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Growth and leaf physiology of monkeyflowers with different altitude ranges

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Abstract Every species is limited both geographically and ecologically to a subset of available habitats, yet for many species the causes of distribution limits are unknown. Temperature is thought to be one of the primary determinants of species distributions along latitudinal and altitudinal gradients. This study examined leaf physiology and plant performance under contrasting temperature regimes of sister species of monkeyflower, *Mimulus cardinalis* and *Mimulus lewisii* (Phrymaceae), that differ in altitude distribution to test the hypothesis that temperature is the primary determinant of differences in fitness versus altitude. Each species attained greatest aboveground biomass, net photosynthetic rate, and effective quantum yield of photosystem II when grown under temperatures characteristic of the altitudinal range center. Although both species exhibited greater stem length, stomatal conductance, and intercellular CO_2 concentration in hot than in cold temperatures, these traits showed much greater reductions under cold temperature for *M. cardinalis* than for *M. lewisii*. Survival of *M. lewisii* was also sensitive to temperature, showing a striking decrease in hot temperatures. Within each temperature regime, the species native to that temperature displayed greatest growth and leaf physiological capacity. Populations from the altitude range center and range margin of each species were used to examine population differentiation, but central and marginal populations did not differ in most growth or leaf physiological responses to temperature. This study provides evidence that *M. cardinalis* and *M. lewisii* differ in survival, growth, and leaf physiology under temperature regimes characterizing their contrasting low and high altitude range centers, and suggests that the species' altitude range limits may arise, in part, due to metabolic limitations on growth that ultimately decrease survival and limit reproduction.

Keywords Range boundary · Distribution limit · Altitude · Temperature · Photosynthesis

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Introduction

No species occupies an unlimited area. Rather, every species is limited both geographically and ecologically to a subset of available habitats. Understanding the patterns and processes governing the distribution of species is a central goal of ecology, yet for many species the causes of distribution limits are unknown. Even a mechanistic understanding of the relationship between environmental variables and distribution limits presents an evolutionary conundrum: why does natural selection not continually improve adaptation to limiting environmental variables and overcome current distribution limits (Antonovics 1976; Kirkpatrick and Barton 1997; Holt and Keitt 2005; Holt et al. 2005)? To answer this question, we must identify which environmental variables exert natural selection and which traits are the target of natural selection at and beyond the range boundary.

Identifying the causal mechanisms of distribution limits is challenging because environmental variables are often spatially correlated and dissecting organismal responses to even a single environmental variable is a complex task. However, temperature is thought to be one of the primary determinants of species distributions along latitudinal and altitudinal gradients. Evidence for the role of temperature in distribution limits comes from a diverse array of studies, including correlations between isotherms and distribution boundaries (e.g., McNab 1973; Grace 1987; Root 1988), temperature tolerance and latitudinal or altitudinal distribution (e.g., Loik and Nobel 1993; Cunningham and Read 2002; Kimura

2004), extreme temperature events and periods of reproductive failure or high mortality at range boundaries (e.g., Silberbauer-Gottsberger et al. 1977; Jarvinen and Vaisanen 1984; Olmsted et al. 1993; Mehlman 1997), and studies of latitudinal and altitudinal changes in response to both historic and recent global warming trends (e.g., Huntley 1991; Parmesan et al. 1999; Hughes 2000; Thomas et al. 2001). Further, temperature exerts a ubiquitous influence on many important cellular properties such as the rate of enzymatic reactions, protein conformations and membrane stability.

Temperature may influence species distributions in a multitude of ways, from imposing direct lethal limits to regulating processes of growth, development and reproduction (Cossins and Bowler 1987; Orfanidis 1993; Molenaar and Breeman 1994; Sewell and Young 1999). Study of the sensitivity of metabolic processes to temperature can elucidate the mechanisms underlying limitation at distribution boundaries (Heller and Gates 1971; McNab 1973; Criddle et al. 1994; Anthony and Connolly 2004). For plants, measurements of leaf physiological parameters such as instantaneous net photosynthetic rate (A_{net}) and chlorophyll fluorescence offer a way to detect functional limitations on plant metabolism imposed by environmental factors (Bolhar-Nordenkampf and Öquist 1993; Llorens et al. 2004).

This study examines leaf physiology and whole-plant performance under contrasting temperature regimes of sister species of monkeyflower, *Mimulus cardinalis* and *Mimulus lewisii* (Phrymaceae), that differ in altitude distribution (Hickman 1993; Beardsley et al. 2003). The use of phylogenetic hypotheses to identify closely related species is important when testing the adaptive significance of traits and trait divergences (Monson 1996; Ackerly et al. 2000). In the context of range limits, the study of closely related species partitioning an environmental gradient is valuable because evolution from a common ancestor toward each species' native environment has occurred, allowing examination of what causes and constrains adaptation to different ends of the gradient.

Reciprocal transplants of *M. cardinalis* and *M. lewisii* demonstrate that each species has high growth, survival and reproduction at its altitude range center and lower growth, survival and reproduction at its altitude range boundary and at altitudes beyond its present altitude range (Angert and Schemske 2005). Here I test the hypothesis that temperature is the primary determinant of these differences in plant fitness using temperature regimes measured in the field to simulate natural low and high altitude environments during the growing season. To examine adaptive differentiation among populations in response to natural selection at the range margin, populations from the altitude range center and range margin of each species were used as source material for the experiment. Specifically, this study asks:

1. Do *M. cardinalis* and *M. lewisii* differ in performance under temperature regimes characterizing their contrasting low and high altitude range centers?
2. Do differences in leaf physiological traits underlie differences in performance under contrasting temperature regimes?
3. Are populations from the range center and range margin of each species differently adapted to temperature?

Materials and methods

Study system

Mimulus cardinalis and *M. lewisii* (Phrymaceae) are rhizomatous perennial herbs that grow along seeps and stream banks in western North America. The species are self-compatible and animal pollinated (Hiesey et al. 1971; Schemske and Bradshaw 1999). *M. cardinalis* occurs from southern Oregon to northern Baja California, Mexico and from the coast of California inland to Arizona and Nevada. *M. lewisii* is composed of two races, a northern form occurring from southern coastal Alaska to southern Oregon and eastward to the Rocky Mountains, and a southern form, occurring primarily in the Sierra Nevada Mountains of California (Hiesey et al. 1971; Hickman 1993; Beardsley et al. 2003). The two races are partially incompatible, and recent phylogenetic analysis suggests that the two races are sister to one another and together are sister to *M. cardinalis* (Beardsley et al. 2003). Here I study only the Sierran form of *M. lewisii*.

