Functional Ecology 2000
14, 166–175

Photosynthetic responses to a climate-warming manipulation for contrasting meadow species in the Rocky Mountains, Colorado, USA

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Summary

1. Microclimate was measured and photosynthetic responses to a climate warming manipulation were compared for the evergreen shrub *Artemisia tridentata* and the herbaceous forb *Erigeron speciosus* in the Rocky Mountains, Colorado, USA.
2. Soil was warmer and drier under infra-red heaters compared with control plots.
3. Midday xylem pressure potential did not differ for *A. tridentata* on heated *vs* control plots but was lower for *E. speciosus* on heated plots compared with controls. Leaf temperatures did not vary for the two species on heated or control plots.
4. There were no significant treatment or species differences in the diurnal patterns of CO_2 assimilation or stomatal conductance to water vapour. Also, there were no differences in responses to leaf temperature.
5. The quantum yield for CO_2 assimilation over a range of PPFD was lower for plants on heated plots. There was a marked difference between species in the pattern of stomatal conductance to water vapour over a range of PPFD, but no differences as a result of the heating treatment.
6. The quantum efficiency of PSII electron transport was significantly affected by heating. Non-radiative energy dissipation was greater for *A. tridentata* compared with *E. speciosus*. There was recovery of F_V/F_M for *A. tridentata* but not for *E. speciosus*.
7. Heating appears to affect plants via changes in soil water content rather than by increasing leaf temperature. The deciduous species *E. speciosus* appears to undergo some permanent closure of PSII on heated plots, in contrast to the evergreen shrub *A. tridentata*. Such differences may help explain the increase in above-ground biomass accumulation in response to heating for shrubs, compared with the decrease observed for deciduous herbaceous species.

Key-words: *Artemisia tridentata*, chlorophyll fluorescence, *Erigeron speciosus*, gas exchange, global warming, leaf temperature, microclimate, photoinhibition, soil moisture, transpiration, water potential

Functional Ecology (2000) **14**, 166–175

Introduction

Atmospheric concentrations of carbon dioxide are predicted to double relative to the pre-industrial value sometime in the next century. The enhanced infra-red radiation from increased CO_2 concentrations and other greenhouse gases is predicted to result in a 1·5–4 °C increase in average global air temperatures, with high elevations being especially affected (Houghton & Bolin 1992). An increase in atmospheric temperature is expected to produce a variety of climatic changes, with the potential for dramatic ecological effects on terrestrial vegetation (Peters & Darling 1985). Changes in the exchange of mass, energy and momentum resulting from atmospheric warming will influence the establishment, survival and reproduction of plants (Woodward 1992).

Climate change may cause significant changes in air and soil temperatures and soil water content for continental interior regions, including those of the western United States (Roads *et al*. 1994). Indeed, the results from a global warming experiment in Colorado, USA, indicate an increase in soil temperature and a decrease in soil moisture for plots exposed to infra-red (IR) heating (Harte *et al*. 1995). Under the heating treatment, biomass accumulation was enhanced for shrubs such as *Artemisia tridentata* Pursh. and was decreased for herbaceous perennial species including

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Erigeron speciosus de Candolle and *Potentilla gracilis* (Harte & Shaw 1995). The heating treatment caused species-specific changes in leaf thermal tolerance, relative water content and water potential for a variety of species (Loik & Harte 1996, 1997). The changes in soil moisture content and leaf water relations caused by the IR treatment may also result in reduced stomatal opening, CO_2 uptake and carbon fixation. Differences in responses among different plant functional groups may help to explain the patterns of above-ground biomass accumulation observed by Harte & Shaw (1995).

It is increasingly apparent that photoprotection of PSII is important when plants are subject to multiple environmental stresses (Demmig-Adams & Adams 1996). Photoprotection may occur via a number of mechanisms, including non-radiative energy dissipation (non-photochemical quenching) from PSII via the xanthophyll cycle (Björkman & Demmig-Adams 1995). Down-regulation of a portion of PSII reaction centres can also be important for plants in response to simultaneous stresses (Valladares & Pearcy 1997). The ability to maintain some form of photoprotection may take on increased importance for plants exposed to warmer and drier conditions predicted for global warming scenarios of the future. At present, it is unclear how changes in air and soil temperatures, soil nutrients, and plant resource uptake and allocation patterns will interact to influence the ability to process excitation energy in PSII.

For plants exposed to soils dried by elevated atmospheric temperatures, water potential may be decreased, leading to reductions in stomatal conductance and photosynthetic CO_2 fixation. Also, the requirement for photoprotection may be enhanced or else the number of open PSII reaction centres may be decreased. Such responses may vary for functional groups with different evolutionary backgrounds, leaf phenology patterns and survival strategies. In this regard, the changes in above-ground biomass accumulation exhibited by plants exposed to a warming manipulation in the Rocky Mountains, CO, USA (Harte & Shaw 1995), lacks a mechanistic explanation.

In the present study, we tested the general hypothesis that plants exposed to a climate warming manipulation exhibit less photosynthetic gas exchange and more non-photochemical quenching compared to controls. We compared mechanistic responses for two species: the evergreen shrub *A. tridentata*, which is widespread in cool deserts of the western United States, and the deciduous, herbaceous forb *E. speciosus*, which is common in montane ecosystems of the western United States (Weber 1976; Hickman 1993). These two species were chosen because: (1) at our study site *A. tridentata* represents about 85% of the above-ground shrub biomass and *E. speciosus* represents 25% of the above-ground herbaceous forb biomass; (2) the biomass of *A. tridentata* is greater on heated compared to control plots, whereas the opposite is true for *E. speciosus*; (3) they co-occur within the relatively dry microhabitats of our study site; (4) they have different leaf phenology patterns and survival strategies; (5) they well represent low-elevation shrubs and high-elevation forbs that overlap in distribution at high-desert/subalpine ecotones throughout the inter-mountain United States. This study was conducted at the ecotone between the high-desert shrub and the subalpine flora of the Rocky Mountains of CO as plant responses to climate change at such borders may influence future ecosystem structure and function (Hoffman & Blows 1994). Our goal was to identify the effects of infra-red heating on physiological performance to help explain the above-ground biomass responses to IR (Harte & Shaw 1995) for these two species. We measured microclimatic conditions including soil water content, PPFD, air and soil temperature, and vapour pressure deficit, and their effects on leaf temperature and tissue water potential. In order to identify effects of the heating treatment on physiological performance, we measured diurnal patterns of photosynthetic gas exchange (CO_2 assimilation, A, and stomatal conductance to water vapour, g_s), responses of A and g_s to PPFD and temperature, transpiration and chlorophyll *a* fluorescence from Photosystem II.

