Int. J. Plant Sci. 171(7):749–760. 2010.
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1058-5893/2010/17107-0004$15.00 DOI: 10.1086/654845

PLANT-SOIL WATER RELATIONS AND SPECIES BORDER OF *CLARKIA XANTIANA* SSP. *XANTIANA* (ONAGRACEAE)

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Low precipitation can limit plant distributions. Soil variation might interact with precipitation gradients to define species borders. Analyzing the eastern species border of the California annual *Clarkia xantiana* ssp. *xantiana*, we assessed the following: (1) the geography of plant water status, precipitation, and soil; (2) soil control of plant water status; and (3) water status control of plant performance. Plant water potential declined toward the border in consecutive years. Precipitation declined in parallel and was lower in the year of lower water potential. Many border soils are derived from metasedimentary rock, while igneous rock dominates the species range to the west and unoccupied areas to the east. Compared with igneous soils, metasedimentary soils were found to have greater penetration resistance and finer texture, and they exhibited greater water storage capacity but also stronger restrictions on water release. Within populations, plant water status was inferior on shallow slopes with hard, fine soils. Among populations, plant size and fruit production increased with water potential, though seedling-to-adult mortality was independent. Low precipitation and an abrupt change in bedrock likely contribute to the species border of *C. xantiana* ssp. *xantiana*. Understanding adaptation and distribution shifts under climate change requires a consideration of both climate and soils.

Keywords: plant water relations, species borders, *Clarkia xantiana*, soil texture, soil penetration resistance, demography.

Introduction

The positions of species' geographic range borders are determined by some combination of environmental gradients that limit individual and population performance, genetic constraints on adaptation, and dispersal limitation (Antonovics 1976; Gaston 2003; Antonovics et al. 2006). Thorough investigations of these factors for particular species and borders are rare, however, and are sorely needed to understand species borders for the sake of basic ecology and evolutionary biology as well as for conservation and climate change research (Gaston 2003, 2009; Parmesan et al. 2005; Samis and Eckert 2007, 2009; Geber 2008). To characterize possible causes of species borders, a critical step is to evaluate the joint geographic distributions of features of individual performance and the environmental factors that limit them (Caughley et al. 1988; Brown and Lomolino 1998; Gaston 2003; Parmesan et al. 2005; Sexton et al. 2009).

In plants, a major control of species distributions is geographic variation in precipitation. Water limitation due to low precipitation, for example, can hinder establishment, survival, and reproduction (e.g., Jordan and Nobel 1979; Royce and Barbour 2001; Hampe 2005; Engelbrecht et al. 2007). Precipitation is not the only factor capable of influencing distributions via water relations. Topography, for example, can limit plants to slopes that face away from the equator because of their lower solar radiation and evaporative demand (Pigott and Pigott 1993; Foden et al. 2007; Warren 2008, 2010). Variation in soil properties can also be important. Species distributions sometimes shift toward more xeric or more mesic topographic locations, depending on soil parent rock (Whittaker 1960; Branson et al. 1965; Whittaker and Niering 1965; Kruckeberg 2002). Parent material might affect water relations and reduce performance, in part by affecting soil resistance to penetration, which can reduce water infiltration, restrict root growth, and increase capillary forces binding water to soil (Kozlowski 1999; Gomez et al. 2002; Passioura 2002; Webb 2002; Hillel 2004; Godefroid and Koedam 2004; Godefroid et al. 2005; Whalley et al. 2008). Parent material can also affect soil texture (Parsons and Herriman 1975; Kruckeberg 2002), which correlates with penetration resistance (finer soils being harder; To and Kay 2005). When compared with coarse soils, fine soils are more resistant to air entry and loss of hydraulic conductivity, which are properties that can reduce plant water stress in humid climates (Hacke et al. 2000). In arid climates, however, fine-textured soils are sometimes associated with high water stress (Barnes and

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Manuscript received March 2010; revised manuscript received May 2010.

Harrison 1982; Sperry and Hacke 2002; Rosenthal et al. 2005) and low plant performance (Hererra 2002; Miller et al. 2006), likely because coarse texture increases infiltration, reduces evaporative loss, and weakens capillary forces (Alizai and Hulbert 1970; Noy-Meir 1973; Lane et al. 1998; Hamerlynck et al. 2002; Hillel 2004). A complete accounting of water limits to plant distribution, particularly in relation to species borders, therefore requires a characterization of the geography of plant water stress and its possible geologic and climatic sources.

Clarkia xantiana ssp. *xantiana* A. Gray is a winter annual with a well-characterized distribution in central and southern California (Lewis and Lewis 1955; Eckhart and Geber 1999). Water relations likely influence its distribution limits. In the Kern River drainage, where the species is most abundant, the westerly North Pacific storm track and the north-south orientation of the mountain ranges combine to produce a west-east gradient of declining precipitation (Western Regional Climate Center 2010). Transplanting seeds beyond the eastern species border of this region reveals patterns of phenotypic plasticity and individual fitness that appear to arise in part from water stress (Eckhart et al. 2004; Geber and Eckhart 2005). The geology of this region suggests that soil properties also influence plant water status and the position of the range edge. While igneous rocks dominate most of the species range, substantial areas of metasedimentary rocks do occur, most commonly in the vicinity of the Kern Canyon Fault and the proto Kern Canyon Fault, along the North Fork of the Kern River, and continuing to the south (Saleeby et al. 2008). The highest frequency of metasedimentary surface rock within this area (Nadin and Saleeby 2008) coincides with the eastern species border of *C. xantiana* ssp. *xantiana* (Eckhart and Geber 1999). In similar climatic conditions, soils derived from metamorphic substrates tend to be finer than those from igneous substrates (Parsons and Herriman 1975). Caughley et al. (1988) proposed that species borders defined by climatic gradients will tend to exhibit gradual declines in individual performance (“ramps”) across the range to the border, while effects of discontinuous environmental variation (such as bedrock substrate) will tend to cause abrupt decline in performance (“steps”) at the border. *Clarkia xantiana* ssp. *xantiana* enables an assessment of the possibly interactive contributions of gradual and abrupt forms of environmental variation.

Here we analyze contributions of precipitation and soils to plant water stress and evaluate whether water stress helps to define the eastern species border of *C. xantiana* ssp. *xantiana*. Specifically, we ask three questions. (1) What is the nature of geographic variation in plant water potential, growing season precipitation, and soil properties that are likely to affect plant water status (penetration resistance, texture, and water-release characteristics as influenced by parent rock)? (2) Can variation in soil properties in this system cause variation in water stress independent of precipitation? (3) Does among-population variation in plant water potential explain variation in plant size, fruit production, and mortality? We report that precipitation and soil properties together drive variation in plant water potential and that plant water potential predicts variation in plant size and fruit production. In this way, “stepped” environmental variation in the form of exposed metasedimentary rocks at the species border likely aggravates the effects of a “ramped” decline in precipitation on the position of a plant species border.

