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### Title

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### Permalink

<https://escholarship.org/uc/item/24t3k2c3>

### Journal

Functional Ecology, 31(2)

### ISSN

0269-8463

### Authors

Fischer, Dylan G  
Wimp, Gina M  
Hersch-Green, Erika  
[et al.](#)

### Publication Date

2017-02-01

### DOI

10.1111/1365-2435.12733

Peer reviewed

# Tree genetics strongly affect forest productivity, but intraspecific diversity–productivity relationships do not

Dylan G. Fischer<sup>\*,1</sup>, Gina M. Wimp<sup>2</sup>, Erika Hersch-Green<sup>3</sup>, Randy K. Bangert<sup>4,5</sup>, Carri J. LeRoy<sup>1</sup>, Joseph K. Bailey<sup>6</sup>, Jennifer A. Schweitzer<sup>6</sup>, Clarissa Dirks<sup>1</sup>, Stephen C. Hart<sup>7</sup>, Gerard J. Allan<sup>4</sup> and Thomas G. Whitham<sup>4</sup>

<sup>1</sup>The Evergreen State College, 2700 Evergreen Parkway NW, Olympia, WA 98505, USA; <sup>2</sup>Biology Department, Georgetown University, Reiss Science Building, 37th and O Streets NW, Washington, DC 20057, USA; <sup>3</sup>Department of Biological Sciences, Michigan Technological University, 1400 Townsend Drive, Houghton, MI 49931-1295, USA; <sup>4</sup>Department of Biological Sciences, Northern Arizona University, PO Box 5460, Flagstaff, AZ 86001, USA; <sup>5</sup>School of Earth Sciences and Environmental Sustainability, Northern Arizona University, PO Box 5694, Flagstaff, AZ 86011, USA; <sup>6</sup>Department of Ecology and Evolutionary Biology, University of Tennessee, 569 Dabney Hall, Knoxville, TN 37996, USA; and <sup>7</sup>Life & Environmental Sciences and Sierra Nevada Research Institute, University of California, Merced, CA 95344, USA

## Summary

1. Numerous studies have demonstrated biodiversity–productivity relationships in plant communities, and analogous genetic diversity–productivity studies using genotype mixtures of single species may show similar patterns. Alternatively, competing individuals among genotypes within a species are less likely to exhibit resource-use complementarity, even when they exhibit large differences in their effects on ecosystem function.

2. In this study, we test the impact of genotype diversity and genetic identity on ecosystem function using an ecosystem-scale common garden experiment. Distinct tree genotypes were collected across the entire natural range of the riparian tree *Populus fremontii* in the USA, and grown in 1–16 genotype combination forest stands. Due to the warm climate and irrigation of the planting location along the Colorado River (AZ, USA), mature forest physiognomy with trees up to 19 m tall was achieved in just five years.

3. Several key patterns emerged: (i) genotype richness did not predict forest productivity, suggesting a lack of net biodiversity effects; (ii) we found differences among genotype monoculture stands comparable to differences in average productivity across all forest biomes on Earth; (iii) productivity was predicted based on genetic marker similarity in trees; (iv) genetic-based differences in leaf phenology (early leaf-on and late leaf-fall timing) were correlated with > 80% of the variation in tree and forest productivity irrespective of home-site conditions.

4. Large differences in productivity among genotypes can result in dramatic differences in forest productivity without resulting in diversity–productivity relationships that are present in species-scale biodiversity studies.

**Key-words:** biodiversity–ecosystem function, cottonwood, genes-to-ecosystems, genotype diversity, *Populus*

## Introduction

A major frontier in genes-to-ecosystems research lies in understanding how ecological patterns that have been demonstrated at the interspecific (among species) level apply at the intraspecific (within species) level. Biodiversity–ecosystem function (BEF) research has repeatedly demonstrated that increases in productivity occur with

greater plant diversity at the interspecific scale (e.g. 0–16 species mixtures) and in a broad range of ecosystems world-wide (Loreau *et al.* 2001; Hooper *et al.* 2012; Bukowski & Petermann 2014; Tilman, Isbell & Cowles 2014; Tobner *et al.* 2016). Testing of this pattern at the intraspecific scale suggests that genetic differences within species can also result in increased productivity (e.g. Crutsinger *et al.* 2006; Hughes *et al.* 2008; Bukowski & Petermann 2014).

\*Correspondence author. E-mail: fischerd@evergreen.edu

Genetic differences in trees can have large ecological consequences. Recent research has also repeatedly demonstrated that genotypes within the same species are ecologically differentiated (see Whitham *et al.* 2012; Fischer *et al.* 2014), and this diversity has predictable effects on ecological communities (e.g. Wimp *et al.* 2005; Cook-Patton *et al.* 2011; Zytynska *et al.* 2011; Bangert *et al.* 2013; Busby *et al.* 2013; McArt & Thaler 2013; Abdala-Roberts & Mooney 2014; Barton *et al.* 2015; Campos-Navarrete *et al.* 2015). It is unknown, however, whether such genetic differences warrant differential niche occupation and resource use among genetic individuals within the same species – a prerequisite for true complementarity effects (Tilman, Isbell & Cowles 2014). In fact, it is a fundamental concept in biology that competition is generally higher among individuals of the same species than between species, and many classic ecological species definitions depend on the predictability of the ecological niche within a species. To date, it is unclear whether intraspecific differences can be significant enough in forested ecosystems to result in increased productivity in genetically diverse stands of trees (but see Aspinwall *et al.* 2015). In some cases, more genetically diverse plant assemblages can even show decreased productivity due to competitive interactions, particularly in more extreme environments (Bailey *et al.* 2014).

If plant phenotypes within a species are different enough to result in differential niche occupation, we would expect diversity–productivity relationships. On the other hand, if plants are phenotypically different, but otherwise similar in niche occupation, complementarity resulting in diversity–productivity effects might not be realized.

