Midday depression in net photosynthesis and stomatal conductance in *Yucca glauca*

Relative contributions of leaf temperature and leaf-to-air water vapor concentration difference

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Summary. *Yucca glauca* in the Colorado shortgrass prairie undergoes a pronounced midday depression in net photosynthesis and stomatal conductance under summer field conditions. This phenomenon can be duplicated in the laboratory using potted plants by simulating a typical summer daily pattern of leaf temperature and leaf-to-air water vapor concentration difference (Δw). The decrease in photosynthetic rate appears to be due primarily to high leaf temperatures, while the decrease in stomatal conductance can be attributed mainly to high Δw values. Stomatal conductance also decreases when leaf temperatures exceed a critical threshold value, even when Δw is artificially maintained at a constant level. The threshold temperature is commonly attained for leaves in situ, but only after substantial stomatal closure has already occurred as a result of high Δw values.

The photosynthetic temperature optimum and threshold temperature which promotes stomatal closure increases substantially as the growing season progresses. As a result, the midday depression in photosynthesis occurs at higher temperatures in mid-summer than in late spring. Preliminary evidence suggests that the photosynthetic temperature optimum closely follows the naturally-occurring morning leaf temperatures, while the threshold temperature for stomatal closure matches afternoon leaf temperatures.

Stomatal conductance and the photosynthetic rate of plants growing in hot, arid environments are often reduced during the midday period when leaf temperatures and leaf-to-air water vapor concentration differences (Δw) are greatest. The primary result of this behavior is believed to be the prevention of excessive water loss via transpiration.

Stomatal conductance in plants which exhibit a midday depression appears to be controlled by both internal and external factors. Studies conducted with the Mediterranean-type sclerophylls *Arbutus unedo* and *Quercus ilex* suggested that there was an increased tendency for midday stomatal closure as the water potential of the leaves became more negative (Tenhunen et al. 1981, 1982). Several desert plants have also been shown to exhibit more pronounced midday stomatal closure under conditions of higher water stress (Schulze et al. 1980). It has also been hypothesized that the levels of certain metabolites reflecting the photosyn-

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thetic capacity of mesophyll cells may play a role in the regulation of stomatal aperture (Wong et al. 1979, Farquhar and Wong 1984).

Midday depressions of photosynthesis and stomatal conductance are commonly observed in situ as temperature and Δw increase simultaneously. This effect can be duplicated in temperature- and humidity-controlled environmental chambers (Tenhunen et al. 1980; Lange et al. 1982). Studies which have attempted to separate the effects of temperature and Δw on decreased stomatal conductance and photosynthesis during the midday period have been few in number, however. Schulze et al. (1974) provided evidence suggesting that decreasing air humidity was the primary factor responsible for the midday reduction in stomatal conductance for *Prunus armeniaca* growing under desert conditions. Increasing temperature had an opposite effect on conductance. Based on the cumulative effect of these two factors, these investigators were able to predict the daily course of leaf diffusion resistance for this species.

The reduction of photosynthesis during the midday depression is often attributed to a reduced availability of CO_2 to mesophyll cells due to the decrease in stomatal conductance (e.g., Schulze et al. 1974; Tenhunen et al. 1981). However, the high temperatures which occur during these periods can have direct effects on photosynthesis (Tenhunen et al. 1984), although studies concerning this aspect of the midday depression are few in number.

In this paper we report a large midday depression in stomatal conductance and photosynthetic rate for the shortgrass prairie sclerophyll *Yucca glauca* growing under natural conditions. In addition, we have attempted to evaluate the relative contributions of leaf temperature and Δw as controlling factors which lead to these responses.

