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# Epidermal conductance as a component of dehydration avoidance in *Digitaria californica* and *Eragrostis lehmanniana*, two perennial desert grasses

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## Abstract

Epidermal conductance ( $g_{\min}$ ) is water lost through the cuticle and stomata of plants when stomatal conductance is minimal. Low  $g_{\min}$  may affect survival of perennial grasses by maintaining tissue hydration during drought. If true, populations from environments where drought is severe may exhibit reduced  $g_{\min}$  compared to those from less arid environments. Success of invasive grasses may also be associated with reduced  $g_{\min}$  compared to non-invasive competitors. Using plants grown in a single environment, we measured  $g_{\min}$  of leaves from populations of *Digitaria californica* from environments with similar annual precipitation but differing in average drought severity (southern Arizona and western Texas, USA), and a population of the exotic species *Eragrostis lehmanniana* that has invaded sites occupied by *D. californica* in Arizona. Epidermal conductance was lower in the *D. californica* population from the more arid environment (Texas). Likewise,  $g_{\min}$  was lower in *E. lehmanniana* than in the Arizona *D. californica* population. Shoot biomass production as a fraction of  $g_{\min}$  was higher in *E. lehmanniana* than in the *D. californica* populations and was higher in the Texas

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*D. californica* population than in the Arizona population. This suggests that low  $g_{\min}$  may be a component of drought avoidance in these grasses.

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## 1. Introduction

Characterizing the growth and survival of herbaceous plants in arid environments has often emphasized physiological processes affecting water use during periods of active plant growth (Maroco et al., 1997; Fernandez and Reynolds, 2000; Chaves et al., 2002; Van de Water et al., 2002). However, an equally important component of fitness in these environments may be the ability to avoid or postpone lethal dehydration when stomatal conductance is low. This may be especially important in herbaceous perennial plants, such as many desert grasses, where survival of above-ground meristems through drought periods allows for rapid canopy redevelopment when soil water is sufficient for high stomatal conductance (Burgess, 1995). Many traits may affect dehydration avoidance in such plants including increased leaf and tiller shedding, depth of water extraction, leaf water storage, and decreased lethal cellular relative water content (Ludlow and Muchow, 1990; Chaves et al., 2002). Dehydration avoidance may also be related to epidermal conductance (Muchow and Sinclair, 1989), which is associated with biophysical properties of cuticle-associated waxes. Also referred to as cuticular transpiration and residual transpiration (Clarke et al., 1991), epidermal conductance includes water lost via the cuticle and the stomatal complex during periods of minimal stomatal conductance (Kerstiens, 1996).

Sinclair (2000) used a simple water balance model to predict that plant survival through periods of extended drought would be substantially increased by low conductance of water through the cuticle and stomatal complex. The relationships between epidermal conductance and response to drought have been investigated in crop plants (Muchow and Sinclair, 1989; Araus et al., 1991; Kerstiens, 1996). Although genetic variation in epidermal conductance has been demonstrated in some crop species, productivity has not been consistently associated with this trait under sub-optimal soil water conditions (Clarke et al., 1991).

The overall evolutionary and ecological significance of epidermal conductance is not well characterized in herbaceous plants in arid environments. Based on transpiration of isolated cuticles in a diverse array of species, Pisek and Berger (1938) demonstrated positive relationships between rates of epidermal conductance and average soil water content in their native environments. Association between epidermal conductance and average precipitation in drought-prone environments may indicate that this trait represents a significant component of fitness and a factor in local adaptation. This notion is supported by data showing that epidermal conductance was generally lower from detached leaves in populations of the winter annual grass *Aegilops geniculata* Roth from xeric environments in the Middle East

and North Africa than in populations from mesic environments in southern Europe (Zaharieva et al., 2001). There are no data from perennial plants that address whether natural selection affects this trait in response to precipitation in drought-prone environments.

