

## Drought Resistance in *Welwitschia mirabilis* Hook. fil.

D. F. GAFF

Botany Department, Monash University, Clayton,  
Victoria, 3168, Australia.

Walter (1931) categorised plants into poikilohydrous (i.e. where water stress in the plant followed closely stress fluctuations in the environment) and homoiohydrous (water stress does not vary greatly with external stress). He pointed out that the tolerance of water stress, which was generally implied in poikilohydrous adaptation was more commonly found in the "lower" non-vascular plants (algae, lichens, mosses, liverworts) than in the vascular plants. In the latter a greater degree of organization allows the development of the drought avoidance\* mechanisms that are essential for the homoiohydrous condition. The trend for extreme drought tolerance to become less common as one ascends the evolutionary series can be detected even within the vascular plants:

T A B L E 1

Drought tolerant vascular plants reported in the literature †

Group	Number of drought tolerant species in group	Total number of species in group +	∴ Number of tolerant species per 100,000
Ferns	35	11,000	315
Gymnosperms	0	665	0
Angiosperms:			
Monocots	3	34,000	9
Dicots	7	166,000	4

\* As defined by Levitt (1956)

† Literature up to 1970

+ According to Altmann &amp; Dittmer (1964)

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The apparent absence of drought tolerant Gymnosperms may be related to (a) the relatively small number of species, (b) the facts that whereas the Gymnosperms are predominantly arborescent, the drought tolerant flowering plants are predominantly herbaceous (Table 2), — a situation that probably reflects the difficulties of re-establishing water continuity in the xylem from the roots to the leaves in trees after complete desiccation.

T A B L E 2

Growth habit of drought tolerant angiosperms \*

Growth Habit	Number of species
Herbs < 0.5 m	17
Shrubs 0.5—1 m	8
Trees	0

\* Including unpublished examples known to the author.

If any Gymnosperms then are drought tolerant, one would expect to find these in the order Gnetales which contains relatively low-growing desert shrubs, such as the *Ephedra* species of North America, and more particularly *Welwitschia mirabilis*, which occurs in the Namib desert, — one of the most arid regions of the world (mean annual rainfall = 0 to 30 mm per annum, Kers 1967).

The drought tolerance of *Welwitschia* was investigated using the basal 10 cm of the leaf collected on the Uis Road west of the Brandberg Mountains, and from a dry watercourse in the Namib Desert near Gobabeb. Plants were growing in full sunlight. Leaf material was cut into strips (10 x 2 mm) which were randomized and divided into samples. Some samples were used to determine the initial water content of the leaves relative to the water content at full saturation (strips of leaves were floated on water in darkness for 4 hours). Other samples were allowed to dry rapidly to various levels of water stress on the laboratory bench and were tested for survival by neutral red uptake (Sullivan & Levitt 1959) and evans blue exclusion\* (Gaff and Okong'o-Ogola, 1971). In order to determine the relative humidity equivalent to the water stress at the death point, further samples were allowed to come into equilibrium with air of known relative humidities, which were controlled by sucrose solutions of various osmotic potentials (Levitt 1956). Sucrose solutions were poisoned with Hg<sub>2</sub>Cl<sub>2</sub> to prevent microbial degeneration. Equilibration was attained in three days (c.f. 32 hours Slatyer 1958) at 28°C. Samples were found to survive dehydration to water contents of 56% of the water content when the tissue was fully saturated<sup>†</sup> (water content at full saturation =

\* applied as the stronger solution 0.5% as the cytoplasm of damaged cells failed to adsorb discernible amounts of evans blue.

† c.f. a drought tolerance of 26% saturated water content in an *Ephedra* sp. grown in a greenhouse.

268% of the dry weight). This corresponded to a relative humidity of 91% (equivalent to a water potential of -126 bars). The next level of water stress tested, 90% R.H., was lethal. The value of 91% R.H. for the drought tolerance of *Welwitschia* was at the hardy end of the range of drought tolerance values found in the agricultural plants (91 to 98% relative humidity; Sullivan, Levitt, and Krull, 1960) and was equivalent to the levels that some crop plants species may attain after artificial hardening in dry conditions. However, it was in no way comparable to the levels of desiccation tolerance that the author found in the "resurrection" plants of Southern Africa, viz. from 15% R.H. in *Doryopteris concolor* (Langsd. & Fischer) Kuhn down to almost 0% R.H. in *Xerophyta humilis* (Baker) Dur. & Schinz respectively. The fact that

- (a) the relative humidity equivalent to the drought tolerance would be considerably in excess of the humidity in the surrounding air,
- (b) that the leaves collected during the dry season in an unusually arid year were well hydrated (leaves sampled at Gobabeb 10.00 a.m. 26.8.70 had a water content of 88% of full saturation),

implied that the drought tolerance of *Welwitschia* depended on mechanisms of drought avoidance rather than drought tolerance. Avoidance adaptations must almost certainly involve a low rate of cuticular transpiration once the onset of water stress causes stomatal closure. The fact that the cuticle was thick reinforces this view. The cuticle was 6  $\mu$  thick in the leaves studied here, but as much as 10  $\mu$  was reported by Zemke 1939 (c.f. approximately 1  $\mu$  for the nine other species Zemke studied in association with *Welwitschia*, and 3—8  $\mu$  for *Euphorbia* spp., and 11—16  $\mu$  for *Aloe* spp.).

