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INFLUENCE OF WATER DEFICIT ON GAS EXCHANGE AND DRY MATTER ACCUMULATION IN SUNFLOWER CULTIVARS AND A WILD SPECIES (*Helianthus argophyllus* T&G)

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SUMMARY

The influence of water stress on gas exchange and dry matter accumulation in a wild sunflower (*Helianthus agrophyllus* T&G) and four cultivated sunflower (*Helianthus annuus* L.) cultivars (HA 89, RHA 856, 207 A and C) was compared in a glasshouse experiment during 1989-1990. Plants were maintained in a well-watered condition until physiological maturity, while in the drought stress treatment, the irrigation was suspended just before flowering. Measurements were made of leaf photosynthetic and transpiration rates, relative leaf water content, pre-dawn leaf water potential, leaf area index and total dray matter at harvest. Under dray conditions, the water deficit was smaller in the wild species than in the cultivated lines, and photosynthesis and leaf hydration decreased more rapidly with drought in the cultivars. These results, together with the wild sunflower's smaller reduction in dry matter production, its increase in root/shoot ratio under drought at harvest and the unchanged leaf area after 12 days of drought, indicate it has a dehydration avoidance mechanism. The hydration avoidance may be due to the larger roots of *H. argophyllus* and higher root/shoot ratio under drought, compared with the cultivars.

Key words: drought stress, *Helianthus annuus*.

INTRODUCTION

Until now, drought resistant genotypes have been developed by empirical breeding methods involving selection for yield and its stability over many locations and years, which are expensive, laborious and time concuming (Blum, 1987). Different environments have special water stress conditions which require a particular breeding strategy. Water stress can be mild or strong, develop early in plant growth or in the last phase, and may moreover be continuous or interrupted by limited rains. All these situations need different mechanisms of drought resistance which essentially can be summarized as follows: "drought escape", a mechanism that is most useful in regions subjected to foreseeable periods of drought (Turner, 1979; Fischer and Maurer, 1978); "dehydration avoidance", with the maintenance by the plants of a satisfactory leaf water status; "dehydration tolerance", i.e., tolerance of plants to internal water deficit (Turner, 1979). Each of these mechanisms is related to the natural drought period and involves different

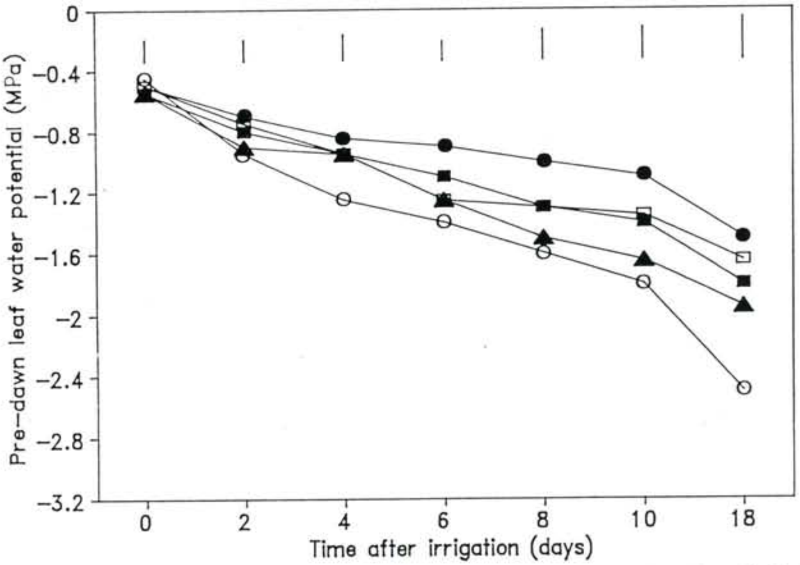

Figure 1 - Change in pre-dawn leaf water potential over time after the suspension of irrigation (0 is the first day after the last irrigation) for HA 89 (○), 856 (■), 207 A (▲), C (□) and H. argophyllus (●). The vertical bars represent the LSD value (n = 3 for each genotype) at P = 0.01 for each measurement day.

