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Huarong Zhang
Northern Arizona University, Flagstaff, zhrnau@gmail.com

Laura E. DeWald
Western Carolina University, Cullowhee, North Carolina, ldewald@wcu.edu

Thomas E. Kolb
Northern Arizona University, Flagstaff, tom.kolb@nau.edu

Dan F. Koepke
Northern Arizona University, Flagstaff, dan.koepke@nau.edu

GENETIC VARIATION IN ECOPHYSIOLOGICAL AND SURVIVAL RESPONSES TO DROUGHT IN TWO NATIVE GRASSES: *KOELERIA MACRANTHA* AND *ELYMUS ELYMOIDES*

Huarong Zhang[1], Laura E. DeWald[2], Thomas E. Kolb[1], Dan F. Koepke[1]

ABSTRACT.—Genetic variation in ecophysiological and survival responses to drought was studied in 2 northern Arizona native grass species, *Koeleria macrantha* (Ledeb.) Schult. (prairie Junegrass) and *Elymus elymoides* (Raf.) Swezey. ssp. *elymoides* (squirreltail). Low- and high-elevation populations of each species were compared in a greenhouse common garden experiment that included simulated drought. Leaf gas-exchange characteristics were significantly affected by simulated drought and often by population elevation, but gas-exchange responses to drought were similar for high- and low-elevation populations. Compared to high-elevation populations, low-elevation populations of both species had higher net photosynthetic rate and predawn water potential, and for *E. elymoides* had higher stomatal conductance. Leaf-level water-use efficiency did not differ between populations for either species. Populations also differed significantly in leaf morphological characteristics related to water use. Compared to high-elevation populations, low-elevation populations of both species had smaller leaves. Low-elevation populations of both species survived aboveground longer than high-elevation populations during drought, with a larger difference in *K. macrantha* than in *E. elymoides*. These results suggest strong selection for drought adaptation and water use along an elevational and water-availability gradient in native grasses.

RESUMEN.—Se estudió la variación genética en respuestas ecofisiológica y de sobrevivencia a la sequía en dos especies de pasto nativo del norte de Arizona, *Koeleria macrantha* (Ledeb.) Schult. ("prairie Junegrass") y *Elymus elymoides* (Raf.) Swezey. spp. *elymoides* ("squirreltail"). Se compararon poblaciones de cada especie a elevaciones altas y bajas durante un experimento de jardín común en un invernadero que simulaba condiciones de sequía. Las características relacionadas con el intercambio de gases a nivel de hoja se vieron afectadas significativamente por la sequía simulada y con frecuencia por la elevación de la población, pero la respuesta del intercambio de gases a la sequía fue similar en las poblaciones de alta y baja elevación. En comparación con las poblaciones altas, las poblaciones bajas, en ambas especies, tuvieron una elevada tasa neta de fotosíntesis y un mayor potencial hídrico previo al amanecer; *E. elymoides* tuvo mayor conductancia estomática. La eficiencia en el uso del agua (EUA) a nivel de hoja no difirió entre poblaciones en ninguna especie. Las poblaciones sí difirieron significativamente en las características de la morfología de la hoja relacionadas con el uso del agua. Comparadas con las poblaciones altas, las poblaciones bajas de ambas especies tuvieron hojas más pequeñas. Durante la sequía, la parte de la planta que estaba encima de la tierra sobrevivió por más tiempo en las poblaciones bajas de ambas especies que en las poblaciones altas, con una mayor diferencia en *K. macrantha* que en *E. elymoides*. Estos resultados indican que hay una fuerte selección para la adaptación a la sequía y el uso del agua a lo largo de una gradiente de elevación y de disponibilidad de agua en pastos nativos.

In the southwestern United States, water availability is the most important resource and determines survival and productivity of plants (Hadley and Szarek 1981, Boyer 1982). An expected result of climate warming is an increase in frequency of drought and high-temperature events that will stress native species. For example, Seager et al. (2007) predict an increase in the frequency of severe drought in the southwestern United States, and elevated plant mortality attributed to severe drought has already been reported in this region (Gitlin et al. 2006, van Mantgem et al. 2009). Improved understanding of drought responses of native plants in arid regions will increase our ability to predict future changes in plant communities and provide information for ecological restoration (Jump and Penuelas 2005, Parmesan 2006).