Material and Methods

Study Species

Clarkia xantiana ssp. *xantiana* A. Gray occurs most commonly on steep slopes at low-to-moderate elevations (500–1500 m) in grasslands, pine-oak woodlands, and openings in chaparral (Lewis and Lewis 1955; Eckhart and Geber 1999). Seeds germinate in fall and winter, and plants mature in late spring and early summer. Seeds disperse passively during the summer and early autumn drought in this area’s Mediterranean climate. Outcross pollination is accomplished mainly by bees that specialize on the genus *Clarkia* (Moeller 2006). *Clarkia xantiana* ssp. *parviflora*, a sister subspecies that is phenotypically distinct (Moore and Lewis 1965; Lewis and Raven 1992; Eckhart and Geber 1999), self-fertilizing (Moore and Lewis 1965; Runions and Geber 2000; Mazer et al. 2004), and reproductively isolated (Moore and Lewis 1965; D. Moeller and P. Tiffin, unpublished observations) from *C. xantiana* ssp. *xantiana*, has a more easterly distribution, with ~10 km of overlap (Eckhart and Geber 1999).

We have spent over 14 yr searching the lower Kern River drainage for *C. xantiana* ssp. *xantiana* populations (e.g., Eckhart and Geber 1999; Moeller 2003). We are confident that we have located stable positions of several of the easternmost populations, all of which occur within 1 km of 118.41°W (= 372 km easting in UTM units, zone 11 North, NAD 27). We therefore classified sample sites as lying beyond the species border simply if they are east of the easternmost known populations at a given latitude, rather than resorting to more complicated approaches to delineating the border (Fortin et al. 2005).

Geography of Plant Water Status, Precipitation, and Soils

Plant water status. During the last week of May and the first 3 wk of June 2006 and 2007, we measured midday water potential (ψ_{mid}) using a pressure chamber (PMS Instruments, Albany, OR) as an indicator of the water stress plants experience during the peak of the flowering season at the warmest, least humid times of day (Barnes and Harrison 1982). Highly negative ψ_{mid} values reduce plant growth and survival via wilting, hydraulic failure, and/or carbon starvation (McDowell et al. 2008). We estimated stem water potential rather than leaf water potential because *C. xantiana* ssp. *xantiana* petioles frequently collapse before readings can be taken at the high pressures necessary to balance xylem sap tension. Stem water potential represents an upper limit on leaf water potential, as leaf water potential must be lower than stem water potential for water to flow from stems to leaves. Our field observations and pilot experiments (A. J. Keledjian, unpublished data) indicate that the stem water potential at which *C. xantiana* ssp. *xantiana* leaves wilt (but recover) is approximately −2 MPa, varying among individuals from −1.8 MPa to −2.5 MPa. For our physiological sampling, we selected plants with at least one green leaf and at least one clearly fresh, turgid flower, regardless of whether leaves showed signs of wilting. Familiarity with geographic variation in flowering time in the study species (Eckhart and Geber 1999) allowed us to sample each population near its peak of flowering (i.e., the date with the highest density of flowering individuals).

We scored ψ_{mid} for 400 plants in 2006: 20 plants in each of 20 populations across a 30-km east-west transect (fig. 1*A*). This sample was intended to represent reasonably dense coverage from within 5 km of the western species border to the limit of the eastern species border, at similar elevations. In 2006 we set up two 20-m-long sampling transects within each population, selecting individual flowering plants every ~2 m along each transect. In 2007 we scored 15–20 plants in each of 10 of the populations sampled the previous year (fig. 1*A*). Lower plant densities in 2007 compelled us to sample by selecting individuals at regular intervals along haphazard walks through the populations. In both years we measured the height of each sampled plant to the nearest 0.5 cm. We then cut the central stem 5 cm from the top and placed it in the pressure chamber within 2 min (usually <1 min). All ψ_{mid} readings were taken between 1000 and 1400 hours solar time. We noted ambient temperature and relative humidity before and after taking the set of ψ_{mid} measurements for each population, estimating vapor pressure deficit for the midpoint temperature and humidity. Vapor pressure deficit did not explain any significant variation in ψ_{mid}, and therefore we dropped this variable from the analyses. As precipitation declined approximately linearly from west to east (see below), we asked whether geographic variation in ψ_{mid} also declined linearly. We applied ANCOVA with year as a categorical variable and easting (UTM NAD 27 longitude, in km) as a covariate. As the interaction term was not significant, we left it out of the final model.

Precipitation. We installed automated precipitation sensors (Onset Computers, Bourne, MA) at locations throughout the sampling area and at sites up to 13 km beyond the eastern range edge (fig. 1*B*). Stations recorded precipitation

