Photosynthetic characteristics of *Lactuca serriola* L.

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Abstract. Gas exchange responses of intact leaves of *Lactuca serriola serriola* and *L. serriola integrifolia* were examined. The light, temperature and intercellular CO_2 dependence of photosynthesis of these two forms of *L. serriola* were indistinguishable. Dependence of photosynthesis on leaf temperature differed only slightly between plants grown at approximately $10/3\,°C$ and those grown at $33/25\,°C$ with the thermal optimum shifting $4\,°C$. Transpiration was shown to increase exponentially with leaf temperature. The gas exchange characteristics of *L. serriola* are discussed in relation to water relations, carbon gain and compass leaf orientation under field conditions.

Key-words: *Lactuca serriola*; compass plant; photosynthesis; transpiration; leaf orientation.

Introduction

Lactuca serriola L. is an annual plant, originally European, now occupying a wide distribution globally, especially in disturbed habitats and grasslands. *L. serriola* grows in a wide range of environmental conditions and the growing season can be very long, exposing individuals to a wide range of temperatures. Germination may occur in the winter or early spring when temperatures are near freezing with growth and flowering continuing through the summer when temperatures can exceed $35\,°C$. This ability to grow in such a wide range of environmental conditions may be a result of a physiological capacity which is quite plastic as has been found in a number of other species (Pearcy, 1977; Bjorkman, Badger & Armond, 1978; Mooney, Björkman & Collatz, 1978). The importance of physiological acclimation by *L. serriola* to changes in temperatures, however, may be diminished since the range of daytime leaf temperatures may be somewhat reduced by changes in growth form. In the winter leaves form prostate rosettes, but then bolting occurs and leaves are on flowering stalks 1–2 m above the ground in the summer. These cauline leaves are oriented vertically in a north–south plane so that the lamina are normal to the east and west (Dolk, 1931). The result of this orientation is that the interception of early morning and late afternoon irradiance is enhanced while midday irradiance is reduced (Werk

& Ehleringer, 1984). The change in growth form and the non-random leaf orientation result in a tempering of leaf temperature (Werk & Ehleringer 1984), and, as such, it may be of little advantage for leaves to photosynthetically acclimate to changes in temperature.

The question of whether the gas exchange physiology of these leaves is affected by the cauline leaf orientation needs to be answered. Is the leaf orientation observed a morphological means of avoiding high temperatures, as Geiger (1966) suggested, or is the resulting redistribution of light over the day more important to the overall water and carbon balance of *L. serriola*? We can only begin to answer these questions when we have an understanding of the basic gas exchange characteristics of these cauline leaves.

A distinct leaf shape polymorphism occurs in *L. serriola*. *L. serriola integrifolia* is a highly lobed leaf form, while *L. serriola serriola* is an unlobed form (Lindqvist, 1958; Prince & Carter, 1977). If differences in leaf shape affect the heat transfer characteristics significantly, then the two types may have different leaf temperatures under identical microclimate conditions and we may find correlated differences in the physiology of the two leaf forms. However, since we know that the characteristic dimension (width) of the lobed leaves is larger than that of unlobed leaves of equal length (Werk & Ehleringer, 1984), we do not expect the heat transfer characteristics of the two leaf forms to be very different.

This study investigates the basic photosynthetic gas exchange characteristics of *L. serriola* in order to characterize the responses of net photosynthesis and stomatal conductance to temperature, light, vapour concentration deficits (ΔW) and intercellular concentration of CO_2. These characteristics are considered in relation to possible interactions with the specific cauline leaf orientation observed in the field. The extent of acclimation in the temperature response of photosynthesis to the extremes of freezing temperatures in the winter and hot temperatures during the summer are also investigated. The photosynthetic characteristics of the two leaf forms are compared. Finally, these characteristics are considered in relation to the environmental conditions encountered by *L. serriola* in the field in Salt Lake City where establishment by both forms has been very successful.

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Materials and methods

Laboratory measurements were made on plants which were grown from seed collected from Salt Lake City, Utah. Plants were grown individually in pots.

