

Genetic basis of aboveground productivity in two native *Populus* species and their hybrids

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Summary Demonstration of genetic control over riparian tree productivity has major implications for responses of riparian systems to shifting environmental conditions and effects of genetics on ecosystems in general. We used field studies and common gardens, applying both molecular and quantitative techniques, to compare plot-level tree aboveground net primary productivity (ANPP_{tree}) and individual tree growth rate constants in relation to plant genetic identity in two naturally occurring *Populus* tree species and their hybrids. In field comparisons of four cross types (*Populus fremontii* S. Wats., *Populus angustifolia* James, F₁ hybrids and backcross hybrids) across 11 natural stands, productivity was greatest for *P. fremontii* trees, followed by hybrids and lowest in *P. angustifolia*. A similar pattern was observed in four common gardens across a 290 m elevation and 100 km environmental gradient. Despite a doubling in productivity across the common gardens, the relative differences among the cross types remained constant. Using clonal replicates in a common garden, we found ANPP_{tree} to be a heritable plant trait (i.e., broad-sense heritability), such that plant genetic factors explained between 38% and 82% of the variation in ANPP_{tree}. Furthermore, analysis of the genetic composition among individual tree genotypes using restriction fragment length polymorphism molecular markers showed that genetically similar trees also exhibited similar ANPP_{tree}. These findings indicate strong genetic contributions to natural variation in ANPP with important ecological implications.

Keywords: aboveground net primary productivity, broad-sense heritability, ecosystem traits, genes-to-ecosystems, genetic similarity, growth rate constant.

Introduction

The occurrence of genetically based variation in productivity in natural forests has important and obvious evolutionary and ecological significance. Understanding genetic regulation of key ecosystem traits such as aboveground net primary productivity (ANPP) is important because ANPP likely plays a major role in structuring communities and other ecosystem processes such as nutrient cycling, especially when they occur in foundation species such as riparian cottonwoods (*Populus* sp.: Ellison et al. 2005, Whitham et al. 2006). Extensive work on the genetics of tree productivity (e.g., for *Populus*: Isebrands et al. 1988, Hinckley et al. 1989, Campbell et al. 1993, Bradshaw and Stettler 1995, Riemenschneider et al. 1996, Li et al. 1998) and recent work on genes-to-ecosystem connections in forests (Treseder and Vitousek 2001, Madritch and Hunter 2002, Fischer et al. 2004, 2006, 2007, Schweitzer et al. 2004) suggest plant productivity may be a major pathway through which genes affect external communities and ecosystem processes (also see Crutsinger et al. 2006). Additionally, genetically based variation in ANPP could indicate differential stability and recovery of natural systems in the face of disturbance (Rood et al. 2007a). In fact, work on comparison of species, genotypes and ecotypes in *Populus* forests in the US and Canada indicates that genetic variance may maintain ecophysiological traits related to plant productivity in multiple environments (Guy and Gornall

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2007) or influence adaptation to temperature at the ecotype level (Berg et al. 2007, Rood et al. 2007b).

The genetic basis to *Populus* productivity has been studied for decades (e.g., Farmer and Wilcox 1968, Riemenschneider et al. 1996), making *Populus* forests ideal model systems for understanding genetic–productivity relationships in the wild. In many North American ecosystems, *Populus* sp. naturally hybridize creating a continuum of genetic variation between the parental species and the hybrid crosses in the wild (Eckenwalder 1984; for our studies, see Martinsen et al. 2001), and this variation typically occurs along environmental gradients from drier lowland areas dominated by *Populus* species in the section Aigeros, to colder upland areas dominated by *Populus* species in the section Tacamahaca (Eckenwalder 1984, Rood et al. 2003, Rood et al. 2007a). Where species from the two sections meet, hybrid zones are common with multiple coexisting species and hybrids (Eckenwalder 1984), and both introgression (Martinsen et al. 2001) and ecotype differentiation (Berg et al. 2007, Rood 2007b) are likely. In such naturally occurring *Populus* forests, studies have demonstrated important patterns related to heterosis (or lack of: Campbell et al. 1993, Kalischuk et al. 2001, Fischer et al. 2004), inter- and intraspecific variation in ecophysiology (Fischer et al. 2004, Guy and Gornall 2007), ecotypic variation (Berg et al. 2007, Rood et al. 2007b) and variation in growth among seedlings and saplings (Kranjcec et al. 1998, Rood et al. 1998, Kalischuk et al. 2001). While studies have generally not targeted ANPP, it is clear that genetically based variation in individual productivity could scale to affect ecosystems (i.e., high growth rates in individuals lead to high carbon uptake by ecosystems). Quantitative genetic approaches have also commonly been used in *Populus* breeding programs to maximize tree height, growth rate, biomass yield and other performance traits (i.e., rust resistance, spring leaf flush and bud set), all of which exhibit significant broad-sense heritability (H^2_B) ranging from 0.21 to 0.50 (Farmer and Wilcox 1968, Riemenschneider et al. 1996, Dunlap and Stettler 1998, Marron and Ceulemans 2006). In natural forests (*Populus* or otherwise), the occurrence of heritable variation in productivity has important evolutionary and ecological significance. Understanding genetic regulation of key ecosystem traits such as ANPP is important because ANPP likely plays a major role in structuring communities and other ecosystem processes such as nutrient cycling, especially when they occur in foundation species such as *Populus* (Ellison et al. 2005, Whitham et al. 2006).