Extended drought is common in desert scrub and grassland communities of North American deserts. Precipitation in these environments is highly variable in frequency and amount (230–600 mm) during the two rainy seasons per year (McClaran, 1995). Summer precipitation occurs in brief and intense convective storms that may be separated by prolonged droughts. During the winter and spring, precipitation is usually from broad frontal storms of low intensity (Williams, 1979). A 2–4 month “foresummer” drought precedes the summer rainy season. A complete lack of biologically significant precipitation is highly likely during this period and mean temperatures frequently exceed 30 °C (Shreve, 1964). A shorter drought period occurs in the autumn. Perennial plants in these environments must cope with relatively short-term drought during rainy seasons, and more predictable and severe long-term drought during the foresummer and the autumn (Wright and Van Dyne, 1976).

North American desert scrub and desert grassland communities contain plant species exhibiting a variety of growth forms with differing water-use and conservation strategies. Suffrutescent perennial grasses display many traits associated with opportunistic response to soil water (Burgess, 1995). For example, individual tillers on these species may live up to 3 years and at least portions of leaves may remain photosynthetically competent throughout extended drought (Cable, 1979). This suggests that dehydration avoidance via reduced epidermal conductance could represent a component of tissue and plant survival in these species.

Our primary objective in this research was to compare epidermal (minimum leaf) conductance ( $g_{\min}$ ) (Kerstiens, 1996) in populations of a widely distributed native perennial grass, *Digitaria californica* (Benth.) Chase, from North American desert shrub sites that have similar annual precipitation but differ in the likelihood and extent of drought (NOOA, 2004). Our central hypothesis is that epidermal conductance is related to the ability of perennial grasses to survive drought. Therefore, when grown in a common environment, plants from populations of this species that evolved where droughts are generally more severe will exhibit lower  $g_{\min}$  than those from sites where droughts are less severe. A second component of this research involved comparison of  $g_{\min}$  in *D. californica* with that of *Eragrostis lehmanniana* Nees, a grass of comparable morphology and life history that is native to southern Africa but is now displacing *D. californica* in North American desert shrub and grassland sites (Angell and McClaran, 2001). We speculate that at least some of the success of this alien species may be due to reduced  $g_{\min}$  that results in decreased leaf and plant mortality during drought. The competitive advantage of *E. lehmanniana* would be increased by persistence of additional live above-ground tissue that facilitates the opportunistic production of biomass when soil water permits active growth. Our experiments were conducted with container-grown plants grown outdoors in a rain shelter in Tucson, Arizona, USA with data collected during autumn and spring drought periods.

## 2. Materials and methods

### 2.1. Plant materials and their native environments

*D. californica* is a caespitose suffrutescent  $C_4$  grass native to the Sonoran and Chihuahuan desert scrub and semi-desert grassland biotic communities of the south-western United States and north-western Mexico (Cable, 1979; Brown, 1994) and similar biotic communities in Bolivia and Argentina (Henrard, 1950). Mature tillers of this species may live for up to 3 years. When sufficient soil water is available, tillers may produce leaves from long-lived axillary buds that are located throughout their length (Cable, 1971).

*E. lehmanniana* is native to arid savanna communities in the North Cape Region of South Africa (Cox and Ruyle, 1986). This  $C_4$  species is also caespitose and suffrutescent, and tillers may survive on plants for more than 1 year producing new leaves from axillary buds along their length when soil water is adequate (Angell and McClaran, 2001). An apomictic accession of *E. lehmanniana* was initially introduced to southern Arizona in 1932, has spread extensively (Angell and McClaran, 2001), and likely occurs on at least 595,000 ha in this region (Gori and Enquist, 2003).

We used plants from three populations in this research collected from similar latitudes to decrease confounding effects of response to day length. Caryopses from *D. californica* populations were collected at Robles Junction, Arizona (32.04°N, 111.18°E; mean annual precipitation: 320 mm) in 1990 and Van Horn, Texas (31.02°N, 104.49°E; mean annual precipitation: 294 mm), USA in 1958. To minimize the effects of environment of seed production on progeny performance, seed of this species used in these experiments was produced in a greenhouse in Tucson, AZ in 1996 (Smith et al., 2000). Caryopses of *E. lehmanniana* were collected at the Santa Rita Experimental Range (SRER, 31.50°N, 110.50°E; mean annual precipitation: 361 mm), 45 km south-east of Tucson, Arizona in 1996.

