

Genetic variation in productivity of foundation riparian species at the edge of their distribution: implications for restoration and assisted migration in a warming climate

KEVIN C. GRADY*, SHARON M. FERRIER†, THOMAS E. KOLB*, STEPHEN C. HART‡, GERARD J. ALLAN† and THOMAS G. WHITHAM†

*School of Forestry, Northern Arizona University, Flagstaff, AZ 86011, USA, †Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011, USA, ‡School of Natural Sciences and Sierra Nevada Research Institute, University of California, Merced, CA 95343, USA

Abstract

We examined the hypothesis that genotypic variation among populations of commonly co-occurring phreatophytic trees (*Populus fremontii*, *Salix gooddingii*) and the shrub (*Salix exigua*) regulates aboveground net primary productivity (ANPP) at a hot site at the edge of the species' distribution. We used a provenance trial in which replicated genotypes from populations varying in mean annual temperature were transplanted to a common garden adjacent to the Lower Colorado River in southeastern California. The garden environment represented an extreme maximum temperature for the study species. Four major findings emerged: (1) Genotypic variation in ANPP was significant for all species with broad-sense heritability (H^2) across populations of 0.11, 0.13, and 0.10 for *P. fremontii*, *S. gooddingii*, and *S. exigua*, respectively, and within-population H^2 ranging from 0.00 to 0.25, 0.00 to 0.44, and 0.02 to 0.21, respectively. (2) Population ANPP decreased linearly as mean annual maximum temperature (MAMT) transfer distance increased for both *P. fremontii* ($r^2 = 0.64$) and *S. gooddingii* ($r^2 = 0.37$), whereas it did not change for *S. exigua*; (3) Populations with similar MAMT to that of the common garden were 1.5 and 1.2 times more productive than populations with 5.0 °C MAMT transfer distances for *P. fremontii* and *S. gooddingii*, respectively; and (4) Variation in regression slopes among species for the relationship between ANPP and MAMT indicate species-specific responses to temperature. As these plant species characterize a threatened habitat type and support a diverse community that includes endangered species, ecosystem restoration programs should consider using both local genotypes and productive genotypes from warmer environments to maximize productivity of riparian ecosystems in the face of global climate change.

Keywords: aboveground net primary productivity, assisted migration, climate change, cottonwood, heritability, local adaptation, provenance, riparian, willow

Received 13 April 2011; revised version received 25 July 2011 and accepted 3 August 2011

Introduction

Recent anthropogenically induced increases in atmospheric temperature (Karl *et al.*, 2009) have the potential to exert strong selection on plants. The genetic material required for plant adaptation to novel warmer environments may be unavailable (Savolainen *et al.*, 2007). In fact, it has been generally accepted that many plant populations are adapted to a relatively narrow range of climatic conditions, and populations inhabiting the warm extremes of current ranges are most vulnerable to extirpation due to climate change (O'Neill *et al.*, 2008). The ability of a species to adapt to changing future environmental conditions will influence its long-term viability. However, recent research suggests that the rates at which populations acquire new

genetic material through migration or mutation lags well behind rates of predicted climate change, especially for populations currently living at the edge of the species' distribution (Davis & Shaw, 2001; Aitken *et al.*, 2008). Thus, it appears that without human intervention, many populations may become locally maladapted as temperatures increase within the next century.

To help moderate the negative consequences of maladaptation, such as reduced productivity and increased mortality, it has been suggested that genotypes best-suited to a predicted future climate be preferentially used in ecosystem restoration efforts – termed *assisted migration* (Ledig & Kitzmiller, 1992; Rehfeldt *et al.*, 2003; Aitken *et al.*, 2008). While genetic manipulation of forests is contentious, proponents of assisted migration argue that without such tactics, many populations may face extirpation (Aitken *et al.*, 2008). Effective assisted migration, as well as conventional restoration via refor-

Correspondence: Kevin C. Grady, tel. + 480 254 8620, fax + 928 523 1080, e-mail: kevingrady@gmail.com

estation, requires identification of genotypes that are adapted to a warmer climate for use in transplanting.

Provenance studies increasingly are being used to identify favorable genotypes for assisted migration programs, evaluate plant responses to climate change, and assess the role of climate in determining evolutionary trajectories of species by explicitly testing the genetic components of local adaptation (Mátyás, 1994; Rehfeldt *et al.*, 1999; Savolainen *et al.*, 2007; Wang *et al.*, 2010). In provenance studies, populations from a variety of environments are transplanted to one or multiple common gardens. A regression function can be calculated relating an environmental transfer distance between population origins and garden sites [e.g., mean annual temperature (MAT), mean annual maximum temperature (MAMT), and/or mean annual precipitation (MAP)] to a quantitative fitness or physiological response trait of each population; this is termed transfer-function analysis (Wang *et al.*, 2006; O'Neill *et al.*, 2008). This function estimates the change in a trait as a result of population differences in environmental response relative to the garden environment. The trait must be heritable and display adaptive variation among populations to use transfer-function analysis (O'Neill *et al.*, 2008; Wang *et al.*, 2010).

Most research about climate change impacts on plant populations has not taken into account intraspecific genetic variation (Monserud *et al.*, 1996; Coops & Waring, 2001; Nigh *et al.*, 2004). Climate change models that predict changes in species productivity or distribution based on climate-physiological relationships rather than climate-genetics-physiological relationships do not consider the intrinsic selection process that influenced population distributions and intraspecific genetic variation. Studies including a genetic component in climate change models generally show that populations are adapted to a narrow climatic range (Morgenstern, 1996; O'Neill *et al.*, 2008; Wang *et al.*, 2010), outside of which populations are maladapted (Crespi, 2000; Davis & Shaw, 2001; St Clair & Howe, 2007). The majority of studies that have employed a genecological approach were in temperate northern latitudes and were focused on conifer species (though see Carter, 1996); studies of other regions and species are less common.

To augment current knowledge of plant adaptation to temperature, and to identify genotypes for use in restoration and assisted migration projects, we used a common garden provenance trial in which multiple provenances from perennially flowing riparian river habitat in the arid southwestern United States were transplanted to a hot common garden (31 °C MAMT) in southeastern California adjacent to the Lower Colorado River. Three species were included: two trees, Fremont cottonwood (*Populus fremontii*) and Goodding

willow (*Salix gooddingii*), and one shrub, coyote willow (*Salix exigua*). Several populations of each species were collected across a temperature gradient ranging in MAMT by approximately 6.5 °C, approximating the predicted increase in mean temperature in the southwestern United States over the next 80 years (Karl *et al.*, 2009), and were transplanted to a common garden near the warmest end of this temperature gradient and at the warm edge of these species distribution. This novel experimental design allows characterization of the potential adaptive responses of multiple species to temperature, and hence, is an initial step to assess the need for assisted migration. We tested the following hypotheses: (1) aboveground net primary productivity (ANPP), a common measure of plant production, varies by population and genotype, is heritable, and is influenced by provenance temperature; (2) ANPP is higher in populations with MAMT most similar to the common garden MAMT (i.e., shortest transfer distance); and (3) patterns of genetic variation in ANPP are consistent for multiple co-occurring riparian species.

