 1). Inflorescence leaves retained desiccation tolerance until unfolding of opposite leaves from the bud was almost complete (Table 3).

Inflorescence buds grow very rapidly on rehydration; floating leaves grow to the surface within 2 to 4 days of pools filling with water, Hickel (1967), Smook (1969).

*Craterostigma monroi*. Vegetative parts of this plant, both air-dry and fully hydrated, show a remarkable resemblance to *Lindernia intrepidus*. Inflorescence shoots

however, are quite distinct, being erect with leaves separated by distinct internodes instead of in a terminal rosette of 4. Shallow pools, in which it occurred in Zimbabwe, were similar to those inhabited by *L. intrepidus*. Both basal rosette leaves and inflorescence leaves were desiccation tolerant, with the optimal tolerance value 0% RH (Table 1).

### **Injury Mechanisms**

The detailed data for desiccation tolerant tissue show death of tissue during prolonged equilibration to humidities of 52% and above (Table 4), as well as partial injury at 0% RH.

Observations such as these led to the suggestion (Gaff 1980) that more than one mechanism of injury was involved in the onset of injury during water stress. The particular mechanism probably varies with the degree of stress, its duration, the temperature, and the species involved. Loss of resistance to microbial infection probably is implicated in injury at water potentials above 50% RH. Similar phenomena have been reported during storage of seed and pollen (literature cited in Gaff 1980).

There was evidence of sublethal injury at 0% RH: *Limosella* shoots from corms which survived equilibration to 0% RH grew more slowly after rehydration than did plants from corms which survived 5% RH (Table 5).

### **Ecology of *Lindernia (Chamaegigas) intrepidus***

**Rates of Dehydration and Rehydration:** Intertwining roots of *L. intrepidus* hold the shallow soil layer so tightly together that soil segments approximately of 8cm diameter could be removed intact without injury to the plants growing in them. When segments were allowed to dry under natural conditions, the soil mass, approximately 1cm deep, dried within 2 hours (Table 6). One hour later, plants in the centre of the soil segment wilted; wilting was first visible at 54% RWC. All plants were air-dry within a further 45 minutes (RWC 8%). Once soil water has been exhausted, plants dry within 1.75 hours. There is little time, then, for biochemical changes for protective adjustments to imminent desiccation. Rehydration is equally rapid: air-dry *L. intrepidus* plants become fully turgid within 1 1/2 hours of immersion in water (Hickel 1967, consistent with the study reported here). Drying and resorption of water then are far more rapid than in non-aquatic resurrection angiosperms, which usually dry over a 2 day period, and rehydrate in 8 to 12 hours (Gaff 1977).

**Time Pools Contain Water:** Despite the approximations involved in the estimates of pool filling and drying (Tables 7—9), they give some notion of likely patterns. Some interesting features emerge. Depending on the pool and season, 20 to 40% of plant rehydrations last less than one day; this emphasizes the importance of rapid rehydration and the retention of chlorophyll in the leaf throughout the drying/rehydration cycle. On the average, plants were rehydrated in the order of 3 to 5 days at a time, but 37 days was reached on one occasion. In general, then, there was relatively little time for assimilation and growth in a single refilling. Pools held water for a total of 42 to 86 days per wet season.

Plants were dry for 172 days continuously in the rainless season from April to October. In addition, they were dry for 5 to 12 days 'on the average' between showers in the wet season.

Despite the differences in the dimensions of the two pools, the numbers of rehydrations were the same (15 and 17 in consecutive wet seasons). The greater depth of pool B apparently compensated for the lower catchment area relative to pool area. However, the two pools differed markedly in the extent to which they overflowed. Pool B did not overflow in 69/70, and only overflowed in one month in the subsequent wet season (Table 7). In February, it was estimated to have overflowed on seven occasions, the total discharge corresponding to 1.6 times the volume of the pool. Pool A, on the other hand, overflowed on 10 occasions during the earlier wet season and 20 during the later season; total volumes discharged were equivalent to 14.0 and 30.8 complete flushings of the pool in the two seasons respectively.

The six sites at which *L. intrepidus* occurs, have annual rainfalls ranging from 93 to 370 mm (mean =  $288 \pm 137$  S.D.; Hickel 1967). By comparison the rainfall for the two wet seasons, studied in Tables 7—9, totalled 173 and 331mm, and would therefore be representative of the most common conditions experienced by the species.

