Leaf movement, stress avoidance and photosynthesis in *Vitis californica*

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Summary. Gas exchange and chlorophyll fluorescence techniques were used to evaluate the hypothesis that leaf movement in *Vitis californica* Benth. (California wild grape) allows a compromise between sunlight interception and stress damage in order to maximize photosynthetic carbon gain over the life of the leaf. Leaves that were restrained horizontally tolerated their increased radiation loads if critical temperatures were not exceeded. Reductions in photosynthetic capacity and the F_V/F_M fluorescence ratio only occurred in leaves that attained high temperatures. Leaf orientation and canopy position were important determinants of leaf temperature. These results indicate that excessive leaf temperature, not high PFD, can be a principle cause of reduced carbon gain and senescence in this species in the wild. Leaf movement appears to protect photosynthetic components in midsummer.

Key words: Heat stress – Leaf movement – Photoinhibition – Photosynthesis – *Vitis californica*

Leaf movement affects physiological performance due to the influence of orientation on leaf energy balance. Various reports have illustrated that diaheliotropism can serve to maximize carbon gain by increasing incident PFD and leaf temperature; on the other hand, paraheliotropism can minimize incident radiation, resulting in more favorable leaf temperatures and water status during drought (Ehleringer and Forseth 1980; Mooney and Ehleringer 1978; Forseth and Ehleringer 1982). Other have hypothesized that paraheliotropism might serve to avoid damage by high irradiance ("photoinhibition") in leaves under drought (Ludlow and Björkman 1984).

Field observations indicated that sun leaves of *Vitis californica* Benth. exhibit an increasing tendency to turn parallel to incoming midday solar radiation as hot, dry summer conditions develop. In order to examine the role of these leaf movements in photosynthetic performance, we posed the hypothesis that leaf movement allows a compromise between light interception and stress damage so as to maximize carbon gain over the life of the leaf. This hypothesis predicted that an altered leaf orientation would result in less carbon gain over the growing season. Because leaf movements of *V. californica* tend to minimize incident PFD

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at midday in midsummer, our experiments primarily focused on the effects of an increase in radiation load on photosynthetic processes by restraining leaves horizontally.

Altering a leaf's radiation load can affect incident PFD, leaf temperature and water status. It is well known that water stress and high temperatures can limit photosynthesis (Berry and Björkman 1980; Berry and Downton 1982; Berry and Raison 1981; Boyer 1976), however the role of excessive PFD in inhibiting photosynthetic processes ("photoinhibition") is less clear, especially under field conditions. Photoinhibition has been widely studied in the lab (Kyle et al. 1987; Powles 1984) but few studies have determined if photoinhibition actually limits carbon gain in natural habitats. Field studies of photoinhibition have been reported for CAM plants (Adams 1988; Adams et al. 1987b), mangroves (Björkman et al. 1988) and phytoplankton (Belay 1981; Elser and Kimmel 1985; Vincent et al. 1984). The studies with terrestrial plants have found declines in fluorescence yield, F_V/F_M and oxygen evolution with exposure to high irradiance, but have not examined the effects on net CO_2 assimilation under field conditions. In addition, most of these studies have not separated the possible effects of PFD from temperature and water status.

The primary objective of this study was to ascertain the role of leaf movements of *V. californica* in its natural habitat in avoiding damage associated with high radiation loads. By examining leaves of different orientations, canopy positions and seasons we were able to distinguish between effects of PFD, temperature and water status on photosynthetic performance.

Materials and methods

The study species, *V. californica*, is a woody, deciduous vine native to riparian areas of northern California and southern Oregon (Munz and Keck 1959). Unless otherwise noted, all measurements were made near Davis, CA on a south-facing bank of a perennial stream in the Putah Creek Reserve, managed by the University of California Natural Reserve System. The study plant appeared to be a single, female clone covering an area of 35 by 25 m, and extending from ground level to a height of 10 m in adjacent tree canopies. Measurements were confined to leaves between ground level and 2 m high that were exposed to full sun at midday. Some additional measurements were made on a second female clone growing in Cold Canyon Reserve of the University of California Natural Reserve System, approximately 32 km west of Davis, CA.

PFD was determined with horizontally-mounted, gallium-arsenide sensors (Hamamatsu Corp., San Jose CA) calibrated against a standard quantum sensor (LI-COR, Inc., Lincoln, NE). Leaf azimuths and angles were determined with a compass and a clinometer, respectively. The angles and azimuths were then used with the measured PFD on a horizontal plane to estimate the incident PFD on individual leaf surfaces (Gates 1980).

Leaf temperature measurements were made with home-made fine-wire copper-constantan thermocouples (0.076 mm diameter) or with an infrared thermometer (model 210, Everest Interscience, Tustin, CA). Thermocouple measurements were made by attaching two junctions to each abaxial leaf surface with surgical tape and then averaging the two readings. Infrared thermometer measurements of leaf temperatures were made on adaxial surfaces and were corrected for instrument drift by frequent calibration against a blackbody target (Telatemp Corporation, Fullerton, CA). The maximum leaf temperatures measured with the thermocouples were, on average, 2–3° C higher than those measured with the infrared thermometer.