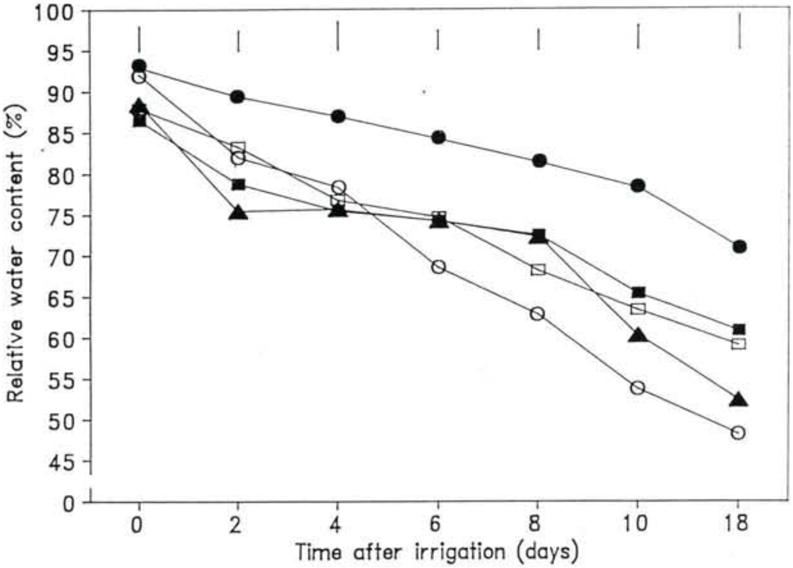

Figure 2 - Relative water content of the leaf (%) over time after the suspension of irrigation for HA 89 (○), 856 (■), 207 A (▲), C (□) and H. argophyllus (●). The vertical bars represent the LSD value (n = 3 for each genotype) at P = 0.01 for each measurement day.

and sometimes incompatible phenological, morphological, and physiological processes, which may or may not limit the seed yield potential.

Various studies on *Helianthus* spp. have contributed to evaluation of the variability present in cultivated sunflower (Rawson et al., 1980; Blanchet and Merrien, 1984; Fereres et al., 1986; Gimenez and Fereres, 1986) and have identified some physiological processes related to seed yield under drought. One line of research, no less important, is based on the exploitation of wild species coming from dry environments. Many authors have reported that *H. argophyllus* is an interesting source for improving drought resistance in cultivated sunflower (Serieys, 1980; Seiler, 1988), because physiological studies indicate a greater efficiency in water use as compared with cultivated sunflower under wet conditions (Blanchet and Gelfi, 1980; Iouras and Voinescu, 1984). In the exploitation of wild sunflowers, seed yield may not be a useful criterion for drought resistance because of their indeterminate and multiflowering habit (Blum, 1987; Sobrado and Turner, 1983) as is observed in *H. argophyllus*. In this case the employment of physiological selection criteria, that present mechanisms of drought resistance, may be useful, in breeding. The aim of this study is to evaluate differences in physiological activity and dry matter yield under drought among *H. argophyllus* and four sunflower cultivars in order to assess possible mechanisms for adaptation to drought and the possibility of using this species in breeding programmes.

MATERIALS AND METHODS[1]

The wild species, *H. argophyllus*, was compared with four sunflower cultivars, selected for high yield potential (HA89, RHA856, 207A, and C).