Materials and methods

STUDY SITE

This study was conducted in a subalpine meadow located at the Rocky Mountain Biological Laboratory, 10 km north of Crested Butte, CO, USA (38°53′N, 107°02′W, elevation 2920 m). The meadow occurs at the border between the upper elevational limit of Great Basin Desert shrub-steppe and subalpine vegetation characteristic of the central Rocky Mountains (Weber 1976). The meadow vegetation consists primarily of perennial herbaceous winter geophytes, several graminoid species and two woody shrubs. All above-ground biomass senesceses during the autumn, except for *A. tridentata*, which maintains overwintering leaves. The soil in the meadow is a well-drained, deep and rocky glacial till, and classified as a subalpine soil (Erickson & Smith 1985). Further details of the study site appear in Harte *et al*. (1995) and Harte & Shaw (1995).

EXPERIMENTAL DESIGN

Five control and five heated plots (3 m × 10 m each) were placed along the ridge of a south-facing slope in 1990 (Harte *et al*. 1995). For each of five heat-treatment plots, three 1·6 m long electric heaters (Kalglo, Inc., Lehigh, PA, USA) were suspended 2·5 m above the soil surface by a series of steel cables and towers. The five heated plots were continuously treated (24 h day^{-1}, 365 days $year^{-1}$) with infra-red radiation at an intensity of 22 W m^{-2}. This level of IR was used because it

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generates surface warming comparable to the combined effects of doubling of CO_2, the contribution of major feedbacks (such as increased atmospheric water vapour content) and a small additional flux associated with convective warming. Although the IPCC predicts elevated night-time air temperatures (Houghton & Bolin 1992), our manipulation warms the soil and is stronger in daytime than at night because of soil drying and the Bowen effect (Harte *et al*. 1995). The heaters give off no UV radiation and in the far-red (700–800 nm) the downward flux is equal to 10^{-6} of solar input. Approximately 0·5% of the area of the heated plots is shaded by the heaters for less than one-third of the daytime.

Weather measurements were collected from a National Dry Deposition Network station maintained by the United States Environmental Protection Agency *c.* 100 m away from the plots. Air temperature and daily precipitation were measured at standard meteorological height and recorded on a personal computer. Temperature and precipitation were measured with an air temperature-humidity sensor and tipping-bucket rain gauge (R. M. Young Company, Traverse City, MI, USA).

Permanently placed thermocouples and calibrated gypsum blocks were installed in both control and heated plots to monitor soil temperature and moisture. The sensors were coupled to multiplexers and data loggers to collect data every 2 h throughout the year. The upper, middle and lower region of each plot contained three sets of two probes at 5, 12 and 25 cm depth. We focused on the 5 and 12 cm depths where most roots are located.

PLANT MATERIAL

Ten individuals (one plant per plot) each of *A. tridentata* and *E. speciosus* were randomly selected during July 1997. Average plant height was 0·48 ± 0·08 m for *A. tridentata* and 0·50 ± 0·10 m for *E. speciosus*. At the present study site, *E. speciosus* exhibits full above-ground senescence beginning in August; plants with an onset of colour change were avoided.

All measurements were made on leaves that were at least 10 leaves away from the apical meristem. Such leaves were on the east side of the plant in a portion of the plot that was not shaded by the overhead heaters for most of the day (the plants on the east side of plots are not shaded until mid- to late afternoon).

LEAF TEMPERATURE AND WATER POTENTIAL

Leaf temperature was measured over a diurnal period with a nickel chromel constantan thermocouple (1·27 mm diameter) appressed to the abaxial surface of the same leaves that were used for chlorophyll fluorescence measurements. For water potential measurements, 10 cm-long stem segments were carefully removed with a razor blade and rapidly inserted into a pressure chamber. Water potential was measured as xylem pressure potential between 11.00 and 13.00 h with a pressure chamber (PMS Scientific, Corvallis, OR, USA).

PHOTOSYNTHETIC GAS EXCHANGE

Photosynthetic gas exchange was compared for *A. tridentata* and *E. speciosus* in terms of: (1) diurnal patterns of CO_2 assimilation and stomatal conductance to water vapour; (2) responses of assimilation to leaf temperature; (3) the relationship of transpiration to assimilation; (4) responses of assimilation, stomatal conductance and chloroplastic CO_2 concentration to photosynthetic photon flux density (PPFD; 400–700 nm).

All measurements were conducted for five, randomly selected plants of each species in both the control and heated plots; for each set of experiments (1 through 4 above) a different set of plants was used. Leaves were selected as described above; for diurnal measurements, leaves were marked so that the same leaves were used throughout the day. For *A. tridentata*, three leaves were used and carefully arranged to avoid overlapping; for *E. speciosus* one leaf per plant was used. Measurements were made during the period 22 July–7 August 1997.

CO_2 assimilation, stomatal conductance to water vapour and transpiration were measured using an open-mode portable photosynthesis system (Model LI-6400, Li-Cor, Inc., Lincoln, NE, USA). The CO_2 concentration within the leaf measurement chamber was maintained at 360 μmol mol^{-1}. Leaf area used for gas-exchange measurements was determined by tracing the leaf onto paper and subsequent comparison of the image to a known area and mass of paper.

Measurements of assimilation in response to leaf temperature were made at different times of the day as temperature increased. Leaf temperature was initially measured, the cuvette was applied to the leaf and then temperature was held constant at the measured ambient level using the thermoelectric block within the cuvette. Leaves were illuminated at 1500 μmol m^{-2} s^{-1} using the LED light source to avoid differences owing to changing PPFD levels during the day. VPD was maintained at 1·5 kPa by controlling the flow rate of source air through desiccant or by adding a water-vapour source to the air inlet.