In this study, we used a *Populus* riparian forest as a model system for three additional reasons. First, cottonwoods and their hybrids are a major component of riparian forests across western North America (Eckenwalder 1984, Rood et al. 2003, Whitham et al. 2006). While sometimes representing a small portion of the larger non-riparian landscape, the riparian forests they dominate represent a hotspot of biodiversity (Noss et al. 1995, Naiman and Décamps 1997, Brinson and Verhoeven 1999). Second,

the genus *Populus* has been widely employed as a model for genetic studies in forest tree breeding and was the first tree species to have its genome sequenced (Tuskan et al. 2006). Third, we used a system dominated by the species *Populus angustifolia* James, *Populus fremontii* S. Wats. and the hybrids between the two which closely resemble similar well-studied systems in Alberta, Canada, dominated by *P. angustifolia*, *Populus deltoides* Bartram ex Marsh. and hybrids between those two species. Because *P. fremontii* has been treated as indistinguishable from *P. deltoides* (e.g., see Cooper et al. 1999), we expected to find patterns similar to those found for the *P. angustifolia* × *P. deltoides* system (Campbell et al. 1993, Kranjcec et al. 1998, Rood et al. 1998, Kalischuk et al. 2001).

We examined the genetic component to tree productivity in both riparian forests and common gardens containing *P. fremontii*, *P. angustifolia* and their naturally occurring hybrids from Northern UT. Using 11 natural stands and four common gardens with trees of known genotype spanning a range of environmental conditions, we hypothesized that (1) natural stands of *Populus* trees that vary in the composition of species and hybrid cross types would vary predictably in tree ANPP; (2) differences in tree ANPP among common gardens that vary in the composition of cross types and specific tree genotypes would be predictable across different environmental conditions, and this variation would reflect patterns found in the wild; (3) tree ANPP would exhibit significant broad-sense heritability (H^2_B) among *Populus* tree genotypes within cross types; and (4) genetically similar trees, as quantified using molecular markers, would exhibit similar tree ANPP across the hybridizing complex.

Materials and methods

Study sites

Along the Weber River, UT, where the ranges of *P. fremontii* and *P. angustifolia* overlap, the two species naturally hybridize (Martinsen et al. 2001). As a result, cottonwood forests along the Weber River are composed of distinct zones (Figure 1) dominated either by *P. fremontii* at lower elevations (~ 1280–1330 m), *P. angustifolia* at higher elevations (~ 1500–2350 m) and a > 13 km overlap or hybrid zone with both parental species and their natural F₁ and backcross hybrids living in sympatry (~ 1330–1500 m; Figure 1; Martinsen et al. 2001).

We first sampled 11 natural stands of cottonwood (five *P. fremontii*, three hybrid and three *P. angustifolia*) using 89 circular permanent plots that spanned a 100 km stretch of the river, 290 m of elevation change, mean annual precipitation variation of 150 mm (448–600 mm), mean annual temperature variation of 3 °C (7.7–10.7 °C) and high variation in growing season temperature and cumulative degree days (Table 1; stands were located among common garden