### **Nutrient Balance**

Such extensive flushing of the pool must have a major leaching effect on the mineral nutrients held in the thin layer of soil. On the other hand, earlier authors (Heil 1925; Hickel 1967) have commented on the deposition of urine and dung on the rock surfaces by the varied fauna of the area (baboon, bock, leopard); much of these are washed into the *L. intrepidus* pools. It is feasible then that pool nutrient levels are high after the small isolated showers, which usher in the wet season, carrying in urine accumulated on the catchment area during the long dry season. Nutrient uptake by the plants at this stage may well provide internal mineral reserves to support growth later in the wet season when water is relatively plentiful but external nutrients have been leached away.

Analysis of soil collected from *L. intrepidus* pools at Okahandja in December (Table 10) indicates moderate to good levels of five major minerals (potassium, calcium, magnesium, nitrogen, and sulphur) but with low phosphorus. The relatively high levels of nitrogen are consistent with an appreciable input of urine from the catchment.

*L. intrepidus* exists then in a finely balanced ecological situation in which it is indirectly dependent on the surrounding fauna. Elimination of the current fauna could cause nutrient depletion of the pools and possibly threaten survival of the species within a few years. The far-sighted establishment of the Fritz Gaerdes Nature Park near Okahandja hopefully has ensured the continued existence of this rare and fascinating species.

*L. intrepidus* pool soil from Okahandja and Omaruru registered mildly acidic pH values: 6.15 and 6.35 respectively (c.f. 5.7 to 6, Hickel 1967). Nutrient minerals should be readily available to plants at this pH.

**Temperature:** Limited data on the temperature of *L. intrepidus* pools at Okahandja in December of the wet season indicate a wide fluctuation in the air temperature and the temperature of the water, which ranged from 6°C to 41°C. The bare rock outcrops, on which the pools occur, doubtless amplifies temperature fluctuations. The nearest weather station, Windhoek, reporting temperature, has monthly mean maximum and minimum temperatures of 29.7 and 16.7°C in December. Air-dry *L. intrepidus* plants probably suffer more extreme temperatures in the dry season when skies are mainly cloudless.

### **Ecology of Other Species**

Pools occupied by other species were visited too briefly to obtain firm data on temperatures. Consequently it is only possible to speculate, on the basis of pool depth, that *Limosella* plants would experience similar temperatures to *Lindernia*. In the case of *Aponogeton*, one would expect rock-surface temperature fluctuations to be considerably damped down by the insulating effect of gravel overlying the rhizomes, and by the heat capacity of the considerably greater volume of water than in *Limosella* and *Lindernia* pools.

The water balance of *Limosella* pools probably resembles that of *Lindernia* pool B, but with even less frequent overflow, since they lack the marked dip in their pool rim which leads to overflow in the case of *Lindernia* usually well before the whole depression is filled. A more uniform rim height and smaller catchment area might lead to slower but continual accumulation of nutrients. The position of *Aponogeton* pools in major drainage runnels of the rock outcrops would probably lead to flushing of pools to become the predominant influence. Nutrient conditions in the pools of the different species then may be very different, and would be worthy of further investigation. If evaporation rates are similar to those at Okahandja, full pools of *Aponogeton* would take 70 days to dry without further rain falling.

*Craterostigma monroi* pools resemble *L. intrepidus* pools, but, being in a higher rainfall zone, *C. monroi* pools probably are filled for longer periods and for more days per year. *C. monroi* is the only desiccation tolerant pool species which extends beyond the pool to intermix with non-pool species close to the rim of rock depressions.

### **CONCLUSION**

The various rock pool species are exposed to extreme fluctuation in temperature, aridity, and probably in nutrient supply. Despite the hydrophytic nature of their leaves, all four species are drought resistant xerophytes. Drought resistance mechanisms vary between species and might be related to pool depth. The deepest pools allow growth of the largest species, *Aponogeton desertorum*, and probably allow the longest growth period free of water stress. In this species, drought resistance is confined to the rhizomes, by which its plants perennate through the long dry season. Although *A. desertorum* rhizomes have better protoplasmic drought tolerance than leaves, their drought resistance depends more on drought avoidance mechanisms such as relatively bulky rhizomes, with relatively water impermeable surface layers, and positioning of the rhizomes at the base of the gravel soil.