The two *D. californica* populations are native to environments with similar mean annual precipitation, but they differ in pattern and amount of precipitation that occurs during the winter, spring and foreshadow periods (Table 1). The climate of the southern Arizona location is typical of the Sonoran Desert where about 55–65% of annual precipitation occurs in a 4-month summer rainy season, when most  $C_4$  plant growth occurs (Shreve, 1964; Cable, 1975), and an additional 30–35% falls in a 5-month winter–spring rainy season (Table 1). Precipitation averages 15.5 mm month<sup>-1</sup> in the generally arid 3- and 5-month periods preceding and following the 4-month summer rainy season (Table 1). Van Horn, Texas has a climate typical of the Chihuahuan Desert, where the summer rainy season is on average longer than that of the Sonoran Desert (Table 1). More than 80% of annual precipitation at this western Texas site occurs in the summer rainy season because this area receives relatively little winter–spring precipitation. Importantly, monthly precipitation outside the 6-month summer rainy season averages 7.3 mm month<sup>-1</sup>, which is about one-half that of the Arizona site.

*E. lehmanniana* in southern Arizona is represented by descendants of a single accession ('A-68') that was collected in the Griqualand West region, North

Table 1  
 Mean monthly precipitation and temperature (NOAA, 2004) for three periods of contrasting environmental conditions relative to the growth of *C<sub>4</sub>* perennial grasses for the 30-yr period preceding seed collection at Robles Junction, Arizona and Van Horn, Texas

Locale	Parameter	Period of year/months <sup>a</sup>		
		Winter–spring	Foresummer	Summer growth
Van Horn, Texas		November–February	March–April	May–October
	Mean temperature range (°C) [monthly mean]	5.9–10.4 [7.8]	12.1–16.0 [14.1]	16.6–25.7 [22.4]
	Total precipitation (mm) [monthly mean]	33.5 [10.9]	10.2 [5.1]	250.7 [41.8]
Robles Junction, Arizona		November–March	April–June	July–October
	Mean temperature range (°C) [monthly mean]	9.8–13.9 [11.7]	17.3–27.2 [22.1]	19.7–29.2 [25.7]
	Total precipitation (mm) [monthly mean]	103.1 [20.6]	20.6 [6.9]	196.5 [39.3]

<sup>a</sup>Winter-spring: mean monthly precipitation  $\geq 8$  mm and mean monthly temperature  $< 14$  °C; foresummer: mean monthly temperature  $\geq 12$  °C and mean monthly precipitation  $< 10$  mm; summer growth: mean monthly temperature  $\geq 14$  °C and mean monthly precipitation  $\geq 10$  mm.

Cape Province, South Africa (Crider, 1945; Cox and Ruyle, 1986). Precipitation in this region of South Africa (mean: 250–500 mm yr<sup>-1</sup>, 414 mm yr<sup>-1</sup> at Kimberley, RSA) occurs primarily as thunderstorms during a 6-month summer rainy season (75–85% of annual precipitation) when mean temperatures may be above 20 °C. Mean monthly precipitation outside the summer rainy season is similar to that in southern Arizona (13.2 mm month<sup>-1</sup> at Kimberley) (Vose et al., 1992).

The 5 years preceding collection of seed of the *D. californica* population in Texas (1958) were unusually dry for this environment. Mean annual precipitation at Van Horn, Texas during this period was 236 mm and the mean Palmer Drought Severity Index (PDSI) was -2.07, which indicates a period of moderate long-term drought (Palmer, 1965). In contrast, the 5 years prior to seed collection of both *D. californica* and *E. lehmanniana* in Arizona had near-normal precipitation. The mean PDSI at Robles Junction, Arizona for this period was -0.17 and that at SRER was 0.94.