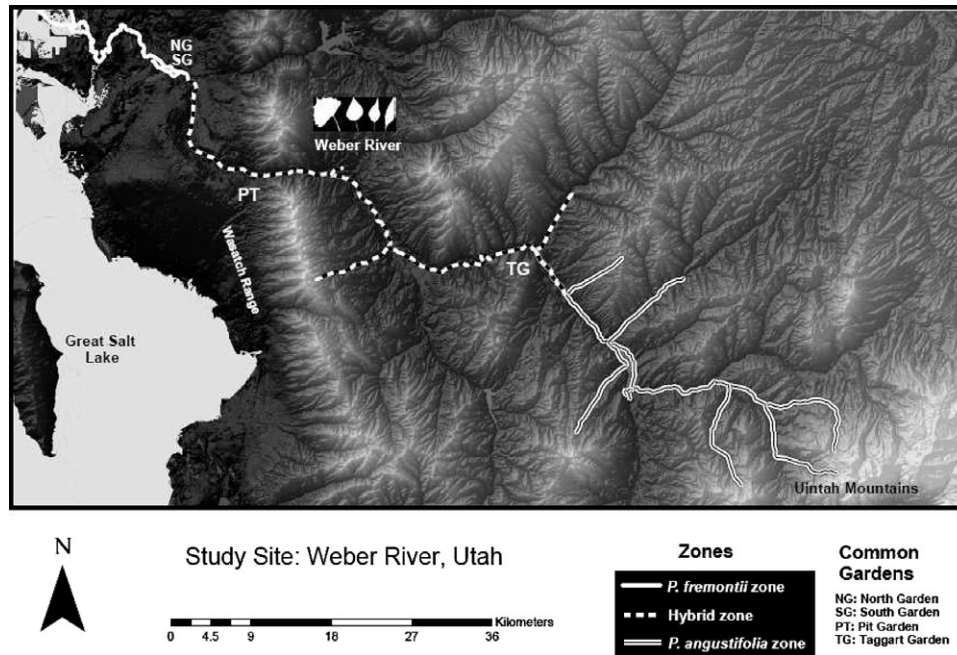


Figure 1. Approximate site locations for natural stands and common gardens along the Weber River, UT. Common gardens are named NG, SG, PT and TG. Extent of natural stands and hybrid zones is indicated by line shading where the white line represents *P. fremontii* dominated reaches, the hatched line represents the hybrid zone where both parental species and hybrids coexist and the double line represents reaches dominated by *P. angustifolia*. Icons representing leaf types are displayed above the Weber River label.

locations). All trees ($n = 1359$) in each randomly located circular 116.9 m^2 plot ($n = 3\text{--}12$ plots per stand and $1\text{--}24$ trees per plot) were repeat-measured for diameter at 1.4 m height on the stem (diameter at breast height, DBH) on the same dates in summer of 2003, 2004 and 2005. Trees in each plot were identified as one of the three cross types (*P. fremontii*, *P. angustifolia*/backcross hybrid or F_1 hybrid) by leaf morphology, which is a reliable estimator of parent/hybrid status for these cross types (Campbell et al. 1993, Martinsen et al. 2001).

Our field measurements were matched with the measurements of tree DBH in 2003 in four common gardens (North Garden, NG, South Garden, SG, Pit Garden, PT and Taggart garden, TG) composed of clones derived from naturally occurring genotypes of each of four cross types (i.e., *P. fremontii*, F_1 hybrid, backcross hybrid with *P. angustifolia* and *P. angustifolia*). Previous studies have demonstrated that this system exhibits unidirectional introgression such that natural backcrosses with *P. fremontii* are rare (Keim et al. 1989). The pure and hybrid status (cross types) of individual genotypes within these common gardens has been characterized and applied in multiple studies (see Keim et al. 1989, Martinsen et al. 2001, Whitham et al. 2006) using 35 *P. fremontii* species-specific restriction fragment length polymorphism (RFLP) markers. Keim et al. (1989) and Martinsen et al. (2001) provide extended details on the RFLP analysis. Each garden was planted between 1300 and 1590 m spanning the historical range of the *Populus* hybrid zone adjacent to the Weber River (see Table 1 for

garden descriptions; Figure 1). The gardens were planted between 1981 and 1992 using cuttings taken from randomly selected genotypes along the Weber River (Keim et al. 1989, Martinsen et al. 2001). Random placement of trees (including all replicates) within each garden assured that there were no systematic site biases or spatial auto-correlations that might affect the response variables.

Productivity and relative growth rate constant measurements

Allometric equations relating tree dry biomass to DBH (Crow 1988) were developed by destructively sampling eight cottonwood trees (four *P. fremontii*, one F_1 hybrid, two backcross hybrid and one *P. angustifolia*) with a DBH range of $7.1\text{--}37.9 \text{ cm}$ growing along the Weber River, UT. Each tree was separated into four components: stem and large branches ($> 2.54 \text{ cm}$ diameter), small branches ($< 2.54 \text{ cm}$ diameter), foliage and dead branches. Subsamples from each component were dried at $70 \text{ }^\circ\text{C}$ to determine wet to dry biomass conversions. We then developed the following two predictive equations: wood biomass (g) = $-38248.29 + 359.69 \times (\text{DBH})^2$ ($r^2_{\text{adj}} = 0.95$, $P < 0.0001$) and foliar biomass (g) = $386.88 + 113.58 \times (\text{DBH})$ ($r^2_{\text{adj}} = 0.89$, $P < 0.001$). Biomass values for occasional trees smaller than 10 cm DBH were estimated using a best-fit linear model forced through zero using only the two smallest trees (7.11 and 12.95 cm) for foliar ($= 187.17 \times \text{DBH}$) and stem ($= 258.30 \times \text{DBH}$) biomass.

Table 1. Climatic data and planting descriptions of four common gardens used along the Weber River, UT.