Drought avoidance mechanisms are likely to be inadequate in the face of the severe aridity and length of the dry season in cases where plants are small, in shallow pools and with very shallow soil. Drought resistance must then be based on tolerance of protoplasm to desiccation. *Limosella grandiflora* shows partial expression of this, in that corms, including their apical buds, show about 50% survival of complete desiccation, whereas leaves are not unusually drought tolerant. In shallower pools, the minute plants of *Lindernia intrepidus* have basal leaves, 50% of which survive complete desiccation, but desiccation tolerance weakens in maturing inflorescence leaves. *L. intrepidus* is unique, then, in possessing mature leaves simultaneously, one type being desiccation tolerant, the other being desiccation sensitive. Equally minute plants of *Craterostigma monroi* occupy similar pools to *L. intrepidus* but may extend beyond the pools; this species has complete desiccation tolerance in both basal and inflorescence leaves. It is interesting to note that these three genera are all in the family Scrophulariaceae, which seems to have a predisposition for the evolution of protoplasmic drought tolerance.

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Table 1: Water potential, relative water content, (RWC), and drought tolerance of plants in the field late in the dry season. Water potentials are expressed as the corresponding equilibrium relative humidity at 28° C. Drought tolerance is the lowest air relative humidity with which tissue can survive full equilibrium.

Species and organ	Water potential, % RH (or RWC) when collected and at start of tolerance test	Drought Tolerance, % RH (or RWC)
<i>Aponogeton desertorum</i> Zeyher ex Sprengel f.		
leaves	— (dead)	97* (19% RWC)
rhizome	— (87% RWC)	89 (38% RWC)
<i>Limosella grandiflora</i> Benth.		
leaves	— (dead)	94* (18% RWC)
corms	— (12% RWC)	0*
<i>Lindernia intrepidus</i> (Dinter) Oberm. (syn. <i>Chamaegigas intrepidus</i> )		
I "floating" inflorescence leaves		
A. field:	30 (folded in bud)	5
	(half open)	5
	(mature leaves dead)	—
B. laboratory grown	mature	96 (10.5% RWC)
II basal "underwater" leaves		
	30 (7% RWC)	0*
<i>Craterostigma monroi</i> S. Moore		
leaves	— (6% RWC)	0

\* only approximately 50% of tissue survived.

Table 2: Dry matter content (D.WT) of aquatic plants found in ephemeral pools in granitic outcrops. Data are expressed as a percentage of the fresh weight of the tissue when fully turgid (T.WT).

Species and Organ	D.WT/T.Wt (%)
<i>Aponogeton desertorum</i>	leaves: 6.7    rhizomes: 44.5
<i>Limosella grandiflora</i>	6.0            corms: 22.8
<i>Lindernia (Chamaegigas) intrepidus</i>	
"floating" inflorescence leaves:	10.6
plants (= basal leaves, rhizomes, and roots)	14.6
<i>Craterostigma monroi</i>	16.5

Table 3: Survival of air-drying (~40% RH) by fully turgid inflorescence leaves at different stages of unfolding in buds on intact plants of *Lindernia intrepidus*.

Angle formed by opposite leaves	Cells surviving
0 (fully folded)	79%
~ 45°	67%
~ 90°	57%
~ 135°	75%
~ 180° (fully open)	19%

Table 4: Recovery of tissue on rehydration following 4.5 months equilibration to the designated air humidities at 28°C. Plants had been collected air-dry in the field at the commencement of equilibration.

Equilibration Air Humidity % R.H.	<i>Lindernia intrepidus</i>		<i>Limosella grandiflora</i> corms
	basal leaves	Inflorescence leaves	
100	0% (decayed by 10 days)	0%	0%
76	0	0 (dead at 3.2 months)	0
52	0	0	0
30	100	100	100
20	100	100	100
11	100	100	100
5	100	100	100
0	54	0	44

Table 5(a): Height of foliage which had grown after rehydration from leafless corms of *Limosella grandiflora* previously equilibrated to the air humidities indicated.

