Oecologia (Berlin) (1983) 58:309-313

Oecologia

A comparison of the water relations characteristics of *Helianthus annuus* and *Helianthus petiolaris* when subjected to water deficits

M.A. Sobrado[1] and Neil C. Turner[2]

[1] Department of Environmental Biology, Research School of Biological Sciences, The Australian National University, P.O. Box 475, Canberra City, A.C.T. 2601, Australia
[2] CSIRO Division of Plant Industry, P.O. Box 1600, Canberra City, A.C.T. 2601, Australia

Abstract. The effect of water deficits on the water relations and stomatal responses of *Helianthus annuus* and *Helianthus petiolaris* were compared in plants growing in the glasshouse under controlled conditions. Unirrigated plants of both genotypes were subjected to two different stress rates in which predawn leaf water potentials declined steadily at either 0.15 MPa day^{-1} or 0.50 MPa day^{-1}. In both genotypes water stress induced a gradual and similar decrease in leaf conductance from 1.6. to 0.3 cm s^{-1} as water potential decreased from -0.5 to -2.0 MPa. The relationship between leaf conductance and leaf water potential was not affected by the rate of stress development.

Development of predawn leaf water potentials of -1.3 MPa had no significant effect on the relative water content at zero turgor, the apoplastic water content or the volumetric elastic modulus of whole leaves in either species, but decreased the osmotic potential at full turgor and zero turgor by 0.22 MPa and decreased the turgid weight:dry weight ratio from 10.6 to 8.4 in *H. annuus*, but not in *H. petiolaris*. In *H. annuus* leaves expanded during stress development, changes in the osmotic potential at full turgor induced by water deficits did not disappear on rewatering.

Introduction

In their natural habitat in the USA, *Helianthus annuus* and *Helianthus petiolaris* grow in the same regions, but whereas *H. annuus* is found on heavy fine textured soils, *H. petiolaris* is limited to light sandy soils (Thompson et al. 1981). This suggests that *H. petiolaris* may be better adapted to periodic water deficits than *H. annuus*. While several studies have compared the responses of cultivars and populations of *H. annuus* to water deficits (Rawson et al. 1980; Takami et al. 1981, 1982; Rawson and Turner 1982a, b; Turner and Rawson 1982), comparisons between species of sunflower are much rarer. Sobrado and Turner (1983) compared the tissue water relations characteristics and productivity of two cultivars of *H. annuus* and two wild species, *H. nuttallii* and *H. petiolaris*. Under field conditions water deficits induced major reductions in leaf area development and dry matter accumulation in all species, but only induced a significant decrease in the osmotic potential at full turgor and zero turgor and a decrease in the turgid weight:dry weight ratio in the two cultivated species and not in the two wild species. The relative water content at zero turgor, apoplastic water content and elasticity of whole leaves were unaffected by water deficits in any species. However, a full evaluation of the diurnal water relations and stomatal conductance at similar levels of leaf water potential was not possible in the field because of differences in leaf area development and rates of drying. The present study was, therefore, initiated to compare the water relations and stomatal responses of one cultivated sunflower, *H. annuus*, and one wild sunflower, *H. petiolaris*, under conditions in which the rate of drying could be controlled and manipulated.

Materials and methods

Helianthus annuus L. cv. Hysun 31 and *Helianthus petiolaris* Nutt. ssp. *fallax* were grown in well fertilized soil in a glasshouse with day/night temperatures of 28/22° C. Prior to sowing, the seed of *H. petiolaris* was kept on wet filter paper for 6 weeks at 2° C to break its dormancy. Some plants were kept well watered throughout growth, while in others water deficits were induced by withholding water. In order to vary the rate of development of water deficits, the plants of *H. annuus* were grown in either 9 or 50 l containers and the plants of *H. petiolaris* were grown in either 5 or 50 l containers.

In order to monitor the development of water deficits, the predawn and midday leaf water potentials, predawn and midday leaf osmotic potentials and midday stomatal conductances were measured at intervals as the soil dried. Additionally, the diurnal changes in leaf water potential, leaf osmotic potential and leaf conductance were measured in the water stressed and control plants on several occasions between 45 and 60 days from sowing. During stress and after rewatering, the tissue water relations of leaves were also determined by the pressure-volume technique both in the control plants and in the plants subjected to water deficits.

