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High-temperature tolerance of *Artemisia tridentata* and *Potentilla gracilis* under a climate change manipulation

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Abstract Leaf tolerance to high temperatures, as determined by electrolyte leakage and chlorophyll *a* fluorescence, was compared for *Artemisia tridentata* (Asteraceae), a widespread shrub of the Great Basin, Colorado Plateau, and western slope of the Rocky Mountains, and *Potentilla gracilis* (Rosaceae), a herbaceous forb common to high-elevation meadows of the western United States. Species-specific and treatment-specific differences in leaf temperature, high-temperature tolerance and chlorophyll *a* fluorescence from photosystem II were compared, to test the hypothesis that plants at ecosystem borders will exhibit species-specific responses to climate change. Measurements were made for plants exposed to a climate change warming manipulation on a major ecosystem border at the Rocky Mountain Biological Laboratory, Colorado, United States, in July and August 1995. In July, daily maximal leaf temperatures were significantly higher for *P. gracilis* than for *A. tridentata*. Leaf temperatures were slightly lower in August than July for leaves of both species, on control and heated plots, despite the fact that daily maximum air temperatures were not significantly different for the two months. High-temperature tolerance was determined for leaves treated for 1 h at temperatures ranging from 15°C to 65°C. LT₅₀ was approximately 46°C for both species on control plots, but was 43°C for leaves of both species from heated plots, contrary to the predictions of the hypothesis. No shift in LT₅₀ (acclimation) was apparent between July and August. Changes in chlorophyll *a* fluorescence from photosystem II (F_V/F_M) were used to characterize the photosynthetic response to high temperatures. For both *A. tridentata* and *P. gracilis* in July,

F_V/F_M was about 0.7, but decreased for temperatures above 40°C. The results suggest that plant responses to global warming at ecosystem borders may be influenced by factors other than leaf-level physiological tolerance to elevated temperatures.

Key words Chlorophyll fluorescence · Climate change · Electrolyte leakage · Rocky Mountains · Sagebrush

Introduction

Increasing levels of anthropogenic CO₂ and other greenhouse gases are predicted to cause a warming of the Earth's atmosphere due to the enhanced infrared radiation from such gases (Houghton and Bolin 1992). Various models indicate that global mean surface temperatures will increase by 1.5–4.5°C, with a 3°C increase considered likely (Gates 1993). In addition to the direct affect on planetary boundary layer temperature, indirect climate changes will occur, with dramatic implications for the establishment, reproduction, and survival of plants (Woodward and Williams 1987; Grace and Norton 1990; Peters and Lovejoy 1992).

High-temperatures limit the geographic distribution of plant species through effects on metabolism and cell viability (Levitt 1980). In particular, elevated temperatures directly influence photosynthetic and respiratory rates, as well as the structural integrity of membranes (Björkman et al. 1980). Under a warmer climate predicted to result from an increase in atmospheric CO₂ and other greenhouse gases, the distribution of individual plant species might be influenced by changes in temperature and precipitation, seed dispersal and seedling recruitment, as well as changes in herbivory and host-parasite interactions (Richardson and Bond 1991; Leishman et al. 1992). Based on species-specific responses to increases in air temperature, differences in high-temperature tolerance and acclimation ability may result in changes in species distributions, novel competitive interactions, and extirpations.

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In the Great Basin Desert and Colorado Plateau of the western United States, *Artemisia tridentata* (Asteraceae) is the dominant evergreen shrub species. On the western slope of the Rocky Mountains, *A. tridentata* exists as mosaics among subalpine vegetation, including high-elevation herbaceous forbs such as *Potentilla gracilis* (Rosaceae; Weber 1976). In such regions where ecosystems border upon one another, species-specific responses to climate change may determine the rate and extent of changes in community composition (Hoffman and Blows 1994). For plants exposed to a climate change manipulation at the Rocky Mountain Biological Laboratory, Colorado, United States, above-ground biomass accumulation was greater for *A. tridentata* compared to herbaceous forbs, such as *P. gracilis* (Harte and Shaw 1995). Also, a significantly larger number of *A. tridentata* seedlings were found on heated versus control plots in 1994 (Harte and Shaw 1995). Therefore, there is a potential for increased recruitment of *A. tridentata* at higher elevations under a warmer and drier climate predicted by general circulation models (Manabe and Wetherald 1986; Harte and Shaw 1995).