Relative Humidity to which equilibrated before rehydration	Mean Height of Foliage (mm)	
	3 days rehydrated	5 days rehydrated
0%	7.3	9.4
5%	17.2	21.3

Table 5(b): Length of foliage and adventitious roots which had grown after 24 hours rehydration from leafless corms of *Limosella grandiflora* previously equilibrated to the air humidity indicated.

Relative Humidity to which equilibrated before rehydration	Range of lengths (mm), min. and max.	
	Shoots	Roots
0%	3—15	0— 4
5%	6—35	2— 5
11%	3—32	1—13
20%	5—30	2—20
30%	2—20	5—12

Table 6: Time course of drying of *Lindernia intrepidus* plants and surrounding soil allowed to dry in the sun, commencing 9.00 am, 7.12.70. (Data for plants at the margin of the soil segments are in brackets.)

Time drying (hours)	Appearance		RWC of plants at the centre of soil segments
	of soil	of plants	
0	sodden	fully turgid	100%
2	dry (except at base)	turgid	74%
2.5	dry throughout	turgid (Marginal plants wilting)	59% (54%)
3	dry throughout	wilted (Marginal plants air dry)	32%
3.75	dry throughout	air-dry	8%

Table 7: Estimated number of days per month during which *Lindernia intrepida* pools in Fritz Gaerdes Reserve, Okahandja, contained water. Overflow from the respective pools was also estimated for each month and expressed as a percentage of the pool volume. Monthly rainfall records are from the nearest weather station at Okaundua.

Rainfall during		Total days with water in pool during month.		Overflow % of pool volume	
Month	(mm)	Pool A	Pool B	Pool A	Pool B
Oct 69	0	0	0	0	0
Nov 69	8.0	3.4	2.5	16	0
Dec 69	19.8	8.3	5.7	51	0
Jan 70	80.3	12.0	23.6	816	0
Feb 70	40.8	9.7	12.0	422	0
Mar 70	21.1	7.2	5.1	96	0
Apr 70	3.0	1.7	0.7	0	0
May —					
Sep 70	0	0	0	0	0
Oct 70	48.5	8.0	13.4	555	0
Nov 70	1.0	0	0	0	0
Dec 70	18.0	3.9	6.5	69	0
Jan 71	59.7	14.7	16.9	329	0
Feb 71	166.6	22.9	28.0	1 976	162
Mar 71	37.0	11.5	17.0	200	0

Table 8: Estimated numbers of days during which *Lindernia (Chamaeigias) intrepidus* pools ('A' and 'B') were moist during two successive wet seasons at Fritz Gaerdes Nature Park, Okahandja. Each value represents the duration of a single period rehydrated. Values are grouped in columns according to their magnitude. Estimates are based on rainfall data for the nearest weather station, at Okaundua.

Pool 'A' Oct. 1969 — April 1970									
0.6	1.6	2.3	3.4	4.3		7.4			
0.6	1.7		3.4	4.4					
0.9			3.4	4.9					
			3.4						
Pool 'A' Oct. 1970 — March 1971									
0.1	1.1	2.7	3.4	5.4	6.4	7.4		16.9	
0.1	1.1		3.4	5.4					
0.3	1.6		3.6						
0.6	1.7								
0.6									
Pool 'B' Oct. 1969 — April 1970									
0.1	1.4	2.5	3.6		5.2	7.4	8.8	12.6	
0.4	1.4		3.2						
0.4	1.1								
0.6									
0.7									
Pool 'B' Oct. 1970 — March 1971									
0.1	1.1		3.4	4.5	5.6		8.5	13.8	37.9
0.2	1.3		3.9						
0.4									
0.4									
0.4									
0.7									
0.7									
0.9									

Table 9: Cycles of moistening and drying of *Lindernia (Chamaegigas) intrepidus*, estimated for the wet seasons 1969 to 1971, for two pools ('A' and 'B') at Fritz Gaerdes Nature Park, Okahandja. Rainfall data as for table 7. The intervening dry season 1970 was 172 days with no rain.