*Populus* (cottonwood) forests have become a model system for linking genes-to-community–genes-to-ecosystems processes in both terrestrial and aquatic ecosystems (LeRoy *et al.* 2007; Fischer *et al.* 2014) and may represent an ideal system for examining genetic-based BEF concepts. Genetic variation in naturally occurring genotypes of *Populus* spp. has been associated with effects on soil microbes (Schweitzer *et al.* 2008), lichens and fungi (Grady *et al.* 2015; Lamit *et al.* 2015a,b), browsing ungulates (Bailey *et al.* 2004), canopy arthropods (Wimp *et al.* 2005; Keith, Bailey & Whitham 2010; Ferrier *et al.* 2012), nutrient mineralization (Schweitzer *et al.* 2004; Fischer *et al.* 2010) and carbon cycling (Fischer *et al.* 2007; Lojewski *et al.* 2009, 2012). Genotype identity and molecular similarity also predict tree productivity in naturally occurring *Populus* genotypes (Lojewski *et al.* 2009; Grady *et al.* 2011).

Here, we use an experimental Fremont cottonwood (*Populus fremontii* S. Wats.) riparian forest on the lower Colorado River (Arizona, USA) to examine: (i) how stand tree genotype diversity (16 single-genotype monocultures and five levels of increasing genotypic richness) affects planting survival and productivity (basal area increment and total above-ground biomass accumulation) of riparian forest stands; (ii) whether different genotypes exhibit differential survival and productivity; (iii) whether similar plant genetics result in similar productivities (based on genotype

similarity in neutral microsatellite genetic markers); and (iv) whether variation in genotype home environment conditions and average genotype leaf phenologies correlate with patterns in average genotype productivity. We specifically hypothesized that: (i) more genotypically diverse plantings would result in higher survivorship and higher ecosystem-scale productivity over five years measured by basal area increment and total stand biomass accumulation; (ii) individual tree biomass would be predictable based on tree genotype; (iii) productivity would also be predictable based on the genetic similarity among genotypes (more similar genotypes would have more similar productivities); and (iv) conditions related to the original home environments (latitude, elevation, temperature, precipitation and leaf phenology) would predict individual genotype performance.

## Materials and methods

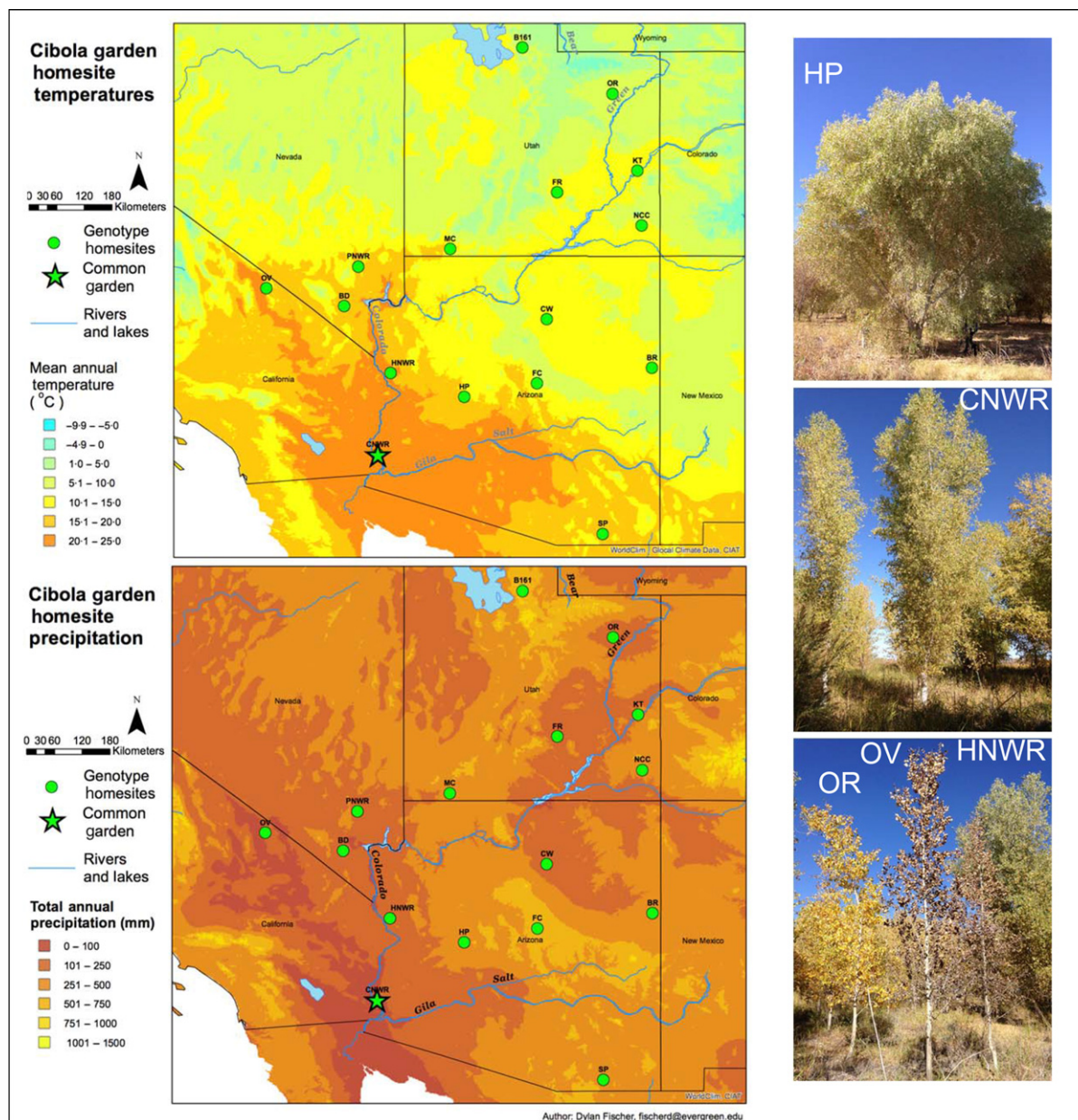
### SITE DESCRIPTION

Cibola National Wildlife Refuge (CNWR) is located in southern Arizona, on the historic floodplain of the Colorado River. Environmental conditions at CNWR are generally hot and xeric, with maximum summer temperatures over 50 °C and minimum winter temperatures of –6 °C. Average precipitation is <1 cm for any given month (total of 7.87 cm per year) and wind speeds average 8 km h<sup>-1</sup> (Western Regional Climatic Center; <http://www.wrcc.dri.edu/>).