Seeds were sown in 10 cm-diameter pots on 20th September 1989 for all genotypes except *H. argophyllus*, which was sown 20 days earlier because of its seed dormancy and its very slow early growth rate, in order to obtain the same stage of development (of both the above-ground part and root system) in all plants for all genotypes at transplanting and approximately the same flowering time. Seedlings were transplanted on 10th October 1989, when all the genotypes had reached the stage of 4-6 true leaves, in two separate benches of identical dimensions (10 metres long, 1.5 metres wide and 0.6 metres deep) with a silty-peaty soil in a glasshouse. During the study period the temperature, regulated via a thermostat, varied from 18° to 20°C during the night, while during the day values varied from a minimum of 20°C to a maximum of 30°C. Relative humidity was of 60-70% during the night and 35-50% during the day. A constant 16 hours photoperiod was provided by a timer connected to four lamps per bench (Philips SGR 200/400), which assured a minimum photon flux density of about 900 μE m^{-2} s^{-1} at the top of the canopy. In the glasshouse, at the top of the canopy level, mean values of photon flux density for all leaf measurements ranged from 900 to 1500 μE m^{-2} s^{-1}, ensuring light saturation for near-optimal water use efficiency in sunflower (Rawson and Costable, 1980). Each genotype was transplanted in 6 rows, with two rows per replication, which were randomized across the benches, with a distance between the plants in the rows and between the rows of 25 cm. Border rows were established at the two ends of each bench. In one

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[1] Abbreviations and symbols: RWC= relative water content; TE= transpiration efficiency

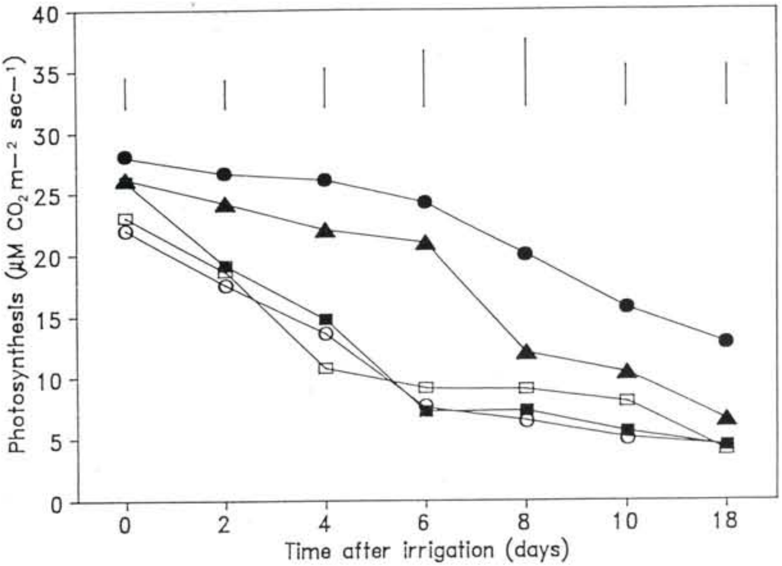

Figure 3 - Photosynthetic rate (μM CO_2 m^{-2} sec^{-1}) over time after the suspension of irrigation for HA 89 (○), 856 (■), 207 A (▲), C (□) and H. argophyllus (●). The vertical bars represent the LSD value (n = 3 for each genotype) at P = 0.01 for each measurement day.