We studied desert-riparian woody species for two major reasons. First, the adaptation of desert-riparian species to climate change has received little attention, presumably due to the notion that climate change is less likely to negatively affect plants with access to perennial water. However, this may not be correct in the southwestern United States because of negative impacts of climate change and increasing human water use on stream flow in this region (Barnett *et al.*, 2008; Sabo *et al.*, 2010) coupled with threshold responses of riparian vegetation to water stress caused by reduced availability of stream and ground waters (Tyree *et al.*, 1994; Smith *et al.*, 1998; Rood *et al.*, 2005; Hultine *et al.*, 2010). Second, populations of these species have experienced severe fragmentation and deforestation in the 20th century due to land conversion to agriculture and urban development, displacement by invasive species, and river flow alteration via dams and human water use (Shafroth *et al.*, 2002, 2008; Richardson *et al.*, 2007); <3% of pre-20th century extent remains (Noss *et al.*, 1995). These ecosystems provide habitat for a large number of dependent community members, including endangered species such as the southwestern willow flycatcher (*Empidonax traillii extimus*), contributing disproportionately to regional biodiversity in semi-arid ecosystems (Knopf *et al.*, 1988; Whitham *et al.*, 2006). Furthermore, riparian forests moderate hydrologic regimes by increasing bank stability and reducing flood damage to human communities (Seavy *et al.*, 2009). Consequently, restoration of riparian ecosystems is a high priority in the southwestern United States (Follstad Shah *et al.*, 2007).

Materials and methods

Site description

Our common garden study site was located at the Palo Verde Ecological Reserve (PVER; Fig. 1), on the historic flood plain (prior to dam construction) of the Lower Colorado River, approximately 5 km from Blythe, California and 0.25 km from the Lower Colorado River (N 33.71391, W -114.49600, elevation 87 m). The PVER garden is a component of the Lower Colorado River Multi-Species Conservation Program (LCR MSCP), a \$626 million ecosystem restoration project fund managed by the Bureau of Reclamation (BOR; Follstad Shah *et al.*, 2007; LCR MSCP, 2010) covering approximately 1030 km of river length and earmarked until 2055. Collaboration with the BOR, as well as Arizona Fish and Game, United States Forest Service, the City of Phoenix, and the Nature Con-

servancy, promotes the application of results of our research, continued research testing, and a centralized genetic testing group for regional riparian studies.

Prior to garden establishment, this flood plain was leveled and converted to agricultural use, formerly supporting cotton and alfalfa. The garden was flood irrigated with approximately 300 L m⁻² (1 acre-foot) of reclaimed water from the city of Blythe every 2–3 weeks in May through September and once every month from October through April. Soil volumetric water content at 10 cm soil depth at PVER throughout the growing seasons in 2009 and 2010 (March–December) ranged from 0.04 to 0.32 m³ m⁻³ (mean of 0.24 m³ m⁻³) as determined by continuous (10 minute intervals) data-logging (Onset Computer Corporation, Bourne, MA, USA) using a ECH₂O Dielectric Aquameter probe (Decagon Devices, Inc., Pullman, WA, USA) permanently installed at the approximate center of the garden. In May, 2009, depth to groundwater was

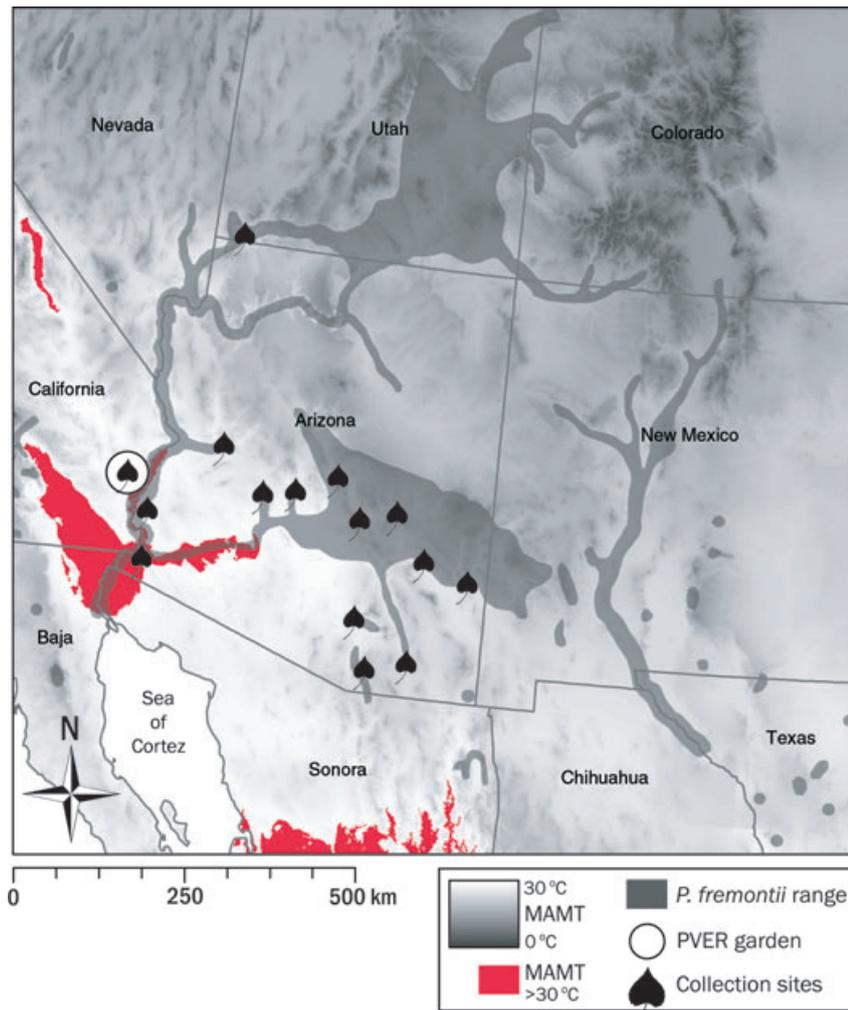


Fig. 1 Locations of provenance collection sites for *Populus fremontii*, *Salix gooddingii*, or *Salix exigua*, the Palo Verde Ecological Reserve common garden, and mean annual maximum temperatures (averaged between 1950 and 2000; WorldClim (2011)) across the range of *P. fremontii* (Little, 1971) in the southwestern United States and northern Mexico. The warmest edge of the range of *P. fremontii* is similar for both *S. gooddingii* and *S. exigua* (Little, 1971, 1976).

approximately 3.3 m as determined using a soil auger. Soils at the garden were composed chiefly of coarse-loamy, mixed, superactive, calcareous, hyperthermic Typic Torrifluvents (USDA NRCS, 2010).

Culture and garden design

Cuttings were collected from 16 randomly selected populations of both *P. fremontii* and *S. gooddingii*, and from seven randomly selected populations of *S. exigua* between December 5, 2006 and January 19, 2007. Cuttings were taken from dormant plants within 10 m of the active flood channel of perennially flowing rivers in Arizona and California within the Basin and Range Hydrogeologic Province (Fig. 1). Initial identification of genotypes was based on spatial discreteness of genets and a minimum distance of 10 m between individuals. Genotype identification was confirmed with genetic-based analyses using Microsatellite technology (S. Ferrier, unpublished data). Cuttings (approximately 35 cm length) were grown in Tinus root-trainers filled with sterilized soil media (equal parts of peat moss, perlite, and vermiculite) in a greenhouse at ambient air temperature to maintain bud dormancy. Soils were radiantly heated to 22 °C to promote root initiation and development. In March, 2007, cuttings were transported from the greenhouse to PVER and transplanted randomly across 66 blocks (16 × 16 rows at 2 m spacing per block). Fre-

quency distribution of *P. fremontii* and *S. gooddingii* in the garden ranged from 9% to 17% of total plants across all blocks, respectively, whereas *S. exigua* was planted at 66–83% of total plants across blocks due to its smaller stature as a shrub and greater abundance in natural communities (Irvine & West, 1979).