Our common garden experiment at CNWR was planted as part of collaborations with the Lower Colorado River Multi-Species Conservation Program and the United States Bureau of Reclamation. We collected *P. fremontii* cuttings from single naturally occurring trees at each of 16 sites that spanned the species' geographic range in the south-west (southern Arizona to northern Utah, USA; Fig. 1) and planted them into one common garden at the warmest location; all cuttings were taken in winter 2004 from healthy, large, established trees and grown in a greenhouse at Northern Arizona University for two years prior to planting at CNWR. The common garden design involved planting 400, 16-tree stands (with trees spaced 4 m apart) as either single *P. fremontii* genotypes or mixtures (2, 4, 8 or 16 genotypes). The design was modelled after multiple species grassland BEF experiments (Tilman 1997; Tilman, Isbell & Cowles 2014), but we substituted multiple genotypes of a single species. Blocks consisting of all 20 treatments (16 monocultures and four mixtures) were replicated 20 times for over 321 clonal replicates of each genotype across the entire garden (total of 6400 trees). Because these plants were two years old at the time of planting, survival rates were predicted to be higher than would be expected under natural regeneration from seeds after a flood. All trees were planted in fall of 2006 and winter of 2007, and by winter of 2012 mean tree height was 12.5 m ± 2.7 m SD, maximum tree height was ~19–12 m, and minimum tree height was ~3–3 m. These rapid growth rates were achieved using flood irrigation in an environment that receives over 320 days of sunshine each year. The common garden was laser-levelled prior to planting to ensure uniformity of irrigation across the experiment.

### INDIVIDUAL TREE AND STAND PRODUCTIVITY

We compared basal area (tree cross-sectional stem area) among genotypes at the individual and stand scale. To accommodate low



**Fig. 1.** Collection locations (circles and star) across the range of *Populus fremontii* and common garden location (star). Photographs demonstrate differences in growth form and leaf-fall phenology among genotypes (white lettering on photos). In all cases, branches begin ~ 0.75 m above the ground. All photographs were taken on 11 November 2014 by Dylan G. Fischer.

branches on tree trunks, tree diameters were measured 0.30 m from the base of each tree. Basal diameters were measured throughout the stand for all surviving trees in early spring, 2012. Basal area values were summed within stands and divided by stand area (256 m<sup>2</sup>) to determine stand-level basal area.

Basal diameters were also converted to equivalent tree diameter at 1.4 m (Diameter at Breast Height or DBH, a more common metric) using an equation from Grady *et al.* (2011) in order to estimate stand biomass. Using modified biomass estimation equations (*sensu* Fischer *et al.* 2007; tree biomass (g) =  $e^{(6.77 + 2.34 \cdot \text{LN}(\text{DBH}))}$ ), we calculated individual tree biomass for all surviving trees within a plot and used these values to estimate stand-level productivity for comparison with other forest types. Biomass-based productivity was calculated for comparison purposes and to understand potential differences in the context of stand carbon pools (where biomass C was assumed 50% of biomass). Statistical

analyses were conducted on stand biomass estimates in addition to stand basal area, but we focus our interpretation of genetic effects on results associated with stand basal area to avoid the pitfalls of assuming that genetically distinct genotypes share the same allometric relationships for the prediction of biomass. We note that similarity in allometric biomass prediction among genotypes is often assumed in other studies (Jenkins *et al.* 2003; Fischer *et al.* 2007; Lojewski *et al.* 2009; Grady *et al.* 2011), but could be a source of error, and results should be interpreted accordingly.

#### GENOTYPE CHARACTERIZATION

Total genomic DNA from the 16 *P. fremontii* genotypes was extracted from dried leaf material using DNeasy Plant Mini Kits (Qiagen, Hilden, Germany) and then standardized for analysis.

We then calculated neutral genetic variation among the 16 genotypes at 15 microsatellites (Van der Schoot *et al.* 2000; Smulders *et al.* 2001; Tuskan *et al.* 2006). Genotyping followed methods outlined in detail in Hersch-Green, Allan & Whitham (2014). Briefly, microsatellite markers were PCR amplified, and fluorescently labelled products were electrophoretically separated on an ABI 3730 automated sequencer (Applied Biosystems™, Foster City, CA, USA) using GENESCAN-600 LIZ (Applied Biosystems™) as an internal size standard, and electropherograms were scored with GENOTYPER v. 3.7 NT software (Applied Biosystems™). Four of the microsatellites were monomorphic across the 16 genotypes and were dropped from subsequent analysis. Data from the remaining 11 microsatellites were combined for each individual to obtain neutral multilocus individual genotypes.

#### STATISTICAL ANALYSIS OF DIVERSITY AND GENOTYPE EFFECTS

The effects of genotypic richness (1, 2, 4, 8 or 16 genotypes in a stand) on both per cent survival and stand basal area were analysed using simple linear regression (SLR), where log-transformed tree basal area and survival were predicted using genotypic richness in each stand. The nature of the experimental design ensures that there are many more replicates of the one-genotype treatment than the 16-genotype mixtures, resulting in an apparent unbalanced design where the least-squared means in regression are biased by the level of the factor with the most replicates. Accordingly, for each analysis we first used a simple *t*-test to determine whether the mean for the monoculture stands was different than the overall mean for the combined mixture treatments (which had equal numbers of replicates). In all cases, we found monoculture treatments did not have significantly different overall means from the mixture treatments ( $P > 0.58$ ), justifying the continued use of the combined least-squared means in SLR, using genotype richness as a predictor variable. All the above parametric analyses were performed using JMP (v12.0, SAS Inc, Cary, NC, USA). Data were tested to meet the assumptions of equality of variance and normality using Levene's tests and Shapiro–Wilk's tests, respectively.

