

Mechanisms of drought resistance of Helianthus annuus and H. argophyllus.

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Summary

Plants of H. annuus and H. argophyllus were grown in a partially controlled environment (drainage lysimeters in the field) during cycles of decreasing water availability, to study the mechanisms of their drought resistance. The plants were grown under optimal conditions of water supply until the formation of the floral buds. The watering was then withheld in a first set of tanks while a second set provided well watered controls. Sap flow data, leaf water potential, RWC, gas exchange of leaves and soil moisture content were measured daily. Pressure-volume curves and root densities were also determined. In the presence of a moderate water stress H. argophyllus had a better WUE; This species showed a lower transpiration, a more efficient stomatal control and osmotic adjustment. The denser root system could also contribute to this performance.

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Introduction

The cultivated sunflower (Helianthus annuus) has a contrasting behavior with relation to its water requirements (Merrien and Greco, 1984; Morizet and Merrien 1990). In non-limiting water conditions its transpiration rate is very high with a low water use efficiency (WUE), quickly depleting the upper soil water

storage; it is, conversely, considered a drought resistant crop, and its yield as a rainfed crop is often only slightly lower than under irrigation. The ratio between its relative evapotranspiration deficit and its relative yield deficit is usually favorable when compared to other species such as grain maize (Morizet et al., 1984). A deep and dense root system is one of the mechanisms considered responsible for this behavior, while the plant shows a good capability for continuing its metabolic activity even at low soil water potential (Cox and Jollif, 1987).

As a result of these characteristics, sunflower acreage increased in many EEC countries as a rain-fed crop in hilly and relatively marginal areas; most of the high yielding varieties and hybrids were, anyway, selected under non-limiting water conditions, and new genotypes selected for drought resistance and higher WUE during good water availability periods are required.

Breeding programs aimed at increasing the resistance to drought have been carried out (Fereret et al., 1986; Gimenez and Fereret, 1986); one of the promising methods involves the interspecific cross between H. annuus and H. argophyllus, a wild species that grows in dry sandy areas of Southern Texas (Heiser, 1978).

Gelfi and Blanchet (1980) report data on the good efficiency in the utilization of water of this species, and credit this character to the hairiness of the leaves. In their study they found that low transpiration rates were associated with low stomatal resistances.

Morizet et al. (1984) report data comparing H. annuus and a H. annuus x H. argophyllus hybrid: they noticed an early wilting in the hybrid type, contrasting with the its xerophytic habit.

Stomatal resistance, and transpiration were similar while differences were pointed out in terms of leaf water potential and net assimilation. Their paper suggests the following factors as responsible for the differences observed: i) mechanical characteristics of vascular bundles ; ii) leaf cell osmotic components and their adjustment during drought cycles; iii) cell modulus of elasticity. These hypotheses were not verified by the authors.

Baldini (1992) in a greenhouse experiment comparing H. argophyllus with five H. annuus genotypes having different characteristics monitored their gas exchange and water status. He found a better WUE at leaf level in H. argophyllus due to a generally higher assimilation rate at both low and high soil water moisture content; transpiration and stomatal resistance were not significantly different. The data were not conclusive as he discarded an osmotic adjustment mechanism (no actual data were reported), but ascribed the superior behavior of H. argophyllus to the maintenance of water uptake. A different root density and root/shoot ratio was also suggested, but not demonstrated, as a possible explanation for differences. These hypotheses contrast with the idea of H. argophyllus being a drought avoider and satisfy, perhaps, the hypothesis of a drought tolerance. Besides, it is frequently found that plants grown in a greenhouse modify their anatomic and physiological characteristics; the xerophytic habit of H. argophyllus could also have had a poor chance to take advantage of a high leaf boundary layer resistance, as the greenhouse climate lacks the wind component.

The aim of this paper is to provide further information on the

different behavior of H. annuus and H. argophyllus grown in a partially controlled environment (drainage lysimeters in the field) during cycles of decreasing water availability and on their mechanisms of drought resistance.