The present study was conducted to characterize the physiological responses of plants to a climate change manipulation in the Rocky Mountains of Colorado, and to assess the potential for the encroachment of *A. tridentata* into subalpine ecosystems. In particular, the high-temperature tolerance of *A. tridentata*, a common shrub of the Great Basin and Colorado Plateau, was compared to that of *P. gracilis*, a widespread herbaceous forb of subalpine meadow ecosystems, to test the hypothesis that low-elevation species have a higher thermal tolerance than high-elevation species. Also, high-temperature tolerance of these two species was measured for plants exposed to an *in situ* climate-change manipulation to test the hypothesis that species from lower elevations have a greater ability to acclimate to the warmer and drier microclimate near the soil surface expected to occur due to increases in atmospheric greenhouse gases.

Methods

Study site

The present study was conducted during July and August 1995 at the Rocky Mountain Biological Laboratory, near Crested Butte, Colorado (38°53'N, 107°02'W, elevation 2920 m). Vegetation at this location consists primarily of shrubs (including *A. tridentata*, *P. fruticosa*, and *Salix* spp.), herbaceous forbs such as *Erigeron speciosus*, *Helianthella quinquevallis*, *Lupinus argentea*, and *Potentilla gracilis*, and trees including *Picea engelmannii* and *Populus tremuloides* (Weber 1976). The experimental manipulation is a series of infrared (IR) heaters (Kalglo, Lehigh, Pa.) suspended by towers and cables over five 3 × 10 m plots (alternated with five unheated control plots) along a ridge of a subalpine meadow. For a typical summer day the average reduction in solar energy due to the shadow cast by the heaters is less than 0.5%, and for a portion of the day the shadow falls outside the plots. The IR heaters give off no UV radiation, and in the visible range they give off 10⁻⁶ of solar radiation.

Soil temperature and moisture were measured with thermocouples and gypsum blocks buried at a depth of 5, 12, and 25 cm at

the top, middle, and bottom of each plot. The heaters were set at 22 W m⁻² in 1993, to generate surface warming comparable to that predicted as a result of a doubling of atmospheric CO₂ (Harte et al. 1995). Detailed descriptions of the study site appear in Harte et al. (1995) and Harte and Shaw (1995).

Meteorological measurements

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

Plant material

Five individuals each of *A. tridentata* and *P. gracilis* were tagged in each plot at the end of June 1995. The plants in different plots were selected for similar aspect and slope. Average plant height for all ten plots was 0.44 ± 0.09 m for *A. tridentata* and 0.14 ± 0.03 m for *P. gracilis*. Leaf temperatures for plants in control and heated plots were measured with an Everest Interscience model 210 infrared thermometer held 8 cm from the leaves. Prior to experiments (at about 0600–0630 hours), five fully expanded terminal leaves were removed from each plant with surgical scissors and immediately placed with their petioles in water inside 30-ml capped plastic bottles for transport to the laboratory.

Temperature treatments

High-temperature treatments were conducted within a modified 0.18 × 0.26 × 0.18 m picnic cooler. Temperature was maintained by a 0.18 × 0.18 m heat exchanger within the picnic cooler. The temperature of the heat exchanger was maintained by a circulating waterbath using 60% (v/v) ethylene glycol as the circulated fluid. Humidity was maintained at the saturation vapor pressure with a beaker of water placed on the heat exchanger.

Immediately prior to experiments, petioles were re-cut under water in small glass vials, and then the vials were placed on top of the heat exchanger in the cooler. Temperature treatments were started at the ambient outside air temperature (generally around 5–10°C) and increased at a rate of 2°C h⁻¹ to the desired temperature. Leaves were treated for 1 h at a particular temperature (15–65°C); leaf temperatures inside the cooler were measured with an Everest Interscience model 210 infrared thermometer.

Chlorophyll fluorescence

Following each temperature treatment, a leaf was removed from the cooler and transferred to the sensor head of a Hansatech MFMS/2S modulated fluorimeter (a total of *n* = 5 leaves from control and heated plots were measured at each temperature). The low-level light source intensity was set to 2 μmol m⁻² s⁻¹ at 583 nm, the demodulator gain was 80, and the response time was 0.1 s. Pulse-modulated light was supplied to the leaves from a Hansatech FLS1 light source and was delivered with a fiber optic cable at an intensity of 8500 μmol m⁻² s⁻¹. The pulses were delivered for 0.5 s at a frequency of 1 s⁻¹. Data acquisition was via a Hansatech IF1/2 interface in a Dell 4100/MX personal computer.