Provenance characteristics and climate

The annual mean of maximum daily temperature (MAMT) ranged from 24.4 to 30.9 °C across provenances. This range represents approximately 50% and 60% of the total MAMT temperature range of *P. fremontii* and *S. gooddingii*, respectively, based on extensive genetic surveys of *P. fremontii* in the western United States (G. Allan, unpublished data) and historical surveys of these species (Little, 1971, 1976) combined with temperature data for the United States (PRISM Climate Group, 2010) and Mexico (WorldClim, 2011). Provenances used in our study represent the warmest edge of the distributional range of *P. fremontii*, *S. gooddingii*, and *S. exigua* (Fig. 1; MAMT) as well as the hottest recorded temperatures (>50 °C) at which these species occur (Table 1). The range of MAMT across provenances (0–6.5 °C for *P. fremontii* and *S. gooddingii* and 0–4.3 °C for *S. exigua*; Table 1) is within the range of predicted temperature increases via climate change over the next century (Karl *et al.*, 2009). For instance, according to the International Panel on

Table 1 Selected climatic and soil characteristics of the common garden at Palo Verde Ecological Reserve (indicated with *) and provenances located throughout Arizona and California

Provenance	Elevation (m)	Climate				Climate Extremes			Soil	
		Transfer (°C)	MAMT (°C)	MAT (°C)	MAP (cm)	VPD (kPa)	MAD > 32 °C	MAD < 0 °C	Record high (°C)	Soil type
Palo Verde*	87	0.0	30.9	22.0	9.4	6.54	178	19	50.0	Typic Torripsamments
Cibola	70	0.0	30.9	22.0	9.4	6.21	178	19	50.0	Typic Torrifluvents
Mittry	49	0.2	30.7	22.0	10.1	5.93	172	10	51.1	Typic Torrifluvents
Bill Williams	357	0.6	30.3	21.5	22.9	6.48	172	22	51.1	Typic Torripsamments
Hassayampa	595	1.8	29.2	18.8	31.0	5.80	150	61	49.4	Typic Torriorthents
Santa Cruz	681	2.1	28.9	19.8	31.5	4.89	156	45	46.1	Typic Torrifluvents
Verde	620	3.1	27.8	19.6	39.6	5.64	138	55	47.8	Aquic Ustifluvents
Virgin	570	3.4	27.5	18.8	19.8	6.13	146	50	48.9	Typic Torrifluvents
Salt	660	3.7	27.2	19.2	42.9	5.58	132	51	46.7	Aquic Ustifluvents
Gila III	1048	4.1	26.9	18.6	34.3	4.59	139	43	46.7	Typic Torrifluvents
Gila	970	4.1	26.8	17.7	25.3	4.59	141	41	47.2	Typic Torrifluvents
Fish	810	4.7	26.3	18.5	50.3	4.96	133	51	45.6	DNA [†]
Sonoita	1234	4.7	26.3	16.1	45.5	3.89	100	93	43.3	Typic Torrifluvents
San Pedro	1268	5.2	25.7	16.5	46.0	3.66	99	60	43.9	Aquic Torrifluvents
Agua Fria	963	6.5	24.4	16.3	41.4	4.57	91	55	46.1	Typic Torrifluvents

Climate variables include: transfer distance in mean annual maximum temperature (MAMT of the garden minus MAMT of the provenance); MAMT; mean annual temperature (MAT); mean annual precipitation (MAP); vapor pressure deficit (VPD); mean annual number of days (MAD) with temperatures >32 °C; MAD with temperatures below 32 °C, and; record high temperature recorded since weather station became operational (approximately 20th century record). For all variables that include a mean value, Western Regional Climate Data (WRCC, 2010) were averaged between 1971 and 2000. For VPD, we report the average for the two warmest months (July and August), calculated using the mean annual monthly temperature and dew point temperature between 2005 and 2010 (WRCC, 2010).

[†]Data not available, area not surveyed.

Climate Change (IPCC), a low or high carbon emission scenario would yield an MAT increase over the historic baseline of 1.7–3.6 °C or 3.9–5.6 °C, respectively, by 2090 (Karl *et al.*, 2009).

Provenance origins ranged in elevation from 49 to 1268 m above sea-level, in MAMT from 24.4 to 30.9 °C, in MAT from 16.1 to 22.0 °C, and in MAP from 9.4 to 46.0 cm (Table 1). Provenance climatic data were compiled for years 1971–2000 from weather stations affiliated with the Western Regional Climate Center (WRCC, 2010) located within a 10 km radius and 80 m of elevation from provenance. Two provenance origins (Verde and San Pedro) did not have weather stations that fit these criteria, and so we used modeled estimates of temperature and precipitation from PRISM data (PRISM Climate Group, 2010). Soils at provenance origins were similar to those at PVER and were primarily Typic Torrifluvents or closely related groups, chiefly derived from calcareous parent material and dominated by sand textural classes (Table 1; USDA NRCS, 2010).

ANPP measurements

We measured diameter at breast height (DBH; 1.4 m height) and diameter at stem base (DSB; 0.3 m height; the height of the tree immediately above basal swelling) between May 2nd and 27th, 2009 when trees were approximately 2.2 years old. We measured DSB to avoid complications in measurements as a result of tree forks below breast height. For forked trees, we predicted DBH from DSB via linear regression calculated from 998 trees for *P. fremontii* (DBH = $-0.8303 + 0.8808$ (DSB); $r^2 = 0.99$, $P < 0.0001$) and 1025 trees for *S. gooddingii* (DBH = $-0.6502 + 0.9309$ (DSB); $r^2 = 0.99$, $P < 0.0001$). For *S. exigua*, as the majority of plants had multiple forks below breast height, we measured DSB on the five largest forks of each plant and DBH on one fork from each of 200 separate plants. We predicted DBH from DSB via linear regression using 200 samples (DBH = $-0.7330 + 0.9553$ (DSB); $r^2 = 0.98$, $P < 0.0001$) on forked *S. exigua*.

For *P. fremontii*, we measured or estimated DBH between 2 and 27 ramets (mean of 10.6) from 4 to 10 clonal genotypes (mean of 7.6) from each of 14 populations (106 genotypes total, 1136 total trees; Table 2). With *S. gooddingii*, we measured or estimated DBH between 3 and 36 ramets (mean of 14.9) from 3 to 15 clonal genotypes (mean of 6.7) from each of 14 provenances (94 genotypes total, 1373 total trees; Table 2). For *S. exigua*, we measured or estimated DBH between 3 and 47 ramets (mean of 17.4) from 5 to 23 clonal genotypes (mean of 16.7) from each of six provenances (100 genotypes total, 1756 total plants; Table 2). We used the individual tree as the independent experimental unit, because plants were randomly planted across the garden and environmental heterogeneity was relatively low. We excluded several areas in the garden that were either exposed to additional treatments, or were inundated with water for prolonged duration due to lower surface topology; this exclusion resulted in a total of 47 blocks in which measurements were conducted. We measured DBH on clonal genotypes that were replicated in at least two different blocks.

We predicted aboveground biomass (wood and foliage) from DBH using previously published allometric equations

for the same or closely related species (*S. gooddingii* from Jenkins *et al.*, 2004, using *Salix* spp. trees; *S. exigua* using Ohmann *et al.*, 1976 for *Salix* spp. shrubs). For *P. fremontii*, we used two separate equations; one for estimating the woody components of aboveground biomass (modified from Lojewski *et al.*, 2009), and an equation derived from trees growing at the common garden in the present study for estimating foliar biomass (K. Grady, unpublished data). For *S. exigua*, we estimated both wood and foliage biomass on each forked stem separately and then summed them to obtain aboveground biomass. An index of ANPP ($\text{kg tree}^{-1} \text{yr}^{-1}$) was estimated using the following equation: ANPP = wood biomass/tree age + foliar biomass. As foliage allometric equations were created using peak standing foliar biomass for each species (i.e., at the end of the growing season when leaves were fully flushed), the component of ANPP attributed to foliar productivity does not include leaves senesced during the growing season or retranslocation of carbohydrates from leaves to woody components prior to senescence at the end of the growing season.