Photosynthetic responses to PPFD were measured between 06.00 and 11.00 h because of the potential for afternoon rainfall and to avoid leaves that had been shaded by the overhead heaters. For the 7 day period prior to measurements, the ambient air temperature ranged from 4 to 22 °C, and PPFD incident on a horizontal surface varied from 100 to 1700 μmol m^{-2} s^{-1}, between 06.00 and 11.00 h. The cuvette temperature was held at 20 °C with a Peltier thermoelectric block, resulting in leaf temperatures of 20–24 °C and leaf-to-air vapour pressure deficits of 1·5–2·3 kPa. The linear slope was utilized as the apparent quantum yield,

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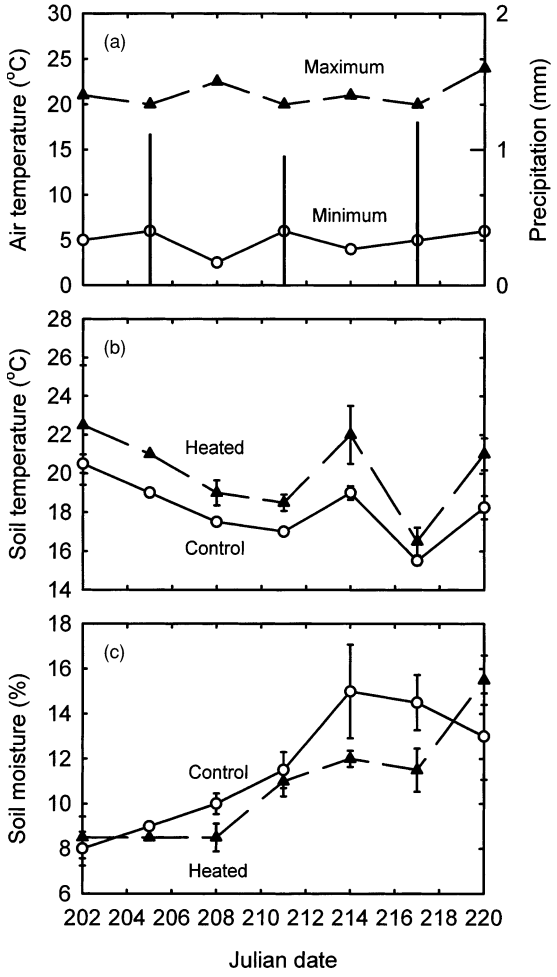


Fig. 1. Meteorological and soil conditions for the 2 week period prior to the study: (a) maximum (○) and minimum (▲) air temperatures and precipitation (vertical bars); (b) soil temperature in the upper region of plots at noon averaged at 5 and 12 cm for control (○) and heated (▲) plots; (c) soil moisture in the upper region of plots at noon averaged at 5 and 12 cm for control (○) and heated plots (▲).

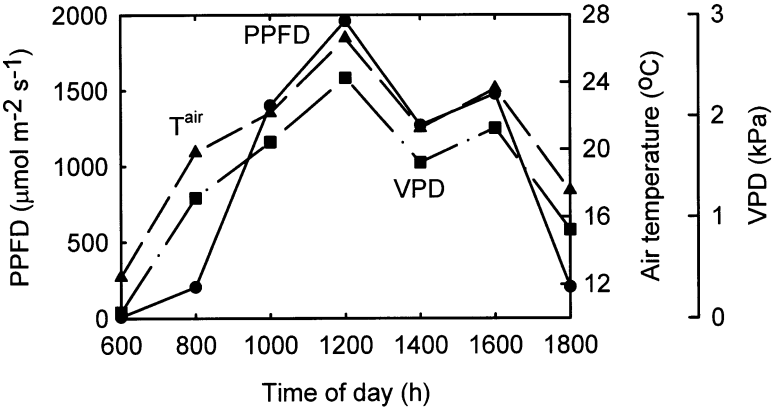


Fig. 2. Photosynthetic photon flux density (PPFD) (●) on a horizontal surface, air temperature (T^{air}) (▲) and vapour pressure deficit (VPD) (■) measured on 27 July 1997. Measurements were made at a station *c.* 100 m from the plots.

the light compensation point was calculated from the intercept of the line with the abscissa and net photosynthetic capacity was determined from the maximal rate of carbon dioxide assimilation.

CHLOROPHYLL FLUORESCENCE

Measurements of chlorophyll fluorescence were obtained with a pulse-modulated fluorimeter (Model FMS1, Hansatech, Kings Lynn, UK). For leaves exposed to ambient PPFD, the intrinsic efficiency of excitation transfer (Barker & Adams 1997) was calculated as $F_V'/F_M' = (F_M' - F_O')/F_M'$. F_O' was determined using a far-red pulse of light to excite PSI preferentially and to oxidize PSII. To assess the recovery of excitation energy transfer, leaves that were measured in ambient light were dark adapted (maximum 1 h owing to sampling time) and the efficiency of excitation transfer was measured as $F_V/F_M = (F_M - F_O)/F_M$. The quantum efficiency of Photosystem II (ΦPSII) was calculated as $(F_M' - F_S)/F_M'$ (Genty, Briantais & Baker 1989). Non-photochemical quenching was calculated as $NPQ = (F_M/F_M') - 1$ (Barker & Adams 1997) for measurements made under actinic excitation at a PPFD of 10 μmol m^{-2} s^{-1} to allow production of reducing power for the de-epoxidation reaction (O. Björkman, personal communication).

STATISTICAL ANALYSES

Two-way analysis of variance (ANOVA) was used to analyse the effect of species and treatment (and their interaction) on each of the dependent variables. Bonferroni's method was used to compare species and treatment groups when they were found to be significant factors in the two-way ANOVA. Throughout means and standard errors are reported and $P < 0{\cdot}05$ is considered significant.

Results

Maximum air temperatures for the 2 week period leading up to the study varied from about 20 to 25 °C and minimum temperatures ranged between 2·5 and 5·5 °C (Fig. 1). A total of 3·3 mm of rainfall occurred over 3 days prior to the study. Mean soil temperature at 5 and 12 cm depth at noon was *c.* 2 °C higher for heated compared to control plots. Soil moisture increased throughout the period and control soils were wetter than heated soils on most of the days. Based on soil moisture release curves for this study site, a gravimetric-based moisture content of 12% (the average for the current study) corresponds to a soil water potential of – 0·10 MPa.