M. cardinalis and *M. lewisii* segregate by altitude, with *M. cardinalis* occurring from sea level to 2,400 m and *M. lewisii* occurring from 1,200 to 3,100 m in California (Hickman 1993). In the Yosemite National Park region where this research was conducted, the species co-occur on larger watercourses between 1,200 and 1,500 m altitude (Angert 2005). Although the published Californian distributions of *M. cardinalis* and *M. lewisii* extend to 2,400 and 3,100 m, respectively, repeated attempts to locate extant populations at these upper limits in the Yosemite region were unsuccessful. Experimental gardens planted at 415, 1,400, 2,395 and 3,010 m on the western slope of the Sierra Nevada Mountains demonstrate that each species is most fit at its altitude range center (415 m for *M. cardinalis*, 2,395 m for *M. lewisii*), less fit at the mid altitude range boundary, and unable to both survive and reproduce when transplanted to altitudes beyond its current range (Angert and Schemske 2005). For *M. lewisii*, reduced fitness at low altitudes results primarily from high mortality within the first growing season. For *M. cardinalis*, reduced fitness at high altitudes is due primarily to limited growth and reproduction (Angert and Schemske 2005).

Genetic material: population collection and crossing design

Seeds from eight plants in each of four populations per species were collected in September 1999 along an

zaltitude gradient from 590 to 2,750 m between 37.49 and 37.95°N latitude (Supplementary Appendix). For each species, the chosen populations represent two locations from central within the range (low altitude for *M. cardinalis*, high altitude for *M. lewisii*) and two locations from the range margin (mid altitude for both species). One plant from each field-collected family was grown to flowering in the University of Washington greenhouse under standard greenhouse conditions. The eight plants from each population were crossed with one another so that each plant served as sire or dam once with no self- or reciprocal pollinations, generating four independent full-sib families. Pollinations were performed by collecting all of the pollen from one flower with a flat toothpick and fully saturating the stigma of one flower. Seeds from four pollinations per full-sib family were pooled. These crosses generated outcrossed seeds from each population in a uniform environment to be used for controlled environment studies.

Chamber conditions

Two incubators (model I-36LL; Percival Scientific, Perry, Iowa) were programmed to simulate low and high altitude temperature regimes for 60 days. To determine representative low and high altitude temperatures regimes during the growing season, data loggers (Hobo Pro Temp/External Temp; Onset Computer, Bourne, Mass.) recorded temperatures at low (415 m, near Jamestown, California) and high (2,395 m, at the White Wolf Ranger Station in Yosemite National Park, California) altitude reciprocal transplant gardens during June–September 2002. These altitudes characterize the range center of *M. cardinalis* and *M. lewisii*, respectively. Two data loggers at each site were mounted at plant height and shielded from direct sunlight with reflective covers.

Incubator temperature programs were set to reflect July average daily maximums and minimums at each altitude, with occasional temperature spikes or dips occurring at natural frequency (Table 1). July temperatures were used because plant growth is at its peak at both low and high altitude during this time. The cold, high altitude chamber was set for a 23°C daytime maximum and 4°C nighttime minimum, with one 0°C freeze on night 15 and a second −2°C freeze on night 36. Although few plants showed visible signs of tissue injury after exposure to 0°C, many plants were injured by the second, −2°C freeze. To quantify tissue damage, I estimated the percentage of total leaf tissue damaged on each plant. The hot, low altitude chamber was set for a 35°C daytime maximum and 15°C nighttime minimum, with 42°C daytime maximums on days 18, 30, and 51. Daily maximum and minimum temperatures were held for 4 h each with gradual ramps between maximum and minimum temperatures. Incubators were programmed for 14/10 h day/night cycles with the maximum possible light output, 200 μmol photons m^{-2} s^{-1} during the daytime period. In natural environments *M. cardinalis* and *M. lewisii* grow in a range of light conditions from full sun on open gravel bars to full shade along riparian corridors (personal observation).

Four replicates of each full-sib family were sown in the Michigan State University greenhouse in January 2003. Five weeks after sowing, seedlings were transferred to either the hot or the cold incubator, for a total of 64 plants per temperature treatment (2 species×4 populations/species×4 families/population×2 replicates per family). Seedlings were placed in random order within wire frames, and wire frames were placed in trays for sub-irrigation within the incubator. Frames were rotated several times per week to minimize position effects. Plants remained in each incubator for 60 days.

Leaf physiological trait measurements

Simultaneous gas exchange and chlorophyll fluorescence measurements were performed prior to all extreme temperature events (day 15) and following the last extreme temperature event for each treatment (day 53 hot, day 37 cold) with a portable open-flow gas exchange system equipped with leaf chamber fluorometer and CO_2 mixer (Li-Cor 6400; Li-Cor, Lincoln, Neb.). The difference in time period preceding final gas exchange measurements reflects natural differences in growing season length at low and high altitudes. However, measurements made after the second extreme heat spike did not produce qualitatively different results, demonstrating that the patterns presented here are not unduly influenced by the length of exposure to low versus high temperatures. Measurements were made at midday during the 4-h daily temperature maximum so that chamber temperature settings were not ramping throughout the course of the measurements. Because of sub-irrigation, plants were not water limited and gas exchange rates remained high at midday. This is realistic because *M. cardinalis* and *M. lewisii* normally inhabit

Table 1 July temperatures recorded in reciprocal transplant gardens at 415 and 2,395 m