Population differentiation, heritability, and regression analyses

Variation in ANPP across populations of each species was tested using restricted maximum likelihood (REML; Conner & Hartl, 2004). Data were log-transformed when the distribution of data violated assumptions of normality or homogeneity of variance. The REML model included population and genotype (nested within population) as random effects. The proportion of phenotypic variation in ANPP that was due to genotype was estimated both across and within populations of each species using the REML model described above (Lynch & Walsh, 1998). Broad-sense heritability (H^2) was estimated using the following equation, where σ^2 denotes variance:

$$H^2 = \frac{\sigma_{\text{among genotypes}}^2}{\sigma_{\text{among genotypes}}^2 + \sigma_{\text{error}}^2}$$

Following REML procedures, the significance of H^2 estimates was tested using log-likelihood ratio chi-squared tests (Shaw, 1987). The degrees of freedom (df) used in within-provenance likelihood tests was calculated as the total number of genotypes per provenance minus one (Table 2). The df used in among-genotype likelihood tests was calculated as the total number of genotypes nested within provenances (i.e., total genotypes minus the number of provenances). The df used among population likelihood tests were calculated as the total number of provenances minus one.

We used linear regression to test relationships between ANPP and climatic variables. Predictions of ANPP from the REML model were used to calculate genotype means and population means (mean across all genotypes within each population). We then quantified a transfer function by regressing ANPP on MAMT, MAT, and MAP between provenance origins and PVER. We used analysis of covariance (ANCOVA) to test for species differences in the relationship between ANPP and MAMT transfer distance. Homogeneity of slopes was tested among species and pairwise between all pairs of species using ANCOVA. If an interaction was present, we rejected the

Table 2 Estimates of broad-sense heritability (H^2) \pm 95% confidence intervals and likelihood ratio tests for within-provenance, among-provenance, and among-genotype variation in aboveground net primary productivity for three riparian woody species (*Populus fremontii*, *Salix gooddingii*, and *Salix exigua*) grown at the Palo Verde Ecological Reserve common garden in the southwestern United States

Within provenance	<i>P. fremontii</i>				<i>S. gooddingii</i>				<i>S. exigua</i>						
	H^2	χ^2	P-value	df	#Ram	H^2	χ^2	P-value	df	#Ram	H^2	χ^2	P-value	df	#Ram
Palo Verde	0.25 \pm 0.24	3.44	0.03	3	32	0.38 \pm 0.52	2.30	0.06	2	21	0.05 \pm 0.04	2.74	0.05	22	340
Cibola	0	0.76	0.19	9	117	0.25 \pm 0.22	6.20	0.006	7	43	0.03 \pm 0.10	0.23	0.31	4	91
Mittry	0.06 \pm 0.26	0.10	0.38	3	23	0.09 \pm 0.07	6.26	0.006	8	215					
Bill Williams		0	0.50	4	39	0.05 \pm 0.12	0.27	0.30	6	77					
Hassayampa	0.21 \pm 0.20	2.72	0.05	7	56	0.09 \pm 0.08	7.14	0.004	5	150					
Santa Cruz	0.23 \pm 0.22	2.87	0.04	6	39	0.23 \pm 0.21	7.83	0.003	4	81					
Verde	0.11 \pm 0.08	5.99	0.007	9	137	0.03 \pm 0.08	0.20	0.33	8	110	0.06 \pm 0.04	8.95	0.001	17	386
Virgin	0.23 \pm 0.14	12.85	0.0002	9	110						0.21 \pm 0.11	14.82	0.0001	21	328
Salt	0.11 \pm 0.09	5.84	0.008	8	143	0.13 \pm 0.35	0.15	0.35	2	46					
Gila III	0.14 \pm 0.15	1.79	0.09	8	95	0.14 \pm 0.13	3.55	0.03	9	121	0.02 \pm 0.03	0.83	0.18	8	212
Gila						0.19 \pm 0.10	16.71	0.0001	14	179	0.17 \pm 0.08	30.83	0.0001	22	399
Fish	0	0.67	0.21	3	11	0.11 \pm 0.09	5.69	0.009	7	129					
Sonoita	0	0.16	0.35	8	81	0.07 \pm 0.18	0.56	0.23	2	25					
San Pedro	0.15 \pm 0.10	12.15	0.0002	8	156	0.44 \pm 0.32	8.75	0.002	2	32					
Agua Fria	0.16 \pm 0.15	4.07	0.02	7	97	0	0.22	0.32	4	144					
Total model															
Among Genotype	0.11 \pm 0.03	40.13	0.0001	92	1136	0.13 \pm 0.04	57.64	0.0001	80	1373	0.10 \pm 0.03	58.72	0.0001	94	1756
Among Provenance	48.02	0.0001	13	1136		29.38	0.0001	13	1373		2.93	0.04	5	1756	

Test details include chi-squared value (χ^2), significance level (P-value), degrees of freedom (df), and total ramets sampled per provenance (#Ram). H^2 is not listed for provenances with less than three representative clonal genotypes.

null hypothesis that slopes were homogeneous. When an interaction was not present, we performed an effects test to discriminate variation in the y -intercept between species. All regression and ANCOVA analyses were performed using JMP 6.0 statistical software (SAS Institute Inc., Cary, NC, USA) using the $\alpha = 0.05$ significance level.

Results

Population differentiation, heritability, and temperature response

Three results support our first hypothesis that ANPP varied by population and genotype, was heritable, and was influenced by provenance temperature. First, likelihood ratio tests showed significant differences in ANPP among populations and genotypes for each species (Table 2). Second, estimates of broad-sense heritability across populations of *P. fremontii*, *S. gooddingii*, and *S. exigua* were 0.11, 0.13, and 0.10, respectively (Table 2; $P < 0.0001$ for each species). Within populations of *P. fremontii*, *S. gooddingii*, and *S. exigua*, estimates of heritability ranged from 0.00 to 0.25, 0.00 to 0.44, and 0.02 to 0.21, respectively (Table 2). These results show that ANPP was under low to moderate genetic control.

Third, in support of our hypothesis, we found significant regressions between population mean ANPP and MAMT transfer distance for both *P. fremontii* ($r^2 = 0.64$, $P < 0.0006$; Fig. 2a, Table 3) and *S. gooddingii* ($r^2 = 0.37$, $P < 0.022$; Fig. 2b, Table 3) suggesting that differences in maximum annual temperature among provenances (Table 1) explains a moderate to large proportion of variation in ANPP. While MAT transfer distance was also correlated to ANPP ($r^2 = 0.49$, $P < 0.005$; $r^2 = 0.36$, $P < 0.017$, for *P. fremontii* and *S. gooddingii*, respectively), we used MAMT as our key environmental variable, because it was more strongly correlated with ANPP, and because MAT and MAMT were strongly associated ($r^2 = 0.87$, $P < 0.0001$). The ANPP of *S. exigua* was not correlated to MAMT ($r^2 = 0.15$; $P = 0.452$; Fig. 2c, Table 3) or MAT ($r^2 = 0.08$; $P = 0.586$). In addition, ANPP varied linearly and positively with MAP transfer distance for both *P. fremontii* ($r^2 = 0.39$, $P < 0.018$) and *S. gooddingii* ($r^2 = 0.46$, $P < 0.007$), but not for *S. exigua* ($r^2 = 0.13$; $P = 0.480$).