	No. of rehydrations	Time moist (days)		Average time plants dry in wet season (days)
		Total days per wet season	Average Time continuously moist	
Pool 'A' Oct '69 to Apr '70	15	42.3	2.8	12.0
Pool 'A' Oct '70 to Mar '71	17	60.9	3.6	6.7
Pool 'B' Oct '69 to Apr '70	15	49.4	3.3	10.9
Pool 'B' Oct '70 to Mar '71	17	86.4	4.9	5.6

Table 10: Mineral nutrient content of soils in *Lindernia intrepidus* rock pools, compared with values from the literature for soils in general.

	Rock pool soil <sup>a</sup>	Range in soils <sup>b</sup>	
		low	high
potassium	0.023%	0.01%	0.03%
calcium	0.13%	0.01%	0.20%
magnesium	0.017%	0.005%	0.03%
nitrogen	0.45%	0.1%	0.5%
phosphorus	0.006%	0.02%	0.2%
sulphur	0.06%	0.01% <sup>c</sup>	2.0% <sup>c</sup>

(a) analysis by the Soil Research Institute, Pretoria, South Africa

(b) based on Allen et al. (1976)

(c) based on data for fertile krasnozem and black earths, and for infertile podsols, from Stace et al. 1972

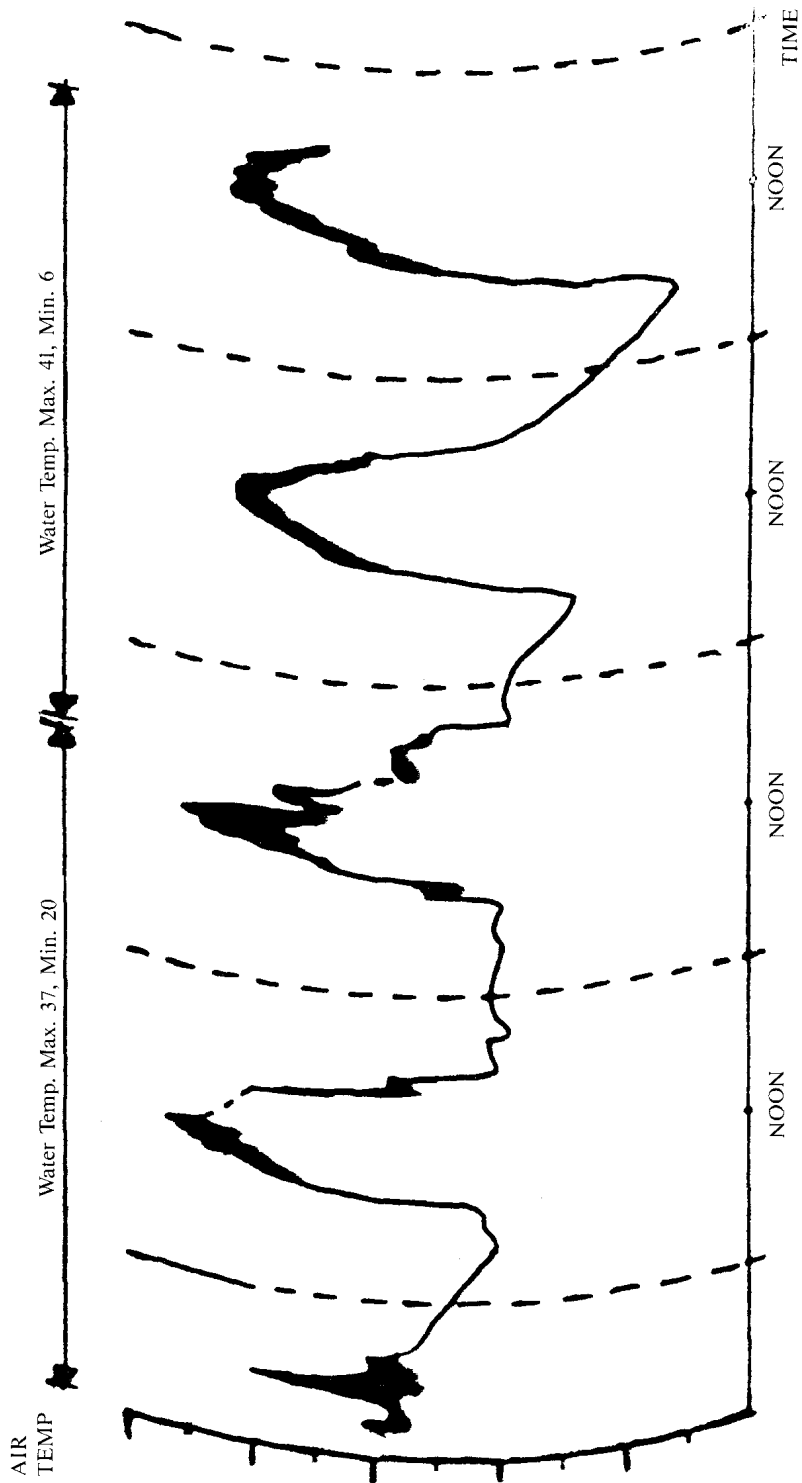