Altitude (m)	Temperature (°C)					
	Average daily maximum	Maximum daily maximum	Days >40	Average daily minimum	Minimum daily minimum	Days <0
415	34.48	41.67	4	14.80	11.67	0
2,395	22.78	27.91	0	4.28	−1.97	2

stream banks or permanent seeps. The youngest fully expanded leaf (second or third node) was enclosed within the leaf chamber. Instantaneous A_{net} (μmol CO_2 m^{-2} s^{-1}), stomatal conductance to water vapor (g_s, mol H_2O m^{-2} s^{-1}), and the ratio of intercellular to air CO_2 concentration (C_i/C_a) were determined at the light intensity in which leaves developed, 200 μmol photons m^{-2} s^{-1}, a reference CO_2 concentration of 400 μmol mol^{-1}, a flow rate of 500 μmol s^{-1}, and block temperatures of 35°C (hot chamber) or 23°C (cold chamber). Vapor pressure deficit (VPD) and relative humidity (RH) within the leaf chamber were not controlled. Leaf temperature (°C) was measured with a fine wire thermocouple on the underside of each leaf. Calculations of g_s assumed a 0.5 ratio of conductances on the upper versus lower side of each leaf. Before statistical analysis, g_s at high temperatures were reduced by 2% per °C above 23°C to normalize for decreased water viscosity with increased temperature (Tyree et al. 1995; Sack et al. 2002). Steady-state fluorescence (F_s) and maximal light-adapted fluorescence during a saturating flash of light (F_m') were also measured simultaneously with gas exchange. These fluorescence parameters were used to calculate the effective quantum yield of photosystem II [$\Phi_{PSII} = (F_m' - F_s)/F_m'$].

Measurement of whole-plant performance

To quantify overall plant performance in each temperature environment, I measured final survival and growth. Traits were measured on day 60, at which time plants were harvested to measure total stem length, number of nodes per stem, and aboveground biomass. Stem length and node number were highly correlated (*M. cardinalis*, Pearson's $r = 0.95$, $P < 0.0001$; *M. lewisii,* $r = 0.79$, $P < 0.0001$), whereas stem length and biomass were less so (*M. cardinalis*, $r = 0.78$, $P < 0.0001$; *M. lewisii*, $r = 0.21$, $P = 0.11$), thus I present only stem length and biomass data.

Statistical analysis

I performed mixed model ANOVA for both temperatures and species combined to model variation in each trait (A_{net}, Φ_{PSII}, normalized g_s, C_i/C_a, aboveground biomass, and height) with respect to growth temperature, species, altitude of origin nested within species, population of origin nested within altitude, family nested within population, and all interactions. I also performed mixed model ANOVA within each temperature treatment to examine the effects of species, population, altitude of origin, and family on leaf temperature. g_s and aboveground biomass were log-transformed to meet ANOVA assumptions. Temperature, species, and altitude of origin were considered as fixed effects, whereas population and family were considered as random effects. To evaluate the significance of fixed effects, I used type III estimable functions, which tolerate unbalanced samples, with denominator *df* obtained by Satterthwaite's approximation. Intraspecific differences between temperatures and interspecific differences within each temperature were evaluated by independent contrasts with a single *df*. Likelihood-ratio tests (comparing each reduced model to the full model including all effects) were used to evaluate the significance of all random effects.

To examine variation in post-freeze tissue damage, I performed mixed model ANOVA as described above, with the following exceptions. Differences in post-freeze tissue damage were examined within the cold temperature regime only, thus the model included only species, altitude, population, and family effects. For this model I also included position within the incubator as a covariate to account for an unexpected temperature gradient from the front to the back of the chamber during the freeze. All analyses were implemented with PROC MIXED in SAS, version 8.2 (SAS Institute, Cary, N.C.).

I used logistic regression to analyze variation in survival with respect to growth temperature and species (PROC LOGISTIC, SAS, version 8.2; SAS Institute). I did not model the effects of population within species or the interaction of growth temperature and species because a lack of variation in some cells of the factorial design (e.g., 100% survival of *M. cardinalis* in the hot temperature treatment) caused model convergence problems.

Results

Leaf physiological traits

Prior to extreme temperature events, interspecific differences in A_{net} and Φ_{PSII} were not present and interspecific differences in g_s and C_i/C_a were small (Table 2, Fig. 1). After prolonged growth in each temperature regime, the main effect of temperature affected g_s and C_i/C_a but not A_{net} or Φ_{PSII}, and the main effect of species only marginally affected photochemical efficiency (Table 2). However, species by temperature interactions affected all four parameters after prolonged growth in each temperature regime, indicating that the species differ in their leaf physiological response to temperature stress (Table 2). Altitude of origin did not affect any leaf physiological trait after temperature stress, and the altitude by temperature interaction affected *M. cardinalis* g_s and C_i/C_a only, indicating that differentiation in leaf physiological traits between range margin and range center populations is low (Table 2). The random effects of population, family, and their interactions with temperature did not affect leaf physiological traits (data not shown).

The species main effect in the model of final Φ_{PSII} indicated that *M. cardinalis* had a marginally higher light-adapted photochemical efficiency than *M. lewisii*. Both species attained higher A_{net} and Φ_{PSII} when grown under the temperature regime of their altitude range center, although the difference was only marginally significant for the A_{net} of *M. lewisii* (Fig. 1a, b, Table 3).

Table 2 Linear mixed model ANOVA summary for four leaf physiological traits [instantaneous net photosynthetic rate (A_{net}), effective quantum yield of photosystem II (Φ_{PSII}), stomatal conductance to water vapor (g_s), and ratio of intercellular to air CO_2 concentration (C_i/C_a)] measured before (*Pre*) and after (*Post*) extreme temperature events. *F*-tests for fixed effects constructed by SAS MIXED procedure, with denominator *df* obtained from the Satterthwaite approximation and indicated *in parentheses* below each *F*-value. All random effects (population nested within altitude of origin, family nested within population, and their interactions with temperature) were estimated to be zero or near zero and were not significant

Time	Trait	*F* for fixed sources of variation				
		Temperature	Species	Species×temperature	Altitude (species)	Altitude ×temperature (species)
	Numerator *df*	1	1	1	2	2
Pre	A_{net}	92.25****	0.49	0.25	2.47	0.61
		(99.5)	(3.58)	(99.5)	(3.14)	(97.7)
Pre	Φ_{PSII}	0.02	0.28	6.48*	0.06	2.27
		(99.5)	(4.1)	(99.5)	(3.72)	(98)
Pre	g_s[a]	13.06***	50.33***	4.04*	4.17*	2.68†
		(100)	(100)	(100)	(100)	(100)
Pre	C_i/C_a	16.49****	34.89**	5.42*	6.08	0.69
		(99.8)	(3.17)	(99.8)	(2.26)	(97.1)
Post	A_{net}	2.13	0.12	27.03**	0.08	0.78
		(3.71)	(3.78)	(3.71)	(3.78)	(3.69)
Post	Φ_{PSII}	1.64	5.90†	44.20***	0.37	1.11
		(56.5)	(3.83)	(56.5)	(3.81)	(55.7)
Post	g_s[a]	94.30****	0.04	56.40****	1.35	4.30*
		(57.6)	(5.24)	(57.6)	(5.21)	(56.80)
Post	C_i/C_a	66.59****	1.32	16.29***	2.99	6.91**
		(56.2)	(4.80)	(56.2)	(4.78)	(55.3)