The effect of genotype on per cent survival, basal area (individual and stand level) and stand biomass was assessed using monoculture stands of single genotypes (one stand of each genotype per block,  $n = 20$  blocks). Responses were compared across genotypes using nested random effects models fit by maximum likelihood in the R-software package LME4 (R Core Team 2014; Bates *et al.* 2015). In the models, block and genotype were treated as random effects. Comparison of each full model with a reduced model lacking the genotype effect was used to test the null hypothesis of no genotype effect using the likelihood ratio test approximated by the  $\chi^2$  distribution in the LME4 package in R. Basal area and biomass data were log-transformed prior to analysis to meet normality assumptions, and in all analyses, an a priori  $\alpha$  of 0.05 was used to determine statistical significance.

#### GENOTYPE ANALYSIS AND MANTEL TESTS OF MULTIVARIATE CORRELATIONS

To evaluate whether there was a relationship between univariate tree basal area and multivariate neutral genetic composition, we performed a matrix correlation with a Mantel test (Mantel 1967; Legendre & Legendre 1998). A Euclidean distance matrix (Legendre & Legendre 1998) of the mean basal areas of the 16 genotypes was correlated with the Queller–Goodnight's genetic relatedness distance matrix (Queller & Goodnight 1989) of the same genotypes. Queller & Goodnight's (1989) genetic relatedness distance matrix does not assume Hardy–Weinberg equilibrium and was

obtained with SPAGED1 v. 1.2 (Hardy & Vekemans 2002). Each distance matrix was composed of all pairwise comparisons between each of the 16 sample units, where there were  $(n*(n-1))/2$  pairs (i.e. 120 pairwise comparisons; Legendre & Legendre 1998). The matrix correlation was performed with R-Package software in R and evaluated with the Mantel *r* statistic ( $r_M$ ), which is related to Pearson's *r* (Legendre & Legendre 1998). Because these matrices contain non-independent data, exact *P*-values were derived from a randomization procedure with 9999 permutations of the data (Manly 1997; R Core Team 2014).

#### PHENOLOGY SURVEYS

Timing of leaf out and leaf fall can be a major, and well-known, genetic-based determinant of tree productivity (e.g. Piao *et al.* 2007; Noormets 2009; Ghelardini *et al.* 2014). We conducted four spring surveys and one fall survey to assess whether genotypes differed in leaf phenology. For spring leaf-out surveys, individual trees were surveyed across five complete blocks within the garden on four dates in 2012 (12 February, 27 February, 14 March and 29 April). On each survey date, the numbers of completely unfurled leaves on terminal branches were counted, and genotypes were ranked from 1 to 16, from first to last tree to leaf out. Fall leaf-senescence surveys were completed in 2014 between 6 and 12 November, when the first trees had begun to drop leaves. For fall surveys, each genotype was also ranked from 1 to 16 based on % leaf dehiscence and % yellowing/browning on terminal branches. Phenology scores in each season were then standardized between 0 and 1 by dividing each value by the highest value in the ranking for each season. Scores closer to 0 represented the first genotypes to leaf out or last to drop, and scores closer to 1 represented the latest genotypes to leaf out or the first to drop. These scores were then averaged for a combined phenology score. To account for the artificial combination of measurements across years, measures of phenology based on spring 2012 surveys and fall 2014 surveys were separately regressed against the combined phenology score using simple linear regression. Both spring 2012 and fall 2014 were similarly auto-correlated with the combined phenology score (spring:  $r^2 = 0.86$ ,  $P < 0.001$ ; fall  $r^2 = 0.81$ ,  $P < 0.001$ ). These analyses were conducted to clarify that a combined score indeed reflected similar autocorrelation trends among genotypes in both the spring and fall surveys and that a combined score was not based solely on either spring or fall trends. Additionally, it confirmed that fall and spring phenology rankings were similar among genotypes. Based on these results, we felt confident using the combined phenology score for all subsequent analyses.

#### HOME-SITE ABIOTIC ENVIRONMENT

We gathered data for 11 environmental/site variables at each collection location (home-site): winter maximum air temperature, winter minimum air temperature, summer maximum air temperature, winter precipitation, summer (monsoon) precipitation, the number of frost-free days (Western Regional Climatic Data Center, <http://www.wrcc.dri.edu/>), elevation, soil pH and three variables related to home-site soil type based on USGS surveys (% sand, silt and clay; <http://websoilsurvey.nrcs.usda.gov/>; last accessed 04/14/14).

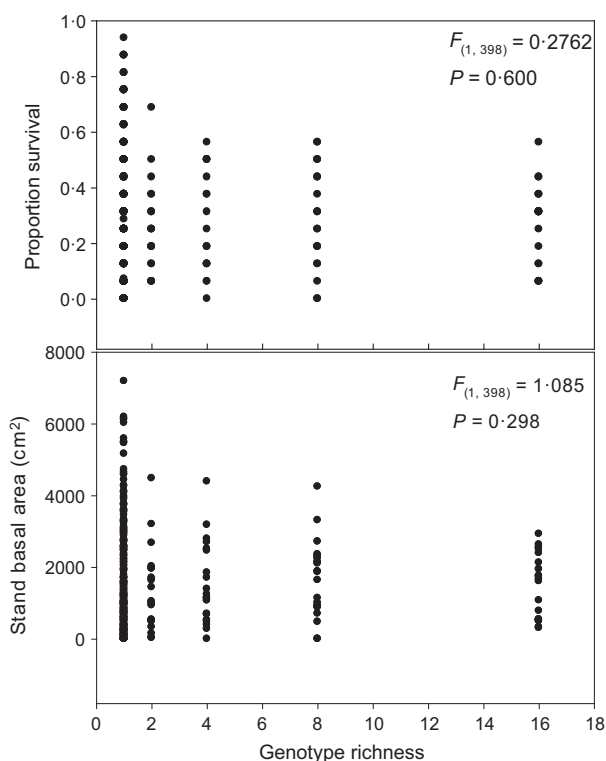
To determine whether any of the 11 abiotic environmental home-site variables were correlated with genotype means of individual tree basal area, stand basal area, % survival and leaf phenology, we calculated Pearson's correlation coefficients. Next, we used structural equation modelling (SEM) to explore whether any differences in productivity may be directly or indirectly related (e.g. through effects on phenology) to the home-site abiotic