Fig. 1: Temperature around *L. intrepidus*. Apparent air temperatures were recorded on a rotating drum recorder unprotected from insolation. Temperatures in water-filled pool were measured with a maximum/minimum thermometer during the periods indicated by the arrows above the chart; 2 to 6.12.70.

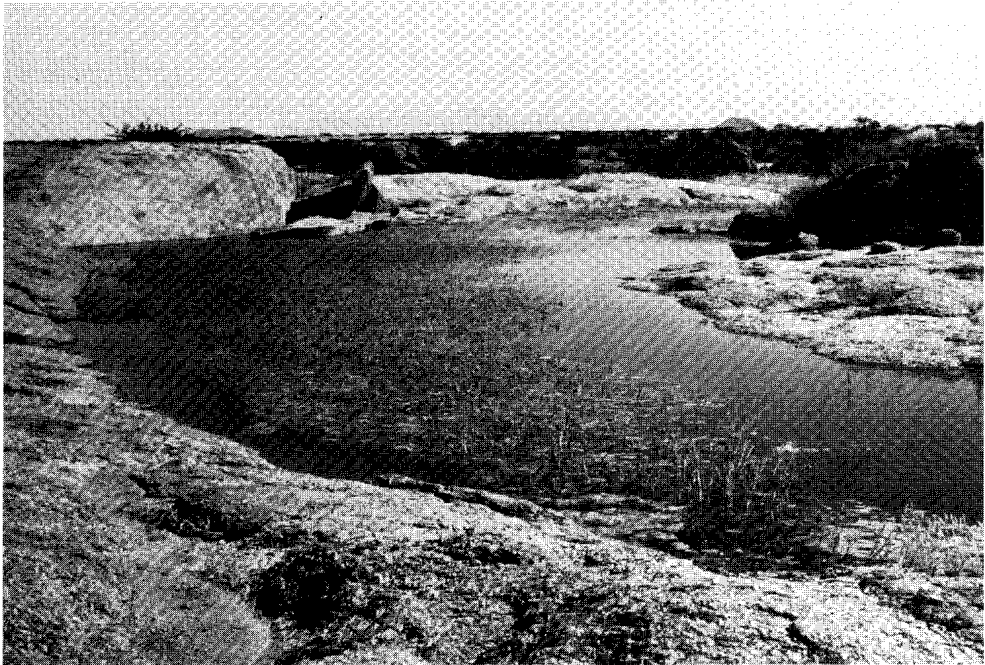


Plate 1: Rock-pool on granite outcrop with *Aponogeton desertorum*. In Damaraland, 34 km east of Uis Mine on road to Omaruru (15.2.1966, W. Giess 9191). Photo by W. Giess.



Plate 2: The same pool in a dry state at the time of collecting the corms in September 1970 with D.F. Gaff in the background. Photo by W. Giess.





Plate 3: Showing the floating leaves and the upright yellow inflorescences of *Aponogeton desertorum* (W. Giess 9191) during February 1966. Photo by W. Giess.



Plate 4: *Limosella grandiflora* with floating leaves and flowers in a circular rock-pool with a diameter of 1 m on a granite outcrop. The whole surface was covered by leaves with flowers inbetween. In Damaraland, 16 km east of Uis Mine on road to Omaruru (18.4.1963, W. Giess, et al. 6273). Locality where the dry corms were collected in September 1970. Photo by W. Giess.