Common garden name	Latitude, longitude	Elevation (m)	Weather station available data years	Mean annual air temperature (°C)	Mean April–October air temperature (°C)	Cumulative degree days (base 50)	Mean annual precipitation (mm)	Date planted	Cross types (# genotypes)	No. of trees
NG	41°15' N, 112°00' W	1300	1924–2007	10.7	25.53	3040	448	1990–1992	POAN (38), POFR (7), F ₁ (14), BC (13)	196
SG	41°15' N, 112°00' W	1300	1924–2007	10.7	25.53	3040	448	1990–1992	POAN (12), POFR (5), F ₁ (7), BC (24)	86
PT	41°8' N, 111°54' W	1384	1914–1991	9.7	24.78	2909	600	1988	POAN (3), F ₁ (5), BC (16)	268
TG	41°4' N, 111°34' W	1587	1903–2008	7.7	23.56	1888	468	1983	POAN (3), POFR (1), F ₁ (2), BC (12)	80

All climatic data and degree days calculations are from <http://www.wrcc.dri.edu> – accessed 3-21-2009. Degree days use base temperature = 10 °C (calculated using 50 °F) where degree days result from the difference between the daily mean temperature and the base temperature. One degree day unit is given for each degree mean temperature above the base temperature. *Populus angustifolia* is represented by POAN, POFR represents *P. fremontii* and F₁ and BC represent F₁ and backcross generation hybrids, respectively.

This prevented negative values for smaller trees possible through the otherwise more robust models above. While ideally we would have sampled enough trees to create separate biomass estimation equations for each species and hybrid, we were unable to harvest any additional trees because the riparian ecosystems where these trees are found are already highly fragmented. While some previous studies have suggested that total tree biomass estimation equations in our study system can be similar across trees and genotypes (Fischer et al. 2004, 2006, 2007), we feel this may be an oversimplification, and results based on these equations should be interpreted with caution. Tree aboveground net primary productivity (hereafter ANPP_{tree}; Hart and DiSalvo 2005) was estimated with the following equations: $ANPP_{tree} = (B_{t2} - B_{t1}) + FB_{t1}$, where B_{t1} is the biomass at time 1, B_{t2} is the biomass at time 2 and FB_{t1} is the foliar biomass at time 1.

In the common gardens, an index of individual tree productivity was generated by fitting aboveground biomass estimated from allometric equations to a geometric growth function and calculating the exponential growth rate constant (GRC; Avery and Burkhardt 2002, pp 354). This approach was used for these trees because repeat measures of tree DBH were unavailable for gardens other than the North Common Garden. The GRC was developed by fitting each tree to the following equation: $B_t = B_0 \times e^{(GRC \times T)}$, where B_t is the biomass measured in 2003, B_0 is the initial biomass (estimated at 9.2 g based on before planting dry weight of 21 saplings), GRC has the units year⁻¹ and T is time (year). In the single common garden, NG, comparison of repeat measures of diameter (2003, 2005 and 2006) in a standardized location (marked with paint) on all trees allowed the estimation of individual ANPP_{tree} over multiple years similar to plot-level ANPP_{tree} estimates in the natural stands. These estimates were then used for heritability measures and Mantel tests (see below). All such analyses were conducted on an average of ANPP_{tree} calculated for the two periods 2003–2005 and 2005–2006.

Data analysis

Data from natural stands were analyzed using a nested ANOVA design, incorporating data from individual plots with stands nested within stand types. Data from all common gardens were analyzed using a mixed model, two-factor ANOVA on genotype means to determine the relative influences of cross type (random effect), common garden (fixed effect) and cross type by common garden interactions (random effect). Cross type was treated as a random effect specifically because exact combinations of cross types and genotypes in each garden are the result of a random sampling of available trees in the wild, and thus are not fixed effects. Sample sizes among cross types at different common gardens varied dependent on the random sampling of trees at the time of garden planting, site history and early planting mortality. A similar mixed model, two-factor ANOVA was also used at the genotype level for

the eight genotypes common to all four gardens but with varying sample sizes reflective of random sampling (26 clones of one F₁ hybrid genotype, 27, 39, 18 and 20 clones of four backcross hybrid genotypes and 48, 36 and 33 clones of three *P. angustifolia* genotypes divided among four gardens). This analysis allowed us to evaluate the influence of genotype, common garden and genotype by common garden interaction (i.e., genetic by environment, or G × E) on productivity with random variation in specific genotype/cross-type membership among gardens.

All hypotheses were tested at $\alpha = 0.05$ to denote statistical significance, and Tukey's Honest Significant Difference (HSD) multiple comparisons test was used for comparison of means in all tests (natural stands and garden data) when ANOVAs were significant. However, because one garden (PT) did not have *P. fremontii*, Tukey's HSD comparisons were not appropriate for this cross type. In this special case, we used least squared means contrasts (with Bonferroni correction) to determine differences for cross-type analyses. Additionally, for each common garden, individual ANOVAs were run independently to clarify differences among cross types within each garden. All ANOVAs were performed using SAS JMP Version 4.0.4 (SAS Institute, Cary, NC).