Materials and methods

Field measurements. Field studies were conducted during the spring and summer of 1983 at the Central Plains Experimental Range in the Pawnee National Grassland in northeastern Colorado, USA (40°42′ N, 104°46′ W). The plants were mature, with leaves ranging from 25 to 35 cm in length, and were located on a well-drained upland site. Measurements of net photosynthesis and transpiration were obtained with a portable gas exchange system which has been described previously (Monson 1984). Cuvette temperature was regulated by two Peltier modules (Melcor, model
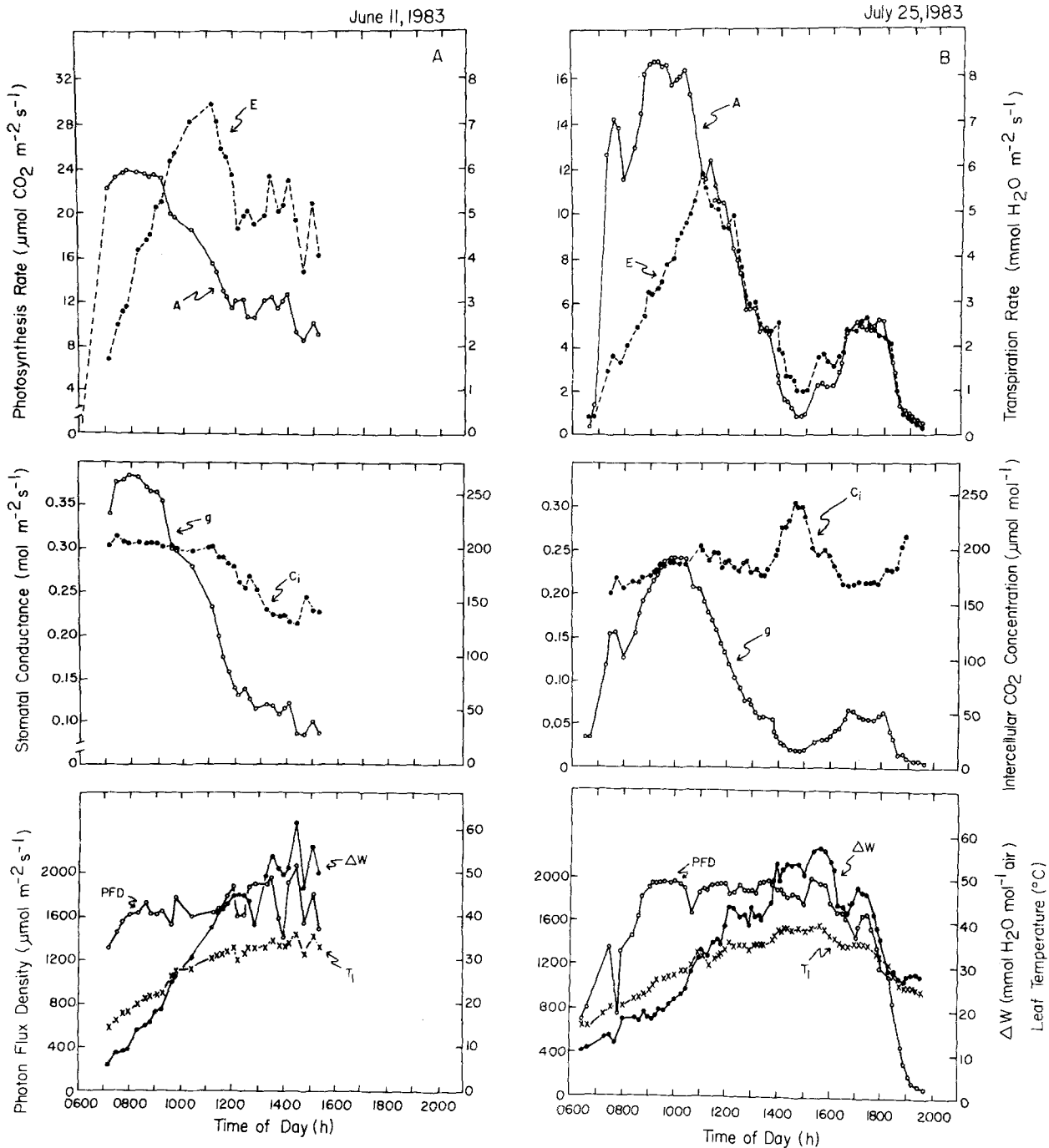
Fig. 1. Daily patterns of gas exchange and microclimate of *Y. glauca* leaves during late spring and mid-summer. For June 11, predawn and midday (1200–1300 h) leaf water potentials were -0.6 ± 0.2 (SD, $n=3$) and -2.0 ± 0.4 MPa, respectively, and C_a ranged from 330 to 344 $\mu mol \cdot mol^{-1}$. For July 25, predawn and midday leaf water potentials were -0.2 ± 0.1 and -0.6 ± 0.1 MPa, and C_a ranged from 318 to 338 $\mu mol \cdot mol^{-1}$

CPI. 4-127-066; Trenton, New Jersey) which were controlled manually or through feedback control from a reference thermistor which monitored the ambient air temperature. The humidity within the cuvette was maintained at a level approximating the ambient air humidity, which was measured by means of a capacitance type chip (Vaisala Humicap, Weathermeasure; Sacramento, California). Leaf temperature was monitored with a thermistor (0.35 mm diameter) appressed to the abaxial leaf surface. Photon flux densities (400–700 nm) incident on the leaves were mea-

sured with a solar monitor (LiCor, model 1776; Lincoln, Nebraska) held parallel to the leaf surfaces. Normally, two leaves were sealed within the cuvette, which was repositioned at various times during the day so that the leaves were exposed to the maximum available sunlight. Leaf areas were measured with a LiCor model LI-3000 leaf area meter. Leaf water potentials were determined with thermocouple psychrometers (Wescor, Inc., model C-52; Logan, Utah).