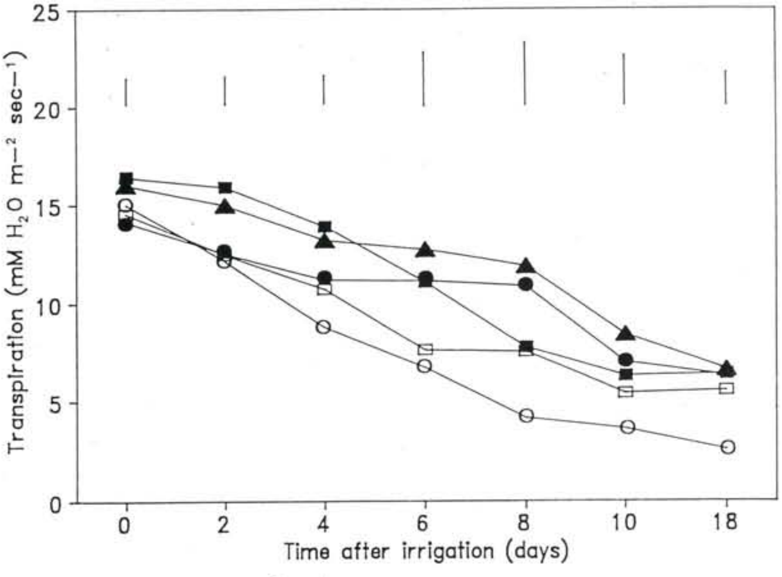

Figure 4 - Transpiration rate (mM H_2O m^{-2} sec^{-1}) over time after the suspension of irrigation for HA 89 (○), 856 (■), 207 A (▲), C (□) and H. argophyllus (●). The vertical bars represent the LSD value (n = 3 for each genotype) at P = 0.01 for each measurement day.

treatment, the soil was maintained at approximately field capacity until physiological maturity, by irrigating every 2-3 days (controls). In the second treatment, irrigation was suspended 35 days after transplanting (DAT, when all the genotypes were at the pre-flowering stage), resulting in progressive water stress until physiological maturity (terminal stress). The measurements were made at 2 day intervals from 35 DAT to 55 DAT (achene filling stage). Gaseous exchanges of the plants as transpiration and photosynthesis were recorded between 0.5 h prior to and 1 h after solar noon, using a commercial ADC (Analytical Development Co., England) open-portable system (Long and Hallgren, 1985; Steduto et al., 1988). The system consisted of a small portable infrared gas analyzer, a flow pump and mater unit, a leaf chamber and a data-logger. Transpiration efficiency (TE) was calculated from the ratio of photosynthesis to the transpiration rate. All measurements were made in the midsection of three fully top expanded leaves of three replicate plants for each treatment.

Relative water content of the leaves (RWC) sampled during the same afternoon (at about 16.00 local STD time), was measured following the methodology suggested by Sobrado and Turner, (1983). From the same leaf per plant on which values of gaseous exchange were obtained, 10 discs of 1 cm^2 each were punched and placed in a tared vial. Fresh weight (Wf), turgid weight (Wt) after rehydration for 12h at 30μE m^{-2} s^{-1} of photon flux density, and dry weight (Wd) after oven drying at 80°C were determined. The RWC was calculated using the equation RWC=(Wf-Wd)/(Wt-Wd). The following morning, using another leaf from the plant on which values of gaseous exhcange were obtained, pre-dawn leaf water potential was measured with a pressure chamber, following the methodology suggested by Turner (1981). Leaf area measurements (LA), to calculate the leaf area index (LAI), were made on two occasions, when irrigation was suspended and 12 days later, and were determined using the relationship, LA = 0.73 LB (Rawson et al., 1980), where L and B are the length and greatest width of the lamina, respectively. At maturity three integral plants per plot were harvested, partitioned into above-ground matter and root and dried at 80°C for 48 h before weighing. Care was taken when pulling cut plants to recover as much of the root system as possible. Root material not recovered when plants were removed, was measured by taking a 10 cm diameter core to a depth of 0.6 m through the crown of each plant. Cores were soaked for 24 h in a dispersing solution of detergent and soil was washed through a 0.3mm screen leaving root material. These roots were then dried and added to the roots pulled previously. The four cultivated cultivars were harvested at 80 DAT and the wild sunflower at 102 DAT.

The data obtained from the control and water-stress experiments were analyzed separately by ANOVA using a randomized block design with three replications, considering as the only source of variation the genotypes within the treatments and the moments of the determinations. The LSDs (bars on the graphs for P-0.01) were calculated (n=3) to check statistical differences among genotypes (Gomez and Gomez, 1984).