$^{\dagger}P < 0.10$, $*P < 0.05$, $**P < 0.01$, $***P < 0.001$, $****P < 0.0001$

[a] g_s was corrected for temperature-induced changes in water viscosity and log-transformed prior to analysis

The main effect of temperature indicated that g_s and C_i/C_a were higher in the hot temperature regime than in the cold temperature regime. Greater g_s and C_i/C_a were detected at high temperature despite greater VPD and lower RH (*M. cardinalis*, VPD_{hot}, 2.13 ± 0.05; VPD_{cold}, 1.98 ± 0.05; RH_{hot}, $19.95 \pm 0.32\%$; RH_{cold}, $31.39 \pm 0.46\%$; *M. lewisii*, VPD_{hot}, 3.06 ± 0.15; VPD_{cold}, 1.80 ± 0.05; RH_{hot}, $14.35 \pm 0.45\%$; RH_{cold}, $33.87 \pm 0.59\%$). After temperature stress, *M. cardinalis* g_s was much lower in cold temperatures than in hot, whereas *M. lewisii* g_s was not significantly different between temperature regimes (Fig. 1c, Table 3). Both species displayed higher C_i/C_a in hot than in cold temperatures, but *M. cardinalis* showed a much larger decrease from hot to cold than *M. lewisii* (Fig. 1d, Table 3). Within the hot temperature regime, *M. cardinalis* displayed greater A_{net}, Φ_{PSII}, and g_s than *M. lewisii* after exposure to temperature stress (Fig. 1, Table 3). Within the cold temperature regime, *M. lewisii* displayed greater A_{net}, g_s, and C_i/C_a than *M. cardinalis* after exposure to temperature stress (Fig. 1, Table 3).

Populations of *M. cardinalis* originating from the low altitude range center differed from populations originating from the mid altitude range boundary in the response of g_s and C_i/C_a to temperature. Low altitude populations showed greater decreases in g_s and C_i/C_a from hot to cold temperatures than mid altitude populations (Table 4), suggesting that mid altitude populations were more adversely affected by hot temperatures than low altitude populations or were not as light-limited as low altitude populations in hot temperatures. However, no other *M. cardinalis* traits and no *M. lewisii* traits displayed a pattern consistent with adaptive differentiation between range center and range margin populations (Table 4).

Within the cold temperature regime, *M. cardinalis* maintained a significantly higher leaf temperature than *M. lewisii* ($F_{1,17.5} = 4.67$, $P = 0.04$). Although statistically significant, interspecific differences in leaf temperature within the cold temperature regime averaged only 0.6°C and leaf temperature of both species was near ambient temperature. Within the hot temperature regime, *M. cardinalis* maintained a significantly lower leaf temperature than *M. lewisii* ($F_{1,43} = 38.02$, $P < 0.0001$). At high temperatures, high conductance enabled *M. cardinalis* to maintain a leaf temperature approximately 10°C below ambient, whereas *M. lewisii* leaf temperature was approximately 7°C below ambient.

Post-freeze tissue damage

Neither species was visibly damaged following the 0°C freeze. Individuals of both species were visibly injured by the −2°C freeze, but *M. cardinalis* exhibited an average of 68.1% visible leaf tissue damage, whereas *M. lewisii* exhibited an average of only 46.3% damage (mixed model ANOVA: species, $F_{1,55} = 14.77$, $P = 0.0003$).

Whole plant performance

Table 5 gives the results of linear mixed model analyses of stem length and log-transformed aboveground biomass. The main effect of temperature affected stem