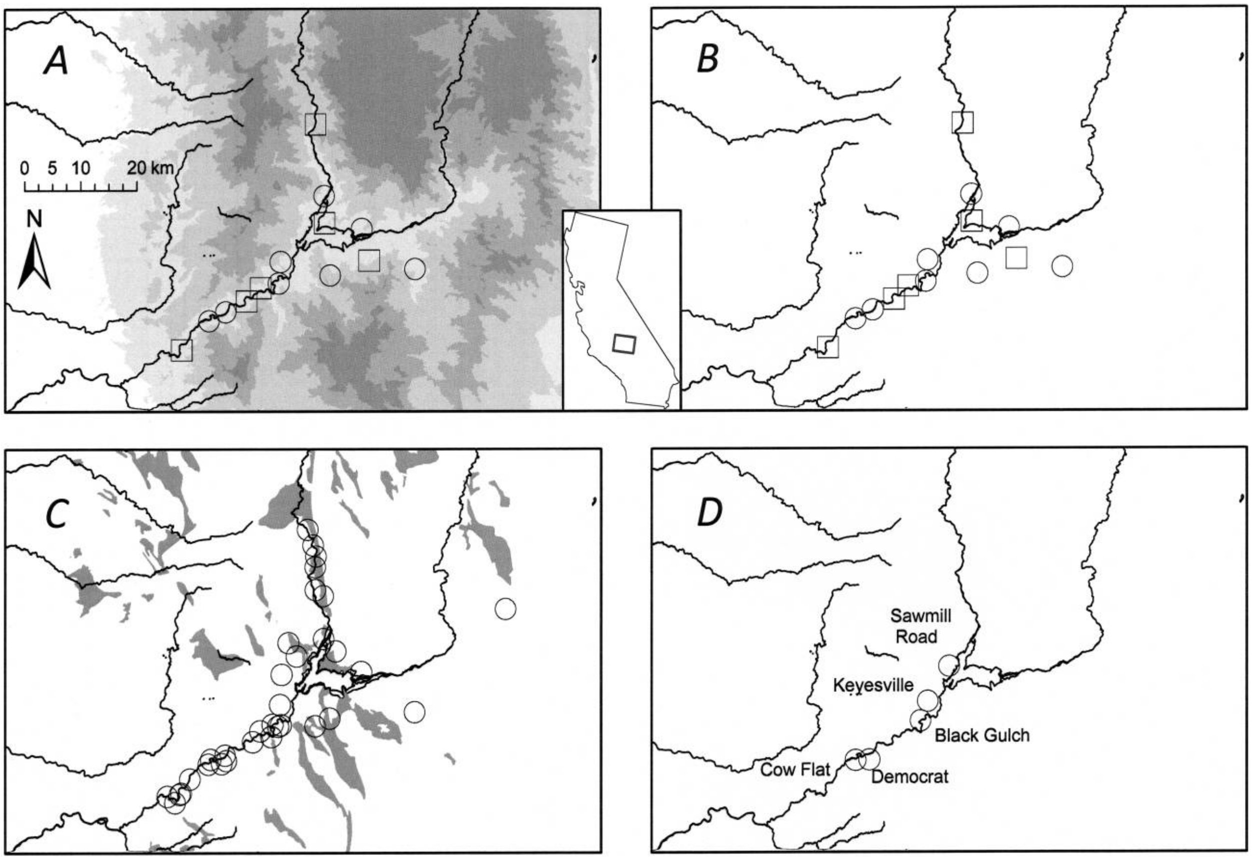

Fig. 1 Maps of study area and site locations. Inset shows location of study area within California. Solid lines are permanent flowing waters. The reservoir outlined in the center is Isabella Lake. *A*, *Clarkia xantiana* ssp. *xantiana* populations where we estimated plant water potential (circles, 2006 and 2007; squares, 2006 only). Shading indicates 500-m contours, ranging from <500 m a.s.l. (white in the San Joaquin Valley at left) to >2000 m a.s.l. (40% gray on Greenhorn Mountains and Sierra Nevada ridges and plateaus in center and right). *B*, Precipitation station locations (circles, 2005–2007; squares, additional stations 2006–2007). *C*, *Clarkia xantiana* ssp. *xantiana* and *C. xantiana* ssp. *parviflora* populations where we determined soil properties in 2006 (circles). Shaded areas are locations of metasedimentary surface rock, the remaining areas being igneous rocks. *D*, *Clarkia xantiana* ssp. *xantiana* populations where we compared water potential between contrasting slopes in 2007 (circles). The majority of field sites are in the Kern River Canyon southwest of Isabella Lake or in the canyon of the North Fork of the Kern River, north of the reservoir, at elevations between 500 and 1000 m.

at 30-min intervals. We analyzed geographic variation in growing season (November–May) precipitation in 2006–2007 (eight stations) and 2007–2008 (13 stations, with a fourteenth omitted because of a suspected malfunction) by ANCOVA of the same design as for ψ_{mid}.

Soils. At all soil sampling sites we noted whether upslope exposed bedrock, surface pebbles, and gravel (i.e., soil parent material) were igneous (granodiorite, granite, quartz monzonite, and/or gabbro, not distinguished from each other in the present analysis; $N = 26$ sites) versus metasedimentary (generally schist; $N = 7$ sites; fig. 1*C*). For a detailed lithology of this area, see Saleeby et al. (2008). As noted above, metasedimentary bedrock is abundant at the species border, with igneous bedrock dominating areas both west and east of it (fig. 1*C*). Border populations of *C. xantiana* ssp. *xantiana* occur on both soil types, though they are underrepresented on metasedimentary substrates (D. Montgomery and V. Eckhart, unpublished observations). If the soil properties of metasedimentary sites differ on average from those of igneous soils, these differences may cause variation in plant performance (1) between border sites and sites away from the border and (2) among sites on contrasting substrates along the border.

We estimated soil penetration resistance with a SC900 static cone penetrometer (Spectrum Technologies, Plainfield, IL) in each of the populations for which we estimated water stress in 2006, plus in eight additional populations and at four sites located beyond the species border on steep slopes that resemble *C. xantiana* ssp. *xantiana* habitat (and where *C. xantiana* ssp. *parviflora* occurs; fig. 1*C*). We estimated resistance (in MPa) at 2.5-cm depth intervals until we encountered rock or very hard soil that the instrument could not penetrate; this point usually occurred near 12.5 cm but occasionally it did not occur until 30 cm. Within sites we took readings every 2 m along four 10-m transects. As correlations between resistances at different depths were very strong (generally >0.8), bedrock differences in resistance at one depth indicate differences in resistances at other depths. We present a subset of the data, three scores of penetration resistance: (1) resistance at 2.5 cm, which had the most complete data set and the strongest correlations with resistances at other depths; (2) resistance at 10 cm, the depth of our soil cores (see below); and (3) the maximum resistance encountered before the substrate became impenetrable. We assessed parent-rock effects on penetration resistance with *t*-tests of the distributions of population means.

We collected a cylindrical 2.5×10-cm soil sample within 1 m of each penetration measurement and scored samples for soil texture. In the lab we combined four random soil samples for each population, dried them in an oven at 105°C for 48 h, and removed gravel by passing each sample through a 2-mm sieve. A Retsch AS200 (Haan) machine-sieved soil through 1-, 0.5-, 0.25-, 0.106-, and 0.053-mm sieves (Six et al. 2000). We weighed the six resulting particle-size fractions and converted them to proportions of total dry weight. We did not separate silt and clay soil fractions (particles <0.053 mm) because silt and clay together constituted such small components of the soils (almost universally <4%).

We generated soil characteristic curves (Bristow et al. 1984; Hillel 2004) for 30 sites, thoroughly mixing four additional random soil samples per site. After drying soil as described above and adding known weights of water, we determined ψ_{soil} at known gravimetric water contents using a dew point potentiometer (Decagon Instruments, Pullman, WA). Soil characteristic curves can be fitted to power functions, $\psi_{\mathrm{m}} = \psi_{\mathrm{e}}(\theta/\theta_{\mathrm{s}})^{-\mathrm{b}}$, where θ is gravimetric water content, θ_{s} is saturated water content, ψ_{m} is soil matric potential, ψ_{e} is soil matric potential at air entry, and the exponent b describes the shape of the function (Bristow et al. 1984; Campbell 1985, 2008). Logarithmic transformation simplified parameter estimation by making the curves linear. We used ANCOVA to estimate characteristic curves for multiple sites and to compare curves of igneous versus metasedimentary soils. In the model, the $\log_{10}$ of inverse ψ_{soil} was the dependent variable, the $\log_{10}$ of gravimetric water content was the covariate, bedrock was a fixed factor, and site nested within bedrock was a random factor. In the output, the slope coefficient for a site estimates b and the Y-intercept estimates $-\log_{10}\psi_{\mathrm{e}}$. A main effect of bedrock would indicate an average difference in Y-intercept (air-entry potential) between metasedimentary and igneous soils. A significant effect of site nested within bedrock would reflect variation in Y-intercept among sites within a soil type. An interaction effect between bedrock and the covariate would represent an average difference in b between soil types. Because we found this interaction to be nonsignificant, we omitted it from the final model. We restricted the data set in two ways before performing the ANCOVA. First, to ensure that the estimated release curves apply in parameter ranges that are likely to matter to plant function (i.e., the range of plant available water: from field capacity at ψ_{m} of ~0.1 MPa for sandy soils to the wilting point at ψ_{m}, approximately -2 MPa; Campbell 1985, 2008), we excluded samples with ψ_{m} values above saturation and samples with ψ_{m} values far below the wilting point (<-10 MPa). Second, to increase confidence in our estimates of each site's response curve, we removed sites for which we collected fewer than five data points in the restricted range of water potentials. With these restrictions, we were able to analyze 14 sites with igneous soils and four sites with metasedimentary soils; without these restrictions, findings did not differ qualitatively.