LEAF WATER RELATION

After suspending irrigation, pre-dawn leaf water potential of all genotypes exhibited a progressive decrease with time (Figure 1). The cultivar HA89 showed a faster decrease in leaf water potential than the other genotypes. The wild sunflower maintained a higher leaf water potential (less negative) than the other genotypes from 4 days after suspending irrigation.

During the whole period of the experiment, *H. argophyllus* also maintained a higher RWC (Figure 2), while cultivar HA 89 had the lowest RWC in the period between 6 and 18 days.

LEAF GAS EXCHANGE

Photosynthetic rates of *H. argophyllus* were greater than those of the other genotypes during the whole period, with the exception of the cultivar 207 A especially in the early stage of the experiment (2,4 and 6 days) (Figure 3).

Transpiration rates per unit leaf area were very similar among the genotypes up to the 6th day (Figure 4), after which the HA 89 line showed a consistently lower transpiration rate indicating that it had greater stomatal limitation of water loss. The wild sunflower had greater transpiration efficiency (TE) during the experiment compared with the other genotypes (Figure 5). TE was almost constant for the whole period.

For the well-watered treatment the genotypes had similar values of leaf water potential, RWC, photosynthesis and transpiration (e.g., see time 0 of Figures 1,2,3 and 4, respectively). These values remained approximately constant for each genotype up to the flowering time, after which they declined progressively in all the genotypes with increasing plant age (data not shown).

DRY MATTTER AND LEAF AREA

When irrigation was suspended (TO), leaf area was different among genotypes and these differences were present 12 days later (T1) (Table 1). Depletion of water from the

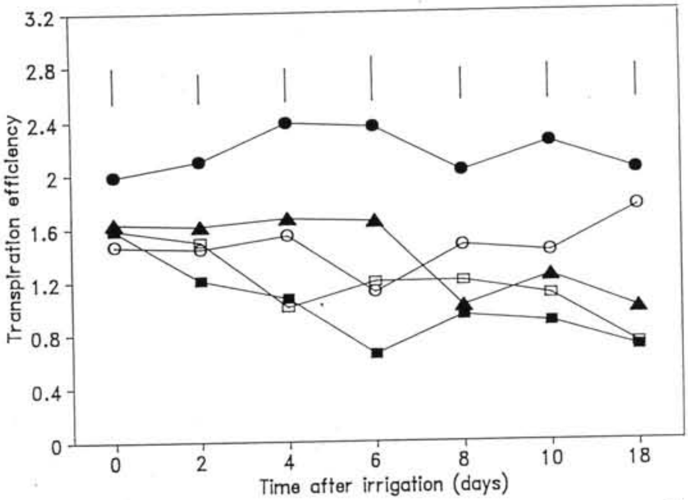

Figure 5 - Transpiration efficiency calculated as photosynthetic/transpiration rates ($\mu M\ CO_2 m^{-2} sec^{-1} / mM\ H_2O\ m^{-2} sec^{-1}$) over time after the suspension of irrigation (is the first day after the last irrigation) for HA 89 (○), 856 (■), 207 A (▲), C (□) and H. argophyllus (●). The vertical bars represent the LSD value (n = 3 for each genotype) at P = 0.01 for each measurement day.

soil during the 12 days following the last irrigation substantially stressed the plants, causing reductions in leaf area. Percentage reduction in leaf area was substantially less for the wild sunflower (19%) than the other genotypes (46 to 52%).

At harvest the effects of water stress on dry matter production were substantial for the cultivars (35 to 45% reduction), but less for the wild sunflower (20% reduction) (Table 2). Considering the ratio between root dry matter and total dry matter, while no differences were apparent among the genotypes in wet conditions, in the stress treatment this ration increased more in *H. argophyllus* than in the other genotypes (Table 2).

Table 1 - LAI at the suspension of irrigation (TO) and 12 days after (T1) and the % reduction. For statistical analysis, the % values were transformed by Arc Sine ??%. Means within a column that do not have a common letter are significantly different by LSD 0.01 test.