Plants usually exhibit reduced photosynthesis and conductance under drought conditions (e.g., Steed et al. 2002), and intraspecific genetic variation in physiological responses has been found among different populations (e.g., Sandquist and Ehleringer 1997). Genetic information about drought adaptation and water-use traits of plants is critical for using native plants in restoration because some current populations may be better adapted to severe drought conditions than other plant populations (Gimeno et al. 2009). For example, plant populations from dry environments

TABLE 1. Geographic origin of *Koeleria macrantha* and *Elymus elymoides* populations sampled from high- and low-elevation populations in northern Arizona.

Elevation group	Latitude	Longitude	Elevation (m)	Dominant tree species[a]
Low	34°18′N	111°02′W	1700	pp with pj
	34°11′N	109°58′W	2058	pp with pj
	35°55′N	112°07′W	2024	pp with pj
	34°53′N	111°41′W	1975	pp with pj
	34°56′N	111°39′W	2015	pp with pj
High	33°33′N	109°20′W	2444	pp
	34°02′N	109°27′W	2525	pp
	33°42′N	109°13′W	2455	pp
	34°48′N	111°28′W	2270	pp
	35°13′N	112°10′W	2160	pp

[a]pp = *Pinus ponderosa*, pj = *Pinus edulis* and *Juniperus* spp.

tend to maintain greater physiological activity during drought than populations from wet environments (Abrams and Kubiske 1990). Because physiological traits related to drought adaptation can be influenced by both plant genotype and the environment (Williams et al. 1995, Premoli and Brewer 2007), comparing physiological response to drought among genotypes in a common environment is essential to documenting the magnitude of genetic control of drought adaptation mechanisms (Easlon and Richards 2009).

The objective of this study was to examine intraspecific genetic variation in survival and ecophysiological responses to drought in populations of 2 native grass species originating from high and low elevations in northern Arizona. The 2 native grasses, *Koeleria macrantha* (Ledeb.) Schult. (prairie Junegrass) and *Elymus elymoides* (Raf.) Swezey. ssp. *elymoides* (squirreltail), co-occur in ponderosa pine (*Pinus ponderosa* C. Lawson var. *scopulorum* Engelm.) forests in northern Arizona. At higher elevations, ponderosa pine is the dominant tree species, while at lower elevations it is mixed with pinyon pine (*Pinus edulis* Engelm.) and junipers (*Juniperus* spp.) (Brown 1994). Many environmental factors covary with elevation, but variation in precipitation and temperature is pronounced in the southwestern United States (Barton and Teeri 1993). For example, plants at low elevations experience higher temperatures and drier soils than plants at high elevations (Pearson 1920, Van de Water et al. 2002). Ecotypic differentiation in flowering time was related to elevation in *K. macrantha* and *E. elymoides* (Robertson and Ward 1970, Clary 1975). However, it is unknown whether there are genetic differences in morphological and physiological traits of drought adaptation between high- and low-elevation populations. In this

study, we compared leaf traits related to water use and drought responses between high- and low-elevation populations of the 2 grass species. We hypothesized that compared to high-elevation populations, low-elevation populations would have (1) morphological traits that confer drought adaptation and result in low water use, such as smaller leaves; (2) leaf gas-exchange characteristics that confer drought adaptation and result in low water use, such as low stomatal conductance and high water-use efficiency; and (3) longer survival during simulated drought.

METHODS

Plant Material and Measurements

We collected seeds from 10 sites in northern Arizona during summer 2004. Five of the sites were randomly located in low-elevation (1700–2100 m) mixed ponderosa pine / pinyon–juniper forest (Table 1). Dominant tree species at the low-elevation sites were mostly *P. ponderosa, P. edulis,* and *Juniperus* spp. Typical understory grasses were *Bouteloua gracilis, K. macrantha,* and *E. elymoides.* The other 5 high-elevation sites (2100–2600 m) were randomly located in a ponderosa pine forest (Table 1) where ponderosa pine was at least 50% of overstory tree density (stems · ha^{-1}). Common understory species included *Poa fendleriana, Festuca arizonica, Muhlenbergia montana, K. macrantha,* and *E. elymoides.* Within each site, we collected seeds from 30 randomly selected mature plants of each species. In May 2005, one seed from each maternal family was germinated and planted in Ray leach Cone-tainer pots (Stuewe & Sons Inc., Tangent, Oregon) in a greenhouse at Northern Arizona University, Flagstaff, Arizona. Each 164-cm^3 pot contained equal parts of peatmoss,

TABLE 2. Leaf traits of high- and low-elevation populations of *Koeleria macrantha* and *Elymus elymoides* grown in a greenhouse common garden. Data are expressed as mean (SE), and *P* values are from one-way ANOVA comparisons between elevations (*n* = 30).