Soil Control of Plant Water Status

In 2007 we analyzed plant water status within five populations, comparing the water potential of plants experiencing contrasting soil properties but equivalent precipitation (fig. 1*D*). Each of these populations occur on soils derived from igneous rocks. Steep sections of hillslopes tend to have soils that are coarser (Churchill 1981; Besler 1987; Brubaker et al. 1993; Tomer and Anderson 1995; Pachepsky et al. 2001) and softer (Wild 1993; Hillel 2004) than level areas, and plants on steep slopes tend to have higher water potential (e.g., Shumar and Anderson 1986). For five of the populations studied in 2007, we paired shallow slopes with adjacent, steep slopes (recent landslides, stream cuts, or road cuts). We quantified soil resistance (five to 15 sample locations per site per slope type), estimated ψ_{mid} values (15–20 plants per site per slope type), and collected bulked samples for soil texture analysis. We measured plant water potential and sampled soils in the same way as for the main 2007 data sets. We analyzed ψ_{mid} and $\log_{10}$ soil resistance at 2.5 cm by

ANOVA, with population treated as a random blocking factor and slope type as a fixed factor. Bulking soil samples within populations and slope types left no replication for soil texture within sites. We therefore compared arcsine-square-root-transformed soil particle size fractions between slope types with paired *t*-tests, using populations as replicates.

To determine whether soil properties (or, more accurately, slope as a correlate of soil properties) affect diurnal cycles of plant water status, we measured plant water potential three times over a 17-h period in one of the five populations mentioned above (Sawmill Road; fig. 1*D*), comparing plants on a relatively shallow hillslope with others located on a steep road cut. We measured predawn stem water potential (ψ_{prd}) between 0400 and 0500 hours, ψ_{mid} between 1200 and 1300 hours, and evening water potential (ψ_{eve}) between 1800 and 1900 hours ($n = 15$ plants per group, per location, and per time interval; sampling as described above). We analyzed diurnal courses by ANOVA, with slope type and time of day as factors.

Because populations on metasedimentary-derived soils mainly occur at the species border (and therefore in areas of similar and low precipitation), it is a challenge to disentangle precipitation effects from soil parent material effects. We took a preliminary step to address this issue by analyzing the 2006 ψ_{mid} data by ANCOVA, with bedrock as a factor and easting (a close correlate of precipitation) as a covariate. The nonsignificant interaction term was omitted from the model. This analysis should be regarded cautiously, as the covariate is partly confounded with the factor (i.e., metasedimentary substrates occur only near the border).

Plant Water Status Control of Plant Performance

Associated long-term demographic studies provided estimates of individual fruit production and population mortality rates to supplement the data on plant height collected from plants whose water status we assessed. The demographic data came from a core sample of 20 populations where we established permanent plots in October 2005 (30 1×0.5-m plots along four to five transects, with 2.5 m of spacing between plots within transects, near the centers of populations), as well as from an extended sample of 21 additional populations that we have sampled repeatedly, though without permanent plots. Fourteen of the 20 populations where we estimated plant water potential and height were part of the core sample, and the remaining six were in the extended sample. At the core sample of 20 populations, we recorded the number of seedlings in each plot in late January to early February of 2006 and 2007, returning in June of those years to record the number of surviving fruiting plants. For all 41 populations, we estimated the average numbers of fruits per surviving plant. In 2006 we did this by sampling all fruiting plants and counting their fruits in randomly positioned 1×0.5-m plots spread across the sites. We followed the same procedure in 2007, except that 30 of the sample plots at the core sample of 20 populations were the permanent plots. For each population in each year, we computed the mean number of fruits per plant and seedling-to-fruiting mortality (as a *k* value: $\log_{10}$ [seedling density/fruiting plant density]; Begon et al. 2006). One population (with no influence on statistical conclusions) was excluded from this analysis because its estimate of fruiting plant density exceeded its estimate of seedling density, suggesting that we failed to capture a late pulse of germination at that site. Sample sizes of fruiting plants at the populations and in the years where we studied plant water status ranged from 75 to 349. We used linear regression to assess whether variation in ψ_{mid} explained variation in plant performance (height at flowering; total fruit production) and demography (seedling-to-fruiting mortality) among populations, separately for each year. Log_{10} transformations of height and fruit number improved model fits.

Results

Geographic Variation in Plant Water Status, Precipitation, and Soils

Plant water status declined toward the eastern species border. Mean ψ_{mid} values across populations varied almost twofold, from -2.25 MPa to -1.3 MPa (extreme individual values ranging over sevenfold, from less than -3.5 MPa to greater than -0.5 MPa). Average values declined significantly from west to east, with a drop of ~0.6 MPa across the range in both study years ($\beta \pm \mathrm{SE} = -0.020 \pm 0.003$ MPa km^{-1}, $F_{(1,27)} = 42.05$, $P < 0.00001$; fig. 2*A*). Water potentials were significantly lower (~0.2 MPa) in the second year ($F_{(1,27)} = 8.03$, $P = 0.008$).

Patterns in precipitation mirrored those in water status. Precipitation varied among weather station sites and years from a minimum of 70 mm to a maximum of almost 350 mm (fig. 2*B*). Growing season precipitation declined significantly to the east ($\beta \pm \mathrm{SE} = -4.8 \pm 0.5$ mm km^{-1}, $F_{(1,18)} = 79.21$, $P < 0.00001$), and the second year (when plant water potential was lower) was 100 mm drier than the first year ($F_{(1,18)} = 81.71$, $P < 0.00001$).

Physical properties of soils derived from metasedimentary versus igneous bedrock differed substantially (figs. 3, 4). Sites with metasedimentary soils were, on average, twice as resistant to penetration at 2.5 cm and ~50% more resistant at 10 cm and at their maximum recorded values (fig. 3*A*; $t_{(6)} = 2.80$, $P = 0.031$; $t_{(9)} = 3.05$, $P = 0.014$; and $t_{(12)} = 3.80$, $P = 0.003$, respectively). Compared with igneous soils, metasedimentary soils were finer (fig. 3*B*). Sites with metasedimentary soils had proportionately less coarse sand (1–2 mm: $t_{(23)} = -2.61$, $P = 0.016$; 0.5–1 mm: $t_{(8)} = -3.75$, $P = 0.006$) and proportionately more fine sand (0.106–0.0253 mm: $t_{(12)} = 2.68$, $P = 0.02$; 0.053–0.106 mm: $t_{(7)} = 4.59$, $P = 0.003$).