Materials and Methods

The experiment was carried out using eight drainage lysimeters (1.1 x 0.8 x 0.65 m) filled with sandy-loam soil, under a rain shelter. Six pregerminated seeds of H. argophyllus were planted in each of four lysimeters; after ten days the four other tanks were planted with an equal number of H. annuus seeds; this delay was in order to synchronize the flowering time. The plants were grown in optimal conditions of water supply until the formation of the floral buds.

The day before beginning the measurements on the two species all the tanks were irrigated; watering was then withheld in a first set of two tanks containing respectively the H. annuus and the H. argophyllus plants, while a second set of two tanks provided well watered controls.

In the not-irrigated lysimeters stem flow gauges (Dynamax 19) were secured to the basal section of the stem of a H. annuus and of a H. argophyllus having similar stem diameter and leaf area. The sap flow data were determined at 15 s intervals and logged as 30 min averages on a Campbell 21x data logger. Every day the following determinations were taken between 11.00 and 12.00 a.m.:

- Leaf water potential (ψ) using a pressure bomb on leaves that were wrapped the previous evening with aluminum foil and on uncovered leaves;

- Relative water content (RWC) of leaf disks punched with a 16 mm cork borer.

- Carbon exchange rate (CER) of fully developed leaves sampled in the upper part of the plants; the ADC portable system used gave also the leaf transpiration rate (T) and the stomatal conductance (g_s). When the natural radiation level was low because of clouds it was brought to saturation level (around $1000 \text{ mol m}^{-2} \text{ s}^{-1}$) by means of a 1000 Watt metal halide lamp.

- Soil moisture content measured at 0-20 and 20-40 cm depth.

A WUE was calculated as the ratio between CER and stomatal conductance g_s (also calculated from the gas exchange data); following Morgan and LeCain (1991) this ratio is preferable to the more common CER/T, when using a system lacking the humidity control in the cuvette.

After seven days the plants had depleted most of the available soil water and leaves were sampled to construct pressure-volume curves (Martin and Zerbi, 1991) and soil cores were sampled at three depths for root density determinations. The plants used for the stem flow measurements were harvested and their leaf area and dry weight were determined.

At the end of this seven day period the same procedure was repeated on a second set of four lysimeters. This time, due to the different environmental demand it took twelve days to reach the same level of soil depletion obtained in the first experiment.

Results

Stem flow measurements

The sap flow in the plants was accurately monitored by the sen-

sors. Figure 1 reports an example of the data retrieved on August 28 (a cloudy morning followed by a sunny afternoon); the flow is clearly related to the radiation regime and the H. annuus has an higher flow. The total daily sap flow of the two species during both experiments (fig. 2) shows that H. annuus transpires more than H. argophyllus particularly when the soil water depletion is intermediate. It should be considered that the total leaf area of the plants under examination was not the same. In both experiments H. argophyllus exceeded H. annuus (0.29 m^2 versus 0.23 m^2 in the first and 0.56 m^2 versus 0.36 m^2 in the second experiment). Calculating the daily flows on a per leaf m^2 basis the difference between the two species is even larger (fig.3).

Gas exchange measurements

The average net assimilation (CER) measured on leaves of the two species was not different in the first experiment, while it decreased as an effect of water stress (on the second day, the artificial light system was not used and the particularly low values are due to the cloudy day and consequent low radiation) (fig. 4). In the second experiment the H. annuus showed an higher assimilation activity in most of the days monitored. The same species transpired much more in both tests (fig. 5) and as a result H. argophyllus had an overall better WUE. In the second experiment this effect was particularly evident during the last period of the cycle when the stress increased.

Leaf water potential.