For cold temperature treatment, plants were grown outside on the roof during November and December 1981. To simulate natural soil temperature conditions as best as possible, the plant pots were set in a large soil box and only removed for gas exchange measurements. Diurnal leaf and air temperatures were measured with thermocouples and monitored continuously with a datalogger (model CR21, Cambell Scientific, Logan, Utah). Overnight minimum air temperatures ranged from 0 to 5 $°C$, while daily maxima ranged from 5 to 12 $°C$. Leaf temperatures never differed more than 6 $°C$ from air temperatures. The photoperiod was approximately 9 h/15 h day/night. For high temperature treatment plants were grown in a temperature-controlled greenhouse during March–May 1983. Overnight leaf temperatures were maintained at 25 $°C$ and daily maximum temperatures ranged from 30 to 35 $°C$. The photoperiod was approximately 12 h/12 h day/night. The plants in both treatments received adequate water to maintain favourable soil moisture conditions. No nutrient supplements were provided.

Plants used to characterize photosynthetic responses to light, water vapour concentration deficit and intercellular CO_2 concentration were grown in pots constructed with 15-cm diameter PVC pipe 75 cm deep. These pots allowed the use of a large soil volume in a small floor area and allowed the roots to grow as deeply as they would in the field. These plants were grown in an HID-lamp supplemented greenhouse. Temperatures were maintained at 25 $°C$ overnight and 30–35 $°C$ during the day. Photoperiod was 14 h/10 h day/night. Daily incident photon fluence rate (400–700 nm) averaged 30 mol m^{-2} d^{-1} with a midday peak fluence rate of approximately 1.0 mmol m^{-2} s^{-1}.

Gas exchange measurements were conducted on an open gas-exchange system similar to that described by Ehleringer (1983). A small gas exchange cuvette specifically designed for the leaves of *L. serriola* was used. This chamber was constructed of nickel-plated brass and was temperature controlled with a thermoelectric peltier block (Melcor Inc., Trenton, NJ, U.S.A.). A small 12 V fan (Micronel, Fallbrook, CA, U.S.A.) in the chamber provided wind speeds of 6 m s^{-1}.

Measurements were conducted on single, attached leaves. To avoid any possible leaf age effects, the youngest fully expanded leaf was used for each plant measured.

For measurements of the effect of growth temperature on the temperature dependence of photosynthesis, a single leaf was sealed into the cuvette with a photon fluence rate of 1.8 mmol photons m^{-2} s^{-1} (400–700 nm), ambient CO_2 concentration of 340 cm^3 m^{-3}, 21% O_2, ΔW of 5–10 mPa Pa^{-1} and a leaf temperature of 5–15 $°C$. The leaf temperature was raised in steps of approximately 5 $°C$, waiting at each step for photosynthesis and leaf conductance to stabilize before changing leaf temperature again. Occasionally throughout these measurements, the leaf temperature was lowered between points to insure repeatability and a lack of dependence on the direction of the temperature changes.

To eliminate the possible interaction of the temperature dependence of photosynthesis and conductance with a sensitivity to humidity, ΔW was maintained as close as possible to 10 mPa Pa^{-1} by adjusting the dew point of the air sent to the cuvette. ΔW averaged 10.2 ± 0.34 ($\bar{x} \pm SE$) for all the temperature dependence measurements. In 1981 six plants were used and in 1983 five plants were used.

Light dependence of photosynthesis was determined by exposing the leaf to an ambient CO_2 concentration of 340 cm^3 m^{-3}, 21% O_2, leaf temperature of 30 $°C$, and ΔW of 10 mPa Pa^{-1}. A fluence rate of approximately 2.0 mmol photons m^{-2} s^{-1} was used to begin each run. When net photosynthesis and leaf conductance were stable the fluence rate was decreased in steps to less than 0.1 mmol photons m^{-2} s^{-1}, waiting for stability between each step. Five plants of each leaf form were measured.

The dependence of photosynthesis on the intercellular CO_2 concentration was determined by adjusting the ambient CO_2 concentration in the cuvette. The first point determined was always at about 340 cm^3 m^{-3} CO_2. The CO_2 concentration was then dropped in steps of 100–150 cm^3 m^{-3}. After these low intercellular CO_2 concentration measurements the conditions were returned to 340 cm^3 m^{-3}. The ambient CO_2 concentration was then raised in steps of 100–200 cm^3 m^{-3} until the intercellular CO_2 concentration was 330 cm^3 m^{-3} or greater. All measurements were made at 21% O_2 and approximately 1.8 mmol photons m^{-2} s^{-1}. Four plants of each leaf form were measured.