Soil-type differences in characteristic curves were also evident (fig. 4). There was no average difference in slope between soil types ($F_{(1,87)} = 0.09$, $P = 0.77$), with the overall slope (*b*) estimated as 1.405 ± 0.07 ($t = 20.45$, $P < 0.0001$). Curves of metasedimentary soils were significantly displaced to the right along the soil water axis (fig. 4; $F_{(1,88)} = 5.16$, $P < 0.037$). This pattern means that metasedimentary soils can hold more water than igneous soils, on average, but the water they hold becomes unavailable to plants at higher water contents than in igneous soils. Variation within soil types was substantial, especially among sites with igneous

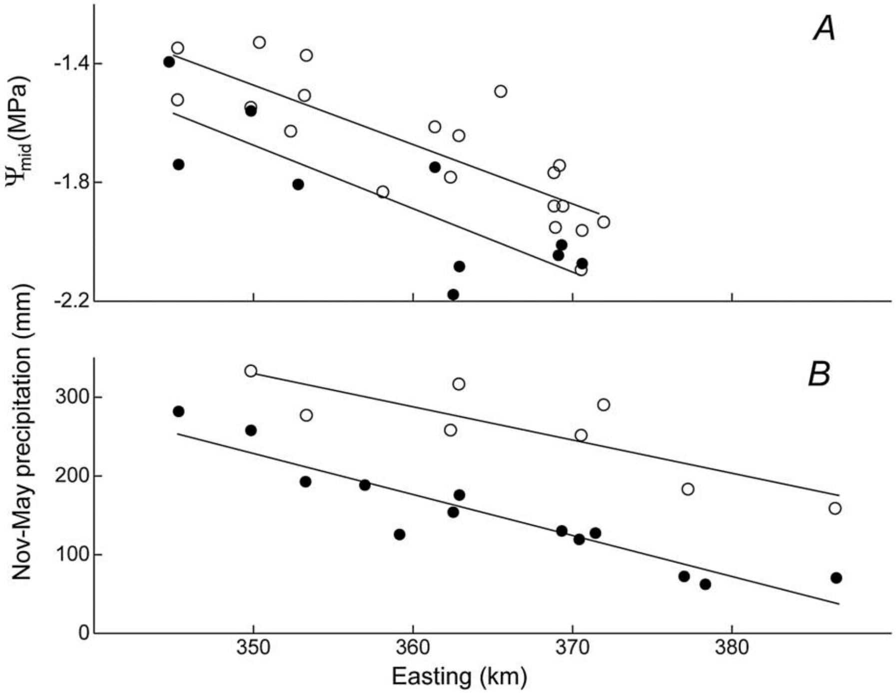

Fig. 2 Geographic variation in plant water stress and precipitation. *A*, Scatterplot of midday water potential versus easting in 2006 (open circles) and 2007 (filled circles). Each point represents the mean of 15–20 individuals. *B*, Scatterplot of November–May (i.e., growing season) precipitation in 2005–2006 (filled circles) and 2006–2007 (open circles). For both (*A*) and (*B*), regression lines are fitted separately by year, although ANCOVA calculated homogenous slopes (see text).

soils (fig. 4; $F_{(16,88)} = 20.00$, $P < 0.0001$). Overall, the model explained 85.2% of the variation in soil water potential.

Soil Control of Plant Water Status

Soil variation within populations was associated with substantial variation in plant water status, equal to 40% of the average decline across the large-scale data set. Values of ψ_{mid} averaged 0.25 MPa higher on steep, rapidly eroding slopes than on adjacent, more stable ones ($F_{(1,169)} = 45.06$, $P < 0.0005$; fig. 5). The soil of steeper slopes was 50% to several times softer ($F_{(1,87)} = 12.11$, $P < 0.0001$), and it was coarser in texture, though the only individual soil fraction that differed significantly was silt plus clay (higher on intact slopes [mean ± SE = 0.068 ± 0.003] than on eroding slopes [mean ± SE = 0.046 ± 0.004], $t_{(4)} = 4.49$, $P = 0.011$).

Diurnal courses of plant water potential on contrasting soils at the Sawmill Road site were 0.3–0.4 MPa higher on the steep slope at all times of day (slope-type effect: $F_{(1.84)} = 25.53$, $P < 0.0005$; fig. 6*A*). As expected, ψ_{prd} was highest and ψ_{mid} was ~0.5 MPa lower; ψ_{eve} showed recovery of about 0.1 MPa (time effect: $F_{(2,84)} = 31.91$, $P < 0.0005$). The absence of an interaction ($F_{(2,84)} = 0.41$, $P > 0.5$) indicates that slope (and, presumably, soil properties) had relatively small effects on the rate of decline in water potential from dawn to midday or on the rate of recovery afterward.

Analyzing the 2006 ψ_{mid} data by ANCOVA, with bedrock as a factor and easting (as a surrogate for precipitation) as a covariate, revealed a significant negative effect of easting ($\beta \pm \mathrm{SE} = -0.015 \pm 0.003$ MPa km^{-1}, $F_{(1,17)} = 15.9$, $P < 0.001$) and a marginally significant negative effect (approximately −0.15 MPa) of metasedimentary rock ($F_{(1,17)} = 3.53$, $P = 0.077$; fig. 6*B*).

Plant Water Status Control of Individual and Population Performance

Low values of ψ_{mid} (i.e., high water stress) were associated with low plant performance among populations. Plant height increased significantly with water potential in both years (2006: $\log_{10}$ height $= 2.05 + 0.25 \times \psi_{\mathrm{mid}}$, $t = 3.30$, $P = 0.006$, $r^2 = 35\%$; 2007: $\log_{10}$ height $= 2.15 + 0.30 \times \psi_{\mathrm{mid}}$, $t = 2.71$, $P = 0.030$, $r^2 = 35\%$; fig. 7*A*). Fruit number increased similarly with water potential (2006: $\log_{10}$ fruit number $= 1.50 + 0.42 \times \psi_{\mathrm{mid}}$, $t = 2.27$, $P = 0.036$, $r^2 = 22\%$; 2007: $\log_{10}$ fruit number $= 2.18 + 0.78 \times \psi_{\mathrm{mid}}$, $t = 3.11$, $P = 0.014$, $r^2 = 55\%$; fig. 7*B*). Seedling-to-adult mortality rate appears to be independent of adult water stress. In neither year was there a significant relationship between seedling-to-fruiting mortality and water potential (2006: $r = -0.393$, $P = 0.133$; 2007: $r = 0.089$, $P = 0.835$; fig. 7*C*).