At the beginning of both tests, when the water stress was absent or very moderate the water potential of leaves of H. argophyllus

exposed to full radiation and screened from radiation with aluminum foil resembled similarly treated leaves of H. annuus. (fig. 6 and 7)

When the water stress increased the ψ of H. argophyllus leaves were constantly more negative. The difference in between screened and exposed leaves is reported in fig. 8. This difference was calculated to represent the ψ gradient between the stem (screened leaves) and the transpiring leaf; on average and on most of the days the H. annuus showed a higher gradient.

Relative Water Content

The relative water content of the leaf tissues sometimes showed a great variability (fig. 9). The RWC of the leaves of H. argophyllus had a better state of hydration in most of the determinations and slightly lower values at the end of the second test period.

Osmotic adjustment

The osmotic potentials at full turgor (ψ_{s100}) and the apoplastic water fraction (AWF) were calculated from the P-V curves (tab.1). The difference between the ψ_{s100} of control and water stressed plants represents the osmotic adjustment and has values of 0.40 MPa for H. argophyllus and 0.08 MPa for H. annuus. The AWF had values around 0.19 for all the treatments.

Root density

The H. argophyllus had a root density (cm of root per cm³ of soil) that was about 30 % higher than the H. annuus density at all the depths tested (fig 10).

Water consumption

The cumulated water consumption values during the two tests cal-

culated from the gravimetric soil moisture measurements were respectively 26 and 62 mm for the H. annuus tanks and 19 and 50 mm for the H. argophyllus tanks.

Discussion

In the presence of moderate water stress H. argophyllus had a consistently better leaf WUE in respect to H. annuus; since leaf WUE is associated with plant and community WUE (Ludlow and Muchow, 1990) from our results we can formulate a consistent hypothesis on the physiological basis of the resistance of the wild species to water stress.

The higher efficiency is mainly related to the transpiration component of the gas exchange, significantly reduced in H. argophyllus, while the CER was only slightly affected. In turn this lower transpiration affects the water consumption, which being lower in H. argophyllus, permits a longer availability of the stored water.

H. argophyllus shows the capability of maintaining both a higher RWC and a lower ψ stem-leaf gradient. A more efficient stomatal control could be deduced, together with a certain degree of osmotic adjustment; in H. annuus the osmotic adjustment was practically nil. No differences were noticed in terms of AWF or cell modulus of elasticity. The denser root system of H. argophyllus also contributes to the more regular water extraction from the soil reservoir.

The leaf hairiness and the silver-gray color, traits often related to xerophytic conditions could contribute to the better performance of H. argophyllus; the moderately lower transpira-

tion under non-limiting water conditions decreases the excessive water consumption permitting a longer utilization of the soil water storage.

Concluding, H. argophyllus tends to avoid water deficits in its tissues preserving cell turgor: this is achieved via a more regular water uptake, a reduced water loss and a moderate osmotic adjustment.

Further investigations are currently in progress on leaf morphological traits; observation and counting of stomata is particularly difficult in this species, as the thick hair mat denies both direct observation and enamel inprinting. Other possibilities that could be investigated regard the existence and level of root messages affecting the leaf water conductance.

Tab. 1. Means and standard deviations of solute potentials at full turgor and of the apoplastic water fraction (AWF) for control (CTR) and water stressed plants (WS).

		(MPa)	AWF
<u>H. annuus</u>	<u>CTR</u>	- 1.81 + 0.05	0.19 + 0.02
<u>H. annuus</u>	<u>WS</u>	- 1.89 + 0.06	0.18 + 0.02
<u>H. argophyllus</u>	<u>CTR</u>	- 2.38 + 0.07	0.18 + 0.01
<u>H. argophyllus</u>	<u>WS</u>	- 2.78 + 0.06	0.19 + 0.03