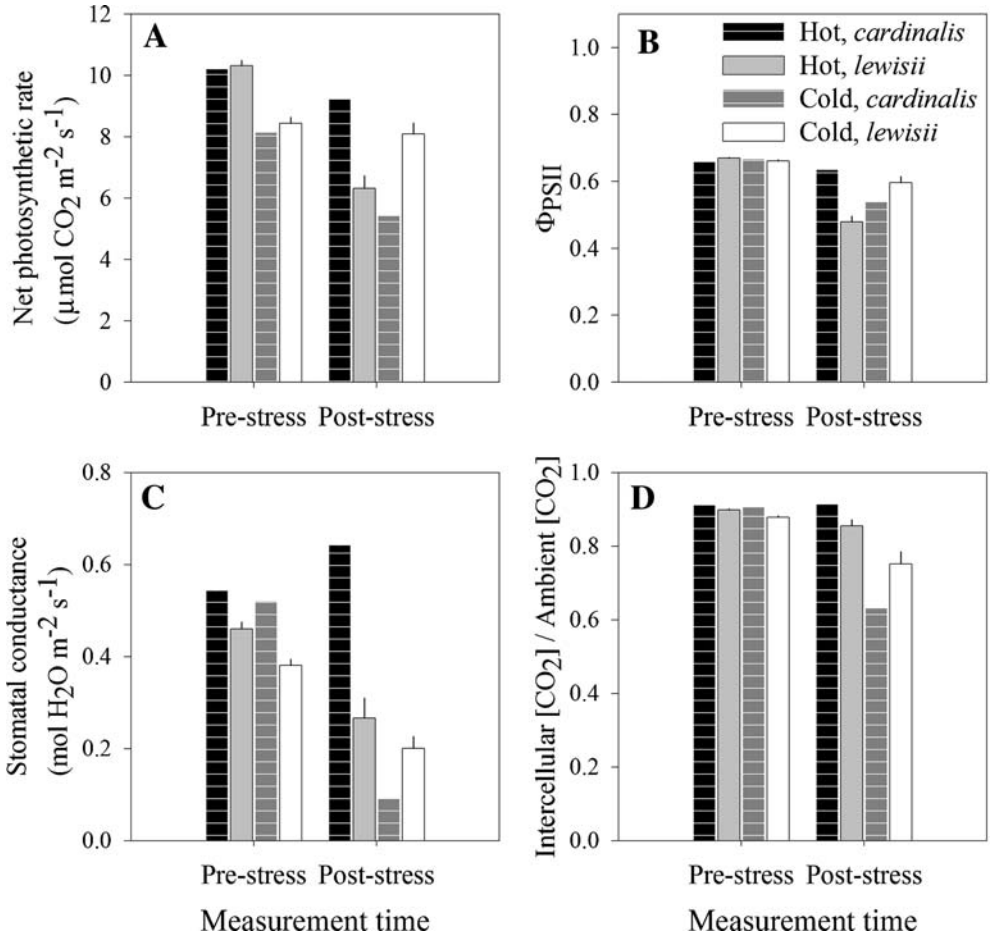

Fig. 1 Species' mean ± SE **a** net photosynthetic rate, A_{net} (μmol CO_2 m^{-2} s^{-1}), **b** effective quantum yield [$\Phi_{PSII} = (F_m' - F_s)/F_m'$, where F_s is steady-state fluorescence and F_m' is maximal light-adapted fluorescence during a saturating flash of light], **c** stomatal conductance, g_s (mol H_2O m^{-2} s^{-1}, corrected for decreased water viscosity at high temperature), and **d** intercellular:ambient [CO_2], C_i/C_a, when measured prior to extreme temperature events (*Pre-stress*) and following prolonged growth in each temperature regime (*Post-stress*)

length, but not aboveground biomass. The main effect of species and the interaction between species and growth temperature affected both traits. Altitude of origin, population, family and their interactions with temperature did not affect either growth trait.

The main effect of temperature in the model of stem length indicated that length was higher in the hot temperature regime than in the cold temperature regime. The main effect of species indicated that *M. cardinalis* had greater stem length and aboveground biomass than *M. lewisii*. However, the interaction between species and temperature indicated that the species differed in growth response to temperature. Both species achieved greater stem length in hot than in cold temperatures, but the magnitude of difference between temperatures was much greater for *M. cardinalis* than for *M. lewisii* (Fig. 2a). Further, within the cold treatment, *M. lewisii* stem length was greater than *M. cardinalis* stem length (Table 6). Although *M. cardinalis* aboveground biomass was greater than *M. lewisii* biomass in both temperatures, *M. cardinalis* aboveground biomass was greater in hot than in cold temperatures, whereas *M. lewisii* biomass was greater in cold than in hot temperatures (Fig. 2b, Table 6).

Species and growth temperature significantly affected the likelihood of survival (logistic regression:

Table 3 Single *df* independent contrasts of least square means testing the null hypothesis that the difference between two means is equal to zero for measurements conducted after extreme temperature events. For abbreviations, see Table 2

Trait	Intraspecific contrasts		Interspecific contrasts	
	Mimulus cardinalis hot vs. *M. cardinalis* cold	*Mimulus lewisii* hot vs. *M. lewisii* cold	*M. cardinalis* hot vs. *M. lewisii* hot	*M. cardinalis* cold vs. *M. lewisii* cold
A_{net}	0.0123	0.0601	0.0201	0.0376
Φ_{PSII}	0.0002	< 0.0001	0.0008	0.1309
g_s [a]	< 0.0001	0.1393	0.0004	0.0005
C_i/C_a	< 0.0001	0.0065	0.1560	0.0080

[a] g_s was corrected for temperature-induced changes in water viscosity and log-transformed prior to analysis

Table 4 Population means (SE) for four leaf physiological traits[a] measured after extreme temperature events and two final growth traits[b]. For abbreviations, see Table 2

Species	Elevation	Population	Hot						Cold					
			Leaf physiology				Growth		Leaf physiology				Growth	
			A_{net}	Φ_{PSII}	g_s	C_i/C_a	Length	Biomass	A_{net}	Φ_{PSII}	g_s	C_i/C_a	Length	Biomass
M. cardinalis	Low	Mariposa	9.55 (0.36)	0.67 (0.01)	0.78 (0.07)	0.92 (0.00)	50.4 (2.0)	3.80 (0.34)	6.71 (1.14)	0.53 (0.10)	0.09 (0.02)	0.68 (0.03)	10.4 (1.7)	1.51 (0.25)
		Bear	9.50 (0.38)	0.64 (0.01)	0.68 (0.04)	0.92 (0.00)	49.9 (1.7)	5.35 (0.40)	2.80 (0.31)	0.53 (0.04)	0.02 (0.00)	0.23 (0.15)	12.5 (0.9)	1.36 (0.26)
	Mid	Tenaya	8.35 (0.42)	0.59 (0.02)	0.59 (0.07)	0.91 (0.01)	43.1 (1.7)	2.72 (0.43)	5.07 (1.09)	0.53 (0.05)	0.10 (0.02)	0.72 (0.05)	10.5 (1.4)	1.86 (0.15)
		S. Fork	9.59 (0.22)	0.64 (0.01)	0.62 (0.03)	0.91 (0.00)	45.4 (1.4)	4.24 (0.40)	8.92 (-)	0.63 (-)	0.20 (-)	0.78 (-)	7.5 (1.2)	1.53 (0.22)
M. lewisii	Mid	S. Fork	7.48 (0.74)	0.50 (0.02)	0.27 (0.09)	0.83 (0.04)	28.1 (2.2)	0.57 (0.11)	8.59 (0.37)	0.62 (0.01)	0.14 (0.02)	0.71 (0.04)	17.7 (3.4)	1.05 (0.23)
		Tamarack	5.03 (0.23)	0.45 (0.03)	0.20 (0.06)	0.86 (0.03)	25.2 (2.5)	0.51 (0.10)	7.65 (1.09)	0.60 (0.04)	0.22 (0.06)	0.79 (0.06)	19.4 (3.3)	0.98 (0.20)
	High	Snow	6.27 (-)	0.37 (-)	0.28 (-)	0.87 (-)	21.4 (1.9)	0.35 (0.06)	8.04 (0.55)	0.56 (0.06)	0.25 (0.07)	0.74 (0.12)	15.8 (1.9)	1.05 (0.13)
		Warren Fork	6.21 (0.69)	0.50 (0.03)	0.34 (0.10)	0.88 (0.02)	21.1 (2.5)	0.62 (0.08)	8.06 (0.96)	0.60 (0.03)	0.19 (0.05)	0.77 (0.04)	13.5 (1.7)	0.75 (0.12)