The dependence of photosynthesis, leaf conductance and intercellular CO_2 concentration on ΔW was determined by varying ΔW while maintaining an irradiance of approximately 1.8 mmol photons m^{-2} s^{-1}, an ambient CO_2 concentration of 340 cm^3 m^{-3}, 21% O_2 and a leaf temperature of 30 $°C$. ΔW was controlled by adjusting the dewpoint of the air entering the cuvette.

For all gas exchange measurements calculations of ΔW and intercellular CO_2 concentration were made as described by von Caemmerer & Farquhar (1981), and Comstock & Ehleringer (1984).

Results

The dependence of net photosynthesis on irradiance was measured on both leaf forms of *L. serriola*.

Leaves of *L. serriola serriola* exhibited the same response to light as those of *L. serriola integrifolia*. Both became light saturated above approximately 1.5 mmol photons m^{-2} s^{-1} and attained very similar photosynthetic rates at saturating light levels (Fig. 1). Leaf conductances and intercellular CO_2 concentrations were also similar. When exposed to irradiances above 1.85 mmol photons m^{-2} s^{-1} net photosynthesis in leaves of *L. serriola serriola* averaged 29.9 ± 2 μmol m^{-2} s^{-1} ($\bar{x}$ ± SE), leaf conductance averaged 0.93 ± 0.1 mol m^{-2} s^{-1} and intercellular CO_2 concentration averaged 286 ± 7 cm^3 m^{-3}. In leaves of *L. serriola integrifolia* net photosynthesis averaged 27.7 ± 1 μmol m^{-2} s^{-1}, leaf conductance averaged 0.67 ± 0.07 mol m^{-2} s^{-1}, and intercellular CO_2 concentration averaged 267 ± 9 cm^3 m^{-3}. No statistical differences in these three pairs of means were indicated by Student t tests ($P > 0.1$). The slopes of photosynthesis as a function of light for irradiances less than 1.0 mmol photons m^{-2} s^{-1} in both *L. serriola serriola* and *L. serriola integrifolia* were compared using linear regression analysis. The slopes of the response curves were not significantly different ($F_{1,38} = 0.36$ $P > 0.5$).

For irradiances above 0.5 mmol m^{-2} s^{-1} intercellular CO_2 concentration remained generally constant and was independent of light ($r = 0.115$, $P \gg 0.1$ using the data from both forms). The intercellular CO_2 concentration did increase at irradiances below 0.5 mmol m^{-2} s^{-1}. A weak negative correlation was observed for irradiances between 0 and 0.5 mmol m^{-2} s^{-1} ($r = -0.457$, $P < 0.05$).

The dependence of net photosynthesis on intercellular CO_2 concentration was the same in *L. serriola serriola* and *L. serriola integrifolia* leaves. Both exhibited responses typical of unstressed C_3 plants (Fig. 2). Under high light conditions neither leaf form of *L. serriola* was CO_2 saturated until the intercellular CO_2 concentration was much greater
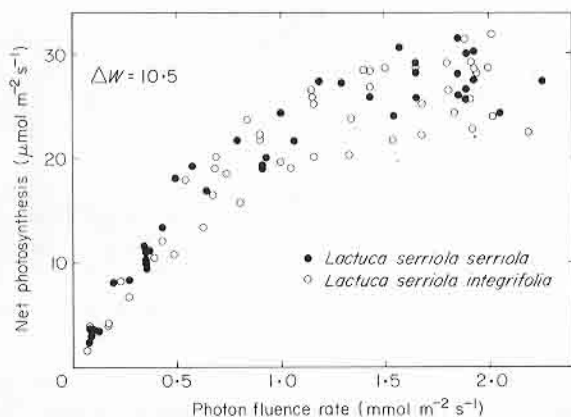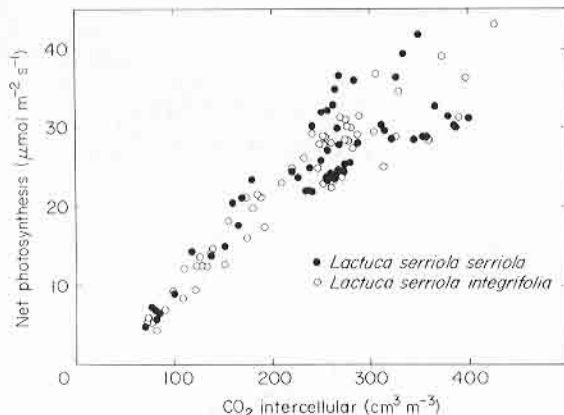