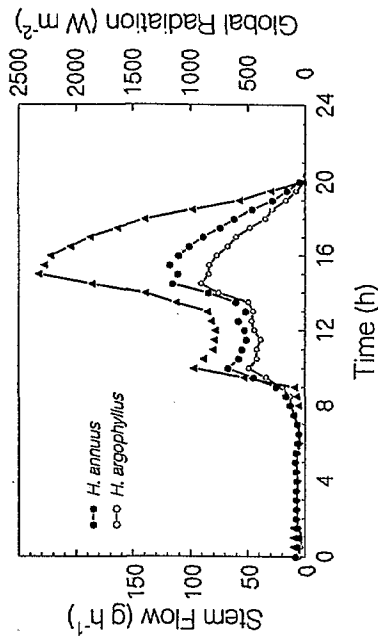


Fig. 1. Daily patterns of stem sap flow in plants of *H. annuus* and *H. argophyllum* on August 28. Global radiation values ($W m^{-2}$) are also reported.

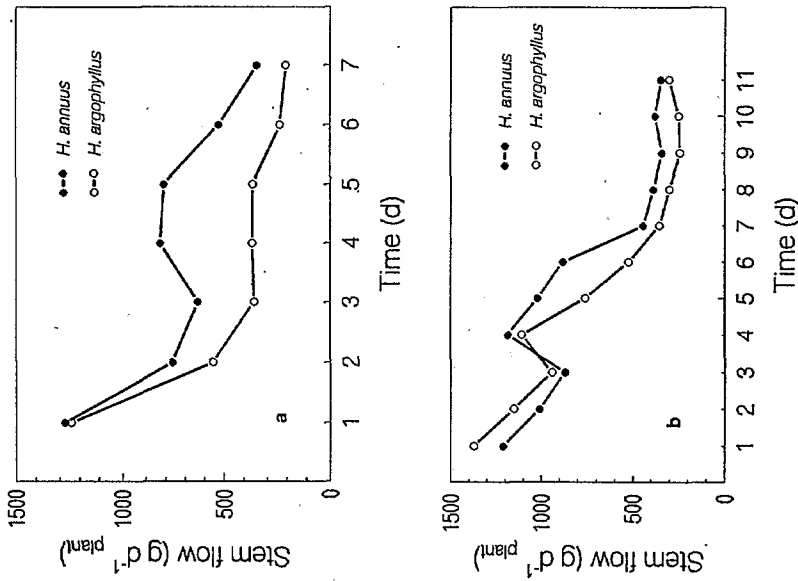


Fig. 2. Total daily stem sap flows, in plants of *H. annuus* and *H. argophyllum* during the first (a) and the second (b) decreasing soil water availability experiments.

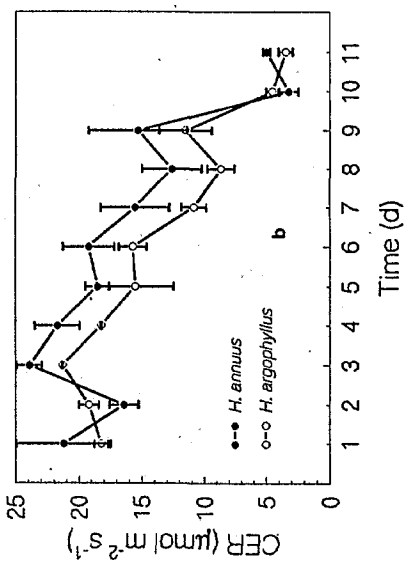
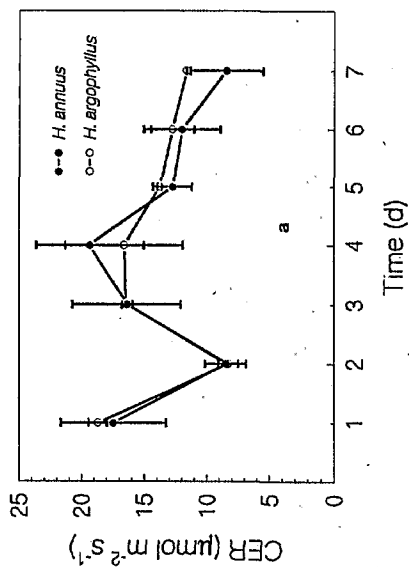


Fig. 4. Leaf carbon exchange rates in plants of *H. annuus* and *H. argophyllus* during the first (a) and the second (b) decreasing soil water availability experiments. Vertical bars represent standard deviations about the mean.