[a] A_{net} (μmol CO_2 m^{-2} s^{-1}), $\Phi_{PSII} = (F_m' - F_s)/F_m'$, g_s (mol H_2O m^{-2} s^{-1}, corrected for decreased water viscosity at high temperature, C_i/C_a (intercellular:ambient [CO_2])

[b] Final growth traits are stem length (*Length*, cm) and aboveground biomass (*Biomass*, g)

Table 5 Linear mixed model ANOVA summary for stem length and log-transformed aboveground biomass (*biomass*). *F*-tests for fixed effects constructed by SAS MIXED procedure, with denominator *df* obtained from the Satterthwaite approximation and indicated *in parentheses* next to each *F*-value. All random effects (population nested within altitude of origin, family nested within population, and their interactions with temperature) were estimated to be zero or near-zero and were not significant

Trait	*F* for fixed sources of variation				
	Temperature	Species	Species×temperature	Altitude (species)	Altitude×temperature (species)
Numerator *df*	1	1	1	2	2
Stem length	489.41**** (84.4)	64.78**** (27.4)	219.02**** (84.4)	8.32 (27.4)	1.03 (84.4)
Log (biomass)	2.36 (8)	92.20**** (8)	38.31*** (8)	0.07 (8)	1.85 (8)

***$P < 0.001$, ****$P < 0.0001$

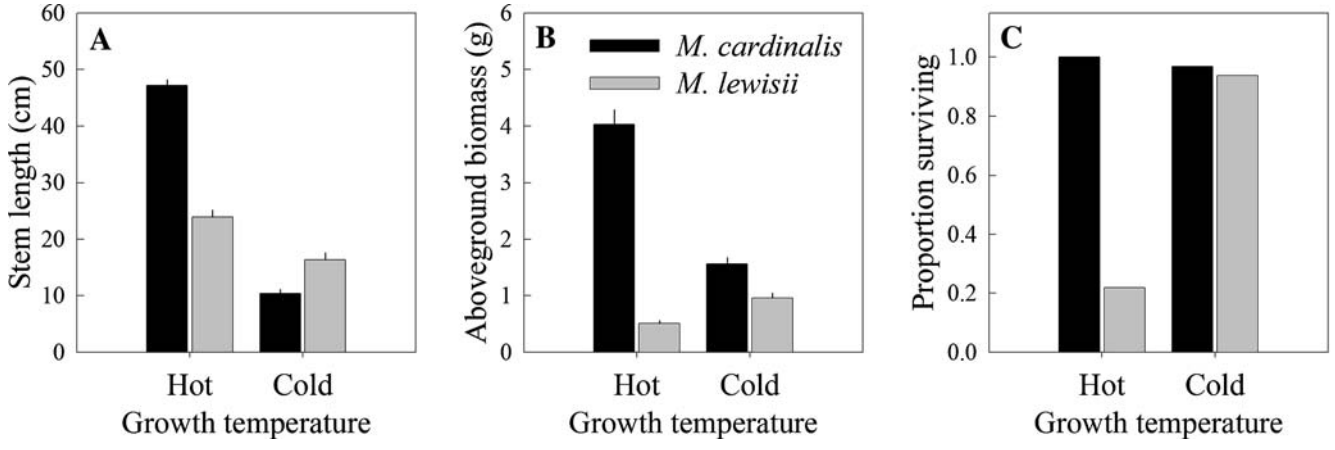

Fig. 2 Species' mean ± SE **a** stem length (cm), **b** aboveground biomass (g), and **c** proportion survival

Table 6 Single *df* independent contrasts of least square means testing the null hypothesis that the difference between two means is equal to zero

Trait	Intraspecific contrasts		Interspecific contrasts	
	M. cardinalis hot vs. *M. cardinalis* cold	*M. lewisii* hot vs. *M. lewisii* cold	*M. cardinalis* hot vs. *M. lewisii* hot	*M. cardinalis* cold vs. *M. lewisii* cold
Length	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Biomass	0.0006	0.0110	< 0.0001	0.0423

species, $\chi^2 = 17.64$, $P < 0.0001$; temperature, $\chi^2 = 21.65$, $P < 0.0001$). In the cold temperature treatment, survival of both species was high. (*M. cardinalis,* 96.9%; *M. lewisii*, 93.8%; Fig. 2c). In the hot temperature treatment, survival of *M. cardinalis* was 100%, whereas *M. lewisii* survival was only 21.9% (Fig. 2c).

Discussion

Interspecific variation in performance versus temperature

Mimulus cardinalis and *M. lewisii* displayed clear differences in performance under contrasting temperature regimes. Each species attained its greatest aboveground biomass when grown under a temperature regime characteristic of its altitudinal range center and displayed reduced mass when grown under a temperature regime beyond its present altitudinal range. Although both species exhibited greater stem lengths in hot than in cold temperatures, the stem length of *M. cardinalis* was more greatly reduced under cold temperatures than was that of *M. lewisii*. Survival of *M. lewisii* was also sensitive to temperature, showing a striking difference of 94% survival in cold temperatures and only 22% survival in hot temperatures. The low survival of *M. lewisii* in hot temperatures did not occur immediately upon exposure to high temperatures, but arose gradually throughout the experiment. Plants appeared to gradually waste away, implicating high respiration rates as the cause of reduced growth and survival (Hiesey et al. 1971). In hot temperatures, *M. cardinalis* displayed greater survival, aboveground biomass and stem length than *M. lewisii*, whereas in cold temperatures, *M. lewisii* displayed greater stem length and resistance to freezing damage than *M. cardinalis*.