We calculated the broad-sense heritability (H^2_B) of ANPP_{tree} as the among-lineage component of variation in the phenotype, (σ^2_S), divided by the total variance in the phenotype for all trees (σ^2_{total}), or $H^2_B = \sigma^2_S / \sigma^2_{total}$ (see Falconer 1989 for details on variance partitioning among lineages using ANOVA). Broad-sense heritability calculations used 20 genotypes (three *P. fremontii* genotypes, six F₁ hybrid genotypes, six backcross hybrid genotypes and five *P. angustifolia* genotypes) that were replicated at least three times in the garden NG; only this common garden could be used for H^2_B analysis because it was the only one with adequate replication of individual genotypes for estimating H^2_B . Broad-sense heritability values were estimated for genotypes within each cross type individually and presented as $H^2_B \pm 95\%$ confidence intervals (CI). The standard error (SE) for H^2_B depends on the intraclass correlation (t), the number of clones (S) and the number of individuals per clone (k). According to Becker (1985), the following formula approximates SE, assuming that t is normally distributed: $SE = \{[2(n-1)(1-t)^2(1 + (k_1-1)t^2)] / [k_1^2(n-S)(S-1)]\}^{1/2}$. To generate 95% CI, we multiplied the standard error by t scores appropriate for sample size (as is standard). When the 95% CI is greater than the broad-sense heritability estimate, the effects of plant genotype on the measured trait are considered non-significant.

We performed a Mantel test (Fortin and Gurevitch 1993) to evaluate the relationship between matrices of individual tree RFLP genetic markers and ANPP_{tree}. The same average ANPP_{tree} values from 20 tree genotypes included in the H^2_B calculations were used in this analysis. As mentioned above, RFLP data were based upon 35 molecular markers for each tree (Martinsen et al. 2001). Our approach was similar to previous work in our study system evaluating

the effect of individual tree genetics on canopy arthropod community composition (Bangert et al. 2006). All Mantel tests were performed using the R package for multivariate and spatial analysis (Version 4.06d; The R Foundation for Statistical Computing, Vienna, Austria).

Results

Comparison of ANPP_{tree} among natural stands

We observed evidence for differences in aboveground growth among cross types in the 11 natural *Populus* stands located across diverse environmental conditions. Naturally occurring *P. fremontii* stands had nearly twice the ANPP_{tree} as either hybrid or *P. angustifolia* stands for two consecutive years (Figure 2; 2004: $F_{(10,88)} = 3.97$, $P < 0.001$; 2005: $F_{(9,84)} = 3.85$, $P < 0.001$). One entire stand (four plots) was lost between 2004 and 2005 due to riverside anthropogenic development in the hybrid zone.

Comparison of GRC among cross types and genotypes in common gardens

Our data from common gardens demonstrated patterns consistent with the natural stands. Using an ANOVA model

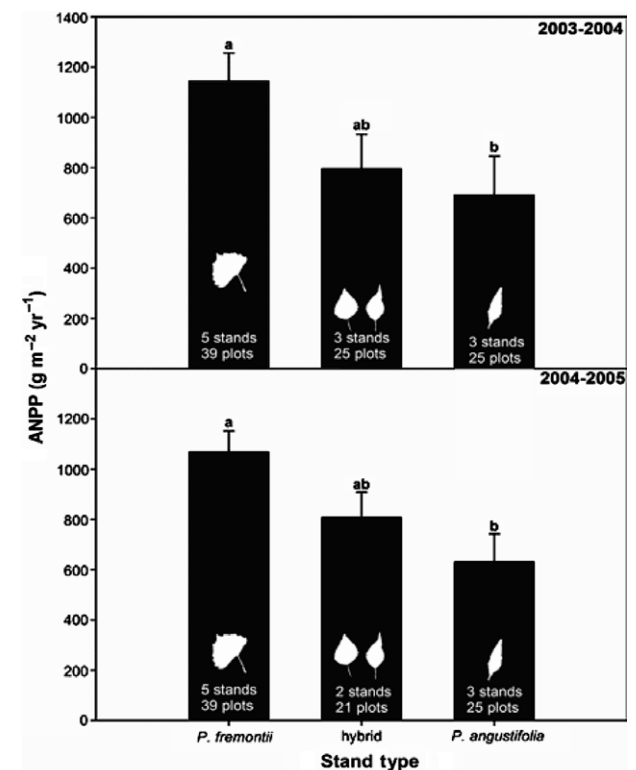


Figure 2. Stand ANPP_{tree} (*Populus* trees only) on the Weber River, UT. The number of stands and total plots in each analysis is indicated in each bar. Different letters denote significant differences using a Tukey's HSD multiple comparisons at $P < 0.05$. Error bars represent one SE of the mean.