Leaf water potentials (ψ) were measured by the pressure chamber technique (Scholander et al. 1965) using the precautions discussed by Turner (1981). Leaf osmotic potentials (ψ_π) were measured on the same leaves by freezing the tissue in Dry Ice and measuring the osmotic potential of the thawed tissue with a Wescor (Wescor Inc., Logan, Utah, U.S.A.) dew point hygrometer. The measurements were not corrected for dilution of symplastic solution by

---

Offprint requests to: N.C. Turner

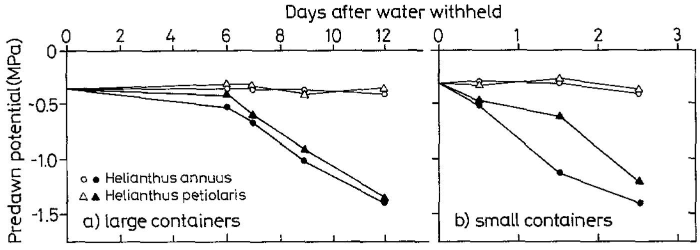

Fig. 1 a, b. Changes in predawn leaf water potential in adequately watered (open symbols) and unwatered (closed symbols) *Helianthus annuus* (○, ●) and *Helianthus petiolaris* (△, ▲) that were grown in either **a** large (50 l) containers or **b** small (9 or 5 l, respectively) containers. Standard errors were less than 0.14 MPa

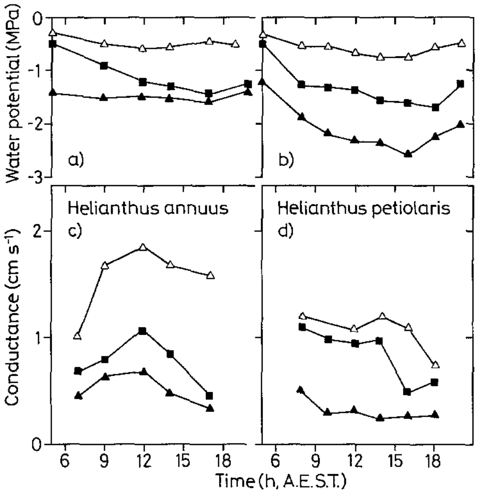

Fig. 2 a–d. Diurnal changes in leaf water potential **a**, **b** and stomatal conductance **c**, **d** in *Helianthus annuus* **a**, **c** or *Helianthus petiolaris* **b**, **d** measured 0 (△), $^1/_2$ (■), and $2^1/_2$ (▲) days after water was withheld from the soil of plants grown in small (9 or 5 l, respectively) containers. Standard errors were less than 0.13 MPa and 0.15 cm s^{-1}

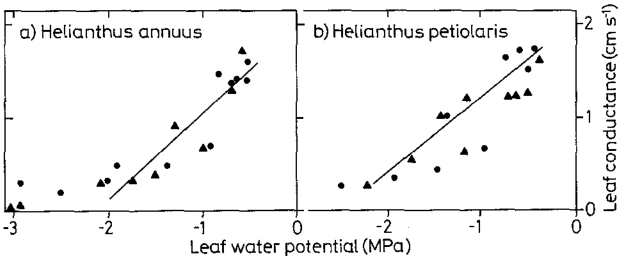

Fig. 3 a, b. Relationship between stomatal conductance (*Y*) and leaf water potential (*X*) measured near midday on **a** *Helianthus annuus* and **b** *Helianthus petiolaris* that were either slowly (●) or rapidly (▲) stressed by growing in large (50 l) or small (9 or 5 l, respectively) containers. The lines give the fitted linear regressions for data above -2.0 MPa. For *H. annuus* $Y=0.9\ X+1.92$ and for *H. petiolaris* $Y=0.8\ X+2.01$

Table 1. The water relations characteristics of *Helianthus annuus* cv. Hysun 31 and *Helianthus petiolaris* ssp. *fallax* that were either watered regularly (Wet) or water withheld until the predawn leaf water potential decreased to -1.3 MPa (Dry). $\psi_{\pi(100)}$ is the osmotic potential at full turgor, $\psi_{\pi(0)}$ is the osmotic potential at zero turgor, RWC_0 is the relative water content at zero turgor, A is the apoplastic water content, and TW/DW is the turgid weight:dry weight ratio measured on either wet or dry plants that had been rehydrated overnight