Potential local adaptation

In support of our second hypothesis that ANPP would be highest in populations with MAMT most similar to the common garden, we found that ANPP varied linearly and negatively with increasing MAMT transfer distance for *P. fremontii* (Fig. 2a) and *S. gooddingii* (Fig. 2b). This result suggests that populations are locally adapted

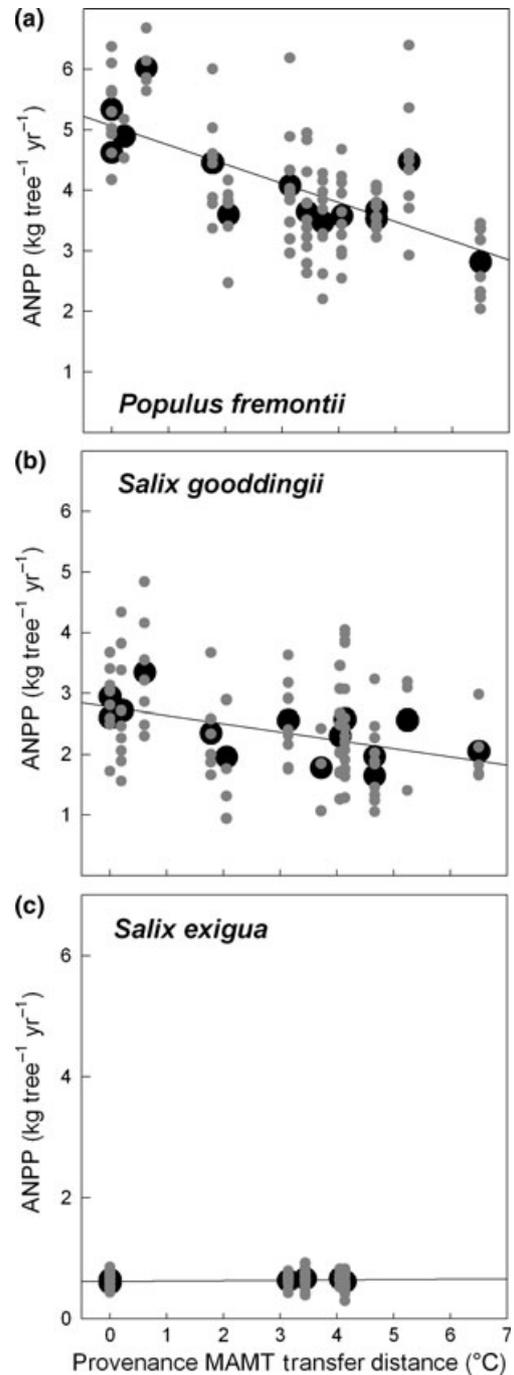


Fig. 2 Relationships between aboveground net primary productivity (ANPP) and provenance transfer distance (mean annual maximum temperature (MAMT) of common garden minus MAMT of provenance origin) for *Populus fremontii* (a), *Salix gooddingii* (b), and *Salix exigua* (c). Population (●) and genotype (●) means are indicated. Regression equation parameters are shown in Table 3.

to temperature (i.e., increasing transfer distance from the garden results in lower ANPP). The ANPP also varied among genotypes within populations (Fig. 2).

Table 3 Comparisons of slope (b_i) and y -intercept (b_o) between *Populus fremontii*, *Salix gooddingii*, and *Salix exigua* for the relationship between aboveground net primary productivity (ANPP) and provenance transfer distance (mean annual maximum temperature (MAMT) of common garden minus MAMT of provenance origin)

	b_i	b_o	r^2	P -value
<i>P. fremontii</i>	-0.32 ^a	5.06 [*]	0.64	0.0006
<i>S. gooddingii</i>	-0.14 ^{bc}	2.78 ^a	0.37	0.022
<i>S. exigua</i>	0.01 ^c	0.62 ^b	0.15	0.452

Different lower case letters following slope and y -intercept indicate significant differences between species ($P < 0.05$). For each species, the relationship between ANPP and MAMT transfer distance (r^2), and the significance of this relationship (P -value) are included.

**P. fremontii* was excluded from analysis because slopes were significantly different compared with both *S. gooddingii* and *S. exigua*.

Interspecific variation in temperature response

Contrary to our hypothesis that responses to MAMT would be consistent across species, we found that individual species differed in population response to temperature. An interaction in the ANCOVA was present between species and MAMT effects on ANPP ($P < 0.018$), and so we performed pairwise comparisons between each pair of species. Significant interaction terms in ANCOVAs between *P. fremontii* and *S. gooddingii* ($P < 0.049$), and between *P. fremontii* and *S. exigua* ($P < 0.023$) showed significant differences in slopes. This result suggests that the magnitude of the response to temperature was different among species (Table 3). An interaction was not present ($P = 0.123$) in the ANCOVA comparing *S. gooddingii* and *S. exigua*, and an effects test showed a significant difference in the y -intercept between these species ($P < 0.0001$; Table 3). This result indicates that the response of ANPP to temperature was similar for *S. gooddingii* and *S. exigua*, but ANPP was lower in *S. exigua*.

Discussion

Population differentiation and heritability

We found that ANPP was a heritable trait for all species and within most populations. Our estimates of broad-sense heritability apply to the growing conditions at the PVER common garden, which is an unusually hot environment for all species, and does not account for genotype \times environmental interactions that would probably influence heritability estimates. However, evaluation of

genetic variation at the warm edge of a species distribution is important for assessing species adaptations to temperature. Our estimates of broad-sense heritability (0.10–0.13 across populations; Table 2) were lower than most estimates of broad-sense heritability in *Salix* and *Populus* species. Other studies have reported broad-sense heritability of ANPP in the range of 0.05–0.51 for plants in the *Salicaceae* family, including both *Salix* (Lin & Zsuffa, 1993) and *Populus* species (Wilcox & Farmer, 1967; Riemenschneider *et al.*, 1996; Lojewski *et al.*, 2009). Low estimates of broad-sense heritability in common gardens may be attributed to small sample size, low phenotypic variability in the trait, or weak genetic control (i.e., Lojewski *et al.*, 2009). We can rule out an effect of low sample size because we found significant heritability in a range of populations that varied in the number of genotypes sampled (3–23; Table 2). Populations at distribution edges often have lower genotypic diversity compared with core populations due to genetic isolation (Durka, 1999; Faugeron *et al.*, 2004).

Population response to temperature

Using a common garden trial, we found population-level variation in ANPP (Table 2) that was related to variation in temperature (Fig. 2) and precipitation among provenances. We consider provenance temperature to be a more likely cause of population variation in ANPP than provenance precipitation. We suggest that the correlation between ANPP and provenance precipitation was not causal for two reasons. First, while precipitation varied across provenances from approximately 10–46 cm (Table 1), water use by desert-riparian trees is predominantly controlled by groundwater availability as opposed to local precipitation (Dawson & Ehleringer, 1991; Kolb *et al.*, 1997; Snyder & Williams, 2000; Cox *et al.*, 2005). Second, if MAP drove variation in ANPP among populations, we would have expected populations with the highest MAP to have the highest ANPP in the well-watered PVER garden, a pattern opposite to our results. We also acknowledge that population variation in ANPP may have been affected by other unmeasured characteristics of provenance origins, such as nutrient availability. Given increasing global temperatures, however, we focus here on population adaptation to temperature.