Gas exchange calculations were conducted according to Field et al. (1982), except that intercellular CO_2 concentra-

tion (C_i) was determined as described by von Caemmerer and Farquhar (1981). Stomatal conductance was calculated as:

$$g_s = (g_t^{-1} - g_b^{-1})^{-1} \quad (1)$$

where g_s is stomatal conductance, g_t is total conductance, and g_b is the boundary layer conductance. Estimates of g_b were made by measuring the rate of evaporation from wetted filter paper leaf replicas placed within the cuvette. Boundary layer conductances were measured as 1.36 mol·m^{-2}·s^{-1} for the adaxial surface and 1.55 mol·m^{-2}·s^{-1} for the abaxial surface. In order to assess how these values compared to those under natural conditions, we estimated typical g_b values for wind speeds of 1 m·s^{-1} and 10 m·s^{-1} (Nobel 1984). For a 20 mm wide V. glauca leaf and a wind direction parallel to the leaf surface, approximate values for g_b would be 1.82 mol·m^{-2}·s^{-1} at a wind speed of 1 m·s^{-1} and 5.78 mol·m^{-2}·s^{-1} at a wind speed of 10 m·s^{-1}. Thus, the g_b values that were observed for leaves sealed within the cuvette are on the low end of the range of values which would occur under natural conditions.

Laboratory measurements. Potted *Y. glauca* plants, grown from seeds collected in Colorado or Montana, were obtained from a local nursery. The plants were watered frequently and kept outside on the University of Colorado campus. Plants were carried indoors for gas exchange measurements, which were made using the same equipment described above with the exception that gas lines consisted of stainless steel tubing for humidified gases and copper tubing for dry gases. The tubing leading from the cuvette to the infrared gas analyzer was maintained at approximately 45° C by the use of heating tape in order to prevent water condensation. Light was provided by a 1000 W metal halide lamp, which was placed over a heat filter consisting of a glass tank containing approximately 10 cm of continuously flowing water. The photon flux density (400–700 nm) at the leaf surface was 1800–2000 μmol quanta·m^{-2}·s^{-1}. Leaf areas were measured with a Delta T area meter (Cambridge, England).

C_a was maintained between 300 and 345 μmol·mol^{-1} for all experiments, although the range for C_a in each individual experiment was typically 20 μmol·mol^{-1} or less.