Air temperature gradients with height were measured with shielded fine-wire thermocouples. Seasonal maximum daily air temperatures at two meters height were obtained from a weather station located 2 km from the study site and monitored by the University of California Department of Land, Air and Water Resources.

Leaves were reoriented to horizontal by supporting them with 20 gauge copper wire loops.

Most measurements of net CO_2 uptake were made with either a LI-6000 (1986) or a LI-6200 (1988) portable photosynthesis system (LI-COR, Inc., Lincoln, NE), modified with a 0.6-l chamber designed to contain an entire leaf. Steady-state gas exchange measurements were made with a portable gas exchange system described by Pearcy (1987), with the following modifications. Measurements of CO_2 concentrations were made with a Binos 1 infrared analyzer (Leybold-Heraus, Hanau, Fed. Rep. Germany). Air of the desired CO_2 pressure was obtained by passing compressed air through an ascarite column to give CO_2-free air. This was then mixed using mass flow controllers (Tylan Corpor-

ation, Carson, CA) with air containing 0.4% CO_2 to give the desired CO_2 pressure in the leaf chamber. Air humidity was controlled by passing humidified air through a Peltier-cooled condenser made from a copper block (Field et al. 1989). Steady-state net CO_2 uptake, conductance and intercellular CO_2 pressure were calculated using the equations of Caemmerer and Farquhar (1981).

Chlorophyll fluorescence at 77K and 690 nm was measured on adaxial leaf disk surfaces with a fluorometer based on the designs of Powles and Björkman (1982) and Björkman and Demmig (1987). 9-mm diameter disks were placed in the fluorometer, given a 3–5 minute dark period at ambient temperature to ensure reoxidation of Q_A (Krause and Weis 1984) and reverse high-energy (delta pH) fluorescence quenching (Krause et al. 1983), and then frozen by addition of liquid nitrogen. The initial fluorescence (F_0) was determined as the essentially instantaneous signal obtained by exposing the frozen, dark-adapted leaf disks to 0.2–0.4 μmol photons m^{-2} s^{-1} at 470 nm. The maximum fluorescence (F_M) was measured by first giving a 1-minute exposure to 2 μmol photons m^{-2} s^{-1}, fully reducing Q_A, and then returning the excitation light to 0.2–0.4 μmol photons m^{-2} s^{-1}. The variable fluorescence (F_V) was the difference between F_0 and F_M.

Fluorescence measurements were made on samples collected shortly before dawn, when maximum recovery from any short-term irradiance effects would have occurred. Samples were collected before sunrise, placed in dark containers on ice, and measured 1/4 to 4 h later. Preliminary studies indicated that leaf disks collected before dawn could be stored this way and assayed up to four hours later with little change in fluorescence characteristics.

Fluorescence data is expressed as F_V/F_M for two reasons. 1) This ratio of two absolute fluorescence values tends to normalize differences due to absorptance, chlorophyll concentration and drift in instrument electronics. 2) There have been several reports that the F_V/F_M ratio is linearly related to the CO_2-saturated photon yield of oxygen evolution (Björkman and Demmig 1987; Demmig and Björkman 1987; Adams et al. 1987a). Others have found a curvilinear relationship (Gamon and Pearcy, in preparation; Greer
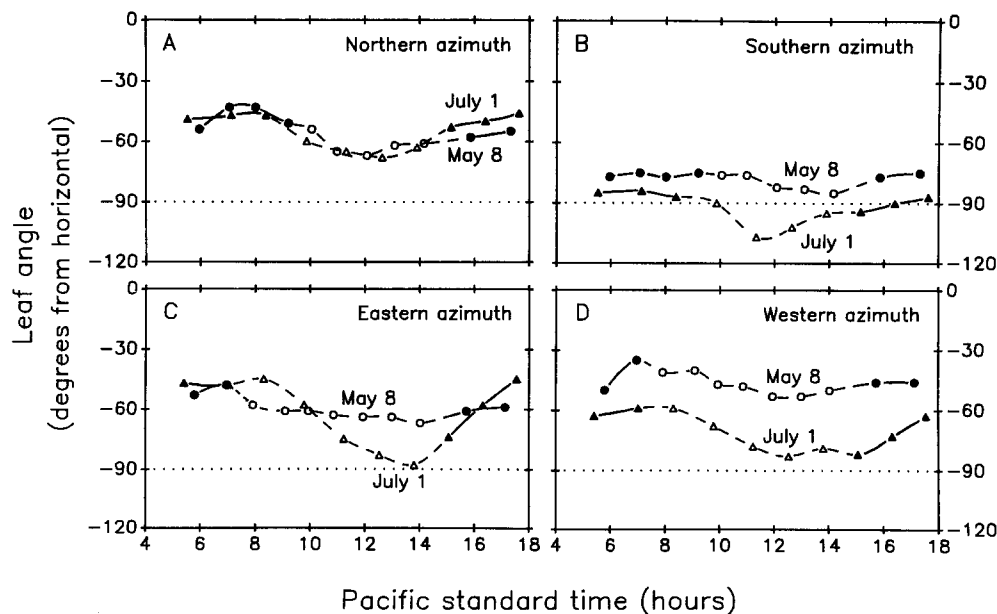