Photosynthetic photon flux density (PPFD; 400–700 nm) incident on a horizontal surface, air temperature (T^{air}) and vapour pressure deficit (VPD) were measured over the course of a typical day for this site (Fig. 2). PPFD increased to a maximum of 1960 μmol m^{-2} s^{-1} at solar noon, decreased owing to afternoon clouds associated with the south-west monsoon and declined early because of a mountain ridge to the immediate west of the study site. T^{air} was 12 °C at sunrise and increased to a maximum of 27 °C, and decreased

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Table 1. Midday leaf water potential for *Artemisia tridentata* and *Erigeron speciosus* exposed to an experimental warming manipulation. Measurements were made between 11.00 and 13.00 h on 28 July 1997. Data are means ± SE ($n = 5$). Values followed by the same letter are not significantly different ($P < 0.05$), across species or treatment

Species	Treatment	Ψ (MPa)
Artemisia tridentata	control	-1.74 ± 0.04^{a}
	heated	-1.99 ± 0.05^{a}
Erigeron speciosus	control	-2.03 ± 0.06^{b}
	heated	-2.36 ± 0.09^{c}

during the cloudy portion of the afternoon. VPD rapidly increased during the morning and fluctuated around 2·0 kPa until the late afternoon. For the 7 day period prior to this day, mean PPFD at noon was 1950 ± 37 μmol m^{-2} s^{-1} (mean ± SE, $n = 7$), mean T^{air} was 19·6 ± 0·3 °C and mean VPD was 1·49 ± 0·10 kPa. Leaf temperatures did not differ for either species between control and heated plots for most of the diurnal period (data not shown). There were no significant differences in water potential for *A. tridentata* leaves on control and heated plots (Table 1). However, Ψ^{xylem} was lower for *E. speciosus* compared to *A. tridentata* on control and heated plots, leading to a significant species ($F = 29.0$, $P < 0.001$) and treatment effect ($F = 22.5$, $P < 0.001$).

The diurnal patterns of CO_2 assimilation (A) were similar for both *A. tridentata* and *E. speciosus* (Fig. 3a,b). Maximal uptake rates were achieved by 08.00 to 10.00 h for both species and considerable variation was exhibited. Assimilation decreased around 14.00 h, at the same time as the common summertime afternoon cloud accumulation at this site. There were no significant differences in A between species or for plants on control compared to heated plots. Stomatal conductance to water vapour (g_s) was relatively low for both species throughout the diurnal period (Fig. 3c,d). For both species on control and heated plots, the diurnal patterns of g_s mirrored those of A. There were no significant differences in g_s owing to species or heating treatment.

Carbon dioxide uptake increased as a function of leaf temperature for both species (Fig. 4). For *A. tridentata*, A was significantly greater for plants on control compared to heated plots at a leaf temperature of 11 °C ($F = 5.1$, $P < 0.05$). For *E. speciosus*, the opposite pattern was observed and the differences in A at a leaf temperature of 26 °C were marginally significant ($F = 3.8$, $P < 0.05$).

For *A. tridentata*, mean transpiration rates measured at midday were 5.90 ± 1.0 mmol m^{-2} s^{-1} for plants on control plots and 8.55 ± 0.85 mmol m^{-2} s^{-1} on heated plots. For *E. speciosus*, mean midday transpiration was 8.61 ± 0.60 mmol m^{-2} s^{-1} for plants on control plots, and 10.7 ± 1.54 mmol m^{-2} s^{-1} on heated plots. There was an exponential relationship between transpiration (E) and assimilation for both species on control and heated plots (Fig. 5).

Photosynthetic responses to PPFD were measured *in situ* for both species on control and heated plots

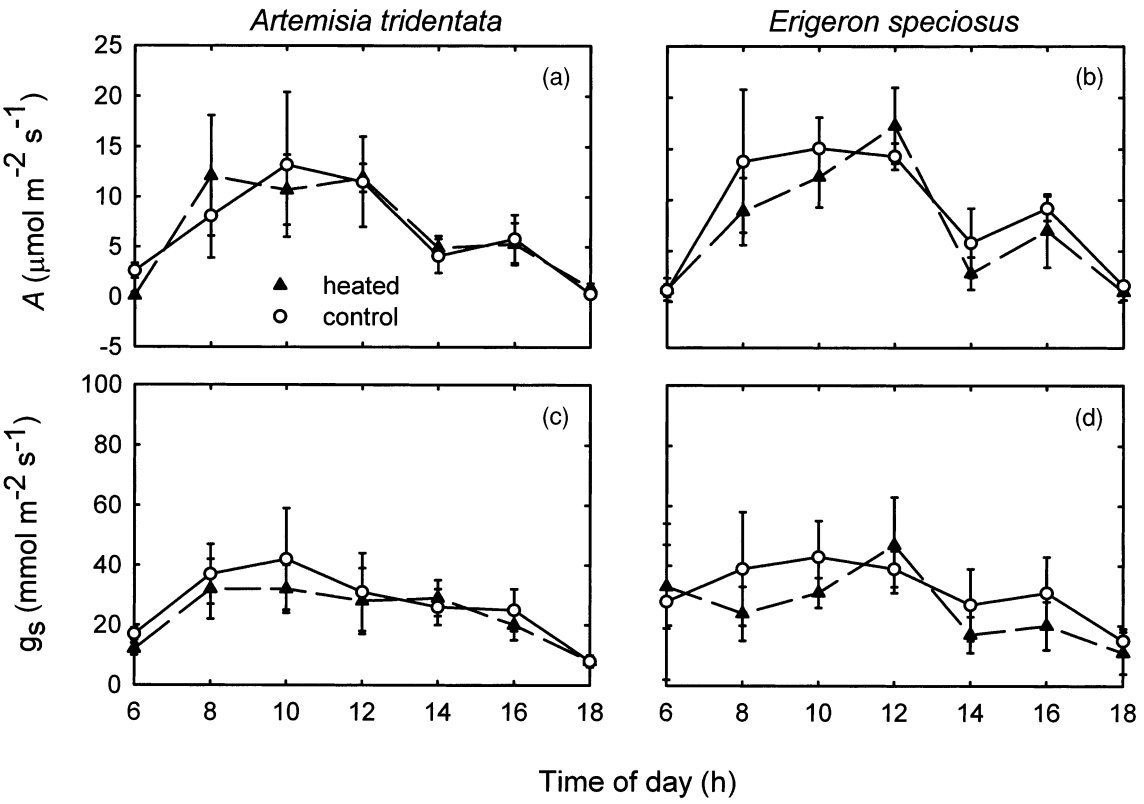


Fig. 3. Diurnal patterns of CO_2 assimilation, A (a,b) and stomatal conductance to water vapour, g_s (c,d), for *Artemisia tridentata* (a,c) and *Erigeron speciosus* (b,d) on control (○) and heated (▲) plots. Measurements were made at ambient PPFD. Data are means ± SE ($n = 5$).