Previous studies have also demonstrated that *M. cardinalis* and *M. lewisii* differ in growth response to temperature (Cline and Agatep 1970; Hiesey et al. 1971). Hiesey et al. (1971) compared growth of *M. cardinalis* from the foothills of the Sierra Nevada Mountains in California and *M. lewisii* from subalpine habitat in the Rocky Mountains of Montana under constant warm (30°C) or cold (10°C) temperatures and found that *M. lewisii* grew poorly under hot temperatures whereas *M. cardinalis* was broadly tolerant of both hot and cold temperatures. Cline and Agatep (1970) grew Sierra Nevadan populations of each species (foothills *M. cardinalis*, subalpine *M. lewisii*) under constant day and night temperatures of 3, 7, 11, 15, 19, 23, or 27°C. Both species attained maximum growth at 19°C. However, *M. lewisii* experienced high mortality under hot temperatures but grew twice as fast as *M. cardinalis* under cold temperatures.

The magnitude of the difference in growth and survival between *M. cardinalis* and *M. lewisii* was greater within the hot temperature regime than in the cold. Several factors may have played a role in producing the observed asymmetrical affect of temperature. First, in its natural habitat, particularly at mid altitudes, *M. cardinalis* is likely to experience occasional freezes and cool daytime temperatures late in the growing season, whereas *M. lewisii* is unlikely to encounter extreme high temperatures anywhere within its natural habitat. Second, high light levels in a natural high altitude environment may exacerbate the effects of cold temperature by inducing photoinhibition (Close and Beadle 2003; Sayed 2003), but in our experiment light levels were relatively low, potentially moderating the harmful effect of low temperatures. Finally, at high altitude, mortality of *M. cardinalis* is concentrated over the winter (A. L. Angert and D. W. Schemske, unpublished data). Because this experiment simulated conditions only during the growing season, it did not simulate the time period when *M. cardinalis* is susceptible to mortality.

The patterns of differential growth and survival presented here are similar to differences in growth and survival observed in reciprocal transplant gardens at 415 and 2,395 m (Angert and Schemske 2005), implying that temperature may be the selective agent largely responsible for differences in fitness versus altitude. For example, after one growing season at 415 m, *M. cardinalis* survival was 77% whereas *M. lewisii* survival was only 2%, but after one growing season at 2,395 m, survival of both species was > 95%. Also, although *M. cardinalis* initial survival was high, growth at high altitude was reduced, with *M. cardinalis* growing roughly two-thirds the size of *M. lewisii* after one growing season.

Interspecific differences in growth response to temperature have been reported for several other congeneric species pairs differing in altitude distribution (Woodward and Pigott 1975; Woodward 1979; Graves and Taylor 1986; Woodward 1990; Kao et al. 1998). For example, growth of the low altitude species *Sedum telephium, Dactylis glomerata*, and *Phleum bertolonii* increases with temperature but growth of high altitude *Sedum rosea, Phleum alpinum*, and *Sesleria albicans* is insensitive to temperature (Woodward 1975; 1979). The

differential sensitivity of *S. telephium* and *S. rosea* growth to temperature results in a switch in competitive dominance between low and high altitudes (Woodward and Pigott 1975). Similarly, Graves and Taylor (1986) found that growth of *Geum urbanum* in cool temperatures was more restricted than growth of *Geum rivale*, which occurs at higher altitudes. However, in field experiments, the species exhibited only slight differences in relative growth rates across altitude. The results of these studies differ from ours in that the effect of temperature was more pronounced in low altitude species, supporting the inference that lower range limits of high altitude species result primarily from biotic interactions such as competition rather than physiological limitation (MacArthur 1972; Woodward 1975; Scheidel et al. 2003). Instead, this study found severe abiotic limitation for *M. lewisii* beyond its lower altitude range limit due to inability to survive and grow under hot temperatures.

Intraspecific variation in performance versus temperature

To demonstrate that temperature limits species distributions requires the use of populations collected from range margins because marginal populations are often phenotypically or genetically divergent from more centrally located populations (Lesica and Allendorf 1995; Perez-Tris et al. 2000; Medail et al. 2002; Van Rossum et al. 2003; Faugeron et al. 2004) and may be differently adapted to temperature conditions at or beyond the range margin. However, in this study, populations from the range center and range margin of each species did not differ in growth or leaf physiological response to temperature, with the exception of *M. cardinalis* g_s and C_i/C_a. In reciprocal transplants at 415 and 2,395 m, a similar lack of adaptive differentiation with respect to altitude of origin was observed among populations of *M. cardinalis* and *M. lewisii* (Angert and Schemske 2005). Although finding no population differentiation in a controlled environment such as in the present study is consistent with results from the field, further experiments that simulate temperatures at the range margin are needed to investigate population variation in performance.

The likelihood of population differentiation depends on the amount of gene flow as well as the degree of environmental difference between populations. Graves and Taylor (1988) also found no difference in the temperature acclimation of photosynthesis between populations of *G. urbanum* and *G. rivale* separated by only several hundred meters. Conversely, Pitterman and Sage (2000) found that a cold-acclimated low altitude population of *Bouteloua gracilis* exhibited depressed rates of net photosynthesis at cold temperatures but that a population originating 1,500 m higher exhibited enhanced rates of photosynthesis at cold temperatures. Patterns of ecotypic differentiation in temperature response have also been found for *Trifolium repens* photosynthesis in populations from 600 and 2,040 m (Mächler and Nösberger 1977), for *Eucalyptus pauciflora* photosynthesis in populations from 915 and 1,770 m (Slatyer 1977), and for *Reynoutria japonica* growth in populations from 700 and 2,420 m (Mariko et al. 1993). Greater altitudinal separation between populations implies not only greater environmental difference but also greater geographic isolation. Populations used in this experiment originated at the altitude range center and range margin of each species, a difference in altitude of 600–1,200 m per species. Estimates of gene flow between range margin and range center populations of *M. cardinalis* and *M. lewisii* would help determine whether gene flow prevents the evolution of local adaptation to the temperature conditions at range margins (Kirkpatrick and Barton 1997).

Interspecific variation in leaf physiology versus temperature

M. cardinalis and *M. lewisii* exhibit differences in leaf physiological response to temperature that are consistent with differences in growth response to temperature and with altitude distributions in nature. Each species attains the greatest A_{net} and Φ_{PSII} when grown under a temperature regime characteristic of its altitudinal range center and displays reduced photosynthetic rate and quantum yield when grown under a temperature regime beyond its present altitudinal range. g_s and C_i/C_a are reduced under cold temperatures compared to hot temperatures, but *M. cardinalis* shows much greater reductions than does *M. lewisii*. Within each temperature regime, the species native to that temperature exhibits greatest leaf physiological capacity.