environmental variables. In order to reduce the number of variables in our model, we used principal components analysis (PCA) to determine the primary axes of separation in the soils and climate data. The PCA identified two primary axes (chi-square = 194.87,  $P < 0.001$ ); PCA1 explained 44.1% and PCA2 explained 20% per cent of the variation in abiotic variables. The PCA1 axis was primarily associated with temperature and elevation (winter maximum temperatures  $r = 0.96$ ; summer maximum temperatures  $r = 0.96$ ; winter minimum temperatures  $r = 0.95$ ; elevation  $r = -0.93$ ; frost-free days  $r = 0.89$ ), and PCA2 was associated with summer precipitation ( $r = 0.48$ ), winter precipitation ( $r = 0.62$ ), % clay ( $r = 0.36$ ), % sand ( $r = 0.66$ ), % silt ( $r = -0.89$ ) and soil pH ( $r = 0.27$ ). Principal component analysis was conducted using JMP (v12.0, SAS). Briefly for SEM, we examined the standardized path coefficients between the direct association of home-site abiotic variables (PCA1, PCA2) with individual basal area, and the potential indirect path whereby home-site abiotic variables influenced leaf phenology, which then determined individual basal area. For structural equation modelling, we used the LAVAAN package in R (Rosseeel 2012). We specifically chose this approach due to the ability to explore potential direct and indirect effects (Grace 2006). Nevertheless, these analyses should be interpreted with caution because of the limited mechanistic factors in the model.

## Results

### GENOTYPIC RICHNESS EFFECTS ON SURVIVORSHIP AND PRODUCTIVITY

We initially hypothesized that stands with greater genotype richness (greater numbers of distinct genotypes) would also



**Fig. 2.** Genotypic richness (1, 2, 4, 8 or 16 genotypes) vs. proportional survival and stand basal area (productivity). Basal area values represent basal area in 16 m × 16 m stands.

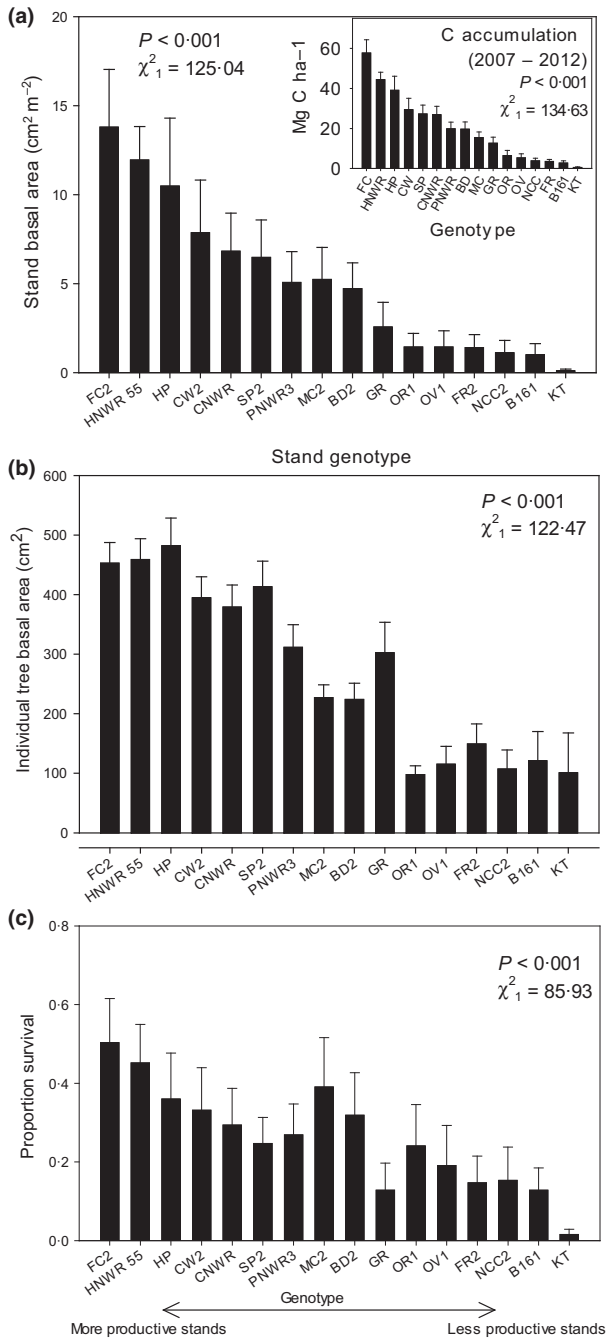
have greater survivorship, yet we found no evidence for this effect (Fig. 2;  $F_{1,398} = 0.2762$ ,  $P = 0.600$ ). While there was variability in monotypic stand survivorship, more diverse stands strongly reflected the average survivorship of monotypic stands. For example, when there was a mixture of two genotypes that each had low monotypic stand survivorship, the resulting mixed stand also had low survivorship. The same was true of high survivorship genotype mixtures, and mixed stand survivorship reflected the average survivorship of genotypes planted in monotypic stands.

We hypothesized that greater genotypic richness would result in greater stand productivity. Nevertheless, total stand productivity, as indicated by basal area and biomass, did not change with stand diversity treatments, consistent with no net biodiversity effect (Loreau & Hector 2001). The most diverse treatment was similar to the average of all monotypic treatments (Fig. 2; basal area:  $F_{1,96} = 0.218$ ,  $P = 0.698$ , biomass:  $F_{1,96} = 0.317$ ,  $P = 0.575$ ). Monotypic stands were variable in average total basal area, but synergistic effects of genotype combinations were not apparent. The lack of relationship was also true when differences in survivorship were taken into account by dividing stand basal area or biomass by the number of surviving trees per stand (basal area:  $F_{1,96} = 0.517$ ,  $P = 0.474$ , biomass:  $F_{1,96} = 0.043$ ,  $P = 0.837$ ; also see below).