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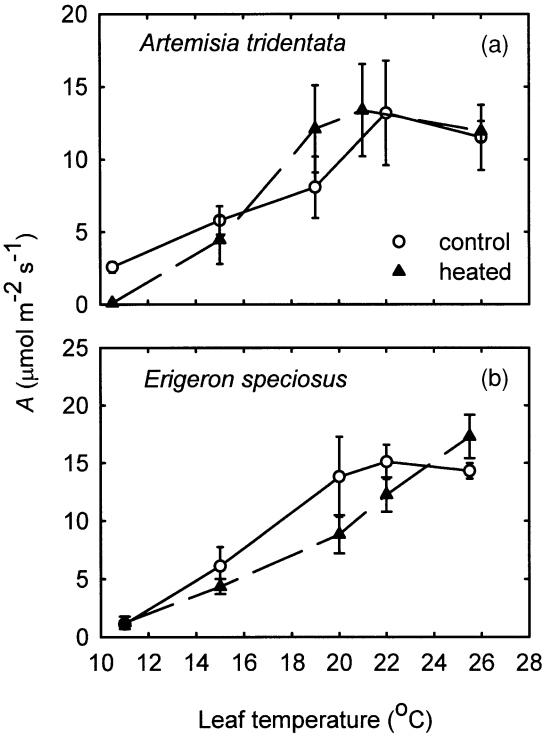


Fig. 4. CO_2 assimilation, A, as a function of leaf temperature for *A. tridentata* (a) and *E. speciosus* (b) on control (○) and heated (▲) plots. Measurements were made at a light saturating PPFD of 1500 μmol m^{-2} s^{-1}. Data are means ± SE (n = 5).

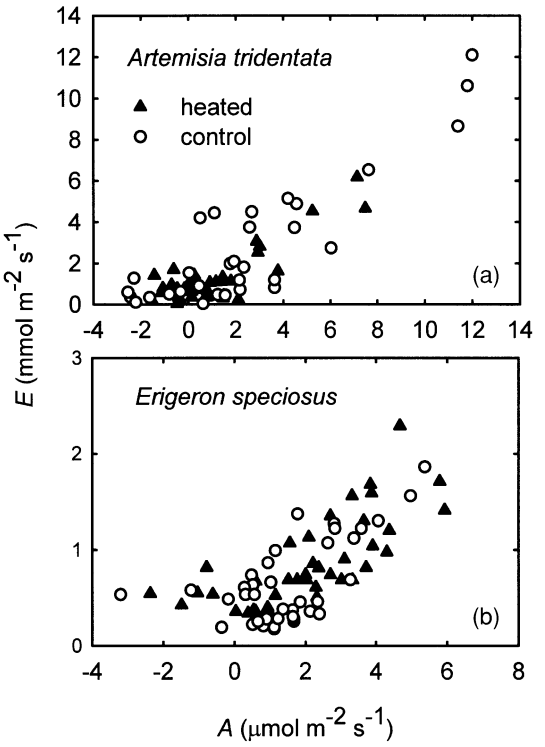


Fig. 5. Transpiration, E, as a function of CO_2 assimilation, A, for *A. tridentata* (a) and *E. speciosus* (b) on control (○) and heated (▲) plots. Data are means ± SE (n = 5). For *A. tridentata*, $E = -1{\cdot}61 + 2{\cdot}8e^{0{\cdot}125A}$, $r^2 = 0{\cdot}82$ (control plots) and $E = -0{\cdot}715 + 1{\cdot}46e^{0{\cdot}2A}$, $r^2 = 0{\cdot}78$ (heated plots). For *E. speciosus*, $E = 0{\cdot}49e^{0{\cdot}22A}$, $r^2 = 0{\cdot}58$ (control plots) and $E = 0{\cdot}26 + 0{\cdot}15e^{0{\cdot}45A}$, $r^2 = 0{\cdot}56$ (heated plots).

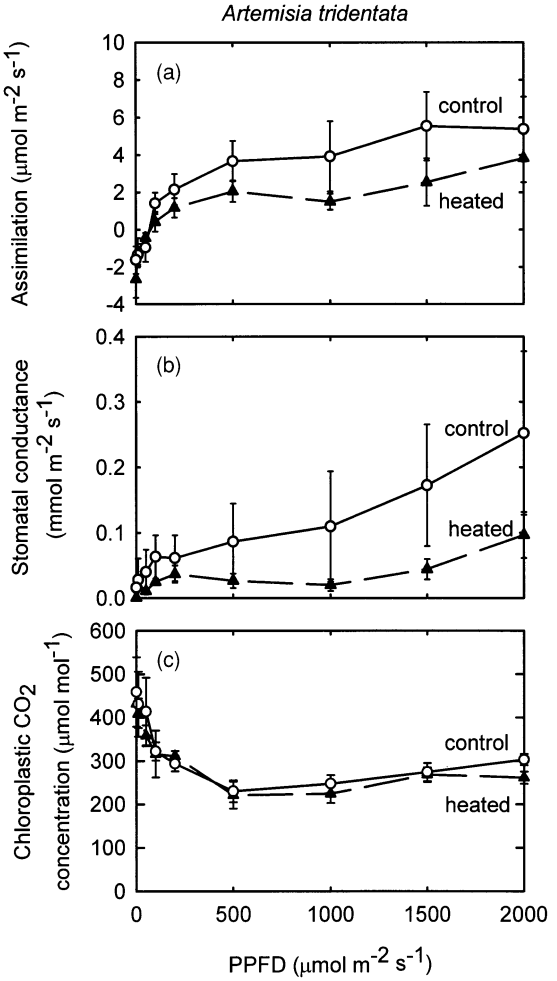


Fig. 6. Assimilation (a), stomatal conductance to water vapour (b) and chloroplastic CO_2 concentration (c) in response to PPFD for *A. tridentata* on control (○) and heated (▲) plots. Data are means ± SE (n = 5).