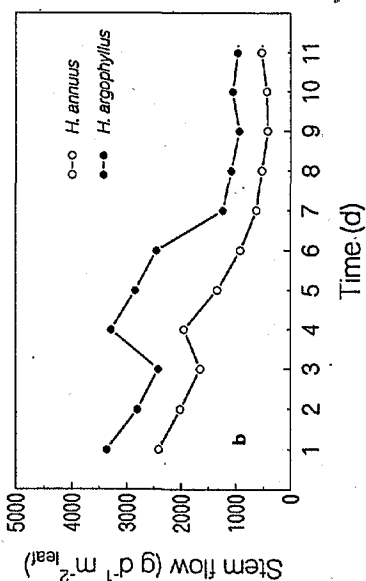
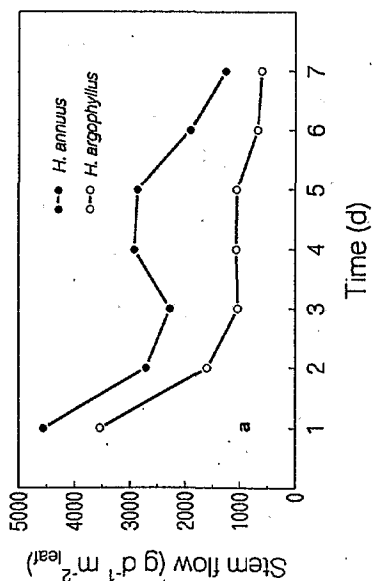


Fig. 3. Daily stem sap flows, per m² of leaf area, in plants of *H. annuus* and *H. argophyllus*, during the first (a) and the second (b) decreasing soil water availability experiments.

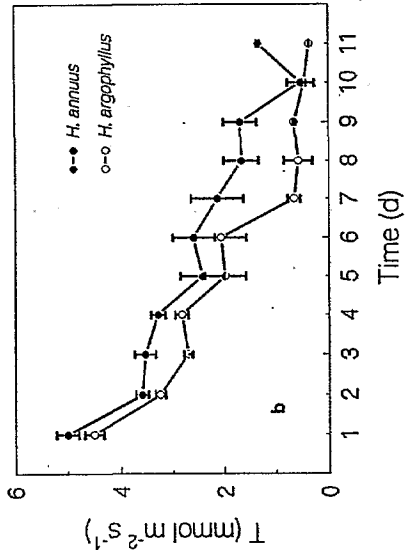
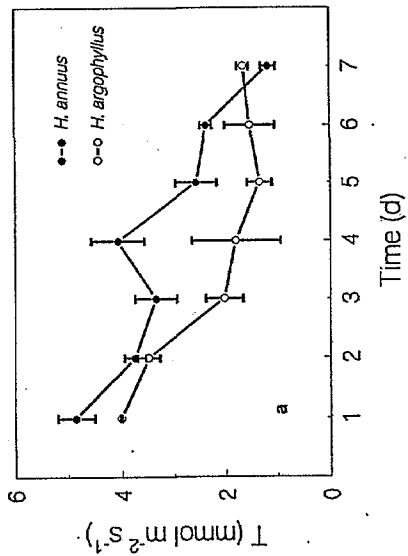


Fig. 5. Leaf transpiration rates in plants of *H. annuus* and *H. argophyllus* during the first (a) and the second (b) decreasing soil water availability experiments. Vertical bars represent standard deviations about the mean.