## 2.2. Experimental design and execution

Beginning in March 2001, 40 individual randomly selected plants per population were grown in 25 × 6.4 cm tapered cylindrical containers filled with soil (656 ml) collected at the SRER from a site where *D. californica* and *E. lehmanniana* occur. This soil, from the Combate-Diaspar Series (thermic Ustic Torrifluent), was taken from the surface 20 cm, and was thoroughly wetted to germinate and then dried to kill all seeds present before experiments began. Plants were grown with regular irrigation in an outdoor shadehouse in Tucson, Arizona until experiments began on 1 July 2002. Plants were then placed in an open-sided fixed-location rain shelter (Svejcar et al., 1999) adjacent to the shadehouse. All plants from each population were randomly placed into one of four groups of 10 individuals each. Plants were arranged using a split-plot design with groups as the main-plot factor and populations as the subplot factor.

Plants were irrigated every 2–4 days by wetting the soil to field capacity, with no irrigation during the 10 days prior to measurement of  $g_{\min}$  to elicit drought acclimatization response as would occur at the initiation of an extended drought. Epidermal conductance was measured on detached leaf blades from all plants under defined evaporative conditions during four, 4-day periods (runs) in 2002 and two, 4-day periods in 2003 (Table 2). In each run, measurements were taken on 4 consecutive days with data collected from one of the four groups in each population (30 plants) each day. The first four runs involved sampling leaves that had grown during the summer growth period while the other two runs were at the beginning of the foresummer and reflected growth during late winter and early spring. The technique used to measure  $g_{\min}$  is based largely on that described by Muchow and Sinclair (1989). Briefly, plants in the group to be evaluated are moved into a dimly lit laboratory (<0.81 μmol m<sup>-2</sup> s<sup>-1</sup>) at 24–26 °C 18–20 h before measurements commence and the soil brought to field capacity. Beginning at 10:00 h on the following day, a 8–10 cm-long fully expanded leaf blade is removed from the third to fifth node of a mature tiller and placed in a 18 × 150 mm glass test tube, immediately weighed

Table 2

Least-squares means for minimum leaf conductance ( $\text{m s}^{-1} \times 10^5$ ) in five late-summer/autumn (Runs 1–4) and two spring (Runs 5, 6) evaluation trials in two *Digitaria californica* populations and one population of *Eragrostis lehmanniana* (40 genotypes per population, evaluated in four groups)

Run number	Date run initiated — mean temperature preceding run ( $^{\circ}\text{C}$ ) <sup>a</sup>	Species/population		
		<i>Digitaria californica</i>		<i>Eragrostis lehmanniana</i>
		Texas	Arizona	Arizona
1	3 Sep—29.8	6.38 b <sup>b</sup>	7.75 a	6.76 b
2	23 Sep—27.7	5.69 b	7.22 a	5.85 b
3	14 Oct—22.4	6.39 b	7.96 a	7.47 a
4	5 Nov—15.5	6.29 b	7.92 a	5.62 c
5	28 Apr—19.2	5.89 c	7.81 a	7.01 b
6	12 May—19.9	5.95 b	7.63 a	6.32 b
(arithmetic mean over runs)		6.09	7.72	6.51

<sup>a</sup>Over 7-day period preceding first measurement of  $g_{\min}$  in each run. Data from the Arizona Meteorological Network, Tucson Station which is located 1 km from the experimental site.

<sup>b</sup>Least-squares means within a row followed by the same letter are not significantly different based on pairwise comparisons using the probability of difference option of PROC MIXED (Littell et al., 1996).

and then placed in an oven at  $30^{\circ}\text{C}$  containing an open container of 25 ml of newly dried Drierite desiccant ( $\text{CaSO}_4$ ) producing relative humidity  $< 3\%$ . Exactly 6 hr later the leaf blade and tube are weighed again and leaf area is then measured using an electronic leaf area meter. Minimum leaf conductance is calculated as  $\text{m s}^{-1} \times 10^5$  (Kerstiens, 1996) using the approach outlined by Muchow and Sinclair (1989) except that it is presented here assuming conductance through both leaf surfaces. Reported  $g_{\min}$  values assume standard atmospheric pressure at  $25^{\circ}\text{C}$ . Mean water content of leaf blades was 75.2% (SE = 0.9%) when initial masses were measured and did not differ significantly among runs or populations. No significant differences were observed between populations when initial leaf tissue water content was expressed on a leaf area basis. After the fourth run, all shoot biomass was harvested 10 cm above the soil surface, dried at  $60^{\circ}\text{C}$  and weighed. The 128-day period in which this biomass was produced included four 10-day drought periods that immediately preceded each run.