### GENOTYPE DIFFERENCES

Our results strongly supported our hypothesis that individual genotypes would differ in stand-scale basal area ( $\chi^2_1 = 125.04$ ,  $P < 0.001$ , genotype represented 93% of explained variance and 53% of total variance; Fig. 3a), stand biomass ( $\chi^2_1 = 134.63$ ,  $P < 0.001$ , genotype represents 92% of explained variance and 61% of total variance), individual tree basal area ( $\chi^2_1 = 122.47$ ,  $P < 0.001$ , genotype represents 81% of explained variance and 46% of total variance; Fig. 3b) and survival ( $\chi^2_1 = 85.93$ ,  $P < 0.001$ , genotype represents 71% of explained variance and 29% of total variance; Fig. 3c).

Differences among tree genotypes resulted in an average maximum  $\sim 114.4$  Mg ha<sup>-1</sup> (57.2 Mg C ha<sup>-1</sup>) difference in stand-scale standing biomass, or approximately 23 Mg ha<sup>-1</sup> year<sup>-1</sup> (11.5 Mg C ha<sup>-1</sup> year<sup>-1</sup>) over five years (Fig. 3a, inset). This difference was partially attributable to differences in genotype survival because stands with high mortality have inherently low productivity. Nevertheless, we compared individual biomass of surviving trees only, and the difference was still large where the maximum difference between genotype biomass was approximately 0.2 Mg tree<sup>-1</sup> over the course of five years. Scaled up to the stand level, the potential difference in stand productivity in the case of 100% survival could amount to an approximately 133.5 Mg ha<sup>-1</sup> difference in stand biomass. Since all biomass was accumulated in only five years, this again amounts to a difference in productivity of  $>20$  Mg ha<sup>-1</sup> year<sup>-1</sup> ( $>10$  Mg C ha<sup>-1</sup> year<sup>-1</sup>).



**Fig. 3.** Individual (a) and stand-level (b) basal area (productivity) is strongly influenced by *Populus fremontii* genotype. Inset on Panel (a) shows associated stand C accumulated through the life of each monotypic stand ( $\text{Mg C ha}^{-1}$ ). Panel (c) shows proportional survival of individual genotypes within monotypic stands. Genotypes are arranged along the x-axis according to stand productivity with less productive stands to the right, and more productive stands on the left. Error bars represent the upper 95% confidence intervals.

Because productivity is dependent on the number of trees alive at a site, it is again important to compare survivorship and stand-level productivity values. No stands had 100% survival, and survivorship and stand basal area were related to each other in the monotypic stands

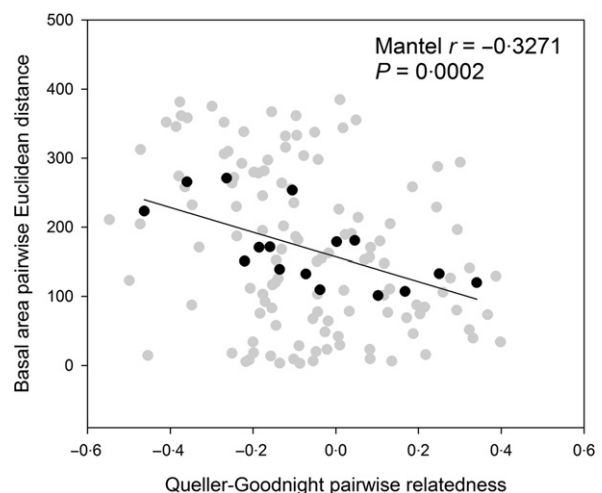
( $r^2 = 0.51$ ,  $F_{(1, 257)} = 262.2$ ,  $P < 0.001$ ). It is important, however, to distinguish between surviving trees that are on average very large and productive, vs. monotypic stands that have high survivorship and low individual tree productivity. This can be reflected in comparisons of productivity patterns among stand-based and individual-based estimates. Our data suggest a strong relationship where average individual tree size predicts stand basal area ( $r^2 = 0.81$ ,  $F_{(1, 14)} = 67.16$ ,  $P < 0.001$ ). When each variable is expressed as a percentage of maximum, the slope of the linear relationship was  $< 1$  (slope = 0.97), indicating some competition that may generally reduce maximum stand biomass among genotypes that are, on average, the most productive individuals. Nevertheless, relative ranking of stand-based and individual-based estimates of productivity was relatively stable (Fig. 3a,b).

GENETIC DISTANCE EFFECTS

Given a strong significant difference among genotypes, we might expect that differences in productivity are predictable based on genetic relatedness among genotypes (dependent, of course, on patterns in neutral markers). We found a significant association between microsatellite markers and individual tree productivity among genotypes (Mantel  $r = -0.33$ ,  $P < 0.001$ ; Fig. 4). Greater Queller–Goodnight relatedness among genotypes at neutral markers was correlated with more similar basal areas. Thus, genetically similar tree genotypes had more similar productivity.

HOME-SITE CHARACTERISTICS AND LEAF PHENOLOGY

Home-site air temperatures (maximum winter, minimum winter, maximum summer) and PCA1 were the strongest correlates with individual tree basal area (Table 1).



**Fig. 4.** Mantel test of Queller–Goodnight genetic distance vs. similarity in basal area among genotypes. As Queller–Goodnight scores reflect greater relatedness, differences in basal area are smaller in pairwise comparisons. Grey dots represent all individual stand comparisons, and black dots represent stand average relatedness and pairwise distance for each genotype.

**Table 1.** Pearson's correlation coefficients comparing individual genotype tree and stand basal area, survival, and leaf phenology to home environment temperatures, number of frost-free days, elevation, winter and summer precipitation, soil pH\*, soil % sand, silt and clay, and both principal components (PCA1 and PCA2) from a principal component analysis

Home-site variable	Individual tree BA	Stand BA	Survival	Leaf phenology
Max. Winter Air Tem.	0.711	0.594	0.437	-0.665
Min. Winter Air Temp.	0.695	0.627	0.495	-0.681
Max Summer Air Temp.	0.634	0.520	0.308	-0.639
Frost-free days	0.583	0.398	0.254	-0.577
Elevation	-0.610	-0.538	-0.356	0.651
Winter precipitation	-0.115	0.088	0.174	0.251
Summer precipitation	0.059	0.047	0.008	0.053
Soil pH*	0.115	0.093	0.055	-0.338
% Clay	0.353	0.271	0.117	-0.331
% Sand	-0.089	-0.005	-0.036	0.089
% Silt	-0.156	-0.261	-0.116	0.143
PCA1	0.638	0.503	0.341	-0.639
PCA2	0.322	0.387	0.247	-0.275

\*pH in H<sub>2</sub>O.