that included cross type, common garden and the cross type by common garden interaction (whole model $P < 0.001$, Table 2), we found significant differences in GRC among *Populus* cross types across all gardens ($P = 0.016$, Table 2; Figure 3). We found significant differences between the parent species using least squared means contrasts among all gardens that contained both parent species (*P. fremontii* and *P. angustifolia*; $F_{(1,147)} = 6.928$, $P = 0.009$), and hybrids were intermediate between parental tree types (Figure 3). Tukey's HSD comparisons within gardens generally yielded similar results (Figure 3). We also found a twofold difference in GRC across common gardens ($P < 0.001$), but we found no significant cross type by common garden ($G \times E$) interaction ($P = 0.973$, Table 2; Figure 3). In a comparison of eight genotypes common to all gardens, we similarly found a significant model ($P < 0.001$), where genotype ($P < 0.001$) and common garden ($P < 0.001$) were significant factors, but the genotype \times common garden interaction was not significant ($P = 0.080$, Table 2).

Broad-sense heritability molecular marker covariance of productivity estimates

Using two different approaches (H^2_B analysis and a Mantel test), we found evidence for genetically based predictability of ANPP_{tree} in a single common garden (NG). Within cross types, plant genetic factors explained $38 \pm 35\%$ ($H^2_B \pm$ CI 95%) and $82 \pm 35\%$ ($H^2_B \pm$ CI 95%) of the variation in ANPP_{tree} for *P. angustifolia* and F_1 hybrids, respectively. In other words, there was significant genetic variation for plant productivity where 38% and 82% of the variation in productivity, respectively, were explained by plant genetic factors. We found no significant (not statistically different from zero) H^2_B of ANPP_{tree} for *P. fremontii*

($H^2_B = -0.06 \pm 41\%$ CI 95%) or backcross hybrids ($H^2_B = 0.07 \pm 17\%$ CI 95%). Using a Mantel test comparing the molecular marker matrices of trees used in the H^2_B analysis, we found that trees with similar molecular composition also had similar ANPP_{tree} (Figure 4; Mantel $r = 0.355$ and $P < 0.001$).

Discussion

We hypothesized that plant genetic factors would exert a readily observable effect on native *Populus* ANPP_{tree} in two species and their hybrids, and we found four main patterns that support this hypothesis. First, *P. fremontii* was generally more productive than *P. angustifolia* with hybrids intermediate between the two parents. While some other studies on *Populus* productivity (e.g., Isebrands et al. 1988, Hinckley et al. 1989, Bradshaw and Stettler 1995, Li et al. 1998) have focused on hybrid vigor, we found that hybrids generally had growth rates intermediate between their parents. Although some select individual hybrid genotypes were among our most productive trees, this was not the case for the average hybrid. This agrees with previous studies comparing parents and hybrids between *P. angustifolia* and *P. deltoides* (Campbell et al. 1993, Kranjcec et al. 1998, Rood et al. 1998, Kalischuk et al. 2001). In fact, recent studies have found a marked lack of heterosis in natural hybrids between *P. angustifolia* and *P. deltoides* (Campbell et al. 1993, Kalischuk et al. 2001). Because some authors have treated *P. deltoides* and *P. fremontii* as the same species (e.g., Cooper et al. 1999), our results support the findings of these earlier studies using wild stands and mature trees in common gardens.

Table 2. ANOVA results for (A) model comparing cross types, gardens and cross type \times garden interactions across all gardens and (B) model comparing common genotypes, gardens and genotype \times garden interactions.

	DF	SS	MS	F ratio	P
(A) ANOVA cross types among gardens					
Model	14	6.508	0.465	42.649	< 0.001
Error	147	1.602	0.011		
Total	161	8.111			
<i>Effects test</i>					
Garden	2	2.780	1.390	191.460	< 0.001
Cross type	2	0.065	0.032	4.288	0.016
Cross type \times garden	8	0.024	0.003	0.276	0.973
(B) ANOVA common genotypes among gardens					
Model	30	5.568	0.186	63.945	< 0.001
Error	214	0.621	0.003		
Total	244	6.189			
<i>Effects test</i>					
Genotype	6	0.108	0.018	4.748	< 0.001
Garden	2	3.807	1.903	468.797	< 0.001
Genotype \times garden	20	0.088	0.004	1.509	0.080

Note: In (A) cross type was treated as a random effect and in (B) genotype was treated as a random effect. Acronyms stand for degrees of freedom (DF), sums of squares (SS) and mean squares (MS).