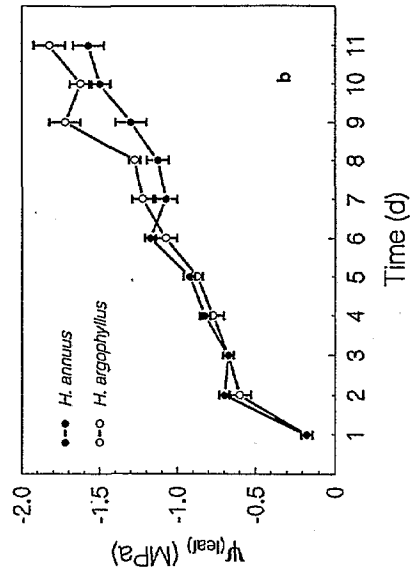
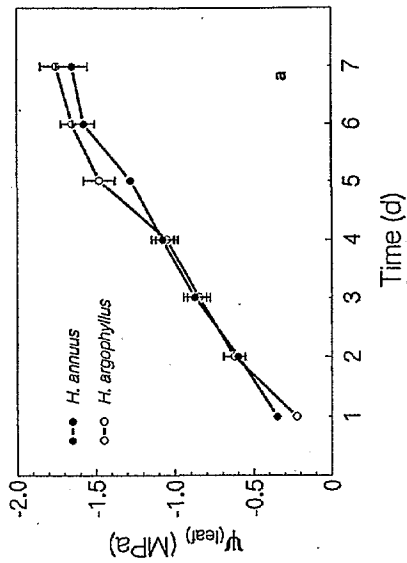


Fig. 6. Leaf total water potentials in plants of *H. annuus* and *H. argophyllus* during the first (a) and the second (b) decreasing soil water availability experiments. Vertical bars represent standard deviations about the mean.

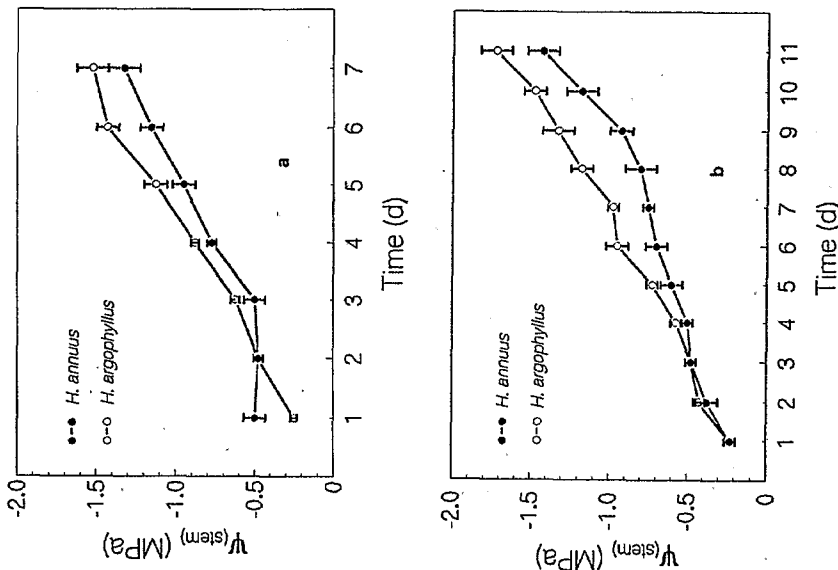


Fig. 7. Stem total water potentials in plants of *H. annuus* and *H. argophyllus* during the first (a) and the second (b) decreasing soil water availability experiments. Vertical bars represent standard deviations about the mean.