Characteristics	*H. annuus*		*H. petiolaris*	
	Wet	Dry	Wet	Dry
$\psi_{\pi(100)}$ (MPa)	−0.82	−1.04[a]	−0.77	−0.87
$\psi_{\pi(0)}$ (MPa)	−0.98	−1.20[a]	−1.03	−1.10
RWC_0 (%)	85.8	85.0	79.3	79.5
A (%)	19.1	16.7	20.3	18.8
TW/DW	10.61	8.39[a]	8.65	8.33

[a] Statistically significant from the wet treatment at $P \leq 0.05$

apoplastic water. The leaf turgor pressure (ψ_p) was calculated from the measured values of ψ and ψ_π using the equation:

$$\psi = \psi_\pi + \psi_p$$

The osmotic potential at full turgor ($\psi_{\pi(100)}$) and at zero turgor ($\psi_{\pi(0)}$), the relative osmotic water content (ROWC), the relative water content at zero turgor (RWC_0), the percentage of apoplastic water (A) and the turgid weight:dry weight ratio (TW/DW) were all determined from pressure-volume relationships established by the pressure chamber technique (Tyree and Hammel 1972; Turner 1981). Leaves were collected after sunset and rehydrated overnight in a humid darkened chamber with their petioles in water. The following day preweighed leaves were allowed to lose water outside the chamber, the balancing pressure was measured and the leaf was reweighed. This procedure was repeated until a pressure-volume curve was established.

Stomatal conductances were measured with a diffusion porometer (Delta-T Devices, Burwell, Camb. U.K.). The adaxial and abaxial surfaces were measured separately on adjacent portions of the leaf and the leaf conductance was calculated assuming the two surfaces acted as parallel resistors.

Results

Development of water deficits

Predawn leaf water potentials of well watered control plants and plants from which water had been withheld are shown in Fig. 1 for plants in large and small containers. In the controls the predawn leaf water potential was always between -0.3 and -0.4 MPa in both *H. annuus* and *H. petiolaris*. However, in the unwatered plants grown in 50 l containers the predawn leaf water potential was similar to the controls for 6 days and declined steadily at a rate of about 0.15 MPa day^{-1} in both species for the following 6 days. When water was withheld from the plants growing in the 9 and 5 l containers the predawn leaf water potential fell rapidly to reach values of -1.4 and -1.2 MPa in *H. annuus*

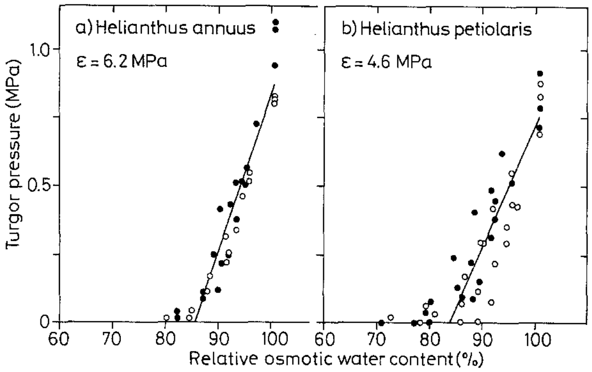

Fig. 4a, b. Relationship between turgor pressure and relative osmotic water content for **a** *Helianthus annuus* and **b** *Helianthus petiolaris* that were watered regularly (○) or from which water was withheld until the predawn leaf water potential reached −1.3 MPa (●). The slope of the regression fitted to data with a relative osmotic water content above 80% gives the volumetric elastic modules (ε) noted: this procedure is consistent with the observations of Melkonian et al. (1982) in wheat

Table 2. The osmotic potential at full turgor $\psi_{\pi(100)}$ of different leaves of *Helianthus annuus* cv. Hysun 31 grown with adequate water (Wet) or with water withheld until the predawn leaf water potential reached −1.3 MPa (Dry) and measured either when **a** stress was maximal in dry treatment or **b** 19 days after rewatering. $\Delta\psi_{\pi(100)}$ gives the difference in $\psi_{\pi(100)}$ between wet and dry treatments. Values are means ± one standard error of the mean of 4 observations taken on leaves rehydrated overnight