Results

Field studies

Typical daily patterns of net photosynthesis (*A*) and stomatal conductance (g_s) for *Y. glauca* during the late spring (June 11) and mid-summer (July 25) are shown in Fig. 1. A pronounced midday depression in both *A* and g_s was clearly evident for both measurement dates. On June 11, maximum values for *A* and g_s were observed in the morning between 0730 and 0900 h (MST). A steady decline in both *A* and g_s then occurred so that by early afternoon (1200–1430 h) *A* and g_s values had decreased to 40–50% and 25–35% of the morning maxima, respectively. After 1430 h, light became limiting for photosynthesis due to heavy cloud cover, which is a common occurence during this time of the year. Transpiration was maximal at about 1100 h, and also exhibited a midday decline. Intercellular CO_2 concentration (C_i) remained between 192 and
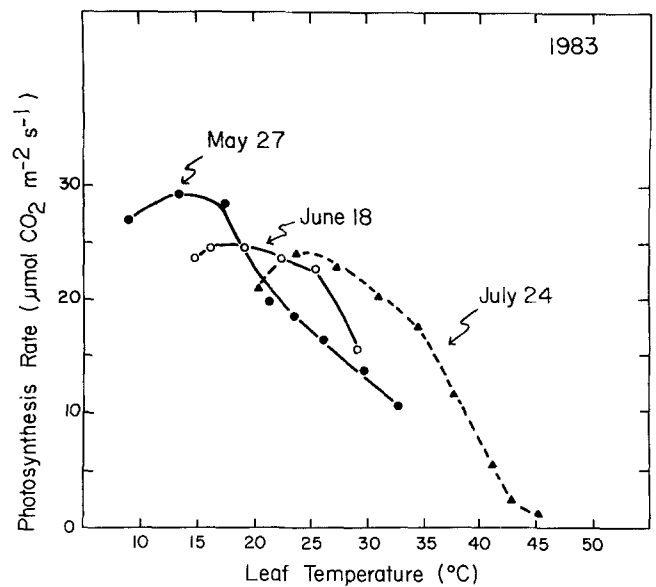
Fig. 2. Effects of leaf temperature on photosynthesis in field-grown *Y. glauca* at different times during the growing season. Δw increased slightly with increasing leaf temperature from 15 mmol H_2O·mol^{-1} at the cooler temperatures to 25 mmol H_2O·mol^{-1} air at the highest temperatures
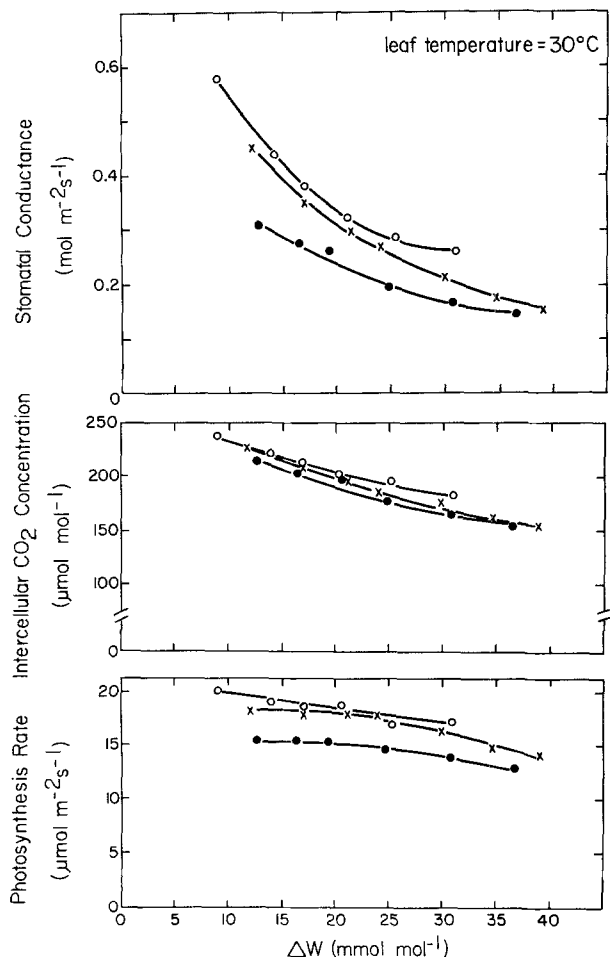