(Figs 6 and 7). Both species exhibited a typical saturating response of assimilation to increasing PPFD and plants on control plots generally had faster CO_2 uptake for PPFD greater than 500 μmol m^{-2} s^{-1}. The pattern of stomatal conductance to water vapour in response to increasing PPFD markedly differed for the two species. In particular, g_s increased with PPFD for *A. tridentata*, and was about 2·5-fold greater at 200 μmol m^{-2} s^{-1} for plants on control compared to heated plots. In contrast, g_s of *E. speciosus* was greater for controls compared to heated plants at a PPFD of 0 μmol m^{-2} s^{-1} and was less than 0·05 mmol m^{-2} s^{-1} for greater PPFD. For PPFD of 0 μmol m^{-2} s^{-1}, there was a significant difference in g_s for the two species ($F = 11{\cdot}1$, $P < 0{\cdot}01$). The chloroplastic CO_2 concentration decreased from around 400 μmol mol^{-1} at low PPFD to 200 μmol mol^{-1} (for *A. tridentata*) to 300 μmol mol^{-1} (for *E. speciosus*), and these differences between the two species at maximal PPFD were significant ($F = 40{\cdot}7$, $P < 0{\cdot}001$). Various photosynthetic parameters were computed from curves such as those in Figs 4 and 5 (Table 2). For both species, the apparent quantum yield,

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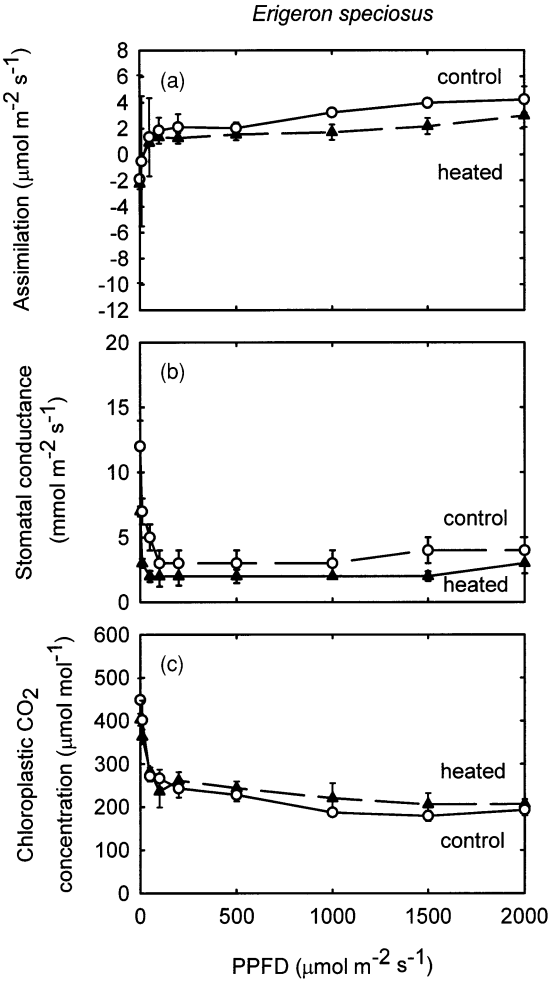


Fig. 7. Assimilation (a), stomatal conductance to water vapour (b) and chloroplastic CO_2 concentration (c) in response to PPFD for *E. speciosus* on control (○) and heated (▲) plots. Data are means ± SE (n = 5).

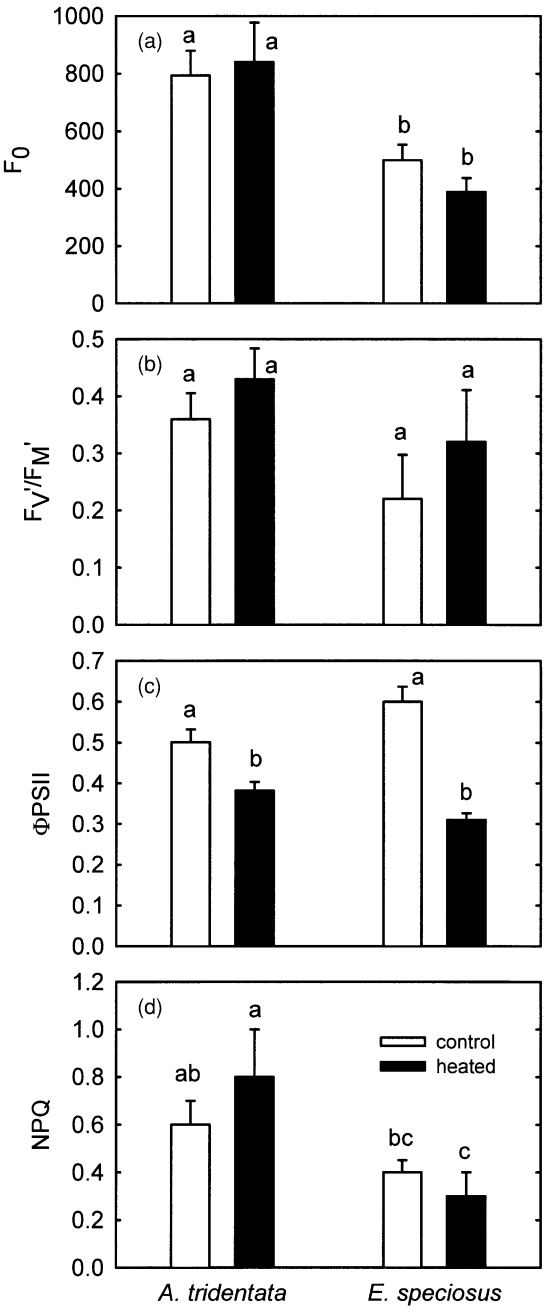


Fig. 8. Chlorophyll fluorescence for *A. tridentata* and *E. speciosus* on control (open bars) and heated (dark bars) plots. Data for open reaction centres (a), the efficiency of excitation energy transfer for plants in ambient light (b), the quantum efficiency of PSII (c) and non-photochemical quenching (d) are means ± SE (n = 5).

determined from the linear slope of the A-PPFD curve, was significantly smaller under the heating treatment (F = 7·99, P < 0·05). There were no significant differences in maximal assimilation rates or the light compensation point for plants on control and heated plots.