Following the final  $g_{\min}$  measurements, stoma densities were measured on leaf blades of all plants in each population. Epidermal impressions were made from abaxial and adaxial leaf blade surfaces with clear nail polish that was then affixed to glass slides using plastic tape. Stomata were counted from a total of ten  $0.275 \text{ mm}^2$  areas on each surface for each plant and mean values used in analyses.

### 2.3. Data analysis

Minimum leaf conductance and stoma density data were analysed using mixed-model analysis of variance with PROC MIXED in SAS (Littell et al., 1996).



Individual runs and groups were considered random effects. In initial analyses a significant negative correlation was observed between leaf blade area and  $g_{\min}$  ( $r = -0.36$ ) so this area was included as a covariate in further analyses of  $g_{\min}$ . Spearman rank correlation coefficients ( $r_s$ ) were calculated for all other correlative comparisons. Least-squares means are reported with pairwise mean comparisons computed using the probability of difference option in PROC MIXED (Littell et al., 1996). Statistical significance was assigned at  $P \leq 0.05$  throughout.

#### 2.4. Validation of experimental approach

Two preliminary experiments were conducted to validate our experimental approach. One indicated that mass lost from the cut end of the leaf blade was insignificant relative to that lost from the remainder of the leaf during the 6 h drying period. In this experiment, the cut end from leaf blades of eight different plants (six *D. californica*, two *E. lehmanniana*) was dipped in petroleum jelly before the initial mass was recorded while a second leaf blade from that plant was not treated with petroleum jelly (Muchow and Sinclair, 1989). Minimum leaf conductance was measured as described above. In this two-replication experiment, there were no significant plant  $\times$  treatment or species  $\times$  treatment interactions and no significant difference was observed in  $g_{\min}$  between the treatments ([least-squares mean  $\pm$  SE] no petroleum jelly:  $9.73 \pm 1.85 \text{ m s}^{-1} 10^5$ , with petroleum jelly:  $9.55 \pm 1.67 \text{ m s}^{-1} \times 10^5$ ).

In a second experiment,  $g_{\min}$  was measured as described above but with ( $110 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ) or without ( $0 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ) light exposure during the drying period to assess stoma closure under the experimental conditions. The experiment was conducted using leaf blades from five randomly selected *D. californica* plants from each population on two dates with two replicate leaves per plant. No significant plant  $\times$  treatment or population  $\times$  treatment interactions were observed and  $g_{\min}$  was significantly less in leaf blades kept in the dark than those in the light ( $7.37 \pm 1.40$  vs.  $8.21 \pm 1.72 \text{ m s}^{-1} \times 10^5$ ) suggesting significant differences in stoma closure between the light treatments.

### 3. Results

Mean temperature varied considerably among runs for the acclimatization periods before  $g_{\min}$  was evaluated (Table 2). However, there was no significant correlation between this temperature and mean  $g_{\min}$  either for individual populations ( $r_s = -0.43$ – $-0.71$ ,  $P > 0.11$ ) or for the mean  $g_{\min}$  over all populations for each run ( $r_s = 0.26$ ,  $P = 0.62$ ).

A combined analysis that included data from all six runs showed a significant ( $P \leq 0.05$ ) population  $\times$  run interaction for  $g_{\min}$  and significant differences in mean  $g_{\min}$  between populations for each of the six runs (Table 2). Minimum leaf conductance was consistently lower in the Texas population than in the Arizona population of *D. californica*. Likewise, in five of the six runs,  $g_{\min}$  was significantly



lower in the *E. lehmanniana* population than in the *D. californica* population from Arizona.