Fig. 3. Effects of Δw on stomatal conductance, net photosynthesis, and intercellular CO_2 concentration of field-grown *Y. glauca*. Leaf temperature was held constant at 30° C while the air humidity within the leaf cuvette was altered to achieve different values for Δw. Measurements were made in 1983 on June 16 ($\times$), June 18 ($\bullet$), and July 24 (o)
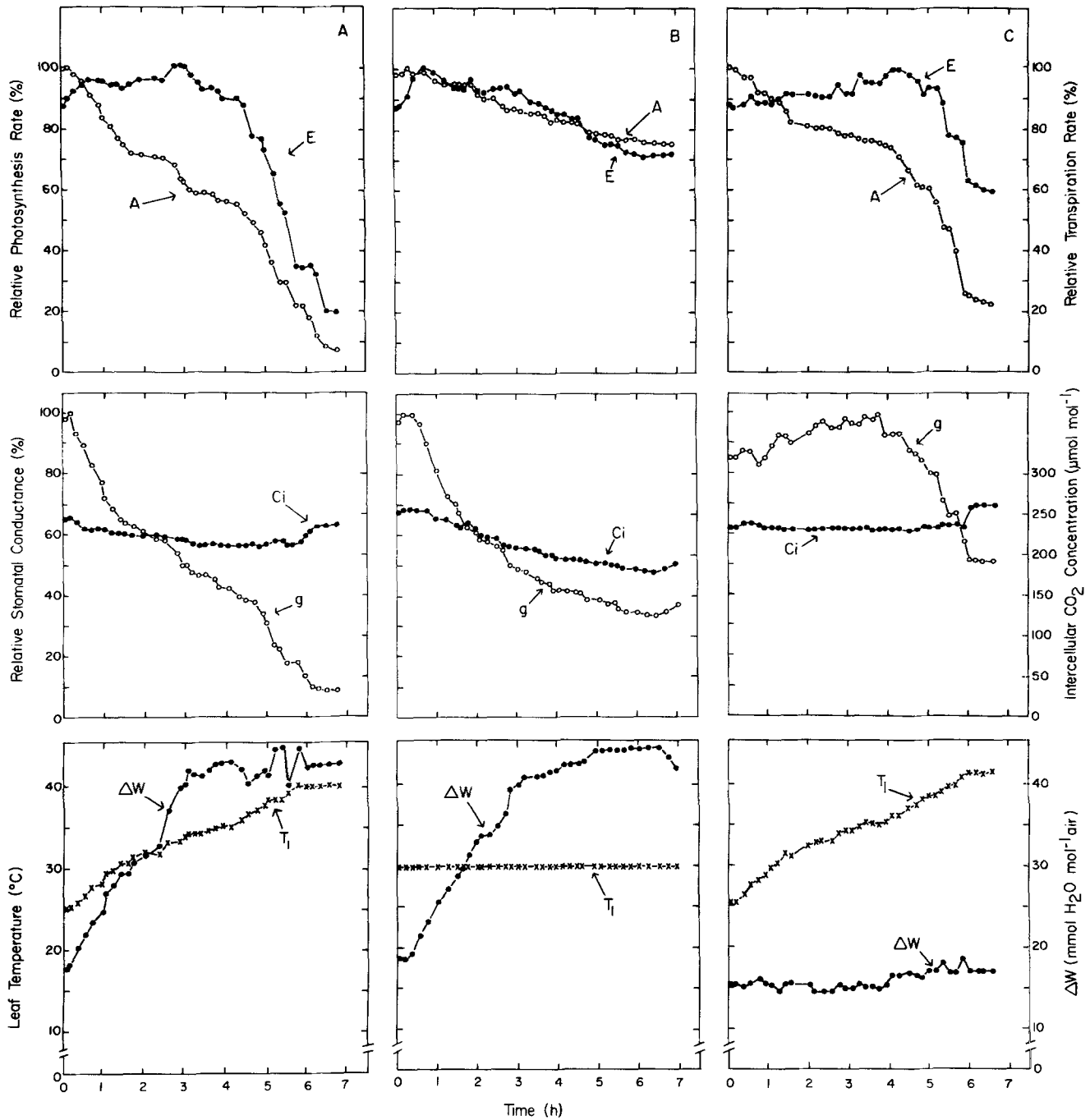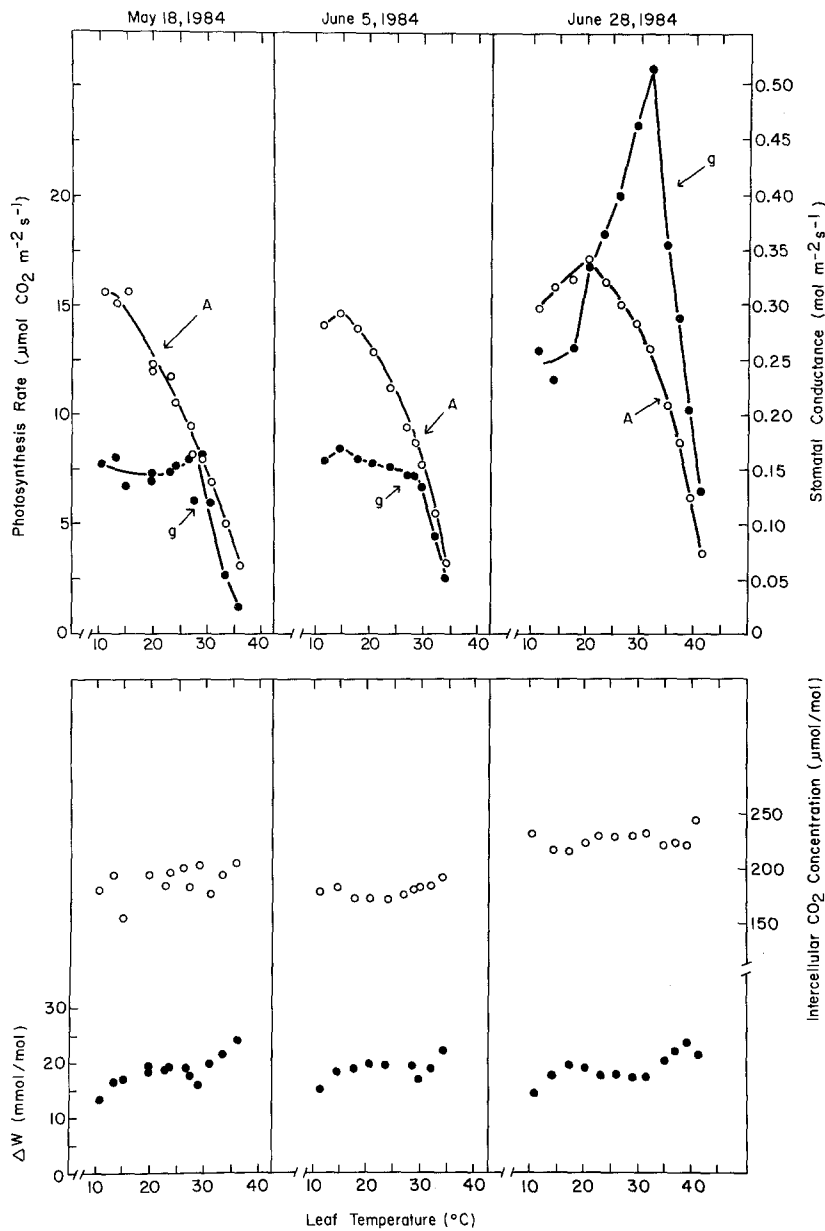
Fig. 4A–C. Effects of leaf temperature and Δw on photosynthesis and stomatal conductance of potted *Y. glauca* plants. **A** Control. Leaf temperature and Δw were increased in a manner which simulated mid-summer field conditions. **B** Leaf temperature was held constant at 30° C while Δw was increased in a pattern similar to that of the control experiment. **C** Δw was maintained relatively constant while leaf temperature was increased in a pattern similar to that of the control experiment. Presented patterns are representative of two replicates. Absolute maximum values for g_s (in $mol \cdot m^{-2} \cdot s^{-1}$), A (in $\mu moles \ CO_2 \cdot m^{-2} \cdot s^{-1}$), and E (in $mmol \ H_2O \cdot m^{-2} \cdot s^{-1}$), respectively, are as follows: **A** 0.388, 18.6, and 7.8; **B** 0.526, 20.8, and 11.1; **C** 0.298, 14.4, and 4.6