Chlorophyll *a* fluorescence was compared for the two species on control and heated plots to test the hypothesis that the heating treatment influences the processing of excitation energy in PSII (Fig. 8). F_O was significantly smaller for *E. speciosus* compared to

Table 2. Summary of photosynthetic parameters for *A. tridentata* and *E. speciosus* exposed to an experimental warming manipulation. Maximal photosynthetic assimilation (A_{max}), apparent quantum yield (Φ) and light compensation point (LCP) were compiled from light dosage-response curves, such as those in Figs 6 and 7. Data are means ± SE (n = 5). Means with the same letter are not significantly different (P < 0·05) across species or treatment

Species	Treatment	A_{max} (μmol m^{-2} s^{-1})	Φ	LCP (μmol m^{-2} s^{-1})
A. tridentata	control	5·38 ± 1·73^a	0·051 ± 0·015^a	55 ± 30^a
	heated	3·83 ± 1·30^a	0·022 ± 0·004^b	71 ± 17^a
E. speciosus	control	4·22 ± 0·80^a	0·065 ± 0·012^a	31 ± 6^a
	heated	2·99 ± 0·90^a	0·032 ± 0·010^b	94 ± 26^a

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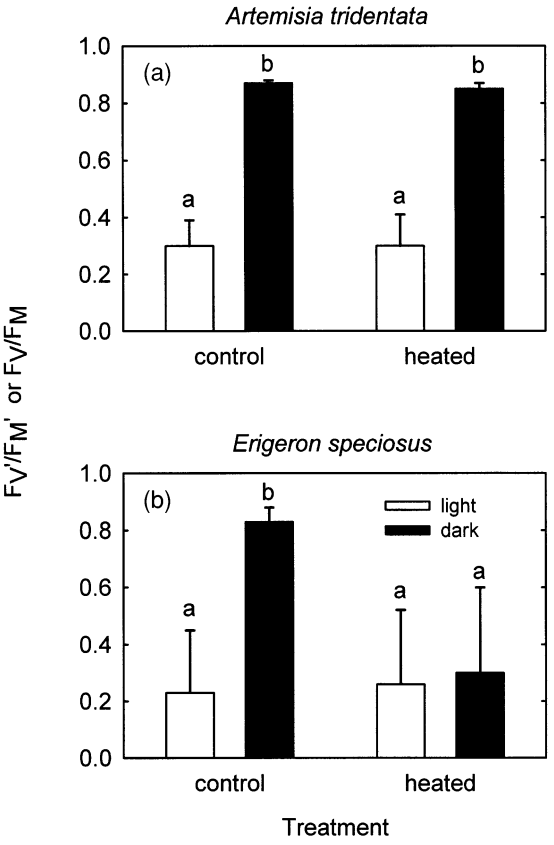


Fig. 9. The efficiency of excitation energy transfer from light harvesting complexes to reaction centres for ambient light (open bars) and dark adapted (dark bars) plants on control and heated plots. Data are means ± SE (n = 5) for *A. tridentata* (a) and *E. speciosus* (b).

A. tridentata (F = 18·0, P < 0·001), although there was no significant treatment effect for either species. The intrinsic efficiency of excitation energy transfer from light-harvesting complexes to reaction centres (F_V'/F_M') was not affected significantly by either species or treatment. The quantum efficiency of PSII was smaller for both *A. tridentata* and *E. speciosus* on heated compared to control plots (for the heating treatment, F = 9·71, P < 0·001). Non-photochemical quenching was greater for plants on heated plots for *A. tridentata* compared to *E. speciosus* (F = 12·9, P < 0·01).

The dynamic nature of excitation energy transfer from light harvesting complexes to PSII reaction centres was examined by comparing F_V'/F_M' in light to F_V/F_M for dark-adapted plants (Fig. 9). For *A. tridentata*, F_V'/F_M' was similar for plants on control and heated plots in ambient light. Following a period of dark adaptation, F_V/F_M was about 0·85 for plants on both control and heated plots. A comparable pattern was observed for *E. speciosus* on control plots, however, for plants on heated plots, F_V/F_M after 1 h in darkness was about 0·3, similar to values of F_V'/F_M' measured in ambient PPFD.

Discussion

The infra-red heating treatment dried the soil in heated compared to control plots, and induced lower water potentials in the herbaceous geophyte, *E. speciosus*, compared to the woody perennial shrub, *A. tridentata* (Fig. 1, Table 1). The heating treatment affects the leaf water content and water potential for a variety of species at this site (Loik & Harte 1997), although there is a great deal of interannual variability in precipitation (B. Barr, personal communication). Soil drying (Harte *et al.* 1995), may reduce above-ground biomass accumulation for herbaceous species at this site (Harte & Shaw 1995) via influences on water relations, the timing of leaf development or leaf longevity. In the present study, photosynthetic rates measured in response to PPFD were lower than those recorded over the daytime (Figs 3, 6 and 7); such variation may have been the result of differences in air temperature, leaf angle, soil or plant water potential, and degree of photoprotection. There were no significant differences in the diurnal patterns of CO_2 assimilation and stomatal conductance owing to the heating treatment for either species. Rather, the heating treatment was associated with a decrease in water potential in *E. speciosus* (Table 1), permanent closure of some PSII reaction centres (Figs 8 and 9) and possibly an earlier onset of senescence for this species. For the evergreen species *A. tridentata*, differences in water potential were not significant and changes in PSII activity did not appear to be permanent. We conclude that physiological responses to the heating treatment are the result of the effect of warming on soil drying, and the resultant lowered plant water potential (Harte *et al.* 1995; Loik & Harte 1997), and it is this which may contribute to species-specific changes in above-ground biomass accumulation (Harte & Shaw 1995).