Fig. 1A–D. Diurnal changes in leaf angle for four leaves on May 8 (*circles*) and July 1 (*triangles*), 1986. *Filled symbols* and *solid lines* (▲, ●, ——) indicate periods of shade; *open symbols* and *dashed lines* (△, ○, ———) indicate periods of direct sunlight

Pacific standard time (hours)

et al. 1988). Regardless of the shape of this relationship, F_V/F_M is an estimate of photosystem II photochemical efficiency (Björkman 1987b) and thus is a useful assay for light- or heat-induced damage to the reaction center.

Results

V. californica leaves in full sun exhibited seasonal and diurnal leaf movements, primarily involving changes in leaf angle (Fig. 1), with little change in azimuth (not shown). These movements tended to reduce incident PFD at midday in midsummer (Fig. 2a) when midday water potentials were low and maximum daily air temperatures were high (Fig. 2b).

The peak daily CO_2 uptake rates of unrestrained leaves reached a maximum early in the season, and then declined gradually during the summer (Fig. 2c). In contrast, the pre-dawn F_V/F_M values of these leaves changed little during this period (Fig. 2c), indicating that photosystem II photo-

chemical efficiency was maintained when leaves were free to move.

There was no evidence for an adverse effect of the increase in PFD following reorientation on net photosynthesis. In May, 1986, when daily maximum air temperatures had not exceeded 35° C (see Fig. 2b), most horizontal leaves had peak daily photosynthetic rates that were equal to or higher than those of unrestrained controls (Fig. 3a). There was a slight decline in predawn F_V/F_M with increased PFD (Fig. 3b). The lack of any large decline in photosynthetic rates or F_V/F_M following horizontal reorientation indicated that these leaves were able to tolerate higher light levels than normally encountered by unrestrained leaves.

In contrast, leaves that were reoriented horizontally in mid-July exhibited an abrupt decline and subsequent partial recovery in both peak daily net CO_2 uptake and predawn F_V/F_M (Fig. 4). At the same time, there was a decline and recovery in both the photon yield region and the light saturated region of the light-response curves of assimilation (Fig. 5). Apparent photon yields calculated from the initial slopes of these curves were 0.032, 0.019 and 0.024 mol CO_2 mol photon^{-1}, respectively. Similarly, net CO_2 uptake plotted as a function of intercellular CO_2 pressure exhibited a decline and recovery at all CO_2 concentrations (Fig. 6). These results suggested a concerted loss of function of many photosynthetic components and an ability of these components to partially recover over several weeks.

PFD on a horizontal plane was essentially equal in May and July, 1986 (Fig. 2a) and thus could not account for the greater inhibition of photosynthetic processes by horizontal reorientation in midsummer as compared to spring. However, it seemed possible that seasonal differences in leaf age, water status or leaf temperature could account for the seasonal differences in photosynthetic performance. Because our 1986 data did not distinguish between the possible effects of these factors, we examined their effects on net CO_2 uptake and fluorescence in more detail in 1988.
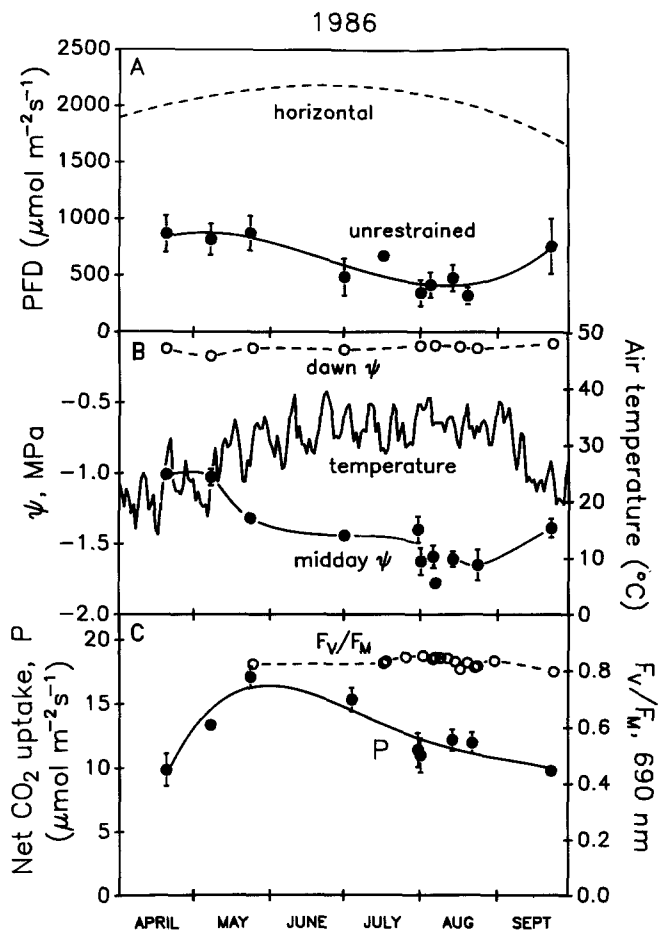