Leaf number[a]	$\psi_{\pi(100)}$ (MPa)		$\Delta\psi_{\pi(100)}$ (MPa)
	Wet	Dry	
a *When stress maximal in dry treatment*			
3^b	-0.82 ± 0.04	-0.92 ± 0.04	0.10
4^b	-0.76 ± 0.06	-0.91 ± 0.02	0.15
5^b	-0.89 ± 0.01	-1.10 ± 0.07	0.21
b *19 days after rewatering*			
6^b	-0.79 ± 0.06	-0.95 ± 0.05	0.16
8^c	-0.82 ± 0.05	-0.80 ± 0.08	−0.02
10^c	-0.75 ± 0.04	-0.73 ± 0.02	−0.02

[a] Numbered from base of plant

[b] Leaves expanded during development of the water deficit

[c] Leaves expanded after rewatering

and *H. petiolaris*, respectively, in $2^1/_2$ days, i.e. the rate of drying was about 0.5 MPa day^{-1}.

Influence of water deficits on diurnal changes in leaf water potential and stomatal conductance

The diurnal changes in leaf water potential and leaf conductance for the rapidly stressed *H. annuus* and *H. petiolaris* plants are shown in Fig. 2. In the control plants of both species, the diurnal range in leaf water potential was in the order of 0.3 to 0.5 MPa, similar to the range found previously in *H. annuus* grown in the greenhouse (Takami et al. 1982). As the predawn leaf water potential decreased the diurnal range of potentials increased, particularly in *H. petiolaris*. Leaf conductance in the control plants reached 1.6 to 1.8 cm s^{-1} during the middle of the day, but decreased in both species as the water deficits developed. Whether stress was imposed slowly at a rate of 0.15 MPa day^{-1} or at a rate of 0.5 MPa day^{-1}, the relationship between leaf conductance and leaf water potential was the same (Fig. 3). Moreover, the relationship was similar in the two species: the conductance decreased almost linearly by 0.8 to 0.9 cm s^{-1} MPa^{-1} from −0.5 MPa to −2.0 MPa. At leaf water potentials below −2.0 MPa the change in conductance was negligible.

Influence of water deficits on tissue water relations

The tissue water relations characteristics of slowly stressed plants and the corresponding well watered controls are given in Table 1. In *H. annuus* the water stress treatment resulted in a significant decrease of 0.22 MPa in the osmotic potential at full turgor ($\psi_{\pi(100)}$) and zero turgor ($\psi_{\pi(0)}$) and a 21% decrease in the turgid weight:dry weight ratio (TW/DW), but no significant changes in the relative water content at zero turgor (RWC_0) or the volume of apoplastic water (A). There were no significant effects of water deficits on the tissue water relations of *H. petiolaris*. This suggests that osmotic adjustment occurred in *H. annuus*, but not in *H. petiolaris*. The volumetric elastic modulus (ε) was calculated from the slope of the regression between turgor pressure and relative osmotic water content (Fig. 4). ε was the same in water stressed and well watered plants in each species and was similar in both the *H. annuus* and *H. petiolaris*.

Finally, $\psi_{\pi(100)}$ was measured at the end of a stress cycle on leaves of *H. annuus* that expanded during the development of stress, and again 19 days after rewatering both on leaves that expanded during the development of stress and also on those that expanded only during the recovery from stress. The leaves that expanded during the development of water deficits all showed a lowering of $\psi_{\pi(100)}$, but 19 days after the relief of stress only the leaves that expanded during stress development had significantly lower values of $\psi_{\pi(100)}$ (Table 2).

Discussion

Several recent studies have shown that differences in physiological responses to water deficits among cultivated *H. annuus*, including ones selected by the North American Indians in the arid south west of the U.S.A., are small (Rawson et al. 1980; Takami et al. 1981, 1982; Rawson and Turner 1982a, b). However, a recent field study (Sobrado and Turner 1983) showed that cultivated sunflowers differed from wild sunflowers in that the former adjusted osmotically and lowered their turgid weight:dry weight ratio (TW/DW) in response to water deficits, whereas the latter did not. The present glasshouse study confirms this, and also confirms that water deficits did not alter the tissue water relations parameters, such as the relative water content at zero turgor, apoplastic water content and volumetric elastic modulus, in either species. Osmotic adjustment is considered a beneficial drought resistance character (Turner 1979), allowing stomata to remain open at lower leaf water potentials and allowing root growth to continue as water deficits develop (Turner and Jones 1980). It is, therefore, surprising that *H. petiolaris* which grows in drier sandier locations does not have osmotic adjustment, where-