Species	Leaf trait	Elevation		*P*
		High	Low	
Koeleria macrantha	Length (cm)	9.46 (0.28)	7.45 (0.40)	<0.01
	Width (cm)	1.15 (0.03)	1.01 (0.03)	<0.01
	Area (cm^2)	10.63 (0.36)	8.11 (0.55)	<0.01
	Number	10.89 (0.53)	9.95 (0.44)	0.20
Elymus elymoides	Length (cm)	20.85 (0.63)	20.75 (0.56)	0.91
	Width (cm)	2.19 (0.05)	1.53 (0.08)	<0.01
	Area (cm^2)	45.36 (1.44)	31.80 (2.03)	<0.01
	Number	5.63 (0.28)	5.48 (0.37)	0.74

perlite, and vermiculite. We grew the grasses under well-watered conditions (watered twice a week) in the greenhouse for 16.5 months (May 2005 to mid-September 2006), and then imposed a simulated drought in mid-September 2006. From May to October in 2005 and 2006, the greenhouse temperatures were 22 °C during the day and 15 °C at night, and from November 2005 to April 2006 they were 10 °C during the day and 5 °C at night.

Before the imposed drought, we measured leaf traits of 30 plants of each species from each elevation group in early September (*n* = 30). None of these plants flowered before or during the experiment. We measured leaf length and width on one representative mature leaf, and counted the total number of leaves on each plant. Leaf length and leaf width were measured by using a ruler and a micrometer, respectively. Individual leaf area was calculated from the product of leaf length and width. We measured gas-exchange traits every 2 days between 11:00 and 13:00 during the imposed drought that started 16 September 2006. Eight randomly selected plants from each elevation group of each species were measured (*n* = 8). As the soil dried, one fully developed leaf from each plant was excised from the plant base; predawn and midday leaf water potentials (Ψ_{pd} and Ψ_{md}, respectively) were measured using a Scholander pressure chamber (PMS Instrument Co., Corvallis, OR). Stomatal conductance (g) and net photosynthetic rate (P_n) were measured on a projected-leaf-area basis by using a portable infrared gas analyzer system (LI-COR6400 with a grass chamber, LI-COR Biosciences, Lincoln, NE). Because the leaves were longer than the chamber, the portion of the leaf in the chamber was marked, and only the marked portion was measured for area. Gas-exchange measurements were made in the greenhouse under near-ambient temperature and humidity, and at moderately high light intensity (1000 μmol · m^{-2}s^{-1}) supplied by the chamber lamp. Intrinsic water-use efficiency (WUE) was calculated using the relationship WUE = P_n/g. We recorded the number of days to aboveground mortality for each plant once all the plant leaves and stems had turned brown.

Data Analyses

One-way ANOVA was used to test for differences between low- and high-elevation populations of each species in leaf morphological traits and survival rates while the plants were under drought conditions; the 30 plants from each elevation served as replicates (*n* = 30). Data were distributed normally. For the simulated drought experiment, 2-way ANOVA was used to compare data on leaf gas exchange and water potential over time between low- and high-elevation populations for each species (*n* = 8). Differences were considered significant at *P* < 0.05. All the analyses were performed with JMP® 4.0 (SAS Institute, Inc., Cary, NC).

RESULTS

The leaves of low-elevation *K. macrantha* populations were significantly shorter and narrower, and had less area than high-elevation populations; however, number of leaves was not different between elevations (Table 2). Low-elevation populations of *E. elymoides* also had significantly smaller leaf widths and areas in comparison to high-elevation populations, but leaf length and number of leaves did not vary between populations (Table 2).