Fig. 2. A Seasonal trends in noontime PFD for adaxial surfaces of unrestrained (●——●) and horizontal (————) leaves. Each point represents a mean ± 1 SEM for 8–21 leaves. **B** Seasonal trends in midday (●——●) and dawn (o———o) water potential and maximum daily air temperature at 2 meters height (——). Each point represents a mean ± 1 SEM for 3–10 leaves (midday) or 3–5 leaves (dawn). Each midday value represents the lowest observed water potential for that particular day (usually between 12:00 and 14:00 Pacific Standard Time). **C** Seasonal trends in the maximum daily net CO_2 uptake (●——●) and pre-dawn F_V/F_M (o——o) for unrestrained leaves. Points represent means ± 1 SEM for 6–14 leaves (net CO_2 uptake) or 3–11 leaves (F_V/F_M)
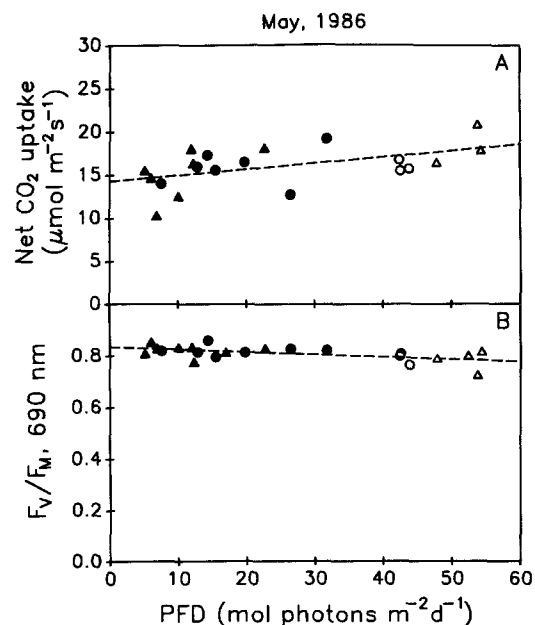

Fig. 3. Daily maximum net CO_2 uptake (A) and pre-dawn F_V/F_M (B) as a function of total daily incident PFD for horizontal leaves (*open symbols*) and unrestrained leaves (*closed symbols*) at Putah Creek Reserve (o, ●) and Cold Canyon Reserve (△, ▲)
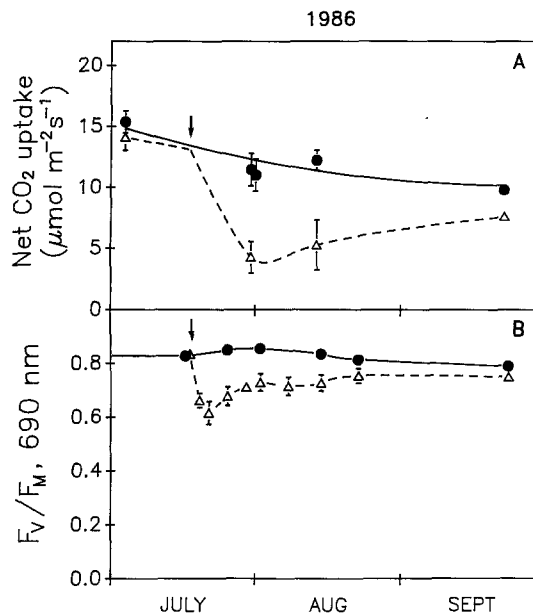
1986

Fig. 4A, B. Trends in daily peak net CO_2 uptake (A) and pre-dawn F_V/F_M (B) for unrestrained, control leaves (●——●) and leaves restrained horizontally (△——△) on July 17, 1986 (arrows). Points represent means ± 1 SEM for 6–14 leaves (A) or 3–13 leaves (B)
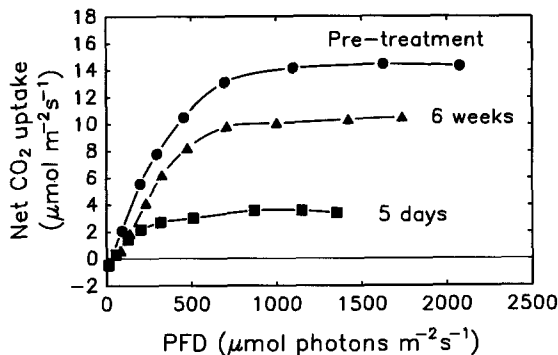
July 28, 1988

Fig. 7. Daily maximum temperature, measured with fine-wire thermocouples, as a function of height above the ground for air (■), unrestrained leaves (●) and horizontal leaves (○) on July 28, 1988