Discussion

Our first question concerned the form of geographic variation in plant water potential, growing season precipitation, and soil properties. We found that ψ_{mid} at the flowering stage declined substantially from west to east, with wilting points

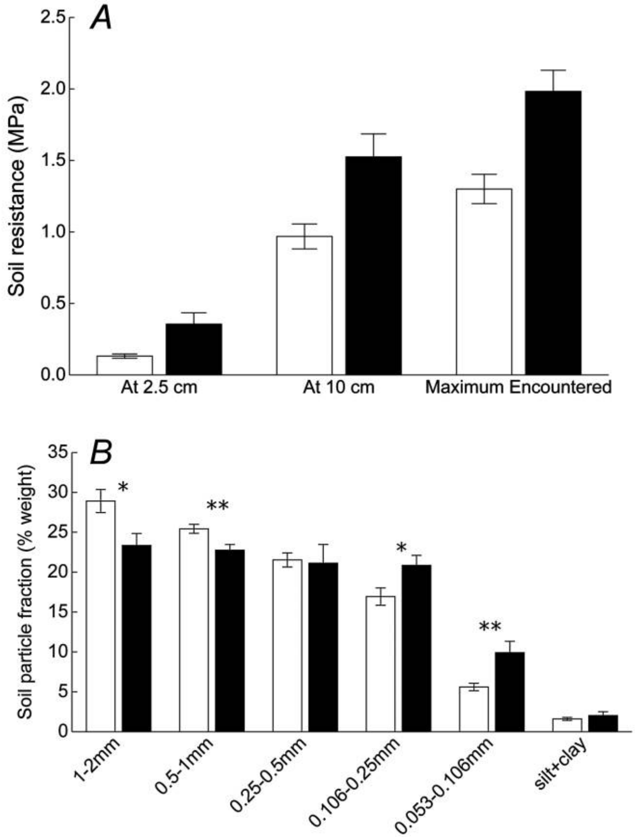

Fig. 3 Penetration resistance and texture of soils derived from different bedrock types. *A*, Resistance at two depths and at the maximum resistance encountered. Bars (open = igneous; filled = metasedimentary) are means of the site means for several populations; error bars are ±1 SE. *B*, Weight fractions of soil particles are for five sand classes plus a combined class of silt and clay. Bars are as in *A*. In *A*, all comparisons are significant (see text); in *B*, one asterisk indicates $P < 0.05$ and two asterisks indicate $P < 0.01$.

frequently being reached, especially near the species border. Lower ψ_{mid} values occurred across the range in the second year. Precipitation varied in parallel. Both spatial (west to east) and temporal (2005–2006 to 2006–2007) patterns matched those of plant water status. Precipitation is a major pathway through which water is expected to limit plant species ranges (Jordan and Nobel 1979; Royce and Barbour 2001; Hampe 2005; Engelbrecht et al. 2007). Our findings are consistent with this expectation.

Declining precipitation alone may not define the species border. Soils derived from igneous rock versus metasedimentary bedrock differed in features capable of affecting plant water stress and performance. Metasedimentary soils, a common substrate for *Clarkia xantiana* ssp. *xantiana* populations at the border but not in the main part of the range or beyond the border, are significantly finer-textured than igneous soils, though both soil types are very sandy. Texture differences are expected to cause differences in penetration resistance, with fine soils being harder (To and Kay 2005), and hydrology, with fine soils providing more surface area for adhesion of water to soil particles (Campbell 1985, 2008; Hillel 2004).

Metasedimentary soils were found to be more resistant to penetration than igneous soils. Average resistances at 10 cm in metasedimentary soils approached 2 MPa, which is sufficient to cause substantial declines in root and shoot growth (Passioura 2002). Aside from the potential for high penetration resistance to harm plant water status by reducing root growth and water availability, hard soils can limit performance even without variation in water content (Whalley et al. 2008). Thus, a high frequency of hard-soiled metasedimentary substrates along the border may exacerbate low precipitation effects on plant water status and performance.

Predicting the effects of contrasting soil hydrology between bedrock types is more complicated. The slopes of characteristic curves did not differ on average between soil types, but the curves of metasedimentary soils were displaced to the right on the water-content axis. This pattern predicts that metasedimentary soils can hold more total water and more plant-available water (i.e., water contained between $\Psi_{\mathrm{soil}} = -0.01$ and $\Psi_{\mathrm{soil}} = -2$ MPa) than igneous soils. The leftward displacement of the curves of igneous soils, however, means that the water they hold is available to plants when it is much less abundant in the soil than for metasedimentary soils. For example, when soil water contents lie between 1% and 2%, water is unavailable to plants in metasedimentary soils but it is available to plants in igneous soils (fig. 3). Thus, igneous soils may be less water stressful for plants than metasedimentary soils when actual water contents are low (Noy-Meir 1973).

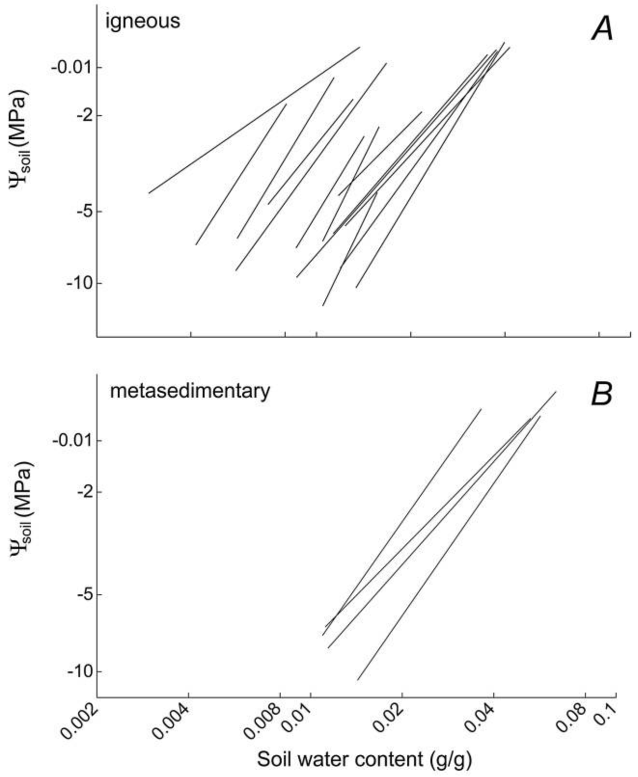

Fig. 4 Water relations of soils derived from different bedrock types. *A*, Soil characteristic curves (linearized by $\log_{10}$ transformation) for 14 sites with igneous soils. *B*, Soil characteristic curves for four sites with metasedimentary soils. Individual symbols omitted for clarity.

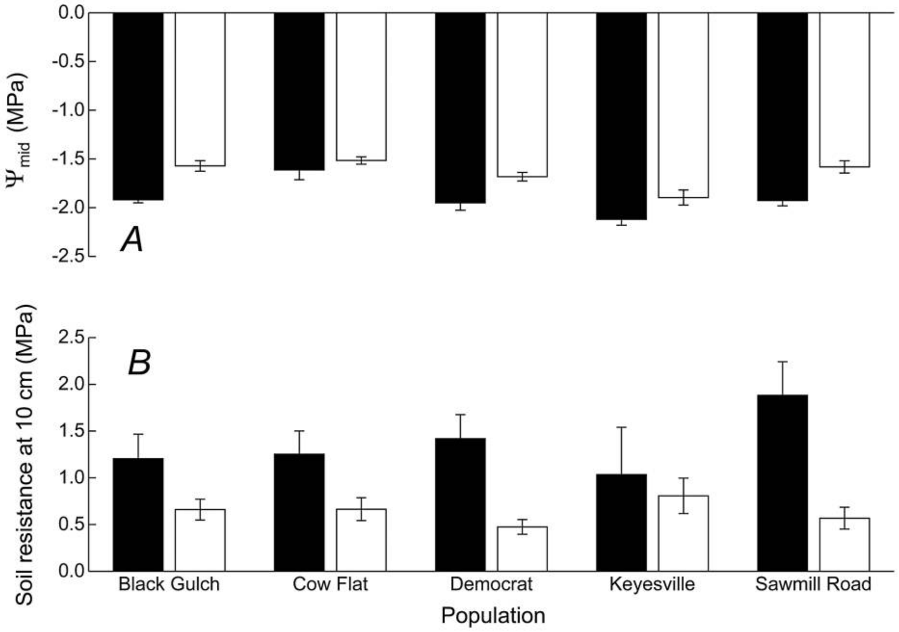

Fig. 5 Plant water status and soil penetration resistance on shallow slopes (filled bars) and adjacent rapidly eroding slopes (open bars) within populations. *A*, Measured midday water potential (Ψ_{mid}). *B*, Soil resistance. Bars are means, and error bars are ±1 SE.