The area of leaf blades upon which  $g_{min}$  was measured differed significantly among the populations with the blades smallest in *E. lehmanniana* (Table 3). Leaf blade area was significantly and negatively correlated with  $g_{min}$  in each population (Table 4). Significant differences were observed among populations in adaxial and abaxial stoma densities (Table 3). However, there was no consistent relationship between  $g_{min}$  and stoma density (adaxial, abaxial or total for both surfaces) of individual plants (Table 4).

The *E. lehmanniana* population produced significantly more shoot biomass per plant than both of the *D. californica* populations (Table 3). Mean shoot biomass produced per plant did not differ between the two *D. californica* populations.

Table 3  
Least-squares means for leaf blade area, stoma density, shoot biomass and the ratio of shoot biomass/minimum leaf conductance in two *Digitaria californica* populations and one population of *Eragrostis lehmanniana*

Trait	Species/population		
	<i>Digitaria californica</i>		<i>Eragrostis lehmanniana</i>
	Texas	Arizona	Arizona
Leaf blade area (cm <sup>2</sup> , adaxial + abaxial)	4.36 b <sup>a</sup>	4.94 a	3.16 c
Adaxial stoma density (stomata mm <sup>-2</sup> )	43.8 c	52.1 b	66.9 a
Abaxial stoma density(stomata mm <sup>-2</sup> )	33.7 ab	37.4 a	31.8 b
Shoot biomass produced over Runs 1-4 (g plant <sup>-1</sup> )	1.88 b	2.17 b	3.68 a
Ratio of shoot biomass/mean $g_{min}$ , Runs 1–4	0.304 b	0.281 c	0.573 a

<sup>a</sup>Least-squares means within a row followed by the same letter are not significantly different based on pairwise comparisons using the probability of difference option in PROC MIXED (Littell et al., 1996).

Table 4  
Spearman rank correlation coefficients between various plant traits and epidermal conductance in two *Digitaria californica* populations and one population of *Eragrostis lehmanniana*

Trait	Species/population		
	<i>Digitaria californica</i>		<i>Eragrostis lehmanniana</i>
	Texas	Arizona	Arizona
Leaf blade area	-0.39 <sup>a</sup>	0.55*	-0.39*
Adaxial stoma density	-0.21	0.01	0.10
Abaxial stoma density	-0.14	-0.24	0.03
Adaxial + abaxial stoma density	-0.17	-0.22	0.08
Shoot biomass	-0.28	-0.35*	0.06

<sup>a</sup>Significant at  $P \leq 0.05$ .  $N = 40$  for each population.

Significant differences were observed among all three populations when shoot biomass was represented as a function of  $g_{\min}$ . This value was consistently higher in *E. lehmanniana* than in the *D. californica* populations and was also about 7% higher in the *D. californica* population from Texas than in the Arizona population. Mean  $g_{\min}$  for Runs 1–4 was significantly and negatively correlated with the amount of biomass produced during this period in the Arizona *D. californica* population (Table 4). Evidence of a negative correlation between these variables also was observed in the Texas *D. californica* population but not in the *E. lehmanniana* population.

## 4. Discussion

### 4.1. Stoma density and leaf area

Muchow and Sinclair (1989) observed a significant positive relationship between epidermal conductance and stoma density in *Sorghum bicolor*. This led them to conclude that transpiration from incompletely closed stomata or peristomatal transpiration was a significant source of leaf water loss in their experiments designed to measure epidermal conductance. Based on correlation analyses, stoma density was not related to  $g_{\min}$  in our experiments (Table 4). This along with results from our preliminary experiments with leaves desiccated in light and dark suggests that stoma closure was likely to be complete in our experiments and that open stomata were not a significant component of  $g_{\min}$ .