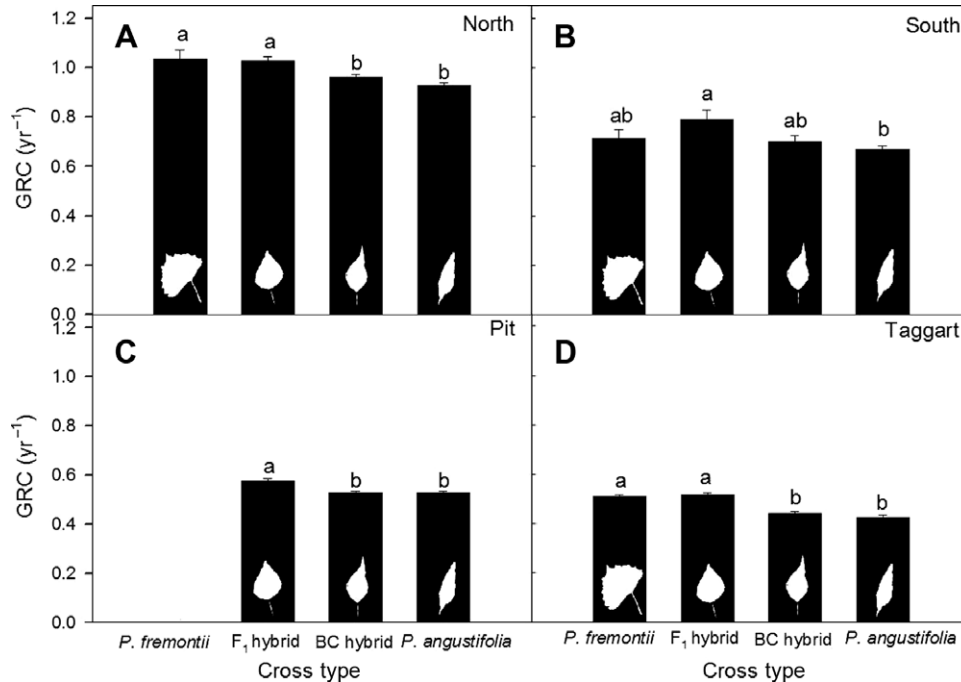


Figure 3. Comparison of exponential GRCs, year⁻¹ among all cross types of *Populus* in four common gardens across a range in environmental conditions: (A) NG, (B) SG, (C) PT; note no *P. fremontii* trees and (D) TG. The cross types are represented by *P. fremontii*, F₁ hybrids, BC hybrid (backcross hybrids) and *P. angustifolia*. Different letters denote significant differences within a garden at $P < 0.05$ using a Tukey's HSD multiple comparisons test. Error bars represent one SE of the mean.

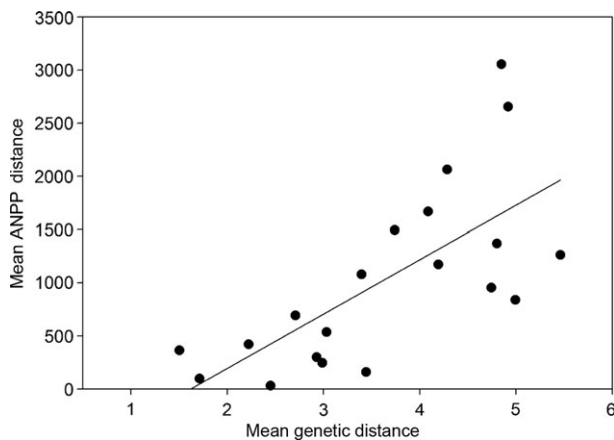


Figure 4. Comparison of molecular genetic composition to ANPP of 20 genotypes using a Mantel test. The axes are unitless and denote relative differences in genetic and ANPP distances among trees. As trees become more similar genetically, ANPP_{tree} also becomes more similar (Mantel $r = 0.355$ and $P < 0.001$).

Second, our findings show that despite a doubling of productivity among common gardens, genetic by environment interactions in this trait were not obvious (Figure 3). We did not find a significant interaction between common garden and productivity of cross types or genotypes, indicating that differences in productivity remained relatively constant. Trees were generally less productive at higher

and cooler sites (consistent with Kalischuk et al. 2001), but similarly so among cross types and genotypes. The two gardens that showed the greatest potential difference in cross type patterns from individual Tukey's HSD tests within gardens were adjacent to each other (SG, NG; see Table 1), but one (SG) appears drier due to distance from a nearby stream. However, gardens separated by the greatest distances (e.g., NG and TG) did not show different relative patterns in productivity among cross types (Figure 3). Genetic effects on many measures of tree productivity have been previously quantified for forest tree species (e.g., for *Populus*, see Riemenschneider et al. 1996, Guy and Gornall 2007, Rood et al. 2007b), but $G \times E$ interactions may reflect ecotypic variation or local adaptation (Rood et al. 2007b, Guy and Gornall 2007), preventing consistent patterns among cross types in multiple environments. Our results suggest predictability in genetic effects across a limited range of elevations. It should be noted that this may be an artifact of the elevations used for common gardens in our study. For example, our highest elevation common garden was at the lower reaches of the *P. angustifolia* zone, and our lowest elevation garden was at the higher reaches of the pure *P. fremontii* zone. A lack of statistically significant $G \times E$ effects in our study does not mean $G \times E$ are not present. Important $G \times E$ effects likely exist but our sample size and study design did not detect them. Thus, our results suggest that where these species naturally coexist with hybrids, relative productivity among genotypes and

cross types may be relatively consistent, and $G \times E$ effects may not be strong enough to detect with low sample sizes. This implies that within this limited elevation band changes in species and genotype range might not change relative productivity among genotypes.