Similarly, home-site air temperatures (minimum winter, maximum winter, maximum summer), elevation and PCA1 were best correlated with stand basal area. Due to regular flood irrigation, our site may actually have been less extreme than some home-sites in terms of water availability. Accordingly, home-site precipitation was never a strong correlate with individual or stand basal area responses. Winter air temperatures had the strongest correlations with survivorship in this study ( $r = 0.44$ – $0.50$ ; Table 1). Nevertheless, trees collected from the site of the common garden (CNWR) did not have the highest survivorship. The genotypes that had the highest survivorship were sometimes from sites differing from the planting site average air temperature, precipitation and elevation (e.g. genotype FC; Figs 1 and 3).

Individual tree genotype basal area and average stand-level basal area of single-genotype stands were both strongly correlated with leaf phenology (respectively, Pearson's  $r = -0.91$ ,  $P < 0.001$  and Pearson's  $r = 0.80$ ,  $P < 0.001$ ). Such relationships are intuitive because the difference in growing season between the genotype with the lowest phenology ranking (shortest period of dormancy), and the species with the highest value (longest period of dormancy) amounted to more than 100 days. Survivorship was also inversely related to leaf phenology ranking, but not as strongly as productivity measures ( $r = -0.57$ ,  $P = 0.022$ ). Leaf phenology itself was best correlated with temperatures, elevation and frost-free days at the home-site (Table 1), where trees that leafed out earlier generally came from sites with higher minimum temperatures. This finding may reflect a trade-off where low temperatures and

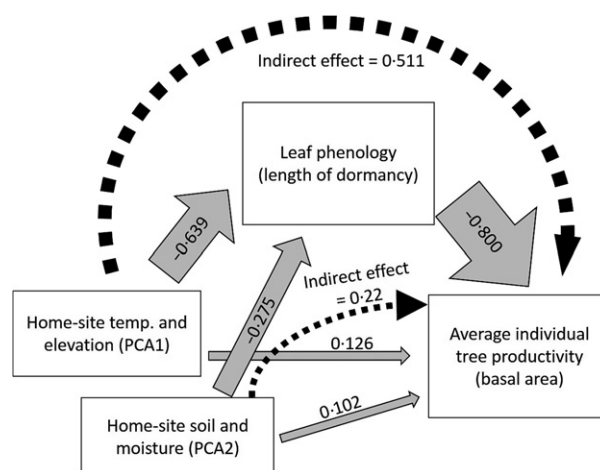
fewer frost-free days at higher elevation home-sites result in late leaf-out times and early leaf drop (and thus low frost damage), but also result in a productivity disadvantage.

Our structural equation model supported indirect effects where climate and elevation (represented by PCA1) correlate with phenology ( $r = -0.64$ ,  $z = -3.56$ ,  $P < 0.001$ ), which then correlates with average tree basal area for each genotype ( $r = -0.80$ ,  $z = -5.75$ ,  $P < 0.001$ ). This indirect path (indirect effect =  $0.511$ ,  $P = 0.003$ ) was much stronger than the non-significant direct correlations between abiotic home-site variables (PCA 1 and PCA2) and genotype average basal area (PCA1:  $r = 0.13$ ,  $z = 0.95$ ,  $P = 0.34$ ; PCA2:  $r = 0.10$ ,  $z = 0.95$ ,  $P = 0.34$ ; Fig 5). These results should be taken with caution based on the lack of data on other traits (e.g. leaf nitrogen content, specific leaf area, leaf area index, photosynthetic rate or stomatal conductance) which may vary greatly between genotypes, and could be strongly related to productivity.

## Discussion

Despite evidence for positive intraspecific diversity–productivity relationships (Crutsinger *et al.* 2006; Hughes *et al.* 2008; Bukowski & Petermann 2014), there may be significant variation in the magnitude of such effects. Our study was unique in that we both sampled from tremendous phenotypic variation in a tree single species (by sampling genetic stock from throughout the range of the species), and out planted all genotypes in a single environment. Thus, we were well positioned to determine diversity–productivity effects, yet we found no evidence of these patterns.

There may be several related reasons we did not find clear genotypic diversity–productivity relationships in this



**Fig. 5.** Structural equation model (SEM) for the effects of abiotic home-site variables related to air temperature and elevation (PCA1) and precipitation and soils (PCA2) vs. average genotype tree size after five years (basal area). Leaf-off phenology (length of dormancy) is included as a potential intermediate factor. Size of arrows reflects the approximate strength of SEM correlation coefficients between variables.



study. First, this finding may be related to true lack of resource-use complementarity in traits that determine annual productivity in individual genotypes. Similar results with forest trees at the species-level have recently been reported by Tobner *et al.* (2016). While genetic differences in dominant forest trees can be large enough to affect biological diversity and ecosystem function in natural systems (review by Whitham *et al.* 2012), niche differentiation among trees of the same species may be insufficient to generate patterns in complementarity of resource use. In this case, trees will still be essentially competing for the same resources (water, light, nutrients), with similar requirements, but some genotypes may be physiologically superior to others in terms of annual growth rate. Similarly, while correlations between canopy arthropod diversity and plant genetic diversity exist in this system (Ferrier *et al.* 2012), such patterns need not invoke changes in productivity. Herbivory and pathogen impacts that are also affected by plant diversity (as discussed by Tilman, Isbell & Cowles 2014) may be insufficient to alter productivity patterns or be unresponsive to our genotype diversity treatments (e.g. airborne or soil pathogens might reduce productivity of certain genotypes across the experiment regardless of monoculture/diversity treatments).