Electrolyte leakage

Immediately following fluorescence measurements, leaf discs were removed from treated leaves with a number 1 cork borer (diameter 3.5 mm). Ten discs from individual leaves were removed

from each of five leaves per high-temperature treatment. The discs were placed in 5 ml of distilled water in a 30 ml glass vial and then vacuum infiltrated for 2 min. The vials were placed on a rotary shaker at a rotation of 60 min⁻¹ for 24 h. Conductivity was measured with a Cole-Parmer Chemcadet pH/conductivity meter calibrated with authentic standards. Electrolyte leakage was expressed as a percent of maximum for discs removed from leaves treated at 70°C for 1 h.

Statistical analyses

Maximum and minimum air temperatures in July and August were compared with an unpaired *t*-test. Maximum leaf temperature, electrolyte leakage, and chlorophyll *a* fluorescence (at the maximum leaf temperature, and at the temperature leading to half-maximal electrolyte leakage) were analyzed using a three-way ANOVA. The model included the three main effects of species, heating treatment, and time, and all two-way interactions. The residuals from the model did not deviate from normality.

Results

Maximum air temperatures ranged from 12°C to 21°C, and minimum air temperatures varied from 3°C to 6°C during the experimental periods (10 days each) in July and August (Fig. 1A). Mean maximum temperature was $17.5 \pm 2.7^\circ\text{C}$ for July and $19.3 \pm 1.7^\circ\text{C}$ for August; mean minimum air temperatures were $4.9 \pm 1.6^\circ\text{C}$ and $6.8 \pm 1.4^\circ\text{C}$ for July and August, respectively. Average maximal air temperature was not significantly different in July and August ($t = -1.22$, $df = 18$, $P = 0.237$). The total amount of rainfall in July was over 3 times the

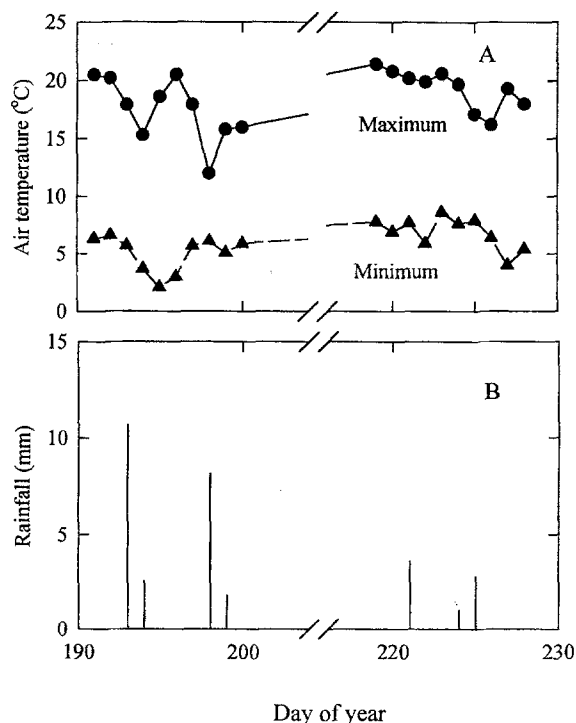


Fig. 1 Daily maximum (●) and minimum (▲) A air temperatures, and B daily rainfall totals measured for the two 10-day study periods in July and August of 1995 at the Rocky Mountain Biological Laboratory, Colorado, United States

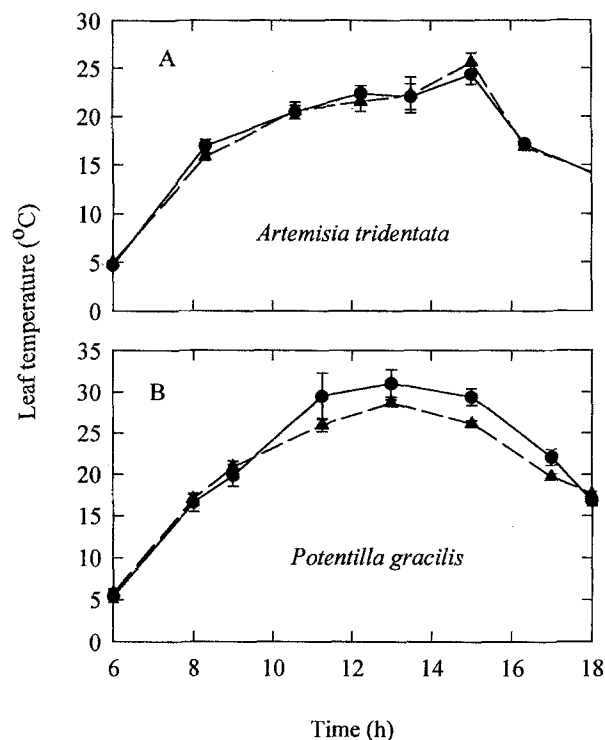


Fig. 2 Daytime patterns of leaf temperature for A *Artemisia tridentata*, and B *Potentilla gracilis*. Data are means $\pm$ 1 SE ($n = 5$) for leaves measured on control (●) and heated (▲) plots

amount that fell in August, and such rainfall events were associated with low maximum air temperatures (Fig. 1).