Differential sensitivity of A_{net} of *M. cardinalis* and *M. lewisii* to growth temperature demonstrates that each species is limited in its ability to acquire primary resources when grown under a temperature regime beyond its altitude range. Hiesey et al. (1971) also demonstrated that *M. cardinalis* and *M. lewisii* differ in photosynthetic response to temperature. When both species were grown at a constant temperature of 20°C, *M. lewisii* exhibited a light-saturated photosynthetic optimum that peaked at 25°C, but *M. cardinalis* photosynthesis did not decline until temperatures exceeded 30°C. Contrary to our results, Graves and Taylor (1988) found little difference in the temperature response of photosynthesis between two species of *Geum* with different altitude distributions. The authors suggested that growth differences between the species were driven by differences in the ability to utilize assimilated C for growth, rather than by differences in the ability to assimilate C.

Because photosynthesis is the primary source of energy and substrates for all other biosyntheses, when differences in photosynthetic rates are observed it is tempting to conclude that differences in C assimilation are directly related to differences in growth. However, although the observed differences in *M. cardinalis* and

M. lewisii C assimilation rates are consistent with their growth responses to temperature, instantaneous A_{net} is often a poor indicator of growth (Nelson 1988; Arntz et al. 1998). To fully dissect differences in growth requires measurement of respiration rates, plant architecture, and patterns of allocation in addition to measurement of photosynthetic rate (Poorter et al. 1990). Traditional growth analysis offers a means by which the mechanistic link between growth and assimilation can be quantified (Poorter et al. 1990), and future studies of *M. cardinalis* and *M. lewisii* should use this tool identify how relative growth rates, physiology, and morphology vary between species and with temperature to further clarify growth limitations beyond the species' altitude ranges. Likewise, measurements of N economy can illuminate differences in the C economy of plants (Poorter et al. 1990), making future measurements of N concentration and allocation desirable.

Interspecific differences in the response of light-adapted quantum yield to temperature indicate that each species is able to use a larger fraction of incoming light energy for photochemical reactions when grown under the temperature regime of its altitude range center. Φ_{PSII} is determined by the efficiency of excitation energy capture by open reactions centers and by the number of open reaction centers available for photochemical reactions (Schreiber et al. 1994). Decreases in the Φ_{PSII} may result from temperature-induced damage to electron transport processes or from feedback inhibition of PS II activity resulting from temperature-induced reductions in C metabolism (Falk et al. 1996; Laisk et al. 1998). To distinguish between these alternatives requires additional data on the temperature sensitivity of particular fluorescence parameters (e.g., minimum fluorescence, variable fluorescence, and non-photochemical quenching) in addition to detailed study of gas exchange metabolism (Owens 1994; Laisk et al. 1998; Xiong et al. 1999; Haldimann and Feller 2004). Without such information, it is difficult to attribute changes in fluorescence yield to any particular process (Owens 1994). However, studies of depression of net photosynthesis in oaks (Haldimann and Feller 2004) and Antarctic plants (Xiong et al. 1999) have concluded that heat-induced damage to thylakoid membranes does not occur until temperatures well above those that depress photosynthesis, and thus that reduced enzymatic activity is the main cause of depressions in photosynthesis under high temperatures in the field. Likewise, low temperature may harm photosynthesis primarily through effects on C metabolism rather than effects on photochemistry (Leegood and Edwards 1996).

Patterns of variation in g_s and C_i/C_a differed from patterns for A_{net} and Φ_{PSII}. In hot temperatures with high VPD and no water limitation, *M. cardinalis* showed high g_s, which allowed greater evaporative cooling of the leaf surface. Even with no water limitation, *M. lewisii* showed lower g_s under hot temperatures than *M. cardinalis*, higher leaf temperatures, and lower intercellular concentrations of CO_2. High C_i/C_a ratios in hot temperatures, particularly of *M. cardinalis*, indicate that photosynthesis at high temperatures was possibly light limited. However, subsequent experiments using higher light levels during growth and measurement find similar patterns of difference in photosynthetic rates between species and between temperature regimes (unpublished data), and it is unlikely that greater light levels would have eliminated the observed differences between *M. lewisii* and *M. cardinalis* in the hot temperature regime.

Without measurement of the CO_2 saturation point for photosynthesis, it is unclear whether lower g_s for both species, particularly *M. cardinalis*, in cold temperatures resulted in greater stomatal limitation to photosynthesis. However, it is likely that lower conductance resulted from, rather than caused, low photosynthesis. Long-term acclimation to growth temperature and light conditions during our study may have allowed changes in stomatal density or aperture that optimized conductance to reduce unnecessary transpiration in conditions of low CO_2 assimilation (Ferris et al. 1996). Several other studies support this hypothesis. Naidu and Long (2004) found that cold-acclimated *Zea mays* did not experience increased stomatal limitation to photosynthesis, despite greatly reduced g_s. Similar results have been reported for tomato (Martin and Ort 1985), olive (Bongi and Long 1987), rye (Huner et al. 1986), wheat (Hurry and Huner 1991), and several C_4 grasses (Pitterman and Sage 2001; Naidu and Long 2004). As in these examples, it is likely that g_s decreased to match assimilatory use of CO_2 and that reduced intercellular concentrations of CO_2 resulted from, rather than caused, low photosynthetic rates.

Some of the observed physiological responses may be due to uncontrolled environmental variables that covaried with temperature, such as VPD or RH, rather than temperature per se (Matzner and Comstock 2001). However, increased g_s was observed at high temperatures despite greater VPD and reduced humidity. Further, although these factors may be confounded in the present study, this represents a realistic natural scenario in temperate environments, where temperature and VPD often increase simultaneously (Iio et al. 2004).

This study provides evidence that *M. cardinalis* and *M. lewisii* differ in performance under temperature regimes characterizing their contrasting low and high altitude range centers. Differences in the species' leaf physiological responses under contrasting temperature regimes are consistent with differences in performance observed in both controlled and natural environments. Altitude range limits of *M. cardinalis* and *M. lewisii* may arise, in part, due to metabolic limitations on growth that ultimately decrease survival and limit reproduction.

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