In the simulated drought experiment, time since last watering had a significant effect on leaf water potentials in both grass species (*P* < 0.01),

TABLE 3. Results (P values) of 2-way ANOVA for hydraulic and gas exchange traits of high- and low-elevation populations of *Koeleria macrantha* and *Elymus elymoides*. Ψ_{pd} = pre-dawn leaf water potential, Ψ_{md} = midday leaf water potential, P_n = net photosynthetic rate, g = stomatal conductance, WUE = water-use efficiency.

Species	Factor	Ψ_{pd}	Ψ_{md}	P_n	g_{-1}	WUE
Koeleria macrantha	Elevation	0.56	0.49	<0.01	0.76	0.96
	Time	<0.01	<0.01	<0.01	<0.01	<0.01
	Elevation × Time	0.45	0.38	0.98	0.94	0.82
Elymus elymoides	Elevation	<0.05	0.56	<0.01	<0.01	0.94
	Time	<0.01	<0.01	<0.01	<0.01	<0.01
	Elevation × Time	0.21	0.43	0.92	0.47	0.41

and the interactions between time and elevation were not significant (Table 3). The Ψ_{pd} declined in response to drought for both species and populations (Fig. 1). There were no significant differences in Ψ_{pd} or Ψ_{md} between high- and low-elevation *K. macrantha* populations. High-elevation *E. elymoides* populations had significantly lower Ψ_{pd} than low-elevation populations, but there was no significant difference in Ψ_{md} between populations (Fig. 1).

There was a significant reduction in P_n and g over time since last watering in both grass species ($P < 0.05$), and the time × elevation interaction was not significant (Table 3). The P_n declined during the latter stages of soil drying, while g increased slightly at the beginning of the experiment and then decreased (Fig. 1). P_n of low-elevation populations was significantly higher than high-elevation populations in both grass species (Table 3, Fig. 1). In *K. macrantha,* there was no significant difference in g between high- and low-elevation populations, but low-elevation *E. elymoides* populations had significantly higher g than high-elevation populations (Table 3, Fig. 1). The WUE did not differ significantly between elevations for both species but did increase significantly with time since last watering in both species (Table 3). The time × elevation interaction was not significant for WUE (Table 3).

The number of days to aboveground mortality in the simulated drought experiment differed significantly between populations in *K. macrantha* where low-elevation populations survived over 4 days longer than high-elevation populations (Fig. 2). In *E. elymoides,* low-elevation populations survived marginally longer than high-elevation populations (21.1 vs. 19.6 days), but this difference was not significant ($P = 0.07$; Fig. 2).

DISCUSSION

Leaf size is an important trait related to plant water use and productivity (Dudley 1996).

Previous studies have shown that smaller leaves are favored in dry compared to wet environments (e.g., Dudley 1996). Similar results were found in this study. Leaves of low-elevation populations of both species were generally smaller than leaves of high-elevation populations, and this variation likely reflects selection for lower water use at lower, drier elevations (Byars et al. 2007). In our study, the differences in leaf size between high- and low-elevation populations helped explain differences in hydraulic and gas-exchange traits. Values of Ψ_{pd} decreased in both grass species in response to simulated drought and were significantly lower (i.e., more negative) for high-elevation *E. elymoides* populations than for low-elevation *E. elymoides* populations. Lower Ψ_{pd} in high-elevation populations of this species was not caused by higher leaf-area-based transpiration from leaves, because g was lower for high-elevation populations than for low-elevation populations, and differences in leaf-area-based transpiration are largely determined by g when atmospheric humidity and temperature are constant for comparisons, as in our measurements (Kramer 1983). Instead, lower Ψ_{pd} in high-elevation *E. elymoides* populations was likely caused by higher transpiration at the whole-plant level, because the high-elevation populations had larger leaves than the low-elevation populations. These results suggest slower depletion of soil water during drought by low- compared to high-elevation populations.