Populations of both *P. fremontii* and *S. gooddingii* from warm environments were more productive than populations from cooler environments when grown in a common garden near the extreme warmest edge (MAMT of 31 °C; Table 1) of the species distribution (Fig. 2a, b). In addition to supporting the hypothesis that populations of both species are locally adapted to temperature, this result suggests that ANPP is a useful

response variable for assessing genotypic variation in adaptation to hot sites. Furthermore, this result suggests that it is important to consider the genetic component of population responses to site-specific variables such as temperature (i.e., providing evidence of local adaptation; Joshi *et al.*, 2001) when designing restoration projects. There is increasing recognition that the effectiveness of restoration strategies depends not only on using appropriate species (Stromberg, 2001) but also on using well-adapted genotypes within species (Hufford & Mazer, 2003; O'Neill *et al.*, 2008; Wang *et al.*, 2010).

Our results demonstrating temperature adaptation in productivity of riparian species are consistent with other research that has shown strong localized temperature adaptation of cottonwoods in both experimental (Rood *et al.*, 2007) and natural settings (Kalischuk *et al.*, 2001; Berg *et al.*, 2007). These studies, however, were conducted using plant populations from much cooler climates than our study. For example, Canadian populations of *Populus trichocarpa* and *Populus angustifolia* from warmer environments were more productive than populations from cooler environments when grown at high temperatures in a common greenhouse environment (Rood *et al.*, 2007). Our results from an extremely hot common garden showed a similar pattern; populations from the warmest environments were the most productive in an extremely hot common garden.

Several lines of evidence suggest that the desert-riparian populations used in our study are often exposed to temperatures that are above optimal for growth. First, provenance temperatures were greater than 32 °C for at least 100 days of the year over the last three decades (Table 1); this is well above the optimal temperature of 25 °C reported for photosynthesis of riparian cottonwoods (Bassman & Zwier, 1991), and at the high end of optimal temperatures (28–33 °C) reported for central Arizona populations of *P. fremontii* and *S. gooddingii* (Horton *et al.*, 2001a). Second, record high temperatures reached 50 °C at four provenance locations (Table 1) and the denaturing of the enzyme regulating carbon fixation in C3 plants, Ribulose-1,5-Biphosphate Carboxylase Oxygenase (Rubisco), occurs at temperatures above 40 °C (Taiz & Zeiger, 2010). Third, in southwestern riparian ecosystems, high vapor pressure deficit (VPD) combined with low precipitation and seasonal and interannual fluctuations in groundwater supply create conditions of water stress to trees (Smith *et al.*, 1998; Horton *et al.*, 2001b). Last, local populations of *P. fremontii* and *S. gooddingii* in our study (i.e., with high MAMT; Table 1) were 1.5 and 1.2 times more productive on average, respectively, than non-local populations transferred to a 5.0 °C warmer environment (Fig. 2a, b). Taken together, this evidence sug-

gests that climate change will expose many southwestern riparian populations of *P. fremontii* and *S. gooddingii* to temperatures that are higher than optimal for a greater portion of the growing season compared with current conditions, probably resulting in decreased productivity.

Interspecific variation in temperature response

Little research has focused on interspecific variation in the strength of adaptive responses to temperature. In our study, regression slopes for the relationship between ANPP and MAMT differed among species (Table 3), suggesting that adaptive responses to temperature also varied among them. While we found similar correlations between ANPP and MAMT for *P. fremontii* and *S. gooddingii* (Fig. 2a, b; Table 3), we did not find similar significant correlations for *S. exigua* (Fig. 2c; Table 3).

Species variation in the effects of temperature on plant traits in semi-arid regions of the southwestern United States is well-documented for riparian species (Sparks & Ehleringer, 1997; Horton *et al.*, 2001a). The relationship between elevation (i.e., which strongly covaries with MAT) and carbon isotope discrimination (a time-integrated measure of water-use efficiency) varied among *P. fremontii*, *P. angustifolia*, and *S. exigua* population across approximately 2000 m of elevational change, with *S. exigua* populations showing less change in isotopic discrimination than *Populus* populations (Sparks & Ehleringer, 1997). Limited change in carbon isotopic discrimination values for *S. exigua* suggests lower stomatal sensitivity to VPD compared with *Populus* species. A relatively fixed low value of stomatal conductance would probably also lead to relatively static and low rates of photosynthesis, potentially explaining similarity in ANPP across a temperature gradient in our study for *S. exigua*. A similar mechanism may be responsible for the difference in slope between *P. fremontii* and *S. gooddingii*, as *S. gooddingii* is known to be more resistant to water stress than *P. fremontii* (Busch & Smith, 1995). Furthermore, leaf gas exchange is more sensitive in *P. fremontii* to atmospheric water stress (high VPD) than *S. gooddingii* (Horton *et al.*, 2001a). These findings suggest that *S. gooddingii* maintains more stable photosynthetic rates than *P. fremontii* across a broader spectrum of environmental conditions, perhaps explaining the lower slope of the regression relating ANPP to MAT of *S. gooddingii* than *P. fremontii*. Taken together, these results illustrate substantial interspecific variation in physiological responses to temperature.

There are several potential explanations for the lack of correlation between ANPP and MAMT for *S. exigua*. First, as we were unable to measure ANPP of adventi-

tious root sprouts in *S. exigua*, our measurements probably underestimate total ANPP. However, we measured the number of adventitious root sprouts within a 0.75 m radius of a subsample of *S. exigua* plants (without assessing parent or biomass of sprouts) and found no population difference between the number of root sprouts produced (data not shown). Second, the lower population sample size ($n = 6$) for *S. exigua* reduced statistical power and our ability to detect a significant correlation. We recognize that low population sample size for *S. exigua* limits the strength of our inference regarding the effects of temperature on growth rates, and therefore, our results for *S. exigua* should be interpreted cautiously.

Information on interspecific variation in plant sensitivity to temperature may be useful for predicting shifts in species composition as a consequence of climate warming. Our study, by assessing ANPP of three riparian species for a range of populations, suggests that climate warming is likely to have the largest impact on growth rates of *P. fremontii* and smaller impacts on *S. gooddingii* and *S. exigua*. Our results suggest prioritizing *P. fremontii* and then *S. gooddingii* for further genetic testing and possible assisted migration. Due to its insensitivity to MAMT, *S. exigua* would not warrant attention at this time. Such prioritization will probably become important as cost effectiveness and risk are evaluated for individual foundation species. Our results, however, apply only to the test conditions of the PVER site, as we did not include multiple common gardens that are required to fully evaluate genotype \times environment interactions (e.g., Lojewski *et al.*, 2009; Pregitzer *et al.*, 2010).

Broader implications

With climate change, the warm climatic edge of a species' distribution is especially important to evaluate, as it often represents the extreme conditions that a species can tolerate. By planting different provenances at such sites, common garden trials can identify well-adapted genotypes that may allow a species to persist in marginal environments where they might otherwise go extinct. Our findings illustrate several important issues that have broad implications for species that are threatened by climate change and shifting distributions.

We established that *P. fremontii* and *S. gooddingii* possess significant within and among population variation in productivity at high temperatures. For example, with *P. fremontii*, the variation in productivity within a population was about one-third of the total species variation, suggesting that local populations have the potential to adapt to changing temperatures. Ecosystem restoration projects concerned with climate change mit-

igation may benefit from identifying and incorporating locally well-adapted genotypes into projects to enhance the probability that evolutionary response to selection will keep pace with climate change. Moreover, restoration projects located in warm portions of current ranges should use genotypes with low provenance MAMT transfer distances (Fig. 2) because these genotypes have higher productivity than genotypes with high transfer distances. Once the adaptive potential of the local variation is exceeded, genotypes from higher temperature source populations can be employed to maintain the species at cooler sites that are becoming too warm for their local populations (Aitken *et al.*, 2008).