Rosenthal et al. (2005) found higher plant water potentials despite lower soil water contents on coarse-textured sand dunes compared with interdune areas in three Great Basin species. They attributed this finding to coarser soil texture on the dunes.

It is impossible to disentangle completely the effects of precipitation and soils in the present study, because the variation is spatially correlated: the finest and hardest soils with distinct water-release curves occur in sites with some of the lowest precipitation. Nevertheless, the associations we found within populations between plant water potential and the texture and penetration resistance of soils (i.e., much lower water potential in areas with harder, finer soils), together with the marginally significant effect of bedrock on plant water potential (fig. 6*B*), suggest that precipitation and soil have independent effects. The net effect of the properties pronounced in metasedimentary soils appears to be increased water stress. If the species border of *C. xantiana* ssp. *xantiana* did not have such a high frequency of metasedimentary soils, then the species might occur farther east. The soft, coarse, igneous soils beyond the border might be suitable for *C. xantiana* ssp. *xantiana* if precipitation were not limiting. The easternmost soil sampling site was within 200 m of a transplant garden from a previous study, where pollen limitation and browsing by ground squirrels, lagomorphs, and deer, in addition to late-season water stress, reduced *C. xantiana* ssp. *xantiana* performance (Geber and Eckhart 2005).

A remaining challenge is to tease apart and quantify the effects of individual soil properties. Species distribution modeling (Latimer et al. 2006; Franklin 2009; Godsoe et al. 2009) would be one approach to characterizing soil effects on population persistence, evaluating whether population occupancy varies with soil parent material, texture, compaction, and topography if the variables vary sufficiently independently on a landscape scale. Experiments that vary compaction and/or texture independently (and that also evaluate the consequences for water-release dynamics) would be necessary to identify the critical property or properties (Whalley et al. 2008). In cultivation, Small (1972) found superior performance in certain other *Clarkia* species in fine-textured soils, though he hypothesized that this pattern arose from a higher phosphorus content in the fine-textured soils in his sample. In the case of *C. xantiana* ssp. *xantiana*, soil resistance to penetration should be assessed at multiple points in the growing season rather than merely at the flowering stage. Wet soils, which occur in winter and earlier spring in the Mediterranean climate of this species, are likely to be softer than the dry soils we scored well after the last spring rains (Whalley et al. 2008). It would also be informative to evaluate soil chemical properties that may contribute to plant water stress and nutrition across contrasting substrates. Preliminary work detected no geographic gradients or substrate differences in soil pH or concentrations of carbon and nitrogen (A. M. Louthan, unpublished observations).

Third, we asked whether among-population variation in plant water potential explains variation in size, fruit production, and mortality rate, which are components of the performance of individuals and populations that should affect population persistence. Studies that link plant water potential to survival and reproduction are surprisingly rare, despite the significance of such studies in understanding physiological mechanisms (McDowell et al. 2008) and understanding how water status affects demography (Breshears et al. 2009). The fact that plant size and fruit production increased with water potential in this study suggests that low water potential represents genuine stress and that water availability increasingly limits plant growth and fecundity as the border approaches.

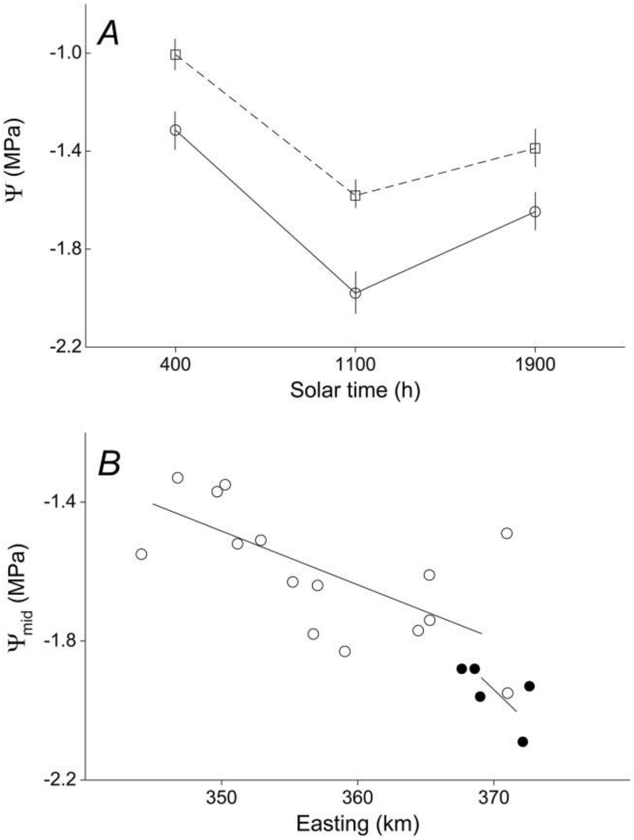

Fig. 6 *A*, Diurnal course of plant water potential on contrasting slopes at the Sawmill Road *Clarkia xantiana* ssp. *xantiana* population. Symbols are means and error bars are ±1 SE. Solid line connects means of plants sampled on a central hillslope. Dashed line connects means of plants sampled on a steeper, softer, rapidly eroding slope. *B*, Scatterplot of mean midday plant water potential of 20 populations in sampled 2006 versus easting (a surrogate for precipitation). Open symbols depict populations on igneous substrates; filled symbols depict populations on metasedimentary substrates. Regression lines are fitted separately by soil type, although ANCOVA did not detect a significant heterogeneity of slopes (see text).

Reproduction in *C. xantiana* ssp. *xantiana* appears to be highly sensitive to flowering-stage water status. Similarly, Aragon et al. (2008) found that effects of plant water potential on reproduction in the Mediterranean subshrub *Helianthemum squamatum* (Asteraceae) were generated by soil water conditions during flowering and not before. Critical effects of water status during flowering might be common in plants of Mediterranean climates. The apparent independence of seedling-to-fruiting mortality from flowering-stage water status in *C. xantiana* ssp. *xantiana* suggests that the effects of water limitation on the species border are mediated mainly by reproduction (and possibly seed-bank dynamics and germination), rather than by survivorship. A recent study of drought-related tree mortality in semiarid areas found strong effects of low water potential on survivorship, likely mediated by carbon starvation (Breshears et al. 2009). We will assess the sensitivity of population performance to variation in different life-cycle stages with additional years of demographic data.