Fig. 5. Steady-state response of net CO_2 uptake to PFD on a representative leaf before horizontal restraint begun on July 17, 1986 (●), after 5 days of restraint (■) and after six weeks of restraint (▲)
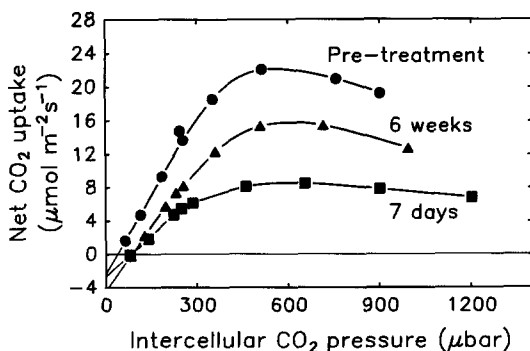

Fig. 6. Steady-state response of net CO_2 uptake to intercellular CO_2 pressure of a representative leaf before horizontal restraint on July 17, 1986 (●), after seven days of restraint (■) and after six weeks of restraint (▲)
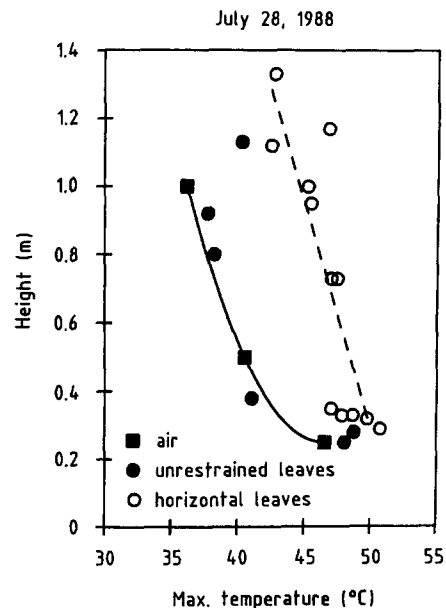
The measurements in 1988 examined the consequences of natural variations in temperature as a function of both orientation and height above the ground (Fig. 7). Maximum daily temperatures of unrestrained leaves were usually closely coupled to air temperature, which decreased markedly with height. In contrast, horizontal leaves typically reached maximum temperatures that were several degrees higher than unrestrained leaves of similar height.

In the spring of 1988 a cohort of leaves of similar sun exposure was divided according to height above the ground (<0.4 meters or >0.7 m) and orientation (restrained horizontally or unrestrained). Seasonal trends in peak daily leaf and air temperatures, midday water potential and net CO_2 uptake for these leaves are illustrated in Fig. 8. These four groups of leaves had essentially equivalent photosynthetic rates at the start of the study in May. In late spring, horizontal leaves developed the highest photosynthetic rates, provided they were high in the canopy where temperatures were low. This supported the earlier conclusion that high PFD *per se* had no adverse impact on net CO_2 uptake. Similarly aged horizontal leaves near the ground consistently reached the highest temperatures and had the lowest photosynthetic rates, and all leaves in this group were dead by August. With the onset of hot, summer conditions in late June, photosynthetic rates in all leaves became inversely correlated with daily peak leaf temperatures regardless of orientation. Differences in water status were probably not responsible for the different photosynthetic rates observed; the lower leaves had slightly higher average midday water potentials than the higher leaves (Fig. 8a). There were no differences in midday water potentials between horizontal and vertical leaves (data not shown). These results indicated that leaf temperature, not incident PFD, water status or leaf age, was the overriding determinant of photosynthetic performance.
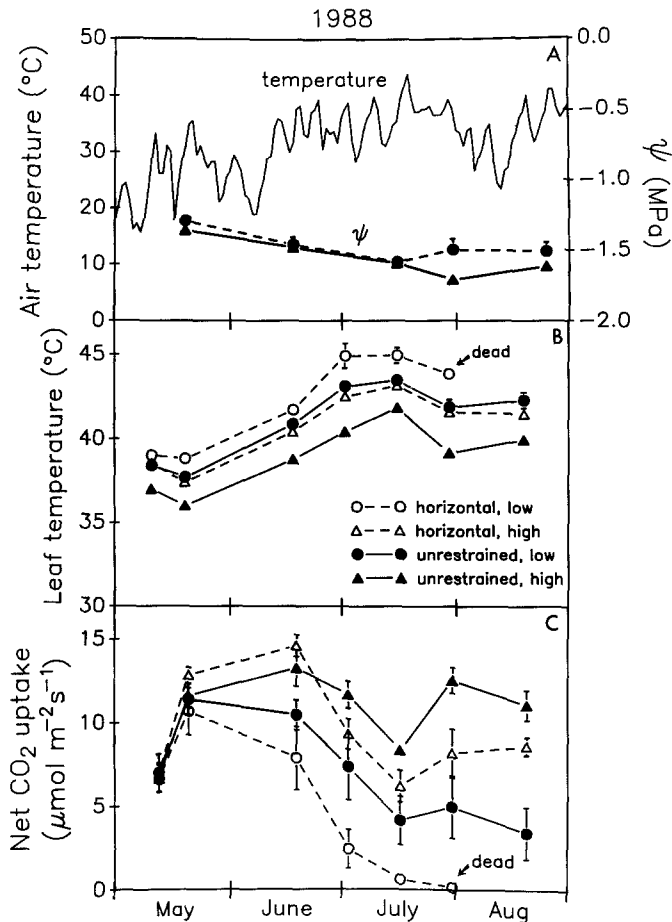
Fig. 9. Peak daily net CO_2 uptake (measured between 9:00 and 11:00 PST on July 29 or July 31, 1988) as a function of maximum leaf temperature (measured with fine-wire thermocouples on July 28, 1988) for horizontal leaves (*open symbols*) or unrestrained leaves (*closed symbols*) above 0.7 m ($\triangle$, $\blacktriangle$) or below 0.4 m (o, ●) above the ground