Figure 2. Dependence of net photosynthesis in both leaf forms of *L. serriola* on intercellular CO_2 concentration. Measurements were made at 30 °C, 21% O_2 and 1.8 mmol photons m^{-2} s^{-1}. Regression equations for the response below 305 cm^3 m^{-3} CO_2 were: NP = 0.11X + 0.37 for *L. serriola serriola* and NP = 0.11X − 1.9 for *L. serriola integrifolia*. Sample sizes were four plants of each leaf form.

than 340 cm^3 m^{-3}. The slopes of photosynthesis as a function of intercellular CO_2 concentrations less than 300 cm^3 m^{-3} were compared using linear regression analysis. The slopes for *L. serriola serriola* and *L. serriola integrifolia* were not significantly different ($F_{1,65} = 0.017$ $P > 0.75$).

The dependence of photosynthesis on leaf temperatures was determined for low growth temperatures in 1981 and high temperatures in 1983. Growth temperatures had a minimal effect on the temperature dependence of photosynthesis in leaves of *L. serriola* (Fig. 3). To calculate the thermal optimum of each set of data least-squares regressions of the form $y = a + a_1 X + a_2 X^2$ were used. The thermal optimum of the plants grown in 5–12 °C/0–5 °C day/night temperatures was 22 °C. The thermal optimum of plants grown in 30–35 °C/25 °C temperatures was 26 °C. Photosynthetic rates remained in excess of 90% of maximum between 13 and 31 °C for the low temperature grown plants and between 16 and 36 °C for the high temperature grown plants. The main difference between the low and high temperature grown plants was the ability of the high temperature plants to maintain relatively high photosynthetic rates at temperatures between 35 and 40 °C. No differences between *L. serriola serriola* and *L. serriola integrifolia* in temperature responses were observed.

The dependence of transpiration on leaf temperature was also determined at the same time as the photosynthesis measurements. Transpiration rate increased exponentially with increasing leaf temperature (Fig. 4). This occurred despite a constant vapour concentration gradient from leaf to air (ΔW). ΔW was maintained close to 10 mPa Pa^{-1} throughout these measurements.

There was a strong response of photosynthesis, leaf conductance and intercellular CO_2 concentration

Figure 1. Dependence of net photosynthesis in both leaf forms of *L. serriola* on photon fluence rate. Measurements were made at 30 °C, 21% O_2, ambient CO_2 concentration of 340 cm^3 m^{-3} and W of 10.5 mPa Pa^{-1}. Sample sizes were five plants of each leaf form.
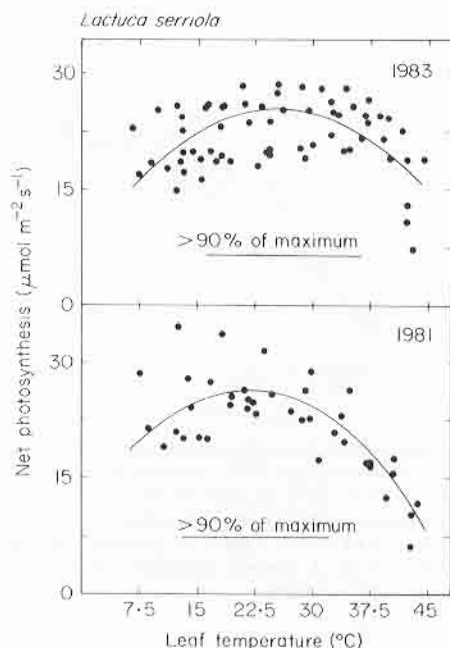
Figure 3. Dependence of net photosynthesis on leaf temperature for both leaf forms grown under low temperature conditions (1981) and high temperature conditions (1983). Regression equations for the temperature responses were: $NP = 10.45 + 1.45T - 0.33T^2$, $r^2 = 0.52$, $P < 0.01$ for 1981 and $NP = 7.14 + 1.41T - 0.027T^2$, $r^2 = 0.31$, $P < 0.01$ for 1983. The horizontal lines represent the temperature range over which net photosynthesis is predicted to remain in excess of 90% of the optimum. Measurements were made at 21% O_2, ambient CO_2 concentration of 340 cm^3 m^{-3}, and ΔW of 10.2 ± 0.58 ($\bar{x} \pm SE$). Sample size was six plants in 1981 and five plants in 1983.