Daytime leaf temperatures in July differed for *A. tridentata* compared to *P. gracilis* (Fig. 2). In particular, leaves of *A. tridentata* reached a maximum temperature of about 25°C at 1500 hours and there was little difference in temperature for leaves on control and heated plots (Fig. 2A). For *P. gracilis*, maximum leaf temperature occurred at 1300 hours (Fig. 2B), and maximum leaf temperature was significantly higher than for *A. tridentata* (Table 1). *P. gracilis* maximum leaf temperatures in August were similar to those in July, contrary to the prediction of the acclimation hypothesis. In both months *P. gracilis* leaves on heated plots were cooler than leaves on control plots, while there was no such effect for *A. tridentata* (Table 1).

A. tridentata and *P. gracilis* exhibited similar patterns of electrolyte leakage for leaves treated for 1 h at temperatures from 15°C to 65°C, contrary to the prediction of the hypothesis that the low-elevation species would be more high-temperature tolerant (Fig. 3). Electrolyte leakage for both species increased from about 20% of maximum at 35°C to 80–90% at 50°C. In the overall model, the heating treatment had a weak effect on electrolyte leakage ($F = 5.57$, $P \leq 0.05$); the other independent variables did not significantly explain the variation in LT_{50} (Table 1). The temperature that resulted in a 50% reduction in electrolyte leakage, LT_{50} (defined as the high-temperature tolerance), was higher in July for leaves from control plants, but not in August, contrary to the

Table 1 Summary of three-way ANOVA results for physiological measurements on leaves of *Artemisia tridentata* and *Potentilla gracilis* from heated and control plots. Data are F values for maximum leaf temperature (T_{leaf}), the temperature causing half-maximal electrolyte leakage (LT_{50}), quantum yield of photosystem-II (PSII) at the maximum leaf temperature ($F_V/F_M^{T_{\text{leaf}}}$), and quantum yield of PSII at the temperature causing half-maximal electrolyte leakage ($F_V/F_M^{LT_{50}}$)

Independent variable	Dependent variable			
	T_{leaf}	LT_{50}	$F_V/F_M^{T_{\text{leaf}}}$	$F_V/F_M^{LT_{50}}$
Species	105.67***	NS	NS	NS
Month	10.24**	NS	25.64***	NS
Heating treatment	NS	5.57*	NS	21.40***
Species X month	5.52*	NS	NS	64.74***
Month X treatment	NS	NS	4.94*	34.28***
Species X treatment	8.13**	NS	NS	NS

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$

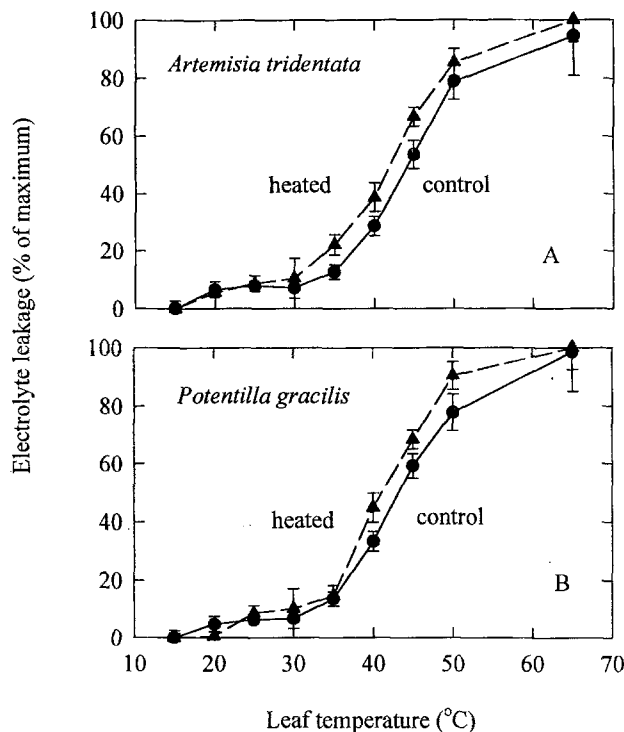


Fig. 3 Electrolyte leakage by heat-treated leaves from plants growing on control (●), or heated (▲) plots in July 1995. Values are expressed as a percent of maximum electrolyte leakage for leaves treated for 1 h at 70°C. Data are means $\pm$ 1 SE ($n = 5$) for **A** *A. tridentata*, or **B** *P. gracilis*