Fig. 8. A Seasonal trends in daily maximum air temperature at 2 m height (——) and midday water potentials for unrestrained leaves above 0.7 m ($\blacktriangle$——$\blacktriangle$) or below 0.4 m (●——●) above the ground in 1988. Each symbol represents a mean $\pm$ 1 SEM for 3–4 leaves, measured between 12:00 and 13:00 Pacific Standard Time. **B** Seasonal trends in maximum daily leaf temperature, measured with an infrared thermometer between 13:00 and 14:30 Pacific Standard Time, for horizontal (*open symbols*) or unrestrained leaves (*closed symbols*), above 0.7 m ($\triangle$, $\blacktriangle$) or below 0.4 m (o, ●) above the ground. Each symbol represents a mean $\pm$ 1 SEM for 12–14 leaves in May, diminishing to a minimum of 3 leaves in July (horizontal leaves close to the ground) due to senescence. **C** Seasonal trends in the maximum daily net CO_2 uptake for a subset of the same leaves illustrated in Fig. 8 B. Symbols as in Fig. 8 B, except each point is a mean $\pm$ 1 SEM for 6 leaves

Fig. 10 A, B. Peak daily net CO_2 uptake (**A**) and pre-dawn F_V/F_M (**B**) for horizontal leaves (*open symbols*) or unrestrained leaves (*closed symbols*) above 0.7 m ($\triangle$, $\blacktriangle$) or below 0.4 m (o, ●) above the ground in July, 1988

The strong correlation of maximum daily leaf temperature with maximum daily photosynthetic rate is further illustrated in Fig. 9. The relationship was the same for all leaves regardless of their orientation or height above the ground. In contrast, when peak photosynthetic rates in July were plotted as a function of daily incident PFD on a subset of the same leaves, a single correlation was not observed. Rather, points fell on one of two relationships according to leaf position in the canopy (Fig. 10a).

Fluorescence measurements in July, 1988, indicated that the substantial decline in F_V/F_M previously observed in midsummer of 1986 upon increased irradiance following horizontal reorientation (Fig. 4b) had partly been due to high leaf temperatures. Results in 1988 indicated almost no decline in F_V/F_M with increasing PFD in leaves high in the canopy where temperatures were cooler (dashed line,
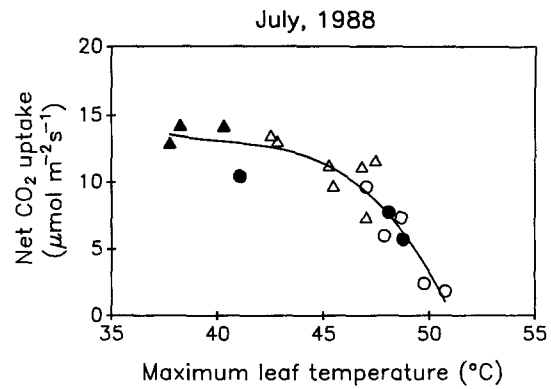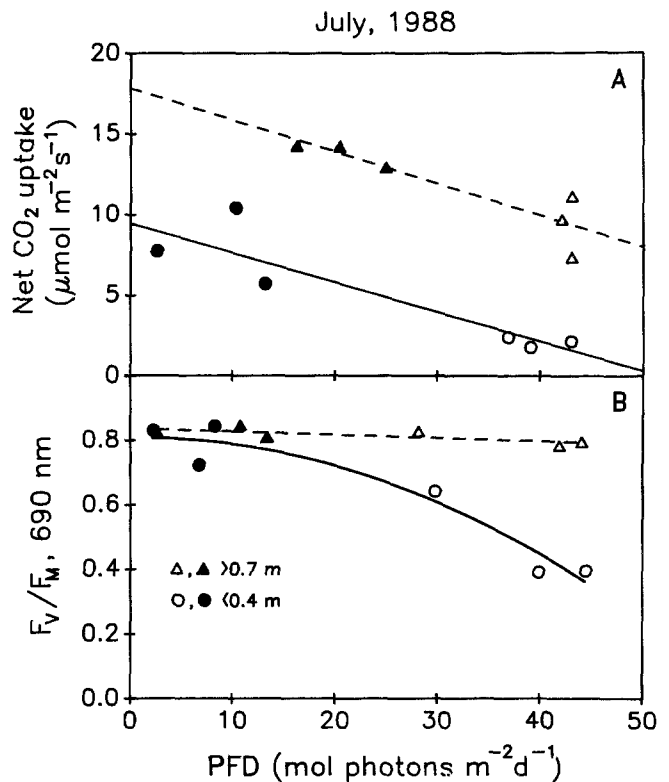
Fig. 10b); however, the hotter leaves close to the ground showed a substantial decline in F_V/F_M with increasing PFD (solid line, Fig. 10b).