The identification of the most favorable genotypes that can survive at the warm edge of a species distribution may have great value in breeding programs that would allow superior traits to be accumulated in individuals, which may further increase tolerance to extreme conditions beyond what naturally occurs in extant populations (Joshi & Nayak, 2010). If successful, such individuals could be used in restoration that would allow a crucial habitat to be maintained where the species has already been extirpated. For example, on the Lower Colorado River in the southwestern United States, a 50-year, \$626 million program was initiated in 2005 to conserve habitat, work toward the recovery of threatened and endangered species, and reduce the likelihood of additional species being federally listed as endangered (LCR MSCP, 2010). Loss of foundational species such as *P. fremontii* and the extended floral and faunal community it supports could have great environmental repercussions beyond the loss of tree itself, which could potentially justify such breeding efforts (Whitham *et al.*, 2006).

Maintaining productivity in a warming climate is important not only for promoting tree performance and survival but is also critical for the conservation of a diverse community of organisms. For example, Stone *et al.* (2010) found that productivity is strongly and positively correlated with the diversity of the canopy arthropod community of pinyon pine (*Pinus edulis*). Preliminary data from the PVER garden suggest a similar pattern for these desert-riparian species; the fastest growing trees support the highest diversity of canopy arthropods (S. Ferrier, unpublished data). Thus, selecting tree genotypes that have higher productivity for restoration and assisted migration should also result in maintaining higher biodiversity in dependent communities.

Acknowledgements

This research was supported by a Science Foundation of Arizona Fellowship Award, the Bureau of Reclamation Grants

CESU-06FC300025, 04FC300039, and NSF FIBR grant DEB-0425908. We thank Chris Updike, Scott Norris, Chris Pope, and Matt House for field and technical assistance. For helpful comments with manuscript preparation, we thank the Whitham lab group and three anonymous reviewers. We thank garden manager Karla Kennedy and the Whitham lab group for help in establishment and maintenance of the garden.

References

- Aitken SN, Yeaman S, Holliday JA, Wang T, Curtis-McLane S (2008) Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications*, **1**, 95–111.
- Barnett TP, Pierce DW, Hidalgo HG *et al.* (2008) Human-induced changes in the hydrology of the western United States. *Science*, **319**, 1080–1083.
- Bassman JH, Zwier JC (1991) Gas exchange characteristics of *Populus trichocarpa*, *Populus deltoides* and *Populus trichocarpa* × *P. deltoides* clones. *Tree Physiology*, **8**, 145–159.
- Berg KJ, Samuelson GM, Willms CR, Pearce DW, Rood SB (2007) Consistent growth of black cottonwoods despite temperature variation across Rocky Mountains ecoregions. *Trees*, **21**, 161–169.
- Busch DE, Smith SD (1995) Mechanisms associated with decline of woody species in riparian ecosystems of the Southwestern U.S. *Ecological Monographs*, **65**, 347–370.
- Carter KK (1996) Provenance tests as indicators of growth response to climate change in 10 north temperate tree species. *Canadian Journal of Forest Research*, **26**, 1089–1095.
- Conner JK, Hartl DL (2004) *A Primer of Ecological Genetics*. Sinauer, Sunderland.
- Coops NC, Waring RH (2001) Assessing forest growth across southwestern Oregon under a range of current and future global change scenarios using a process model. *Global Change Biology*, **7**, 15–29.
- Cox G, Fischer DG, Hart SC, Whitham TG (2005) Nonresponse of native cottonwood trees to water additions during summer drought. *Western North American Naturalist*, **65**, 175–185.
- Crespi BJ (2000) The evolution of maladaptation. *Heredity*, **84**, 623.
- Davis MB, Shaw RG (2001) Range shifts and adaptive responses to quaternary climate change. *Science*, **292**, 673–679.
- Dawson TE, Ehleringer JR (1991) Streamside trees that do not use stream water. *Nature*, **350**, 335–337.
- Durka W (1999) Genetic diversity in peripheral and subcentral populations of *Corrigiola litoralis* L. (Illecebraceae). *Heredity*, **83**, 476–484.
- Faugeron S, Martinez EA, Correa JA *et al.* (2004) Reduced genetic diversity and increased population differentiation in peripheral and overharvested populations of *Gigartina skottsbergii* (Rhodophyta, Gigartinales) in southern Chile. *Journal of Phycology*, **40**, 454–462.
- Follstad Shah JJ, Dahm CN, Gloss SP, Bernhardt ES (2007) River and riparian restoration in the southwest: results of the National River Restoration Science Synthesis Project. *Restoration Ecology*, **15**, 550–562.
- Horton JL, Kolb TE, Hart SC (2001a) Leaf gas exchange characteristics differ among Sonoran Desert riparian tree species. *Tree Physiology*, **21**, 233–242.
- Horton JL, Kolb TE, Hart SC (2001b) Physiological response to groundwater depth varies among species and with river flow regulation. *Ecological Applications*, **11**, 1046–1059.
- Hufford KC, Mazer SJ (2003) Plant ecotypes: genetic differentiation in the age of ecological restoration. *Trends in Ecology and Evolution*, **18**, 147–155.
- Hulline KR, Bush SE, Ehleringer JR (2010) Ecophysiology of riparian cottonwood and willow before, during, and after two years of soil water removal. *Ecological Applications*, **20**, 347–361.
- Irvine JR, West NE (1979) Riparian tree species distribution and succession along the lower Escalante River, Utah. *The Southwestern Naturalist*, **24**, 331–346.
- Jenkins JC, Chojnacky DC, Heath LS, Birdsey RA (2004) *Comprehensive Database of Diameter-Based Biomass Regressions for North American Tree Species*. General Technical Report NE-319. U.S. Department of Agriculture, Forest Service, Northeastern Research Station, Newtown Square, PA.
- Joshi RK, Nayak S (2010) Gene pyramiding-A broad spectrum technique for developing durable stress resistance in crops. *Biotechnology and Molecular Biology Review*, **5**, 51–60.
- Joshi J, Schmid B, Caldeira MC *et al.* (2001) Local adaptation enhances performance of common plant species. *Ecology Letters*, **4**, 536–544.
- Kalischuk AR, Rood SB, Mahoney JM (2001) Environmental influences on seedling growth of cottonwood species following a major flood. *Forest Ecology and Management*, **144**, 75–89.
- Karl TR, Melillo JR, Peterson TC (eds) (2009) *Global Climate Change Impacts in the United States*. Cambridge University Press, New York.
- Knopf FL, Johnson RR, Rich T, Samson FB, Szaro RC (1988) Conservation of riparian ecosystems in the United States. *The Wilson Bulletin*, **100**, 272–284.
- Kolb TE, Hart SC, Amundson R (1997) Boxelder water sources and physiology at perennial and ephemeral stream sites in Arizona. *Tree Physiology*, **17**, 151–160.
- Ledig FT, Kitzmiller JH (1992) Genetic strategies for reforestation in the face of global climate change. *Forest Ecology and Management*, **50**, 153–169.
- Lin JZ, Zsuffa L (1993) Quantitative genetic parameters for seven characters in a clonal test of *Salix eriocephala*. *Silvae Genetica*, **42**, 41–46.
- Little EL (1971) Atlas of United States trees, volume 1, conifers and important hardwoods. U.S. Department of Agriculture Miscellaneous Publication 1146, 9 p., 200 maps.
- Little EL (1976) Atlas of United States trees, volume 3, minor Western hardwoods. U.S. Department of Agriculture Miscellaneous Publication 1314, 13 p., 290 maps.
- Lojowski NR, Fischer DG, Bailey JK, Schweitzer JA, Whitham TG (2009) Genetic basis of aboveground productivity in two native *Populus* species and their hybrids. *Tree Physiology*, **29**, 1133–1142.
- Lower Colorado River Multi-Species Conservation Program (LCR MSCP) (2010) *Palo Verde Ecological Reserve Annual Report 2008*. Bureau of Reclamation, Lower Colorado Region, Boulder City, Nevada.
- Lynch M, Walsh B (1998) *Genetics and Analysis of Quantitative Traits*. Sinauer Associates, Inc., Sunderland, Massachusetts, USA.
- Mátyás C (1994) Modeling climate change effects with provenance test data. *Tree Physiology*, **14**, 797–804.
- Monserud RA, Tchebakova NM, Kolchugina TP, Denissenko O (1996) Change in Siberian phytomass predicted for global warming. *Silva Fennica*, **30**, 185–200.
- Morgenstern EK (1996) *Geographic Variation in Forest Trees: Genetic Basis and Application of Knowledge in Silviculture*. UBC Press, Vancouver, Canada.
- Nigh GD, Ying CC, Qian H (2004) Climate and productivity of major conifer species in the interior of British Columbia Canada. *Forest Science*, **50**, 659–671.
- Noss RF, LaRoe ET III, Scott JM. (1995) *Endangered Ecosystems of the United States: A Preliminary Assessment of Loss and Degradation*. Biological Report 28. U.S. Department of the Interior, National Biological Service, Washington, D.C., USA.
- Ohmann LF, Grigal DF, Brander RB (1976) *Biomass Estimation for Five Shrubs from Northeastern Minnesota*. Research Paper NC-133. U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station, St. Paul, Minnesota.
- O'Neill GA, Hamann A, Wang T (2008) Accounting for population variation improves estimate of the impact of climate change on species' growth and distribution. *Journal of Applied Ecology*, **45**, 1040–1049.
- Pregitzer CC, Bailey JK, Hart SC, Schweitzer JA (2010) Soils as agents of selection: feedbacks between plants and soils alter seedling survival and performance. *Evolutionary Ecology*, **24**, 1045–1059.
- PRISM Climate Group (2010) Oregon State University. Available at: <http://www.prismclimate.org> (accessed 11 November 2009).
- Rehfeldt GE, Tchebakova NM, Milyutin LI, Parfenova EI, Wykoff WR, Kouzmina NA (2003) Assessing population responses to climate in *Pinus sylvestris* and *Larix* spp. of Eurasia with climate transfer models. *Eurasian Journal of Forest Research*, **6**, 83–98.
- Rehfeldt GE, Ying CC, Spittlehouse DL, Hamilton DA (1999) Genetic responses to climate in *Pinus contorta*: niche breadth, climate change, and reforestation. *Ecological Monographs*, **69**, 375–407.
- Richardson DM, Holmes PM, Esler KJ *et al.* (2007) Riparian vegetation: degradation, alien plant invasions, and restoration prospects. *Diversity and Distributions*, **13**, 126–139.
- Riemenschneider DE, Stelzer HE, Foster GS (1996) Quantitative genetics of poplars and poplar hybrids. In: *Biology of Populus and its Implications for Management and Conservation* (eds Stettler R.F., Bradshaw H.D. Jr, Heilman P.E., Hinckley T.M.), pp. 159–181. NRC Research Press, Ottawa.
- Rood SB, Berg KJ, Pearce DW (2007) Localized temperature adaptation of cottonwoods from elevational ecoregions in the Rocky Mountains. *Trees-Structure and Function*, **21**, 171–180.
- Rood SB, Samuelson GM, Braatne JH, Gourley CR, Hughes FM, Mahoney JM (2005) Managing river flows to restore floodplain forests. *Frontiers in Ecology and the Environment*, **3**, 193–201.
- Sabo JL, Sinha T, Bowling LC *et al.* (2010) Reclaiming freshwater sustainability in the Cadillac Desert. *Proceedings of the National Academy of Sciences*, **107**, 21263–21270.