to changes in ΔW. Under saturating irradiances, an ambient CO_2 concentration of 340 cm^3 m^{-3} and a leaf temperature of 30 °C, leaf conductance decreased in direct response to changes in ΔW (Fig. 5). In addition, net photosynthesis and intercellular CO_2 concentrations changed such that their relationship was indistinguishable from that measured in the photosynthesis versus intercellular CO_2 concentration dependence curves.

Discussion

No apparent differences were observed between the gas exchange characteristics of *L. serriola serriola* and *L. serriola integrifolia*. This information, coupled with the lack of differences observed in the pattern of leaf orientation of the two forms (Werk & Ehleringer, 1984) strongly suggests that the two forms are ecologically similar. A detailed study aimed specifically at discerning any subtle differences in physiology or demography would be required to test the hypothesis that *L. serriola serriola* and *L. serriola integrifolia* are ecological equivalents.

L. serriola does not become light saturated until irradiances are above 1.5 mmol photons m^{-2} s^{-1}. This is consistent with the pattern of light received. Although *L. serriola* has vertical leaves, their
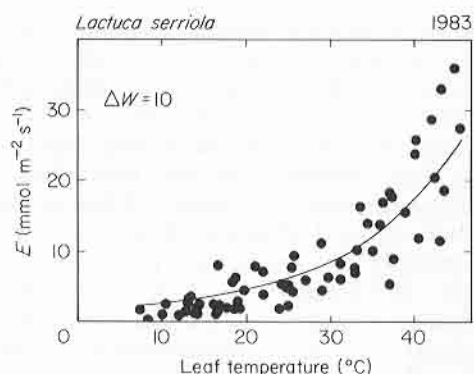

Figure 4. Dependence of transpiration on leaf temperature at constant ΔW for both leaf forms. Measurements were made simultaneously as those presented in Fig. 3, 1983. The regression equation was $E = 1.08$ $e^{(0.069T)}$, $P < 0.01$. The regression equation for leaf conductance (mmol m^{-2} s^{-1}) was $g = 211$ $e^{(0.049T)}$, $P < 0.01$.

east–west orientation results in irradiances of over 1.5 mmol photons m^{-2} s^{-1} for several hours in the morning and afternoon.

Photosynthesis in *L. serriola* has a very broad and flat response to leaf temperature. The response is so broad that it nearly obscures the fact that *L. serriola* has the ability to adjust its photosynthetic response to its growth conditions. Plants grown in temperatures of 5–12 °C had a temperature optimum of
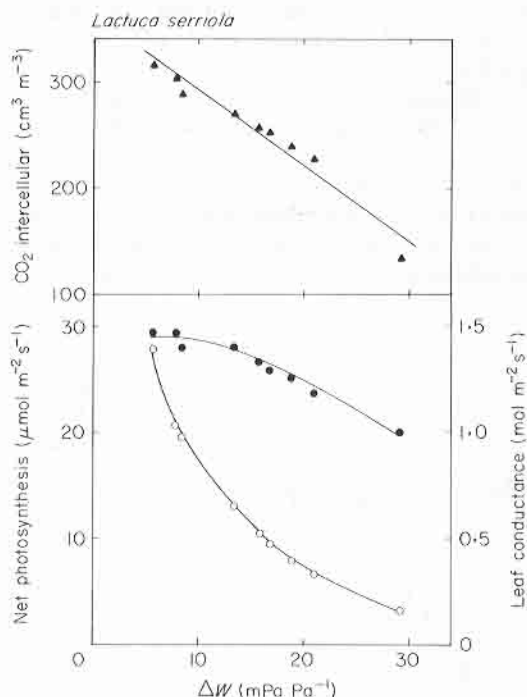

Figure 5. Representative curves of the dependence of net photosynthesis (●), leaf conductance (○) and intercellular CO_2 concentration on leaf to air ΔW (▲). Measurements were made at 30 °C, 21% O_2, 340 cm^3 m^{-3} CO_2 and 1.8 mmol photons m^{-2} s^{-1}. The regression equation for intercellular CO_2 concentration was $C_i = 363 - 7.12$ W, $r^2 = 0.95$, $P < 0.01$. The curves for net photosynthesis and leaf conductance were fitted by eye.