206 $\mu mol \cdot mol^{-1}$ until 1130 h, then decreased to a minimum value of 130 $\mu mol \cdot mol^{-1}$ at 1430 h. Leaf temperature and Δw increased throughout the day until respective maximum values of 36° C and 61.5 mmol $H_2O \cdot mol^{-1}$ air were reached at about 1430 h.

Midday depressions in A and g_s were even more pronounced on July 25. The maximum photosynthetic rate on this date was attained in the morning between 0830 and

1030 h. Stomatal conductance peaked at about 1000 h. After this time, A and g_s declined rapidly until minimum values were reached at 1500 h, at which time the rates were approximately 10% of the morning maxima. A partial recovery was observed in the afternoon, until limiting light intensity again caused a decline. Transpiration also exhibited a two-peaked daily pattern, with a minimum observed at about 1500 h. C_i remained between 161 and 206 $\mu mol \cdot$

Fig. 5. Effects of leaf temperature on photosynthesis and stomatal conductance of potted *Y. glauca* plants at several times during the growing season

mol^{-1} except for a sharp increase between 1330 and 1610 h to around 242 $\mu mol \cdot mol^{-1}$, which corresponded with the midday minima for A and g_s. Leaf temperature and Δw increased throughout the day until maxima were observed between 1400 and 1600 h. At this time, the leaf temperature reached approximately 38° C and Δw ranged between 50 and 60 mmol $H_2O \cdot mol^{-1}$ air. After 1600 h, both leaf temperature and Δw declined rapidly, although the values observed at sunset remained substantially greater than the early morning values.

When the photosynthetic rate of *Y. glauca* was determined as a function of leaf temperature at various times during the growing season, it became apparent that this species exhibits a marked capacity to acclimate to seasonal temperature changes. As shown in Fig. 2, the temperature optimum for photosynthesis on May 27 was approximately 14° C. On June 18 the optimum had increased to between 18 and 19° C, and by July 24 the optimum was 24° C. Thus, over the course of two months the temperature optimum increased by approximately 10° C.

The responses of g_s, A, and C_i to changes in Δw at constant leaf temperature for *Y. glauca* growing in the field are shown in Fig. 3. All three parameters declined as Δw increased both in mid-June and late July. There is significant leaf-to-leaf variability in the shape of the response curves, however, based on the substantially different curves recorded for June 16 and June 18. Therefore, it is not clear whether the slightly higher values for g_s at a given Δw on July 24 represents random variability or an actual acclimatization response to changing environmental conditions.

Laboratory studies

In order to evaluate the role of temperature and Δw in causing the midday depressions in photosynthesis and stomatal conductance which were observed in the field, we utilized potted *Y. glauca* plants and made measurements under controlled conditions in the laboratory. When leaf temperature and Δw were regulated in a manner which simulated mid-summer conditions, reductions in A, g_s, and
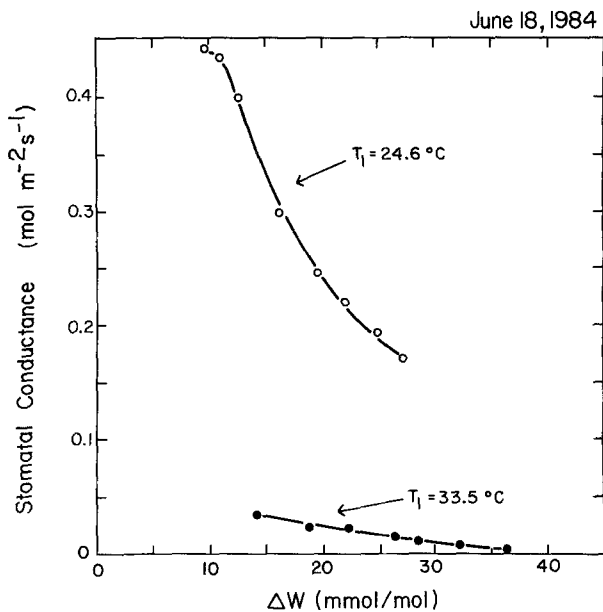
Fig. 6. Effects of Δw on stomatal conductance of potted *Y. glauca* plants above and below the temperature threshold which promotes stomatal closure