The negative relationship between  $g_{\min}$  and leaf blade area (Table 3) may reflect the effects of leaf age and cuticular properties associated with leaf maturation. Schönherr (1976) showed that epidermal conductance from *Pyrus* leaf cuticles decreased significantly as leaves developed to full expansion. Younger leaf blades in these grass species could be subject to much more epidermal conductance than would older leaves. However, only fully expanded leaves were sampled in our experiments, which should have reduced variation in leaf age. The *D. californica* population with larger leaves also had higher mean  $g_{\min}$ . This supports the contention that leaf age was not confounding evaluation of inherent differences among populations in this trait.

### 4.2. Epidermal conductance and drought adaptation

Plant survival and productivity in arid environments involves interactions among a complex set of physiological and developmental processes (Fernandez and Reynolds, 2000). Generally included among these are photosynthetic efficiency and ability of cells to remain physiologically competent at low osmotic potential during drought periods. For grasses that produce perennial tillers, decreasing epidermal conductance could lead to the avoidance or postponement of dehydration in long-lived tillers. This would maintain the morphological potential for rapid re-initiation of growth when soil water levels permit photosynthetic activity.

Modeling by Sinclair (2000) suggested that the survival value of low epidermal conductance would be greatest at about  $0.1 \text{ mm s}^{-1}$ , although he did not estimate effects of epidermal conductances lower than this value, most likely because values observed for crop plants are generally greater than  $0.1 \text{ mm s}^{-1}$ . In our experiments, mean  $g_{\min}$  ranged from 0.066 to  $0.093 \text{ mm s}^{-1}$  ( $5.62\text{--}7.96 \text{ m s}^{-1} \times 10^5$ ), values that would be associated with plant survival of droughts in excess of 20 d in Sinclair's models assuming some leaf loss.

Meteorological records show that the typical length and severity of drought in western Texas is generally greater than that in southern Arizona (Table 1). Plants with reduced epidermal conductance have a lower rate of water loss per unit leaf area that results in increased tissue water conservation during drought. The Texas *D. californica* population exhibited significantly lower  $g_{\min}$  than the population from southern Arizona. Moreover, the lack of a significant difference in shoot biomass accumulation between these two populations suggests that plants from these populations would be expected to have about the same amount of water stored in shoot tissues at the onset of a drought. Thus, at least relative to drought-induced changes in shoot relative water content, plants from the population from the more arid site in Texas may be better able to avoid dehydration than those from the Arizona population. Furthermore, assuming that shoot biomass directly reflects an integrated assessment of whole-plant competitive ability, the significantly higher shoot biomass/mean  $g_{\min}$  ratio in the population from Texas indicates a generally higher level of fitness with regard to water conservation. The negative relationship between  $g_{\min}$  and amount of shoot biomass observed in the *D. californica* populations indicates that increased water conservation during droughts within the experimental period was associated with increased shoot biomass production. This further supports the contention that  $g_{\min}$  represents a component of the overall dehydration avoidance strategy that has evolved in *D. californica* in response to environmental conditions.

The time required for natural selection to affect a trait such as  $g_{\min}$  in a short-lived (usually  $<8$  years) perennial grass such as *D. californica* is unknown. However, differences in  $g_{\min}$  between the two *D. californica* populations could reflect natural selection in response to relatively recent precipitation patterns rather than precipitation over longer time periods (e.g. Table 1). Our interpretation of the possible adaptive significance in differences in  $g_{\min}$  between the populations is consistent given precipitation conditions in the 5 years before seed was collected for this research in addition to long-term precipitation records.

Variation in epicuticular wax structure has been related to seedling drought survival in *E. lehmanniana* (Hull et al., 1978) perhaps via its effects on epidermal conductance. The significantly lower  $g_{\min}$  exhibited by the population of *E. lehmanniana* compared to the *D. californica* population from Arizona suggests that at least a portion of the competitive success of *E. lehmanniana* could be attributable to increased leaf tissue water conservation during drought. In our experiments *E. lehmanniana* also exhibited greatly increased (+69%) shoot biomass productivity relative to that of *D. californica* indicating that maintenance of morphological potential for post-drought growth via dehydration avoidance may also be an important component of its competitive success.

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