prediction of the acclimation hypothesis. Specifically, in July, leaves of *A. tridentata* from control plots had a mean LT_{50} of $44.8 \pm 5.2^\circ\text{C}$ (mean $\pm$ SE, $n = 5$), whereas leaves from heated plots had a mean LT_{50} of $42.9 \pm 3.3^\circ\text{C}$. For *P. gracilis*, mean LT_{50} was $46.8 \pm 4.02^\circ\text{C}$ and $43.6 \pm 1.6^\circ\text{C}$ for leaves from control and heated plots, respectively.

Chlorophyll *a* fluorescence from photosystem II (PSII; F_V/F_M) exhibited a biphasic response as treatment temperatures increased from 15°C to 65°C (Fig. 4). For

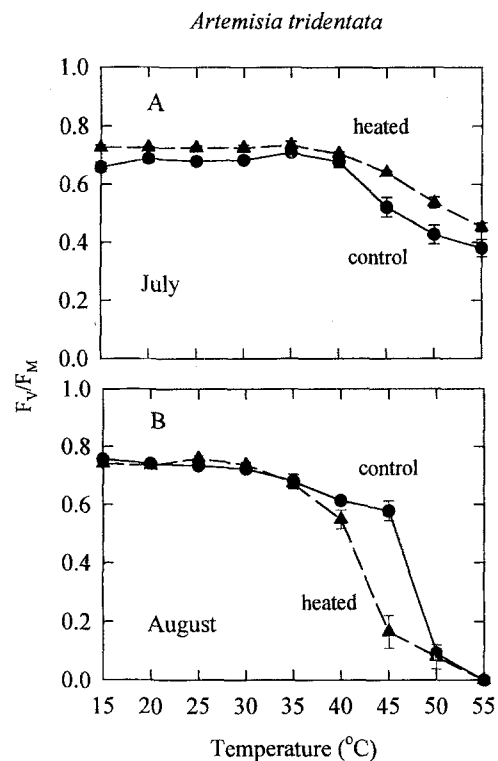


Fig. 4 Quantum yield of photosystem II (PSII) (F_V/F_M) for *A. tridentata* measured as a function of treatment temperature for leaves from plants growing on control (●), or heated (▲) plots in **A** July and **B** August 1995. Data are means $\pm$ 1 SE ($n = 5$)

A. tridentata, F_V/F_M for leaves measured in July was relatively insensitive to treatment temperatures between 15°C and 35°C, but decreased at higher temperatures (Fig. 4A). In August, F_V/F_M was higher for leaves from control plots compared to heated plots, especially at laboratory treatment temperatures greater than 40°C (Fig. 4B). Leaves from both heated and control plots exhibited a more pronounced change in F_V/F_M at high treatment temperatures during August compared to the patterns exhibited in July.

For leaves of *P. gracilis* treated with high-temperatures in the laboratory during July, there was a steady decrease in F_V/F_M between 15°C and 40°C, and the decrease became more pronounced at temperatures above 40°C (Fig. 5A). The decrease in F_V/F_M at temperatures above 40°C was greater in August compared to July (Fig. 5B), but was less than the reduction exhibited for *A. tridentata*. This occurred because F_V/F_M at 65°C in July was lower for *P. gracilis* compared to *A. tridentata*. To compare the dependence of PSII quantum yield on species, time, and treatment, the values of F_V/F_M at the maximal leaf temperature measured in the field (25°C for *A. tridentata* and 30°C for *P. gracilis*) were analyzed by the three-way ANOVA. The results indicated that there was a very strong month effect suggesting a decrease in F_V/F_M between July and August; there was also a weak month $\times$ treatment interaction indicating a difference in F_V/F_M due to the treatment in July but not in August (Table 1).