Although the leaves are thick (1,5 mm) they are sclerophyllous rather than succulent, consequently one would not expect the leaf to survive many months of dry weather solely on the water it contains itself. Mists and dew which are frequent in the coastal zone up to 30 miles inland, Kers 1967, probably allow sufficient water sorption through the superficial root system (Giess 1969) and directly through the leaf surface to offset cuticular transpiration during the previous day. However further inland beyond the mist zone, where the mean rainfall rises to 100 mm, it is difficult to avoid the conclusion that the plants draw on water resources at depth in the soil (Kers 1967). *Welwitschia* has been shown to possess a tap root which attains depths of 1 to 1,5 metres but does not reach the ground water level (Giess 1969). However, plants may withdraw water from soils well below field capacity, — e.g. Slatyer 1957 reported a permanent wilting point of -48 bars for privet and that the permanent wilting point was equal to the osmotic pressure of the leaf cell sap. The osmotic pressure in *Welwitschia* is -32 to -34 bars, Walter 1936. Walter found that, though the surface soil was dry, roots penetrated soil with a moderate water content, 5,9% of soil dry weight, at a depth of 60 cm. It should be noted however that Walter's measurements were made in 1935, following an exceptionally wet year in 1934.

Another possible mechanism of avoidance is that the thick wood which occurs in the first 25 cm below the soil level, may act as a water storage to support at least cuticular levels of transpiration during prolonged dry spells.

Dark fixation of CO<sub>2</sub> during the night followed by stomatal closure during the day, as in Crassulaceae, does not appear to be an adaptation assumed by *Welwit-*

*schia*, since measurements of stomatal resistance made by cobalt chloride papers applied to leaves of potted 3 year old plant (kept in diffuse daylight at approximately 18°C) indicated that the stomata opened more widely during the day than in the night.

T A B L E 3

Stomatal resistance to water vapour diffusion

(Measured as the time for cobalt chloride papers to change to a standard color)

Time of day	Time for colour change (minutes)	
	upper surface	lower surface
6.00 P.M. 1st day	19	9½
10.00 P.M. 1st day	19	12½
2.00 A.M. 2nd day	16½	9
6.00 A.M. 2nd day	14	10
10.00 A.M. 2nd day	12	9
12.00 Noon 2nd day	7½	9
2.30 P.M. 2nd day	9½	5
6.00 P.M. 2nd day	40	10½

#### S U M M A R Y :

*Welwitschia* leaves were found to withstand water stress only to a level of 56% of the water content at full saturation (corresponding to a relative humidity of 91%). This is a reasonably high degree of hardiness for a seed plant but nevertheless implies that the species is dependent on drought avoidance mechanisms (probably low cuticular transpiration, a moderately deep root system and/or water sorption from fogs) for its obvious drought resistance.

#### Z U S A M M E N F A S S U N G :

Die Untersuchung von *Welwitschia*-Blättern hat gezeigt, daß die Wasserspannung nur bis zu einer Höhe von 56% des Wasserinhaltes bei voller Sättigung (entsprechend einer relativen Feuchtigkeit von 91%) Widerstand leistet. Für Samenpflanzen ist dies ein verhältnismässig hoher Grad von Trockenresistenz, deutet aber nichtsdestoweniger darauf hin, daß die Art über einen Austrocknungsmechanismus (wahrscheinlich durch niedere kutikuläre Transpiration, ein tiefes Wurzelsystem und/oder eine Feuchtigkeitsaufnahme durch Nebelniederschläge) für ihre augenscheinliche Trockenresistenz verfügt.

#### O P S O M M I N G :

By ondersoek is gevind dat *Welwitschia*-blare waterspanning kon weerstaan tot slegs 56% van die plant se versadigde waterinhoud (gelyk aan 91% relatiewe vogtigheid). Onder saadplante is dit redelik taai, maar dui nietemin aan dat dié plantsoort afhanklik is van 'n droogte weerstandmeganisme (hoogwaarskynlik laë kutikulare transpirasie, 'n taamlik diep wortelstelsel en/of wateropname gedurende neweltoestande) vir sy bevoegheid om droogtetoestande te kan weerstaan.

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