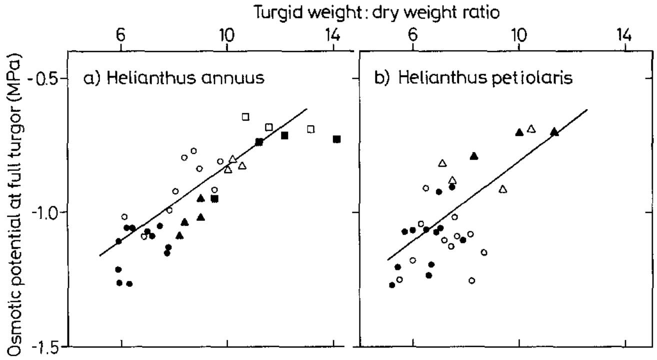

Fig. 5a, b. Relationship between the osmotic potential at full turgor (Y) and the turgid weight:dry weight ratio (X), for **a** *Helianthus annuus* and **b** *Helianthus petiolaris* grown with adequate water (open symbols) or with water withheld (closed symbols) in the field during the summer (○, ●), in the glasshouse during the spring and summer (△, ▲) and in the glasshouse in winter (□, ■). The lines gives the fitted linear regressions: for *H. annuus* $Y = 0.70\ X - 15.2$ and for *H. petiolaris* $Y = 0.75\ X - 15.6$

as *H. annuus* which grown in heavier clay soils does show osmotic adjustment.

The degree of osmotic adjustment observed in *H. annuus* in this study was similar to that observed previously in the field (Sobrado and Turner 1983) and in the glasshouse (Jones and Turner 1980) at the same level of stress: more severe levels of stress induced a greater degree of osmotic adjustment in cultivated *H. annuus* (Jones and Turner 1980; Takami et al. 1981). However, the osmotic adjustment of 0.22 MPa observed in this study had no measurable influence on the stomatal response to leaf water deficits: the change in stomatal conductance with leaf water potential was similar in *H. annuus* which showed osmotic adjustment and in *H. petiolaris* which did not show osmotic adjustment. Moreover, the rate of stress had no effect on the relationship between stomatal conductance and leaf water potential in both *H. annuus* and *H. petiolaris*. This contrasts with the finding by Jones and Rawson (1979) with *Sorghum bicolor* that the rates of drying similar to those in the present study had marked effects on the relationship between leaf conductance and leaf water potential.

Takami et al. (1981) showed a rapid loss of osmotic adjustment in four *H. annuus* cultivars once water stress was relieved, whereas Jones and Turner (1980) showed that prestressed leaves of *H. annuus* still had a significantly lower osmotic potential 7 days after rewatering. The present study clarifies the differences obtained in these two previous studies. In the study by Jones and Turner (1980) only leaves 16 to 18, i.e. those that enlarged during the development of water deficits, were used in the measurement of recovery, whereas in the study by Takami et al. (1981) leaves that developed during the recovery phase were used for later samplings. The present study shows that leaves that emerged during the development of water deficits retain their low osmotic potential, whereas those that develop during the relief of stress have similar osmotic potentials to the controls. This suggests that there are changes in leaves that expand during the development of water deficits that lead to a lowering of the osmotic potential and its persistence after rewatering, i.e. water deficits induce an irreversible change in the transport properties of the plasmalemma.

We noted previously (Sobrado and Turner 1983) that the changes in TW/DW were similar in magnitude to the degree of osmotic adjustment. Similar changes in osmotic adjustment and TW/DW were observed in the present study. Indeed, when we combined the results from the present study with those of the field study, and in addition included data taken in the glasshouse during the winter, it is clear that the osmotic potential at full turgor decreased with the decrease in TW/DW in both *H. annuus* and *H. petiolaris* (Fig. 5). Moreover, the relationship was similar in both plants subjected to water deficits and those not subjected to water deficits. This suggests that some of the observed osmotic adjustment may have resulted from a decrease in cell size while solute amounts remained constant (Cutler et al. 1977), in addition to the active solute accumulation observed in fully expanded leaves of *Sorghum bicolor* and *H. annuus* (Jones and Turner 1978, 1980; Jones and Rawson 1979; Jones et al. 1980). Whether the seasonal changes in osmotic potential at full turgor arise from morphological changes in cell size or from changes at the plasmalemma is worthy of investigation.