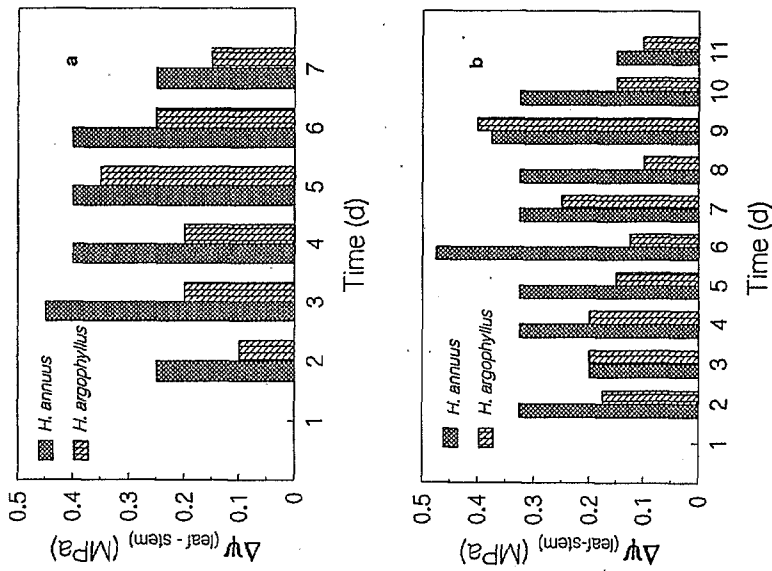


Fig. 8. Difference between leaf and stem total water potentials (respectively un-screened and screened leaves) in plants of *H. annuus* and *H. argophyllus* during the first (a) and the second (b) decreasing soil water availability experiments.

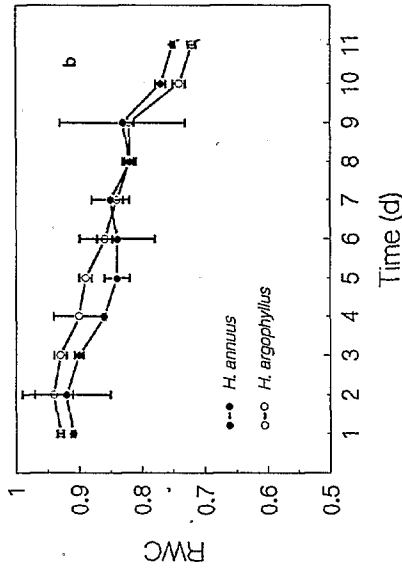
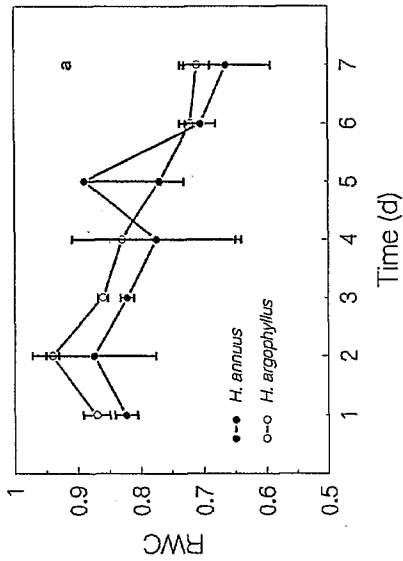


Fig. 9. Leaf relative water content in plants of *H. annuus* and *H. argophyllus* during the first (a) and the second (b) decreasing soil water availability experiments. Vertical bars represent standard deviations about the mean.

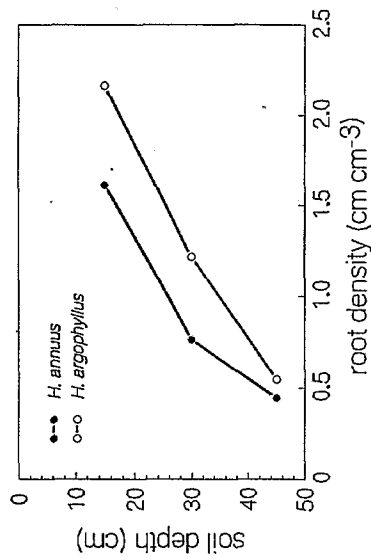


Fig. 10. Root density, at different soil depths, of plants of *H. annuus* and *H. argophyllus* at the end of the second decreasing soil water availability experiment.

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