Genotype	T0	T1	% reduction
HA 89	3.08 ab	1.32 b	57 ab
RHA 856	2.07 c	0.78 c	62 a
207 A	2.52 bc	1.36 b	46 b
C	2.02 c	0.85 c	58 ab
H. argophyllus	3.88 a	3.13 a	19 c

Table 2 - Total plant dry weight (DW), % reduction of dry weight accumulation (DWA) and root to total dry weight ratio at harvest time. For statistical analysis, the % values were trasformed by Arc Sine ??%. Means within a column that do not have a common letter are significantly different by LDS 0.01 test.

Genotype	Control Total DW (g)	Stress Total DW (g)	DWA reduction % of control	Control Root/Total DW	Stress Root/Total DW
HA 89	91 a	59 b	35 a	0.062 a	0.066 b
RHA 856	75 b	41c	45 a	0.063 a	0.068 b
207 A	70 b	45 c	36 a	0.069 a	0.078 b
C	53 c	29 d	45 a	0.062 a	0.065 b
H. argophyllus	99 a	80 a	20 b	0.071 a	0.117 a

DISCUSSION AND CONCLUSIONS

Our intention was to determine whether a wild sunflower species differed from some cultivated genotypes in its physiological responses to drought. The greater transpiration efficiency of the wild sunflower (Figure 5) was due to its greater photosynthetic rate, especially under dry condition (Figure 3) as reported by Morizet et al., (1984), while its transpiration rate was similar to the other genotypes (Figure 4). Maintenance of photosynthetic activity under drought by the wild sunflower was associated with grater relative water content in leaves (Figure 2) and slighty higher leaf water potential at the pre-dawn (Figure 1). Apparently the wild sunflower has greater dehydration avoidance than the cultivars.

Dehydration avoidance in plants has been associated with reductions in water loss (Turner, 1979), but the wild sunflower had the greatest leaf area index, the smallest reduction of dry matter in stressed plants at harvest, very sensitive characters to soil drying (Boyer, 1968; Takami et al., 1982; Davis and Zhang, 1991), and a transpiration rate per unit leaf area similar to the other genotypes. Therefore the water taken up from the soil by this wild species was probably higher.

Consequently, the dehydration avoidance and the high TE of the wild sunflower may be due to its greater allocation of dry matter to roots under drought than the cultivars (Table 2) (Hsiao and Acevedo, 1974). Similar results among peanut cultivars were also observed in glasshouse and field studies (Hubick et al., 1986; Wright et al., 1988).

Although the wild species and cultivar 207 A had similar high photosynthetic activity (Figure 3), the two genotypes did not appear to possess the same level of drought resistance. The difference between them is made clear when one considers that cultivar 207 A reached a leaf water potential of -1.4 MPa within 7 days after irrigation was suspended, while the wild sunflower did not reach this level until no fewer than 19 days after water suspension (Figure 1). It is likely that the increase in root dry matter may have permitted the wild sunflower to exploit a greater volume of soil compared with their neighbours and this can explain the real conflict in our data in which the greater transpired water of the wild species was not associated with more rapid decline in dawn leaf water potential (Figure 1).

The special trial conditions (high plant density and limited amount of soil available to plants) enhanced competition among genotypes for the available water, which contributed to accelerating and intensifying the various differences that could be observed.

This wild species may be a useful source of genes for improving drought resistance in cultivated sunflower since its mechanism of dehydration avoidance would not necessarily limit yield potential in wet conditions (Turner, 1979). Although a negative association between TE and harvest index has been found in other crops (Hubick et al., 1988), and could be present in sunflower, suggesting that concurrent improvement in these traits may be difficult, but progress in this direction should not be impossible.