Thus, in conclusion, we have demonstrated that *H. annuus* and *H. petiolaris* do differ in their ability to osmotically adjust to water deficits. However, in other respects the two species behaved similarly in their response to water deficits. We have also demonstrated a strong correlation between the osmotic potential at full turgor or zero turgor and the turgid weight:dry weight ratio. We suggest that changes in cell size may play a role in osmotic adjustment and drought resitance in sunflower.

Acknowledgements. Financial support for M.A.S. was provided by the National Research Council of Venezuela (CONICIT).

References

Cutler JM, Rains DW, Loomis RS (1977) The importance of cell size in the water relations of plants. Physiol Plant 40:255–260

Jones MM, Rawson HM (1979) Influence of rate of development of leaf water deficits upon photosynthesis, leaf conductance, water use efficiency, and osmotic potential in sorghum. Physiol Plant 45:103–111

Jones MM, Turner NC (1980) Osmotic adjustment in expanding and fully expanded leaves of sunflower in response to water deficits. Aust J Plant Physiol 7:181–192

Jones MM, Osmond CB, Turner NC (1980) Accumulation of solutes in leaves of sorghum and sunflower in response to water deficits. Aust J Plant Physiol 7:193–205

Melkonian JJ, Wolfe J, Steponkus PL (1982) Determination of the volumetric modulus of elasticity of wheat leaves by pressure-volume relations and the effect of drought conditioning. Crop Sci 22:116–123

Rawson HM, Constable GA, Howe GN (1980) Carbon production of sunflower cultivars in field and controlled environments. II. Leaf growth. Aust J Plant Physiol 7:575–580

Rawson HM, Turner NC (1982a) Recovery from water stress in five sunflower (*Helianthus annuus* L.) cultivars. I. Effects of the timing of water application on leaf area and seed production. Aust J Plant Physiol 9:437–448

Rawson HM, Turner NC (1982b) Recovery from water stress in five sunflower (*Helianthus annuus* L.) cultivars. II. The development of leaf area. Aust J Plant Physiol 9:449–460

Scholander PF, Hammel HT, Bradstreet ED, Hemmingsen EA (1965) Sap pressure in vascular plants. Science, 148:339–345

Sobrado MA, Turner NC (1983) Influence of water deficits on the leaf water relations characteristics and productivity of wild and cultivated sunflowers. Aust J Plant Physiol 10:(in press)

Takami S, Turner NC, Rawson HM (1981) Leaf expansion of four sunflower (*Helianthus annuus* L.) cultivars in relation to water deficits. I. Patterns during plant development. Plant Cell and Environment 4:399–407

Takami S, Rawson HM, Turner NC (1982) Leaf expansion of four sunflower (*Helianthus annuus* L.) cultivars in relation to water deficits. II. Diurnal patterns during stress and recovery. Plant Cell and Environment 5:279–286

Thompson TE, Zimmerman DC, Rogers CE (1981) Wild *Helianthus* as a genetic resource. Field Crops Res 4:333–343

Turner NC (1979) Drought resistance and adaptation to water deficits in crop plants. In: Mussell H, Staples RC (eds), Stress physiology in crop plants. Wiley, New York, pp 343–372

Turner NC (1981) Techniques and experimental approaches for the measurement of plant water status. Plant Soil 58:339–366

Turner NC, Jones MM (1980) Turgor maintenance by osmotic adjustment: a review and evaluation. In: Turner NC, Kramer PJ (eds), Adaptation of plants to water and high temperature stress. Wiley, New York, pp 87–103

Turner NC, Rawson HM (1982) Yield and harvest index of sunflower cultivars: influence of duration and water stress. Proc. 10th International Sunflower Conference, Surfers Paradise, Australia, March 14–18, 1982, pp 38–42

Tyree MT, Hammel HT (1972) The measurement of the turgor pressure and water relations of plants by the pressure-bomb technique. J Exp Bot 23:267–282

Received December 20, 1982