22 °C, only four degrees lower than plants grown at 30–35 °C. The temperature optimum of photosynthesis for the low temperature grown plants was approximately 15 °C higher than the growth temperature; however, photosynthetic rates remained in excess of 90% of the maximum down to 13 °C. Thus, the optimum temperature has very little importance in determining the performance of *L. serriola* over a wide range of temperatures. When grown in high temperatures *L. serriola* can maintain 90% of maximum photosynthetic rates at temperatures in excess of 35 °C. It is also clear that these plants do not require the leaf orientation observed in the field to avoid potentially lethal leaf temperatures since stable photosynthesis is maintained at temperatures between 40 and 45 °C (Fig. 3). Leaf temperatures rarely exceed 35 °C in plants growing in the field even when they are artificially held horizontally (unpublished data).

L. serriola has a very stong direct response to ΔW (Fig. 5). The decrease in leaf conductance observed in response to increases in ΔW affects both CO_2 and water exchange. The reduction in leaf conductance is large enough to reduce transpiration at high ΔW's if leaf temperature is maintained constant. At the same time photosynthesis declines because the reduction in leaf conductance lowers the intercellular CO_2 concentration. Intercellular CO_2 concentration declines linearly with ΔW. The ratio of intercellular CO_2 concentration to ambient CO_2 declined linearly with increasing ΔW ($r = -0.84$, $P \ll 0.01$, $N = 68$). Photosynthesis declines at an increasing rate as ΔW increases while transpiration peaks at an intermediate ΔW and declines steadily at higher ΔW's. This points out the trade-off between conserving water and gaining carbon. Although *L. serriola* may become more water-use efficient at high ΔW's the reduction in leaf conductance clearly limits its rate of carbon gain.

Leaf conductance, and thus transpiration, increases with leaf temperature when ΔW is maintained constant (Fig. 4). Similar results have been measured in other species. Hall, Schulze & Lange (1976) indicated that conductance and thus transpiration increased with increasing temperatures at temperatures above the optimum for photosynthesis. In the field, ΔW and temperature vary simultaneously and so just considering the effect of ΔW under constant temperatures might be misleading. Since the ΔW responses were studied at constant temperature and the temperature responses were studied at constant ΔW, we cannot clearly describe the interaction between leaf temperature and ΔW.

The observed leaf orientation in *L. serriola* may be important for water relations under field conditions because of the temperature dependence of transpiration. *L. serriola* leaves have lower midday temperatures in their natural vertical orientation than if they are held horizontally (Werk & Ehleringer, 1984). The dependence of transpiration on leaf temperature (Fig. 4) indicates that this should translate into a reduction in water lost by the vertical leaves.

L. serriola leaf orientation shifts the time of day when the peak irradiance is intercepted. The peak irradiance, and thus the peak heat load, on leaves occurs during the cooler portions of the day (Werk & Ehleringer, 1984). The light response measurements indicate that high rates of photosynthesis can be attained by *L. serriola* during these cooler periods when water loss would be reduced.

Since the leaves of *L. serriola* are oriented vertically, facing east–west, they receive about 20% less incident solar radiation than if they were horizontal (Werk & Ehleringer, 1984). However, the leaves of *L. serriola* receive 75% of their total irradiance before 09:30 h and after 14:30 h, whereas horizontal leaves receive only about 45% of their daily total irradiance during the same period. Thus, 75% of the potential for photosynthesis in *L. serriola* occurs when its potential water loss is reduced because air and leaf temperatures and ΔW's are lowest.

Cowan & Farquhar (1977) discuss how direct stomatal responses to atmospheric humidity can lead to optimal water use by reducing leaf conductance in response to increasing ΔW. The non-random leaf orientation in *L. serriola* results in further increases in water use efficiency since this orientation enhances photosynthetic rates during periods of lower ΔW. Compass plant leaf orientation appears to be a morphological means of improving the integrated water use efficiency of a plant.

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