Low-elevation populations of both species consistently had greater P_n than high-elevation populations during both nondrought and drought periods. This finding is consistent with common garden comparisons of P_n among dry- and wet-habitat populations of red maple (*Acer rubrum* L.) (Abrams and Kubiske 1990) and a perennial grass, *Miscanthus* spp. (Weng 1993). Higher P_n of low-elevation populations was associated with higher g of low-elevation populations of *E. elymoides* but not *K. macrantha,* suggesting a
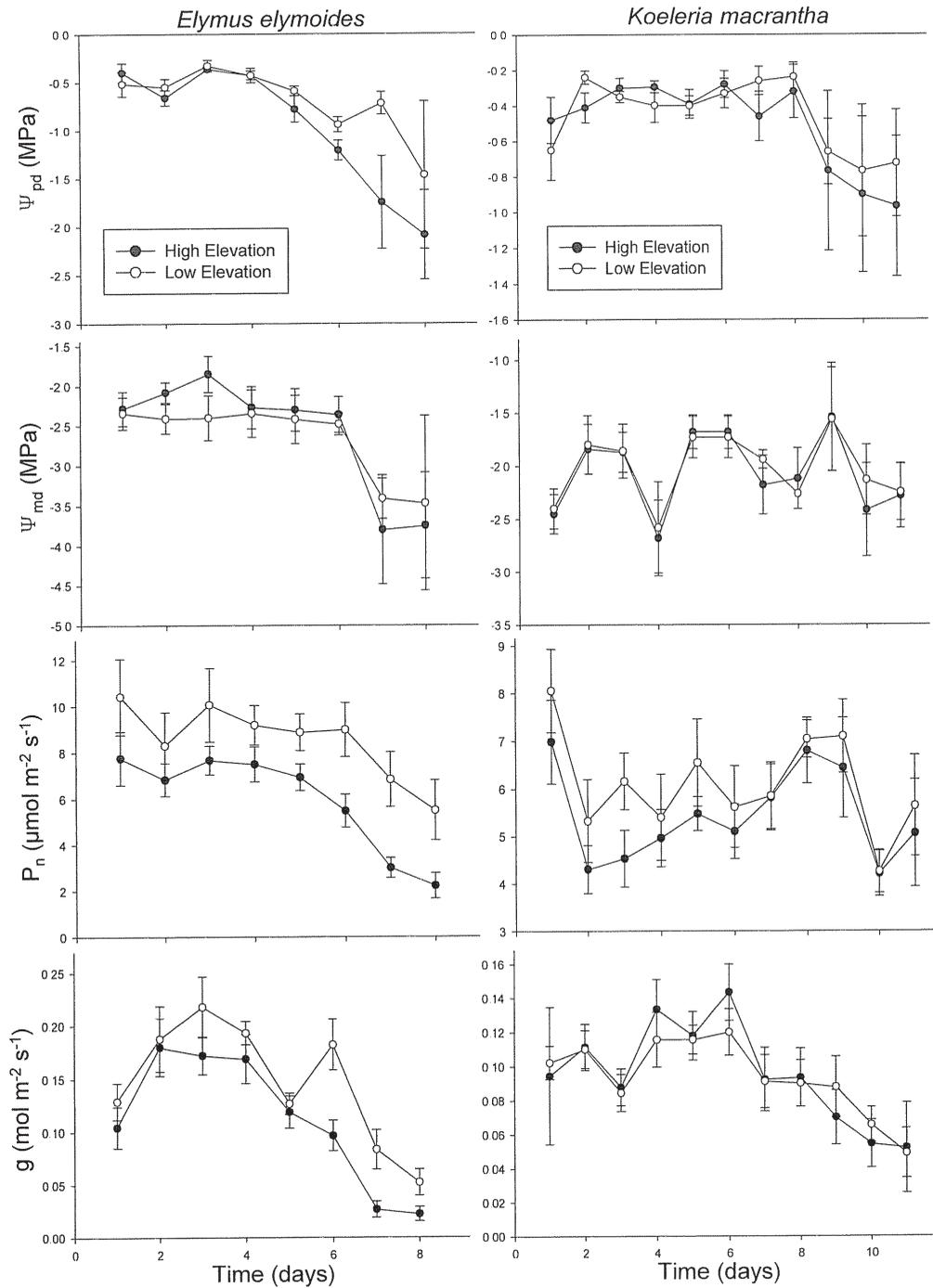
Fig. 1. Response of gas exchange traits to simulated drought, as represented by days since watering. Plants are from high-elevation (solid points) and low-elevation (open points) populations of 2 grass species—*Koeleria macrantha* and *Elymus elymoides*—in northern Arizona. Traits are predawn leaf water potential (Ψ_{pd}), midday leaf water potential (Ψ_{md}), net photosynthetic rate (P_n) and stomatal conductance (g). Means are dipicted with bars representing one standard error around the mean.
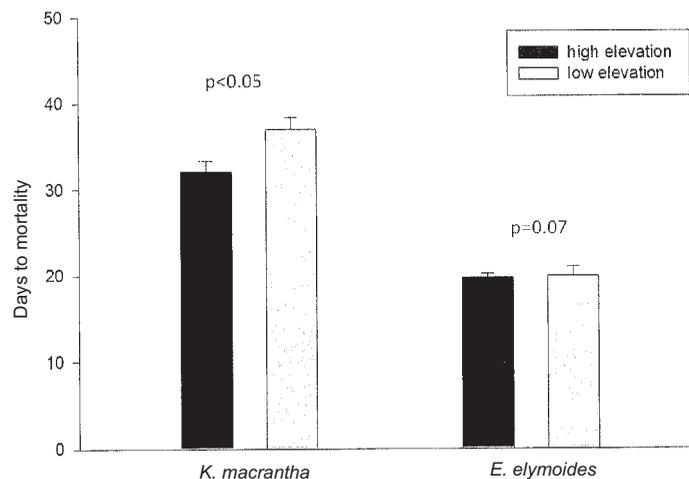
Fig. 2. Average number of days to aboveground mortality in plants from high- and low-elevation populations of *Koeleria macrantha* and *Elymus elymoides* under simulated drought conditions. Error bars represent standard error.