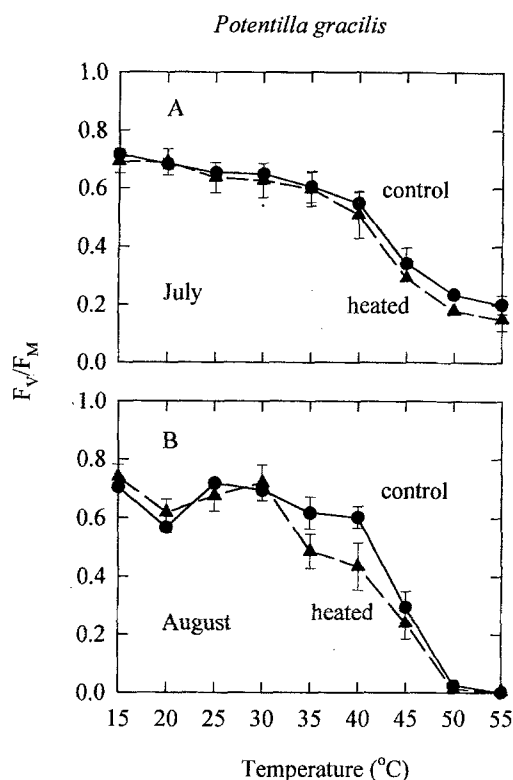


Fig. 5 Quantum yield of PSII (F_v/F_m) for *P. gracilis* measured as a function of treatment temperature for leaves from plants growing on control (●), or heated (▲) plots in **A** July and **B** August 1995. Data are means $\pm$ 1 SE ($n = 5$)

PSII quantum yield at the temperature which caused half-maximal electrolyte leakage (LT_{50}) was also compared for *A. tridentata* and *P. gracilis* (approximately 43°C and 46°C, respectively.) The results of the three-way ANOVA indicate a strong interaction effect of month $\times$ treatment, due to a difference in heated and control values in August, but not in July. There was also a significant species $\times$ month interaction because of a change in F_v/F_m for *P. gracilis* in the two months.

Discussion

High-temperature tolerance was similar (LT_{50} of 43 to 46°C) for the Great Basin dominant species, *A. tridentata*, and the high-elevation meadow species, *P. gracilis*. High-temperature tolerance for a variety of subalpine herbaceous species ranges from 44°C to 54°C, and from 48°C to 54°C for alpine dwarf shrubs (Larcher 1995). For *A. tridentata*, the photosynthetic temperature optimum is around 20°C, corresponding to average leaf temperatures at the time of the year when soil water potential is high enough for root water uptake (Caldwell 1985). In the present study, daily maximum leaf temperatures measured in July and August, the warmest months at this particular site, were 17–25°C below the temperatures causing half-maximal electrolyte leakage (LT_{50}) for *A. tridentata*, and 13–15°C below LT_{50} for *P. gracilis*.

Between 1989 and 1994, daily maximum air temperatures during July and August averaged $24.5 \pm 2.4^\circ\text{C}$ (mean $\pm$ SE, $n = 310$) at this site, and the warmest air temperature recorded was 33°C in 1990 (D. Inouye, personal communication). Therefore, it is unlikely that these two species experience ambient air and leaf temperatures near the measured LT_{50} , and the effects of global warming on membrane integrity and photosynthetic electron transport are not likely to be significant. This suggests that these two species will be able to tolerate a 2.5–5°C change in average air temperatures associated with increased downward infrared radiation flux due to anthropogenic greenhouse gases (Manabe and Wetherald 1986; Schneider 1989). On the other hand, it is not clear how these species will respond to short-term episodes of extreme temperatures such as freezing temperatures in early spring or late autumn (Galen and Stanton 1993, 1995).

High-temperature tolerance measured as electrolyte leakage was higher for leaves from control plots compared to leaves from heated plots, in contrast to the hypothesis that plants under heaters experience an increase in high-temperature tolerance. Plants from geographically and climatically disparate locations generally exhibit differences in the responses of membranes, photosynthesis and respiration to high temperatures (Björkman et al. 1980). In studies under controlled-environment conditions, plants shifted to high day/night air temperatures undergo acclimation whereby gas exchange, metabolic processes, and membrane stability exhibit an upward shift in LT_{50} (Didden-Zopf and Nobel 1982). For example, high-temperature acclimation (measured as the shift in LT_{50} determined by vital stain uptake), averages 5.3°C for several species of cacti after day/night air temperatures in environmental chambers were increased by 10°C, and presumably allows these species to tolerate ambient high temperatures in the field (Smith et al. 1984). For several species of short-statured cacti from the Chihuahuan Desert, high-temperature tolerance measured in the laboratory varies from 60 to 66°C although soil surface temperatures in the field can reach 70°C (Nobel et al. 1986). Under field conditions, interactions between morphology, leaf movements, light intensity, and water status can influence high-temperature tolerance. In this regard, leaves of *Vitis californica* maintain a balance between interception of photosynthetically active radiation and avoidance of high temperature damage by leaf movements on daily and seasonal scales (Gamon and Pearcy 1989).