Discussion

By attenuating radiation loads at midday in midsummer, *V. californica* leaf movements maintained photosynthetic function and avoided premature senescence. This appeared to be particularly important for sun leaves near the ground,

where temperatures reached high values in midsummer. In leaves restrained horizontally, photosynthetic rates were lower over most of the growing season as compared to unrestrained leaves of similar canopy position. In freely moving leaves, incident PFD levels at midday in midsummer (Fig. 2a) were near or slightly below light-saturating levels. Thus any further reduction in PFD would have probably lowered net CO_2 uptake. These observations appear to support the hypothesis that leaf movements allow a compromise between light interception and stress avoidance so as to maximize carbon gain over the life of the leaf.

The main cause of reduced photosynthesis in horizontal leaves appeared to be high temperatures rather than high PFD or low water potentials. In contrast, when F_V/F_M was plotted against PFD (Figs. 3 and 10), the resulting slopes varied with temperature, indicating that the declines in F_V/F_M in this species involved interactive effects of high temperatures with high PFD. Similar interactive effects of light and temperature have been reported for other species (Ludlow 1987; Ludlow and Björkman 1984), and may be due to differences in the temperature sensitivities of damage and repair processes (Greer et al. 1986; Ludlow 1987). To our knowledge, this is the first documentation of such effects in a wild plant. More work needs to be done to further elucidate the possible impact of interactive light and temperature effects on the overall physiology, survival and productivity of wild species, especially those lacking light-avoiding leaf movements.

Our results differ from those of Adams et al. (1987b) who concluded that Opuntia basilaris cladodes exposed to full sun exhibit "chronic" photoinhibition. There is also evidence for severe declines in F_V/F_M and photon yield in a variety of other CAM (Adams 1988) and mangrove (Björkman et al. 1988) species. Because high PFD and high temperature often co-occur in the field, it is possible that the inhibition of photosynthetic processes attributed to high PFD in these species was, in part, due to high temperature during high irradiance. In V. californica, leaf movements ensured that damage by high light and temperature did not occur. Similar observations have been made with potted Macroptilium atropurpureum cv. Siratro exhibiting paraheliotropic movements (Ludlow and Björkman 1984).

Although the lack of photoinhibition in unrestrained V. californica leaves is largely attributable to their movements, other protective mechanisms such as non-radiative dissipation (Björkman 1987a; Demmig et al. 1987) may have been operating. The predawn fluorescence measurements and peak daily photosynthetic rates reported in this study reflect maximal daily values of photochemical efficiency and photosynthetic capacity, respectively. The reductions in these values seen in horizontally restrained leaves exposed to high temperatures imply severe, long-term damage to one or more of the partial processes of photosynthesis. Diurnal changes in leaf gas exchange and chlorophyll fluorescence in V. californica, reflecting readily reversible processes, are described in a separate study (Gamon and Pearcy, in preparation).

References

Adams WW III (1988) Photosynthetic acclimation and photoinhibition of terrestrial and epiphytic CAM tissues growing in full sunlight and deep shade. In: Evans JR, Caemmerer S von, Adams WW III (eds) Ecology of Photosynthesis in Sun and Shade. CSIRO Australia, pp 123–134

Adams WW III, Osmond CB, Sharkey TD (1987a) Responses of two CAM species to different irradiances during growth and susceptibility to photoinhibition by high light. Plant Physiol 83:213–218

Adams WW III, Smith SD, Osmond CB (1987b) Photoinhibition of the CAM succulent Opuntia basilaris growing in Death Valley: evidence from 77K fluorescence and quantum yield. Oecologia 71:221–228

Belay A (1981) An experimental investigation of inhibition of phytoplankton photosynthesis at lake surfaces. New Phytol 89:61–74

Berry J, Björkman O (1980) Photosynthetic response and adaptation to temperature in higher plants. Annu Rev Plant Physiol 31:491–543

Berry JA, Downton WJS (1982) Environmental regulation of photosynthesis. In: Govindjee (ed) Photosynthesis Vol II. Development, Carbon Metabolism, and Plant Productivity. Academic Press, New York, pp 263–343