The possibility of using some physiological criteria to supplement classical breeding for improving drought resistance in sunflower is considered. Already in other species, genotypes with resistance to drought have been developed by a long period of classical breeding together with limited selection for physiological characters as in wheat (Morgan, 1983; Rascio et al., 1988; Schonfeld et al., 1988; Ritchie et al., 1990), barley (Matin et al., 1989), in sorghum (Wright et al., 1983) and soybean (Sloane et al., 1990). *H. argophyllus* may be useful in breeding programmes for drought resistance in sunflower, in that it has some dehydration avoidance due possibly to greater root development and improved water uptake. Since the greater root development only occurred under drought, this mechanism of drought resistance may not limit yield under well-watered conditions.

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INFLUENCIA DEL DEFICIT DE AGUA EN INTERCAMBIO GASEOSO Y ACUMULACION DE MATERIA SECA EN CULTIVARES DE GIRASOL Y EN ESPECIES SILVESTRES (*Helianthus argophyllus* T&G)

RESUMEN

La influencia del *estres* hidrico en el intercambio gaseoso y acumulación de materia seca en una especie silvestre de girasol (*helianthus argophyllus* T&G) y cuatro cultivares de girasol cultivado (*Helianthus annuus*) (HA-89, RHA-856, 207 A y C) fueron compradas en un experimento en invernadero durante 1989-91. Las plantas fueron mantenidas en unas condiciones de buen suministro de agua hasta madurez en fisiológica mientras que en el tratamiento de estrés hidrico el riego fue suspendido justamente antes de la floración. Fueron realizadas medidas de tasas de fotosintesis y transpiración de las hojas y contenido relativo de agua, y potencial de agua en hoja antes del amanecer, indice de área foliar y materia seca total en la recolección. Bajo condiciones de sequia, el deficit de agua fue más bajo en las especies silvestres que en las lineas cultivadas y la hidratación y fotosintesis de hojas decreció màs rapidamente con la sequia en los cultivares. Estos resultados, junto con la menor reducción del girasol silvestre en producción de materia seca, su incremento en la relación raiz/tallo bajo sequia en recoleción y la constancia del área foliar después de 12 días de secano indican la existencia de un mecanismo de evitacion. La evitación puede ser debida a la mayor longitud radicular de *H. argophylus* a la relación raiz/tallo más alta bajo sequia en comparación con los cultivares.

INFLUENCE DU DÉFICIT HYDRIQUE SUR LES ÉCHANGES GAZEUX ET L'ACCUMULATION DE LA MATIÈRE SÈCHE CHEZ DES CULTIVARS DE TOURNESOL ET UNE ESPÈCE SAUVAGE (*Helianthus argophyllus* T&G)

RÉSUMÉ

En 1989-1990, nous avons étudié en serre l'influence du stress hydrique sur les échanges gazeux et l'accumulation de matière sèche chez un tournesol sauvage (*Helianthus agrophyllus* T&G) et quatre cultivars de tournesol cultivé (*Helianthus annuus* L.) (HA 89, RHA 856, 207 A et B). Les plantes ont été maintenues soit dans des conditions d'arrosage favorables jusqu'à la maturité physiologique soit soumises à un traitement de stress hydriques par arrêt des arrosages juste avant floraison. Les mesures concernaient la photosynthèse foliaire, le taux de transpiration, la teneur relative en eau des feuilles, l'indice de surface foliaire et la matière sèche totale à la récolite.

En conditions séches, le déficit hydrique était plus faiable pour l'espéce sauvage que pour les lignées cultivées, alors que la photosynthèse et la diminution de l'hydratation foliaire étaient plus rapides pour les cultivars. Pour l'espèce sauvage nous avons également observé une moindre réduction de la matiére sèche, l'augmentation du rapport racine / pousse à la récolte et une surface foliaire identique après douze jours de sécheresse. L'ensemble de ces résultats indiquerait l'existence de mécanismes permettant d'éviter la déshydratation. Ces mécanisme pourraient avoir comme origine chez *H. agrophyllus* des racines plus importantes et en conditions de sécheresse un rapport racine / pousse supérieur à celui observé pour les cultivars.