In the present study, factors other than interception of infrared radiation may have caused the unexpected decline in high-temperature tolerance. For example, there was a greater amount of rainfall during the July study period compared to the period in August, and it is possible that changes in leaf pubescence in response to drying soil may have altered the interactions between light absorption, photosynthesis and leaf temperature (Smith and Nobel 1977; Ehleringer 1980). Also, the heaters caused a significantly earlier melt date compared to con-

trol plots (Harte et al. 1995) resulting in a 10–15 day difference in phenological stage for plants on heated versus control plots (C. Still, M. Loik, J. Harte, unpublished work), and preliminary measurements indicate an increase in leaf reflectance over the course of the summer (J. Harte, unpublished work). Other microclimatic features such as shading by neighboring plants, differences in soil types, and the presence of rocks could have influenced the thermal responses of leaves via influences on albedo and energy exchange; however, detailed measurements of the microclimate near the soil surface have yet to be made.

Daily maximal leaf temperatures were significantly higher for *P. gracilis* than for *A. tridentata*. Anatomical and morphological features of these two species may have contributed to the observed differences in leaf temperatures. For example, *A. tridentata* has small pubescent leaves about 40–50 cm above the ground with their long axis near to vertical, therefore their leaves may be cooler than for *P. gracilis* because of reduced absorptance of solar radiation as well as convective cooling above the boundary layer at the soil surface. On the other hand, *P. gracilis* has larger palmate leaves which are held parallel to the soil surface at a height of 5–10 cm above the ground, so leaves would be heated by direct solar radiation, minimal air movement near the soil surface, and infrared radiative flux from the immediate microenvironment. Also, leaves of *A. tridentata* are covered on both surfaces with trichomes, whereas *P. gracilis* has a white abaxial surface and a green adaxial surface and may account for the observed lower leaf temperatures for plants on heated versus control plots. The reflectance due to trichomes for *A. tridentata* may increase during the summer as leaves age, or as leaves lose water (J. Harte, unpublished work), thus changing the temperature of leaves on a seasonal time scale. Also, leaves of *P. gracilis* roll along their long axis, exposing the white reflective abaxial surface to the environment, thereby reducing leaf temperatures by reflecting shortwave radiation. Leaf area, angle, height above the ground, and the presence of reflective coverings such as trichomes have all been shown to modify the energy budget of leaves (Mooney et al. 1977; Ehleringer 1980), and may account for the observed higher leaf temperatures for *P. gracilis* compared to *A. tridentata*. Such adaptations may be important for maintenance of leaf temperatures below LT_{50} in an environment where transpirational cooling ability is limited during the hottest and driest portion of the year.

The quantum yield of PSII (F_v/F_m) decreased as air temperatures increased beyond 40°C for *A. tridentata* and *P. gracilis* from both control and heated plots. At ambient leaf temperatures, F_v/F_m was greater in August compared to July, possibly due to differences in leaf temperatures related to water content, or leaf absorptance and reflectance. Leaf pubescence has been shown to influence the thermal balance of leaves of many species (Melcher et al. 1994), and can change over the course of a growing season (Mooney et al. 1977). For high treatment temperatures in the laboratory, F_v/F_m was lower

for plants exposed to the IR heating treatment compared to control plots without IR heaters. These differences may be due to the fact that the snowmelt date is advanced by 10–15 days under the heaters, and many species emerge from dormancy and initiate growth in response to the pulse of snowmelt water, changes in soil surface temperature, or exposure to sunlight following snowmelt (Harte et al. 1995). Therefore, differences in F_v/F_m may reflect seasonal or age-related changes in leaves, such as changes in xanthophyll cycle-associated energy dissipation over time (Adams and Demmig-Adams 1994). An energy budget analysis for leaves of *A. tridentata* and *P. gracilis* on control and heated plots would help to understand the implications of morphology and pubescence on leaf temperatures and thermal tolerance.