Third, the consistency of our findings from wild stands and common gardens suggests that the observed differences in the wild are reflective of genetically based relationships found in the common gardens. This is important because patterns found in the wild could be reflective of environmental influences (e.g., higher and cooler sites restrict tree growth). Alternatively, patterns found in common gardens alone could be an artifact of specific genotypes randomly chosen for the common garden, or an effect that is only present in the absence of natural environmental variation.

Fourth, we found significant heritability of productivity. Estimates of broad-sense heritability represent the combined effects of additive, dominance and epistatic genetic variances, and thus overestimate the amount of variation in measured traits that can be acted on by natural selection (i.e., the additive component). However, our estimates of broad-sense heritability are consistent with other estimates of broad-sense heritability for many measured traits including productivity, phytochemistry, morphology, terrestrial arthropods and soil microbial communities (Whitham et al. 2006, Schweitzer et al. 2008). The H^2_B for *P. angustifolia* of 0.38 (this study) is within the range of values (0.21–0.50) found for the H^2_B of aboveground growth in other studies in trees (Riemenschneider et al. 1996, Osorio et al. 2001), but the H^2_B of 0.82 for F_1 hybrids is higher than in these studies. In contrast, the lack of a statistically significant H^2_B for two of the cross types could be because *P. fremontii* was not well replicated ($n = 3$ genotypes) or because different cross types have different population variability (i.e., *P. fremontii* and backcross hybrids have low variability in $ANPP_{tree}$ across their populations, while *P. angustifolia* and F_1 hybrids show large variability in $ANPP_{tree}$).

Interestingly, our highest heritability estimates are for hybrids which can introgress traits into *P. angustifolia* parent populations through further unidirectional hybridization (see Keim et al. 1989, Martinsen et al. 2001), but by definition they cannot reproduce these traits in their own progeny. The heritability of the important trait of productivity was not uniformly heritable across these species and hybrids. This finding could reflect sample size limitations. However, this finding could also reflect life history trade-offs associated with reproductive strategy (Schweitzer et al. 2002), disturbance (Rood et al. 2007a), environmental variation (Berg et al. 2007, Rood et al. 2007b) and hydrologic regime (Rood et al. 2003) common to where *P. angustifolia* and *P. fremontii* form pure stands. Because trees in the taxonomic section Aigieros may differ in life history strategy compared to trees in section Tacamahaca (e.g., Schweitzer et al. 2002, Rood et al. 2007a), F_1 hybrids may inherently have more variation (and thus a more easily detectable H^2_B ; Whitham et al. 1999) due to inheritance of

divergent traits from both parental species. We would expect that if this were the case, trees with similar genetic makeup would still have more similar productivity across all cross types.

In agreement with our prediction, a Mantel test of the relationship between genetic relatedness and productivity demonstrated a strong correlation. We would not expect this relationship to be significant for simple Mendelian traits, but only for quantitative traits involving genes spread throughout the genome. This finding is analogous to another study from the same system (Weber River; Bangert et al. 2006) in which trees with similar genetic makeup hosted similar arthropod communities. While the finding of our study and that of Bangert et al. (2006) differ in the response variables, together they suggest genetic similarity can play a strong role in structuring ecologically important variables at multiple scales within the same study system. The Mantel test adds another line of evidence suggesting that *Populus* tree productivity displays important and predictable variation based on genetic composition in these two naturally occurring species and their hybrids, and similarity with community-level studies suggests that productivity could be a mechanism driving community patterns (Bangert et al. 2006, Whitham et al. 2006).

Overall, our data demonstrate predictable variation in aboveground productivity within two common, naturally occurring *Populus* species and their hybrids, similar to findings in other *Populus* hybrid studies. These findings are consistent at multiple genetic levels, among cross types and within cross types. However, our results are unique in that they focus on whole plant productivity, and our findings are relevant to a broad community and ecosystem genetics analysis context within *Populus* forests. For example, our findings have implications for recent studies demonstrating a genetic basis to ecosystem-scale carbon allocation in *Populus* (Fischer et al. 2006, 2007). Trade-offs in aboveground growth (this study) may be realized in altered belowground growth or carbon allocation (Fischer et al. 2006, 2007). Additionally, the covariance between the genetic makeup of *Populus* trees and the multiple ecological traits, including aboveground growth, foliar condensed tannins, arthropod community structure, soil microbial communities and soil nitrogen transformation, suggests that plant genetic effects on key traits like productivity may have implications for organization at multiple biological scales (Whitham et al. 2006, 2008). In combination, these studies suggest that the extensive work on the genetic basis to tree productivity could be broadly applied to understanding community structure and ecosystem processes in diverse systems.

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