June 5, maximum photosynthesis occurred at 15° C while the threshold temperature at which substantial stomatal closure began was 29° C. About two weeks later (June 18) the photosynthetic temperature optimum had increased to 20° C, and a decrease in g_s was not observed until the leaf temperature reached 35° C. Laboratory and field measurements conducted in late July sometimes indicated that leaf temperatures as high as 40° C did not result in diminished g_s values.

As shown above, g_s in *Y. glauca* is strongly affected by Δw. Therefore, it was of interest to determine whether stomata still responded to Δw above the threshold temperature which also apparently causes stomatal closure. As shown in Fig. 6, when leaves of potted *Y. glauca* plants were maintained at 33.5° C (approximately 4.5° C above the threshold temperature for that date) an increase in Δw from 14 to 36 mmol $H_2O \cdot mol^{-1}$ air did in fact cause g_s to decrease. However, the rate of decrease was much less than when the same leaves were maintained at 24.6° C (which was below the threshold temperature) and subjected to a similar increase in Δw.

Discussion

Like many other plant species found in hot and arid areas, *Y. glauca* experiences a pronounced midday depression in net photosynthesis (A) and stomatal conductance (g_s) during the summer months. The midday depressions in A and g_s which were observed in field studies do not appear to be a result of water stress, since midday leaf water potentials were -2.0 and -0.6 MPa for June 11 and July 25, respectively. The decrease in A appears to be due primarily to a direct effect of high leaf temperature on the photosynthetic apparatus, rather than to an indirect effect mediated by the effects of large Δw values on stomatal conductance. This conclusion is based on several findings. First, the decrease in A was not accompanied by a decrease in C_i during the initial portion of the midday depression (Figs. 1 and 4A), indicating that the reduced photosynthetic rates were not a result of lowered CO_2 availability. Second, the midday reduction in A observed in field-grown plants occurred at approximately the same temperatures as those which caused decreased photosynthetic rates during temperature response measurements carried out at the same time of the year under conditions of relatively low Δw (Fig. 2). Third, laboratory studies with potted *Y. glauca* plants demonstrated a temperature-dependent decrease in A comparable to that observed with plants in situ, despite the fact that Δw was maintained at a constant level (Fig. 4C).

Increasing Δw appears to be the main factor responsible for the decrease in g_s which is observed during the midday depression. This conclusion is based on experiments with both field-grown and potted plants which indicated substantial stomatal closure as Δw was increased, despite a constant leaf temperature (Figs. 3 and 4B).

High leaf temperatures were also observed to promote stomatal closure (Figs. 4C, 5, and 6). However, the leaf temperature at which stomatal closure occurs is commonly attained in situ only after conductance has already decreased to a low level, due to the effects of a high Δw. Nonetheless, the very low conductance values observed at the minimum of the depression are probably due to the combined effects of high leaf temperature and Δw.

The decrease in g_s at high leaf temperatures may be

E were observed (Fig. 4A). C_i remained between 210 and 245 $\mu mol \cdot mol^{-1}$ during these measurements. Thus, potted plants responded similarly to plants in their natural environment.

We then attempted to separate the effects of temperature and Δw by keeping one of these variables constant while altering the other in a pattern similar to that of the control experiment shown in Fig. 4A. When Δw was maintained relatively constant (between 12.5 and 15.1 mmol $H_2O \cdot mol^{-1}$ air) and leaf temperature was increased from 25 to 41° C, the photosynthetic rate decreased to 25% of its maximum value (Fig. 4C). In preliminary experiments the large reduction in A without a concomitant reduction in g_s resulted in a substantial increase in C_i. In the experiment shown in Fig. 4C, a more accurate simulation of the conditions during the midday depression was obtained by manual manipulation of the external CO_2 concentration in order to maintain C_i at a constant level. In both cases an increase in leaf temperature resulted in a large decrease in A. Stomatal conductance was fairly constant below temperatures of 35° C, but above this temperature there was a rapid decline in g_s to a final value 52% of the maximum. When temperature was held constant at 30° C and Δw was increased from 18.5 to 44.6 mmol $H_2O \cdot mol^{-1}$ air, there was a large reduction in g_s (to 33% of the maximum) while A decreased only slightly to 77% of its maximum (Fig. 4B). The slight reduction in A is presumably due to a decrease in C_i from 256 to 180 $\mu mol \cdot mol^{-1}$. In this case we did not attempt to keep C_i constant.