The responses to PPFD of photosynthetic gas exchange and chlorophyll fluorescence (Figs 6, 7, 8 and 9) suggest that photosynthetic downregulation occurred to some degree for both species. For *A. tridentata*, changes in excitation energy transfer through PSII appeared to be fully reversible and related to non-photochemical quenching, and were only slightly affected by the infra-red heating treatment (Fig. 9). In contrast, the heating treatment caused lowered NPQ and an impairment of the recovery of F_V/F_M in darkness for *E. speciosus*, consistent with permanent PSII closure (Osmond 1994; Valladares & Pearcy 1997). Damage to PSII can result in a loss of excitation energy transfer in response to high temperatures (Loik & Harte 1996) but ambient air and leaf temperatures during the present study were far below those required for decreases in F_V/F_M and membrane damage for *A. tridentata* and *P. gracilis* under similar conditions (Loik & Harte 1996). Reductions in F_V/F_M are species-specific and depend upon interactions between leaf movements, temperature, incident PPFD and water stress (Ludlow & Björkman 1984; Björkman 1987; Gamon & Pearcy 1990a,b; Valentini *et al.* 1995; Huxman *et al.* 1998). Our results suggest that *E. speciosus* may be sacrificing PSII as a form of photoprotection (Epron

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1997; Jagtap *et al*. 1998), which may be important for deciduous species that have a limited period of suitable conditions (about 3 or 4 months) for photosynthate accumulation for growth and reproduction. In contrast, there appears to be a greater reliance on NPQ, such as by xanthophyll cycle activity (Demmig-Adams & Adams 1996), for the relatively long-lived leaves of *A. tridentata*.

The timing of soil drying may determine the extent of changes in photosynthesis and photoprotection. Heating causes snowmelt to be advanced by one to 2 weeks for treatment compared to control plots (Harte *et al*. 1995), leading to changes in plant development and flowering phenology (Price & Waser 1998). The progressive soil drying that occurs at this site over the summer is thus advanced by about 2 weeks, and the rate and magnitude of drying may be enhanced by increasing atmospheric temperatures. This may be especially important for plants at this site late in the summer when soils are driest, as photosynthates are then being translocated to storage organs for the winter. *Artemisia tridentata* is deep-rooted in comparison to *E. speciosus* and most of the other herbaceous species at our site. Roots of *A. tridentata* can extend to depths of 1·5–1·8 m and may help maintain leaf water potentials above those for other species and at values favourable for photosynthesis when surface soil layers are dry (Richards & Caldwell 1987; DeLucia & Heckathorn 1989; Loik & Harte 1997). Moreover, *A. tridentata* exhibits increased cellular solute content, a shift in the cellular distribution of water and changes in cell wall elasticity in response to heating that may extend its ability to extract water from drying soils (Loik & Harte 1997). Species adapted to maintain water uptake and photosynthesis may avoid photosynthetic downregulation under the altered climatic conditions of the future (Ball, Hodges & Laughlin 1991; Raven 1994).

The lack of treatment-induced differences in leaf temperatures may have been the result of species-specific patterns of heat flux. Based on short- and long-wave radiation interception, the total energy input to leaves was greater for *E. speciosus* (control, 1475 W m^{-2}; heated, 1500 W m^{-2}) compared to *A. tridentata* (control, 1340 W m^{-2}; heated, 1360 W m^{-2}); IR emission was about 875 W m^{-2} for both species. For *A. tridentata*, transpiration resulted in a heat loss of 376 W m^{-2} on heated plots and 259 W m^{-2} on control plots. The heat efflux owing to transpiration was greater for *E. speciosus* (control, 379 W m^{-2}; heated, 471 W m^{-2}). The net energy balance would be dissipated by conduction and convection to the bulk air phase, which would be affected by differences in wind speed in the immediate vicinity of leaves, their boundary layer conductance and their emissivity of heat (Nobel 1991). *Artemisia tridentata* has vertically exserted leaves in contrast to the somewhat horizontal leaves of *E. speciosus*, which could influence convective cooling as well as susceptibility to photoinhibition during the morning when air temperatures are cool (Ball *et al*. 1997; Blennow *et al*. 1998). Temporal changes in leaf angle can be important for the interception of PPFD, leaf temperature and reductions in PSII activity (Gamon & Pearcy 1989, 1990a,b; Ryel & Beyschlag 1995; Valladares & Pearcy 1997), although for both *A. tridentata* and *E. speciosus* there were no appreciable leaf movements. The reflectance of trichomes on *A. tridentata* leaves increases by about twofold during the summer (J. Harte, unpublished observations), which could help to moderate leaf temperatures and provide photoprotection (Sandquist & Ehleringer 1998). A detailed energy-budget analysis for plants on heated and control plots would further our understanding of the effects of morphology, pubescence and transpiration on leaf temperatures in a future climate.

Experimental warming influences a number of factors that may limit the survival, growth and reproductive success of plants at our site, including snowmelt date (Harte *et al*. 1995), biomass accumulation (Harte & Shaw 1995), leaf temperature tolerance (Loik & Harte 1996), plant water relations (Loik & Harte 1997) and reproductive phenology (Price & Waser 1998). Altered conditions owing to enhanced IR warming may cause increased fitness for some species and decreased success for others, ultimately leading to changes in species composition at the community scale. For many arid and semiarid ecosystems in the western United States, recruitment within plant populations is often limited by seedling tolerance of the severe conditions near the soil surface (Smith, Monson & Anderson 1997). Recruitment may occur episodically only in years with favourable conditions of soil moisture, temperature, nutrients, predation pressure and disease load. Photoinhibition occurs under a variety of stressful conditions for the seedlings of many species (Farage 1996; Ball *et al*. 1997; Tognetti, Johnson & Michelozzi 1997); although we focused on full-sized plants, the responses of seedlings to altered climatic conditions deserve greater attention.

Acknowledgements

The authors thank the staff of the Rocky Mountain Biological Laboratory for support facilities, Colleen Martin for help with water-potential measurements and the US Environmental Protection Agency for meteorological data. Michael Doyle of PP Systems kindly provided the Hansatech fluorimeter. Perry de Valpine, Jennifer Dunne, Travis Huxman, Becky Shaw and two anonymous reviewers provided useful comments on earlier drafts of the manuscript. Support was provided by NSF award ILI-9651277.

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Received 21 April 1999; revised 1 July 1999; accepted 13 July 1999

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