- Savolainen O, Pyhajarvi T, Knurr T (2007) Gene flow and local adaptation in trees. *Annual Review of Ecology, Evolution and Systematics*, **38**, 595–619.
- Seavy NE, Gardali T, Golet GH *et al.* (2009) Why climate change makes riparian restoration more important than ever: recommendations for practice and research. *Ecological Restoration*, **27**, 330–338.
- Shafroth PB, Beauchamp VB, Briggs MK, Lair K, Scott ML, Sher AA (2008) Planning riparian restoration in the context of *Tamarix control* in western North America. *Restoration Ecology*, **16**, 97–112.
- Shafroth PB, Stromberg JC, Patten DT (2002) Riparian vegetation response to altered disturbance and stress regimes. *Ecological Applications*, **12**, 107–123.
- Shaw RG (1987) Maximum-likelihood approaches applied to quantitative genetics of natural populations. *Evolution*, **41**, 812–826.
- Smith SD, Devitt DA, Sala A, Cleverly JR, Busch DE (1998) Water relations of riparian plants from warm desert regions. *Wetlands*, **18**, 687–696.
- Snyder KA, Williams DG (2000) Water sources used by riparian trees varies among stream types on the San Pedro River, Arizona. *Agricultural and Forest Meteorology*, **105**, 227–240.
- Sparks JP, Ehleringer JR (1997) Leaf carbon isotope discrimination and nitrogen content for riparian trees along elevational transects. *Oecologia*, **109**, 362–367.
- St Clair JB, Howe GT (2007) Genetic maladaptation of coastal Douglas-fir seedlings to future climates. *Global Change Biology*, **13**, 1441–1454.
- Stone AC, Gehring CA, Whitham TG (2010) Drought negatively affects communities on a foundation tree: growth rings predict diversity. *Oecologia*, **164**, 751–761.
- Stromberg JC (2001) Restoration of riparian vegetation in the southwestern United States: importance of flow regimes and fluvial dynamism. *Journal of Arid Environments*, **49**, 17–34.
- Taiz L, Zeiger E (2010) *Plant Physiology*, 5th edn. Sinauer Associates, Inc., Sunderland, Massachusetts, USA.
- Tyree MT, Kolb KJ, Rood SB, Patino S (1994) Vulnerability to drought-induced cavitation of riparian cottonwoods in Alberta—a possible factor in the decline of the ecosystem. *Tree Physiology*, **14**, 455–466.
- United States Department of Agriculture, Natural Resources Conservation Service (USDA NRCS) (2010) Soil Survey Geographic (SSURGO) Database for Arizona and California. Available at: <http://soildatamart.nrcs.usda.gov> (accessed 30 November 2009).
- Wang T, Hamann A, Yanchuk A, O'Neill GA, Aitken SN (2006) Use of response functions in selecting lodgepole pine populations for future climate. *Global Change Biology*, **12**, 2404–2416.
- Wang T, O'Neill GA, Aitken SN (2010) Integrating environmental and genetic effects to predict responses of tree populations to climate. *Ecological Applications*, **20**, 153–163.
- Western Regional Climate Center (WRCC) (2010) Available at: <http://www.wrcc.dri.edu> (accessed 11 November 2009).
- Whitham TG, Bailey JK, Schweitzer JA *et al.* (2006) A framework for community and ecosystem genetics: from genes to ecosystems. *Nature Reviews Genetics*, **7**, 510–523.
- Wilcox JR, Farmer RE (1967) Variation and inheritance of juvenile characters of Eastern Cottonwood. *Silvae Genetica*, **16**, 162–165.
- WorldClim Global Climate Data (WorldClim) (2011) University of California, Berkeley. Available at: <http://www.worldclim.org> (accessed 6 April 2011).