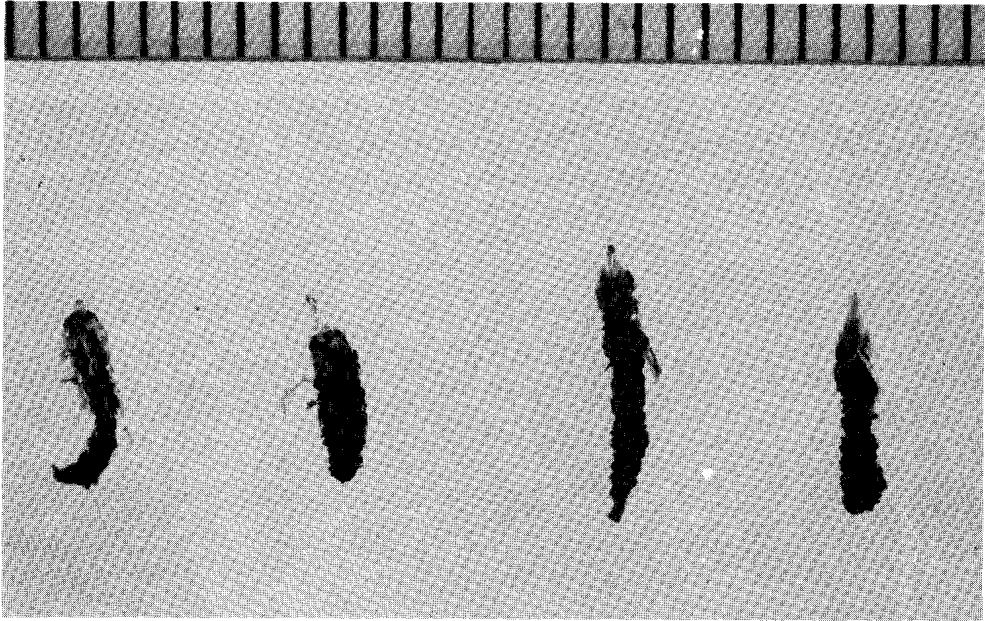


Plate 5: Air-dry corms of *Limosella grandiflora*. Corms are dark, shrivelled, and vertically elongate. A small white apical bud surmounts the corm; pale remnants of adventitious roots can be seen arising below this. Scale 1 div. = 1 mm. Photo by B. Fuhrer.



Plate 6: Flat rock-pool on a granite-glatze at Neikhoes in the Karibib district with *Lindernia intrepida* (16.3.1967, W. Giess 9614). Photo by W. Giess.

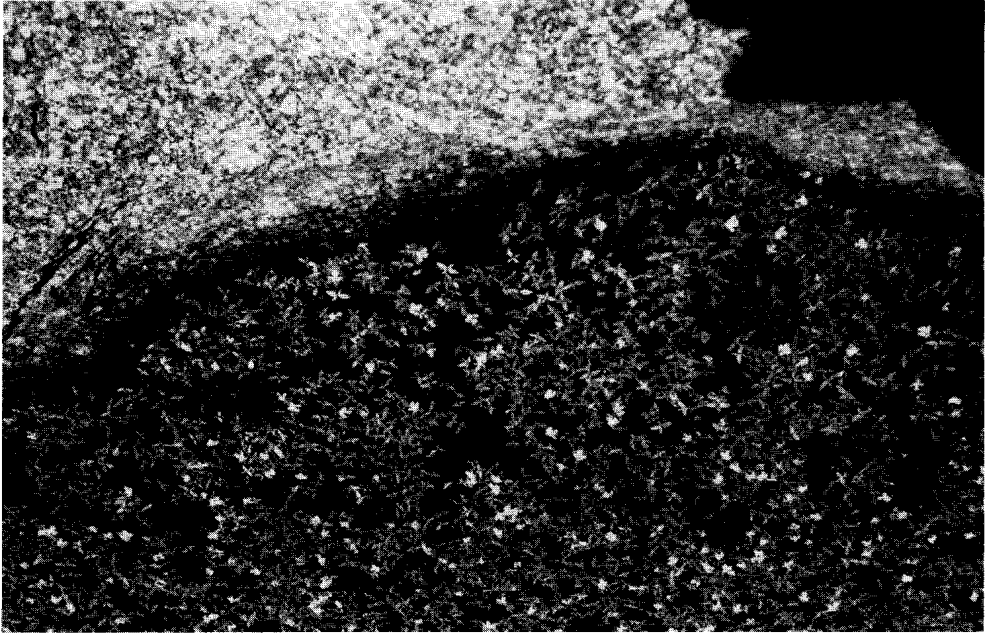


Plate 7: Edge of a flat rock-pool with the white flowers of *Lindernia intrepida* amongst the floating leaves.