Berry JA, Raison JK (1981) Responses of macrophytes to temperature. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds) Physiological Plant Ecology I. Responses to the Physical Environment. Encycl Plant Physiol, New Ser, vol 12A. Springer, Berlin Heidelberg New York, pp 277–338

Björkman O (1987a) High-irradiance stress in higher plants and interactions with other stress factors. In: Biggins J (ed) Progress in Photosynthesis Research, Vol IV. Martinus Nijhoff, Dordrecht, pp 11–18

Björkman O (1987b) Low-temperature chlorophyll fluorescence in leaves and its relationship to photon yield of photosynthesis in photoinhibition. In: Kyle DJ, Osmond CB, Arntzen CJ (eds) Photoinhibition. Elsevier, Amsterdam New York Oxford, pp 123–144

Björkman O, Demmig B (1987) Photon yield of O_2 evolution and chlorophyll fluorescence characteristics at 77K among vascular plants of diverse origins. Planta 170:489–504

Björkman O, Demmig B, Andrews TJ (1988) Mangrove photosynthesis: response to high-irradiance stress. In: Evans JR, Caemmerer S von, Adams WW III (eds) Ecology of Photosynthesis in Sun and Shade. CSIRO Australia, pp 43–61

Boyer JS (1976) Water deficits and photosynthesis. In: Kozlowski TT (ed) Water Deficits and Plant Growth, vol 4. Academic Press, New York, pp 153–190

Caemmerer S von, Farquhar GD (1981) Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. Planta 153:376–387

Demmig B, Björkman O (1987) Comparison of the effect of excessive light on chlorophyll fluorescence (77K) and photon yield of O_2 evolution in leaves of higher plants. Planta 171:171–184

Demmig B, Winter K, Krüger A, Czygan F-C (1987) Photoinhibition and zeaxanthin formation in intact leaves. A possible role of the xanthophyll cycle in the dissipation of excess light energy. Plant Physiol 84:218–224

Ehleringer J, Forseth I (1980) Solar tracking by plants. Science 210:1094–1098

Elser JJ, Kimmel BL (1985) Photoinhibition of temperate lake phytoplankton by near-surface irradiance: evidence from vertical profiles and field experiments. J Phycol 21:419–427

Field CB, Ball JT, Berry JA (1989) Photosynthesis: principles and field techniques. In: Pearcy RW, Ehleringer JR, Mooney HA, Rundel PW (eds) Physiological Plant Ecology: Field Methods and Instrumentation. Chapman and Hall, London (in press)

Forseth IN, Ehleringer JR (1982) Ecophysiology of two solar tracking desert winter annuals. II. Leaf movements, water relations and microclimate. Oecologia 54:41–49

Gates DM (1980) Biophysical ecology. Springer, Berlin Heidelberg New York

Greer DH, Berry JA, Björkman O (1986) Photoinhibition of photosynthesis in intact bean leaves: role of light and temperature, and requirement for chloroplast-protein synthesis during recovery. Planta 168:253–260

Greer DH, Laing WA, Kipnis T (1988) Photoinhibition of photosynthesis in intact kiwifruit (*Actinidia deliciosa*) leaves: effect of temperature. Planta 174:152–158

Krause GH, Weis E (1984) Chlorophyll fluorescence as a tool in plant physiology. II. Interpretation of fluorescence signals. Photosynthesis Res 5:139–157

Krause GH, Briantais J-M, Vernotte C (1983) Characterization of chlorophyll fluorescence quenching in chloroplasts by fluorescence spectroscopy at 77K I. Δ pH-dependent quenching. Biochim Biophys Acta 723:169–175

Kyle DJ, Osmond CB, Arntzen CJ (eds) (1987) Photoinhibition. Elsevier, Amsterdam New York Oxford

Ludlow MM (1987) Light stress at high temperature. In: Kyle DJ, Osmond CB, Arntzen CJ (eds) Photoinhibition. Elsevier, Amsterdam New York Oxford, pp 89–109

Ludlow MM, Björkman O (1984) Paraheliotropic leaf movement in Siratro as a protective mechanism against drought-induced damage to primary photosynthetic reactions: damage by excessive light and heat. Planta 161:505–518

Mooney HA, Ehleringer JR (1978) The carbon gain benefits of solar tracking in a desert annual. Plant Cell Environ 1:307–311

Munz PA, Keck DD (1959) A California Flora. University of California Press, Berkeley

Pearcy RW (1987) Photosynthetic gas exchange responses of Australian tropical forest trees in canopy, gap and understory micro-environments. Functional Ecology 1:169–178

Powles SB (1984) Photoinhibition of photosynthesis induced by visible light. Annu Rev Plant Physiol 35:15–44

Powles SB, Björkman O (1982) Photoinhibition of photosynthesis: effect on chlorophyll fluorescence at 77K in intact leaves and in chloroplast membranes of *Nerium oleander*. Planta 156:97–107

Vincent WF, Neale PJ, Richerson PJ (1984) Photoinhibition: algal responses to bright light during diel stratification and mixing in a tropical alpine lake. J Phycol 20:201–211