One might expect local adaptation to evolve in response to geographic variation in water availability across a species range (e.g., McKay et al. 2001; Heschel et al. 2002; Santamaría et al. 2003; Petrů et al. 2006; Liancourt and Tielbörger 2009). Possible constraints on adaptive evolution include limited genetic variation in species-border populations (Hoffman and Blows 1994; Bridle and Vines 2007; Kawecki 2008; Sexton et al. 2009; but see Eckert et al. 2008), gene flow from the center of the range to the edge that swamps selection (Hoffman and Blows 1994; Kirkpatrick and Barton 1997; Lenormand 2002), and trade-offs between traits that enhance performance at the border and other fitness components (Kawecki 2008; Gaston 2009). The evolutionary sister *Clarkia xantiana* ssp. *parviflora* performs well in arid environments via early reproduction, avoiding drought rather than tolerating it, and via autogamous self-fertilization in environments of low pollinator service (Fausto et al. 2001; Geber and Eckhart 2005; Moeller and Geber 2005; Moeller 2006; and see Guerrant 1989; Runions and Geber 2000; Mazer et al. 2004). Thus, early flowering and an enhanced capacity for self-fertilization (e.g., reduced anther-stigma distance) would be candidate traits for local adaptation in *C. xantiana* ssp. *xantiana* at the border, with introgression from *C. xantiana* ssp. *parviflora* in principle being capable of facilitating adaptation (Kawecki 2008). To date, evidence for local adaptation of *C. xantiana* ssp. *xantiana* range-edge populations is equivocal. In a transplant experiment that included three range-center populations and three range-edge populations of *C. xantiana* ssp. *xantiana*, range-edge populations began flowering at a lower node than did central populations and had less anther-stigma separation (Eckhart et al. 2004), but they did not differ from central populations in actual time of flowering onset or in fitness components (Geber and Eckhart 2005) at a range-edge transplant site.

In sum, our findings indicate that a geographic gradient in flowering-season water plant potential in *C. xantiana* ssp. *xantiana* is caused by declining precipitation and is likely exacerbated near the species border by soil parent material effects on texture, resistance to penetration, and/or hydrology. Significant relationships between plant water potential, size, and fruit production suggest that the water potential decline might reduce population viability and/or seed sources for colonization beyond the range edge. High water stress among individuals in border populations on metasedimentary rock also might influence the location of the border by reducing the frequency of high-quality habitat available for colonization and occupation (see Holt and Keitt 2000; Jump and Woodward 2003; Samis and Eckert 2009).

We have begun to characterize the links between geographic variation in environmental factors, the physiology and performance of individuals, and demography; a research program is necessary to comprehend present environmental controls on species range (Gaston 2009) and how species may respond to climate change (Parmesan et al. 2005; Foden et al. 2007) in geologically complex landscapes. In light of previous findings (Geber and Eckhart 2005) that biotic factors such as pollinators, herbivores, and the density of surrounding vegetation affect *C. xantiana* ssp. *xantiana* performance at coarse spatial scales, we are combining the research presented here with complementary analyses of the geography of biotic factors across the range of *C. xantiana* ssp. *xantiana* (e.g., herbivory;

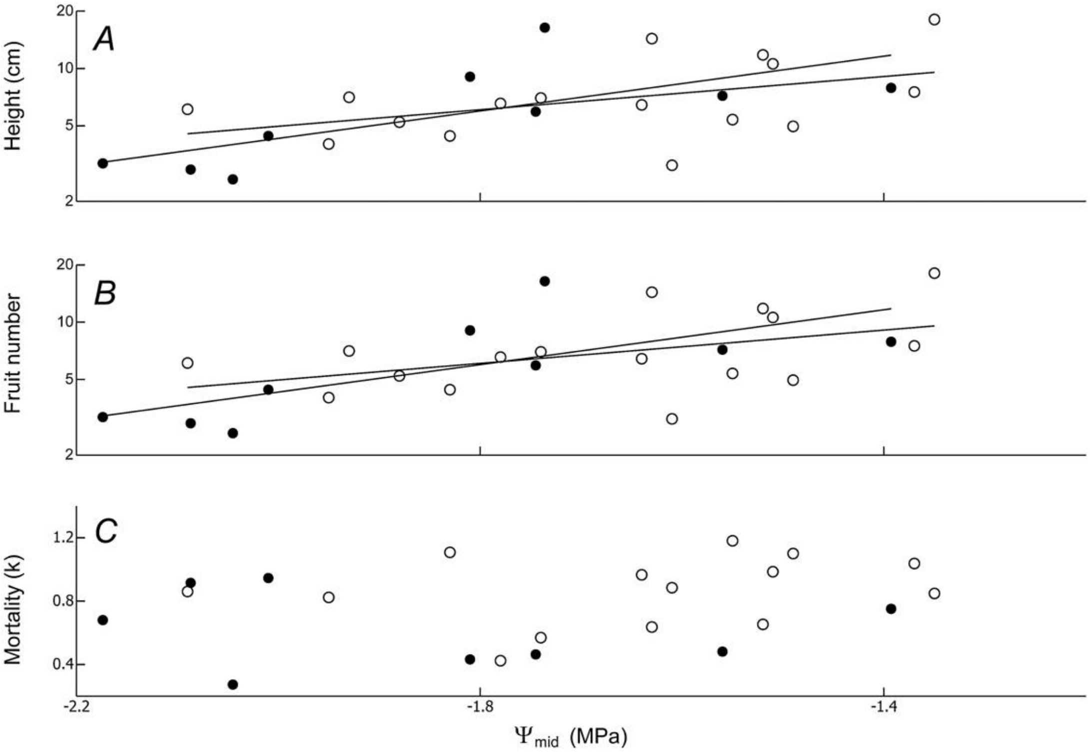

Fig. 7 Relationships among populations between plant water potential, plant performance, and demography. Symbols are as they are in fig. 2. *A*, Scatterplot of plant height (of individuals scored for water potential) versus measured midday water potential (ψ_{mid}), with least squares regression lines for each year. Each point represents the mean of 15–20 individuals. *B*, Scatterplot of fruit number per plant (means of 75–349 individuals per population and year) and ψ_{mid} (means of 15–20 individuals), with least squares regression lines for each year. *C*, Scatterplot of estimated seedling-to-fruiting mortality versus ψ_{mid}. Nonsignificant regression lines are not shown.

D. Moeller, M. Geber, V. Eckhart, I. Singh, R. Bier, and E. Fabio, unpublished manuscript).

Acknowledgments

We thank the U.S. Department of Agriculture Forest Service (Sequoia National Forest) and the U.S. Bureau of Land Management (Caliente Resource District) for granting permission for field studies. Emily Looney provided field assistance, while Peter Jacobson and Carolyn Bosse provided lab technical assistance. Elizabeth Queathem and three anonymous reviewers made helpful comments on the manuscript. Financial support came from the U.S. National Science Foundation (grants DEB-0515409 and DEB-0515428).

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