variable role of stomatal and nonstomatal regulation of ecotypic variation in P_n for each species.

Stomatal control is one mechanism that plants use to reduce water deficiency (Ludlow 1989). Higher stomatal conductance is usually associated with greater photosynthesis because both CO_2 and water vapor diffuse through stomata (Kozlowski and Pallardy 1997), but some plants can change the relative rate of CO_2 and water vapor exchange via stomatal control to increase WUE (Cowan 1982). In this study, we did not detect differences in WUE between high- and low-elevation populations of either species, despite the occurrence of temporal change in WUE during the simulated drought. This result does not support selection for high leaf-level WUE in dry environments as reported for other species (e.g., Monson et al. 1992, Dudley 1996). However, our results are consistent with the lack of ecotypic genetic variation in WUE previously reported for *E. elymoides* (Clary 1975).

Variation in morphological and ecophysiological traits can affect survival of plants under drought (Barton and Teeri 1993). Despite similar gas-exchange responses to simulated drought, low-elevation populations of both species survived longer under drought conditions than high-elevation populations, suggesting morphological and ecophysiological differences between the populations that conferred greater drought adaptation to low-elevation populations. Xeric populations often have higher fitness than mesic populations under water stress because

they are more effective at reducing water loss during drought (Dudley 1996). For example, in our study the smaller leaf size of low-elevation populations likely reduced whole-plant transpiration and thus promoted longer survival during drought.

The significant differences in morphological and ecophysiological traits between low- and high-elevation grass populations suggest that selective pressures have caused genetic differentiation over a water-availability gradient related to elevation (Byars et al. 2007). This genetic differentiation may be maintained by ecotypes that have developed in response to steep elevational gradients of temperature and moisture reported in Arizona (Pearson 1920, Wentworth 1981). Environmental gradients can affect reproduction timing of herbaceous plants (Jackson 1966, Lennartsson 1997), and differentiation of flowering time was reported both in *E. elymoides* and *K. macrantha* populations from different elevations in common garden experiments (Robertson and Ward 1970, Clary 1975). This type of difference in time of flowering would reduce gene flow between elevations, and thus help maintain genetic differentiation among populations caused by natural selection.

In summary, we found genetic differences in leaf morphology and gas-exchange traits between low- and high-elevation populations in 2 grass species native to northern Arizona. Divergent selection along an elevation and water-availability gradient maintained by lack of genetic

exchange likely explains this differentiation. Our finding that low-elevation grass populations are more drought adapted than high-elevation populations should have application in restoration or assisted-migration projects (Marris 2009). Genotypes of native plants from lower elevations or xeric environments could be used in restoration of higher-elevation areas where drought is anticipated to negatively affect survival. However, caution is needed to ensure that lower-elevation, drought-adapted genotypes are adapted in other ways (such as phenology) to higher-elevation conditions before moving these genotypes.

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