Thermal tolerance for leaves of *A. tridentata* and *P. gracilis* may have been influenced by interactions with water stress and light intensity (Berry and Björkman 1980). PSII reaction centers are susceptible to high temperatures, however thermal tolerance for potato and tomato measured by chlorophyll fluorescence can be enhanced by 5°C after exposure to water stress (Havaux 1992). On the other hand, increases in osmotic pressure accompanying drought cause the high temperature tolerance to decrease by about 2.5°C for seedlings of the desert plant species *Agave deserti* and *Ferocactus acanthodes* (Nobel 1984). In the present study, thermal tolerance was lower for leaves from heated compared to control plots, and heated plot soils have lower water content versus control plot soils (Harte et al. 1995), however the present study shows that there was a reduction of thermal tolerance for leaves from heated compared to control plots. The thermal stability of PSII can also be influenced by the interaction between photon flux density (PFD) and high temperatures, as they simultaneously occur in the field. For *Vitis californica*, high PFD levels and high temperatures interact to lower the quantum yield of PSII (Gamon and Pearcy 1990), and this species exhibits leaf movements that maximize the interception of sunlight while at the same time maintaining leaf temperatures below lethal levels (Gamon and Pearcy 1989). In the present study, leaves were collected between 0600 and 0630 hours, therefore they were not exposed to high levels of PFD immediately prior to the high-temperature treatments in the laboratory. Also, the high-temperature treatments were conducted in the dark for at least 1 h (Havaux 1992) thereby allowing for the down regulation of PSII. Further experiments are needed to examine the interactive effects of PFD, water stress and high temperatures on the thermal tolerance for leaves of *A. tridentata* and *P. gracilis* under the climate change manipulation used in the present study.

Differences in the life history strategies of *A. tridentata* and *P. gracilis* may influence how they respond to a warmer and drier climate scenario in the future, and may be more important than effects of increased temperatures on membrane integrity and photosynthesis (as in this study) for species composition in this ecosystem.

For example, *A. tridentata* retains some leaves over the winter and has a low photosynthetic temperature optimum which allows it to rapidly resume growth in response to the pulse of snowmelt water in late spring (Weber 1976; Caldwell 1985). Also, extension of the growing season by 10–15 days due to advanced snowmelt may have dramatic effects on plant phenology (Galen and Stanton 1993, 1995) and exposure of plants to enhanced IR to a clear nighttime sky may result in enhanced freezing damage in spring and autumn. *P. gracilis* is a perennial forb that overwinters as a thickened root system, therefore it must mobilize reserves and grow leaves and inflorescences before the onset of summer drought (Allen-Diaz 1991). *A. tridentata* has photosynthetic inflorescences that are not reliant on vegetative leaves for growth, which increases its capacity to produce flowers and achenes during drought (Evans et al. 1990). Whereas a greater number of *A. tridentata* seedlings were observed on heated versus control plots (Harte and Shaw 1995), no seedlings of *P. gracilis* have been found on any of the plots. Both species produce large numbers of small seeds or achenes that are wind-dispersed, but it is presently unclear how a future warmer and drier soil microclimate due to climate change will affect reproductive effort, seed dispersal and seedling recruitment (Leishman et al. 1992). For many ecosystems in the western United States, establishment, growth, and reproduction within populations is limited by the ability of seedlings to survive in the abiotic environment near the soil surface (Smith and Nowak 1990), so species-specific differences in seedling tolerance of abiotic stress may be more important for seedling recruitment (compared to adults) and may influence the species composition of this ecosystem in a future warmer and drier climate.

Despite species-specific differences in ambient leaf temperature, high-temperature tolerance was similar for both *A. tridentata* and *P. gracilis*, suggesting that small increases in air temperatures due to anthropogenic greenhouse gases will not result in the extirpation of either of these species at this study site. Leaves from heated plots were less thermal tolerant compared to leaves from control plots, contrary to the hypothesis that acclimation will cause an increase in thermal tolerance in response to increased ambient air temperatures. Also, preliminary measurements of leaf reflectance suggest that morphological responses to heating and drying may be more important than physiological responses for plant distributions at ecosystem borders in a future warmer climate. Furthermore, tolerance of freezing temperatures in the spring and autumn, as well as the ability of seedlings to establish in a future warmer and drier climate, may be more important for species' distributions than are the responses of adults to high-temperatures (Loik and Nobel 1993; Jacobos and Romme 1993; Harte and Shaw 1995). Also, ecosystem-level effects of climate change, such as changes in soil microclimate, as well as nutrient turnover rates and availability, may be important for determining plant species and community-level responses to climate change.

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