Plate 8: Close-up of flowering *Lindernia intrepida* (16.3.1967, W. Giess 9614). Photo by W. Giess.

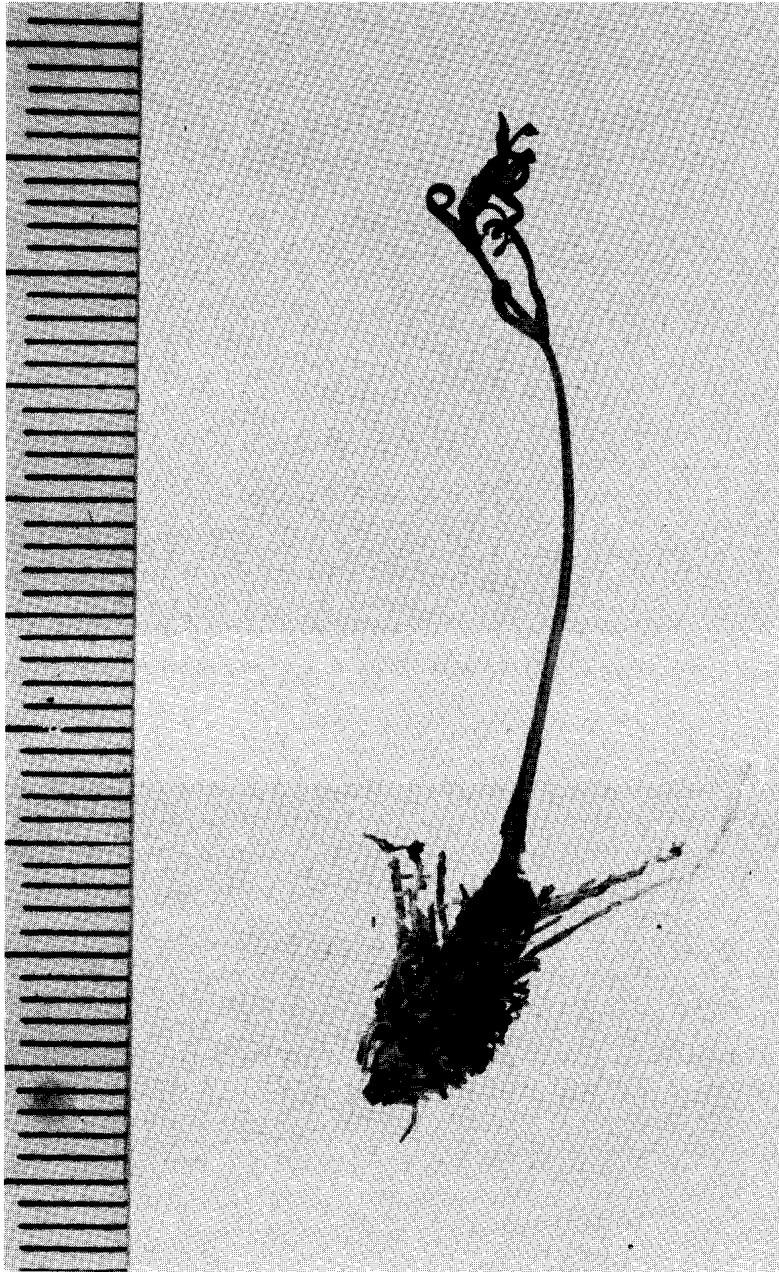


Plate 9: An air-dry plant of *Craterostigma monroi*. The rhizome (approx. 2 cm long here; horizontal in the field) can be seen at the base of the plate, together with adventitious roots. A tuft of about 6 black basal leaves (1 to 2 mm) is visible at the 'upper' end of the rhizome. The stiff, erect inflorescence shoot has been detached and placed near the apex of the rhizome for photographic reasons. Scale: 1 div. = 1 mm. Photo by B. Fuhrer.