Secondly, we note that our study design samples tree genotypes that by definition were not originally collected from individuals in sympatric populations. If genetic differentiation and niche partitioning occur at the intraspecific scale, we might expect that combinations of local genotypes would be more likely to exhibit complementarity than genotypes from geographically separate areas (*sensu* Zuppinger-Dingley *et al.* 2014). Selection for complementarity in local populations might occur in response to the phenotypes and extended phenotypes of conspecifics (Bailey *et al.* 2014). In this context, our results should be interpreted conservatively. Alternatively, our genotype selection scheme (selecting genotypes from distant sources) may have maximized genotypic diversity in our stands, potentially making overestimation of net biodiversity effects more likely (Tack, Johnson & Roslin 2012). Yet even in the presence of this maximized genotypic diversity, intraspecific diversity effects on productivity were not detectable.

Thirdly, strong genetically based variation in productivity (and associated traits) does not necessarily lead to concomitant diversity effects. Simple traits can play a large role in determining productivity without resulting in differential niche occupation and complementarity. Leaf-out/off timing may provide a good example. Genetic determination of leaf phenology may have a common mechanism throughout Salicaceae (including the genus *Populus*) and is clearly associated with growth (Ghelardini *et al.* 2014). Diverse combinations of genotypes may be inherently incapable of resulting in more productive stands if some genotypes leaf out first, and then out-produce genotypes that leaf out later simply due to a longer growing season. Complementarity effects could also be enhanced by differences

in leaf phenology (reflecting differences in timing of resource needs), but this does not seem to be the case in the present study. Variation in other unmeasured factors like leaf nitrogen content, specific leaf area, leaf area index, photosynthetic rates or stomatal conductance could all have a similar effect in terms of over-shadowing variation due to complementarity effects and should be investigated further.

Fourthly, given the relatively young age of the experiment (five years), diversity effects may also have not had enough time to influence productivity and survival (*sensu* Reich *et al.* 2012; but see Crutsinger *et al.* 2006; Hughes *et al.* 2008). Other studies on short-lived species (e.g. Bukowski & Petermann 2014) have found over-yielding associated with plant–soil feedbacks in diverse intraspecific mixtures. In large forest tree species, plant–soil feedbacks may take longer to manifest, and any over-yielding may be driven by selection effects early in forest development (Tobner *et al.* 2016). Similarly, effects associated with shared rhizosphere communities and root contact (Yang, Callaway & Atwater 2015) in diverse mixtures may also not have occurred yet in our study. Nevertheless, our stands consist of sexually mature, large trees, exhibiting full canopy closure, and thus, it is likely that they are already large enough to exhibit competitive, facilitative and complementarity effects above- and below-ground. Further, there were clear differences in survival, but these differences were predictable by genotype regardless of diversity treatments.

Our data provide further evidence for the importance of taking a genetic perspective in interpreting ecological phenomena related to productivity and carbon flux (Schweitzer *et al.* 2012; Fischer *et al.* 2014). In previous studies in cottonwood forests of the western USA, we have found that plant genotype similarity across a hybridizing complex is a strong predictor of major components of ecosystem carbon (Fischer *et al.* 2007; Lojewski *et al.* 2009, 2012). Here, we show that within a single forest tree species, genetic-based differences can be massive, and in fact larger than species-level comparisons. For example, scaling up our measurements to stand-level C based on allometric relationships suggests that intraspecific genotype differences could result in a difference of  $>10 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  in riparian forest C sequestration. Such differences in ecosystem productivity are comparable to average differences between all forest biomes found on Earth (Pregitzer & Euskirchen 2004; Litton, Raich & Ryan 2007). Additionally, it is now well understood that genotypic differences in *Populus* have strong implications for ecological communities from above- to below-ground (Bailey *et al.* 2009), in both terrestrial and aquatic environments (Wimp *et al.* 2005; LeRoy *et al.* 2007; LeRoy, Wooley & Lindroth 2012), and from microbes (Schweitzer *et al.* 2008) to large herbivores (Bailey *et al.* 2004). Thus, the genetic-based variation that we describe here is likely to have cascading implications for dependent community members in ecologically important riparian forests (Whitham *et al.* 2012).

Although trees in our system can be hyper-productive in biomass accumulation (transitioning from a  $<1 \text{ Mg C ha}^{-1}$  field to a  $\sim 57 \text{ Mg C ha}^{-1}$  forest in only five years), the genotypic identity of trees, and not the stand genetic diversity, determined the productivity of the forest. Genetic marker variation was highly predictive of variation in productivity, suggesting that suites of genes are frequently selected together in productive trees, and even without knowing the genes responsible, the genotypic fingerprint of a tree may predict its growth. Individual genotype traits (e.g. leaf phenology) may have driven productivity in our study, and future studies should take a trait-based approach to understanding net biodiversity effects. Overall, these data do not suggest that genotypic diversity is unimportant. Rather, these data highlight that plant genetics can be highly important in structuring forest ecosystems, even when the well-documented mechanism of complementarity in resource use is not playing a clear role.

## Acknowledgements

This common garden was supported by US National Science Foundation grants DEB-0078280 and DEB-0425908 and Bureau of Reclamation grants CESU-04FC300039 and CESU-06FC300025. We thank many individuals for planting and monitoring these trees since 2007. In particular, we thank Gregg Garnett (Bureau of Reclamation) for collaborating on this project, staff and biologists at Cibola National Wildlife Refuge, garden manager Karla Kennedy at Northern Arizona University. We thank The Evergreen State College for sabbatical support for D.G.F. This work was conducted in collaboration with the students of the 2012 Evergreen State College programme 'Field and Laboratory Biology in Southwestern Ecosystems'. We thank all the students of this academic programme for their contributions and participation in the project. Specifically, we would like to thank Claire Cook, Ruth Mares, Abigail Arnold, Morgan Cheyney and Gray Grandy. We also thank Arthur Keith for field assistance.

## Data accessibility

All data in this manuscript are available in the Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.lp2k0> (Fischer et al. 2016).

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Received 13 December 2015; accepted 23 July 2016

Handling Editor: Julia Koricheva