The effects of leaf temperature on photosynthesis and stomatal conductance of potted plants at three different times during the spring and summer are shown in Fig. 5. In these experiments, Δw was maintained at a relatively constant level while the leaf temperature was increased. On May 18 the photosynthetic temperature optimum was between 10 and 15° C. Stomatal conductance was relatively constant until the leaf temperature reached 27 to 29° C; above this temperature conductance rapidly decreased. On

due in part to partially irreversible thermal damage to guard cells, based on the fact that the g_s values observed at low leaf temperatures could not be completely restored after the threshold temperature had been exceeded (data not shown). High temperature disruption of guard cells, leading to a decrease in stomatal aperture, has been observed in *Vicia faba* (Rogers et al. 1981). The apparent increase in threshold temperature observed as the season progresses (see Fig. 5) may represent an acclimation to increasing temperature due to changes in the biochemical and biophysical properties of the guard cells.

The reduction in g_s at high leaf temperatures might also be partly due to a reduced capacity for photosynthesis in mesophyll cells. Recent studies by Wong et al. (1979) and Farquhar and Wong (1984) suggest that under certain conditions g_s responds to the concentration of a photosynthetic metabolite in mesophyll cells. In *Y. glauca*, when Δw and C_i were maintained at relatively constant values, g_s and A did not respond to increased leaf temperature in a parallel manner. Stomatal conductance began to decrease at temperatures approximately 15° C above those which inhibited photosynthesis. It is possible that in this species the postulated response of g_s to changes in A does not occur until some threshold concentration of a photosynthetic metabolite is exceeded at relatively high temperatures. In some cases, however, we did not observe stomatal closure at leaf temperatures as high as 40° C even though A was substantially reduced, suggesting that interactions between g_s, leaf temperature, and the photosynthetic capacity of mesophyll cells are quite complex.

The transpiration rate (E) during the midday depression is a function of both Δw and g_s. With Δw values of ~ 45 mmol $H_2O \cdot mol^{-1}$ air (such as those used in the laboratory simulations, Fig. 4) E was reduced by more than 30% only after g_s decreased below 0.15 mol$\cdot$m$^{-2}\cdot$s^{-1}. In the laboratory simulations, reductions in g_s of this magnitude were only observed when leaf temperatures were increased above the high temperature threshold for stomatal closure (see Fig. 4A). When Δw was increased without a concomitant increase in leaf temperature, g_s was substantially reduced but E decreased only slightly (see Fig. 4B). Likewise, in the field studies we did not observe a significant reduction in E unless concomitant increases in Δw and leaf temperature caused g_s values to decrease below 0.15 mol$\cdot$m$^{-2}\cdot$s^{-1} (Fig. 1). Thus, in *Y. glauca* midday depressions in E appear to be a function of both leaf temperature and g_s.

The photosynthetic system of *Y. glauca* acclimates quite strongly to increasing temperature during the season, as indicated by the increase in the temperature optimum for A both for potted plants kept outside (Fig. 5) and for plants growing under natural conditions (Fig. 2). Similar acclimation potentials have been observed for *Yucca brevifolia* from the Mojave Desert (Smith et al. 1983). According to these results, the temperature at which the midday depression in A occurs would become increasingly higher as the growing season progresses. In support of this, field studies indicated that leaf temperatures which caused a midday depression in A were, in fact, lower in late spring than in midsummer (compare Fig. 1A and B).

Preliminary results indicate that the photosynthetic temperature optimum occurs at leaf temperatures which are commonly observed in situ in the morning (between 0800 and 0900 h) while the high leaf temperatures that initiate

stomatal closure occur in the afternoon (1200 to 1430 h). In fact, the acclimatory increases in photosynthetic temperature optimum and temperature threshold for stomatal closure which occurs as the season progresses parallel the seasonal increases in morning and afternoon leaf temperatures, respectively. This close coupling of physiological processes to naturally-occurring leaf temperatures may play a major role in maximizing seasonal carbon gain with respect to water loss. The correlation between the photosynthetic temperature optimum and morning leaf temperatures fits well with the natural orientation of *Y. glauca* leaves (approximately 45° to 90° from the ground surface), which provides maximal insolation during the morning and late afternoon when temperature and Δw are at low values. Therefore, the morphology of *Y. glauca* is also optimized for maximal carbon gain at times when stomata can remain open without excessive water loss..

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