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Local biotic adaptation of trees and shrubs to plant neighbors

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Natural selection as a result of plant–plant interactions can lead to local biotic adaptation. This may occur where species frequently interact and compete intensely for resources limiting growth, survival, and reproduction. Selection is demonstrated by comparing a genotype interacting with con- or hetero-specific sympatric neighbor genotypes with a shared site-level history (derived from the same source location), to the same genotype interacting with foreign neighbor genotypes (from different sources). Better genotype performance in sympatric than allopatric neighborhoods provides evidence of local biotic adaptation. This pattern might be explained by selection to avoid competition by shifting resource niches (differentiation) or by interactions benefitting one or more members (facilitation). We tested for local biotic adaptation among two riparian trees, *Populus fremontii* and *Salix gooddingii*, and the shrub *Salix exigua* by transplanting replicated genotypes from multiple source locations to a 17 000 tree common garden with sympatric and allopatric treatments along the Colorado River in California. Three major patterns were observed: 1) across species, 62 of 88 genotypes grew faster with sympatric neighbors than allopatric neighbors; 2) these growth rates, on an individual tree basis, were 44, 15 and 33% higher in sympatric than allopatric treatments for *P. fremontii*, *S. exigua* and *S. gooddingii*, respectively, and; 3) survivorship was higher in sympatric treatments for *P. fremontii* and *S. exigua*. These results support the view that fitness of foundation species supporting diverse communities and dominating ecosystem processes is determined by adaptive interactions among multiple plant species with the outcome that performance depends on the genetic identity of plant neighbors. The occurrence of evolution in a plant–community context for trees and shrubs builds on ecological evolutionary research that has demonstrated co-evolution among herbaceous taxa, and evolution of native species during exotic plants invasion, and taken together, refutes the concept that plant communities are always random associations.

While climatic and edaphic factors are known to drive genetic differentiation among plant populations (Hufford and Mazer 2003), the potential for interactions among native plants to result in local biotic adaptation has rarely been studied in herbaceous taxa, (Turkington and Harper 1979, Martin and Harding 1981, Ehlers et al. 2016), and never studied in tree species. Both conceptual models (Shuster et al. 2006) and empirical evidence of rapid evolutionary change within communities because of selection for inter-specific plant interactions (Aarssen 1983, Case and Taper 2000, Thompson 2005) challenge the long-held view that plant communities are random associations of species that do not interact strongly enough nor encounter each other frequently enough to drive the evolution of resource acquisition strategies (Gleason 1926). Evidence of plant interaction-mediated selection upon different plant species belonging to the same community has been found when introduced exotic species invade native species' ranges (Mealor and Hild 2006, Leger 2008, Lankau 2012), or when competitive or facilitative interactions drive co-evolution among forbs and

grasses (Turkington and Harper 1979, Martin and Harding 1981, Chanway et al. 1988).

Competitive and facilitative interactions among individual plants, both within and among species, are expected to alter resource availability and thus have the potential to mediate selection (Thorpe et al. 2011). Selection may lead to coexistence via mechanisms involved in competition avoidance such as niche differentiation (Allard and Adams 1969, Turkington and Harper 1979), in facilitation (Chanway et al. 1988, Proffitt et al. 2005, Dudley and File 2007), or may lead to extinction of weakly competitive genotypes that can occur when exotic species invade native plant ranges (Leger 2008, Rowe and Leger 2011, Lankau 2012). The hypothesis that competition leads to character displacement and niche differentiation and thus divergent strategies for accessing resources is a cornerstone of classical competition and community assembly theories (MacArthur and Levins 1964, Levins 1979, Ackerly 2003). Evolutionary processes that lead to niche differentiation are implicit in these theories, although empirical support for the evolution

of niche differentiation among interacting plant species is rare.

One approach for evaluating the evolutionary consequences of plant interactions, or specifically, if plant species exhibit local adaptation to plant neighbors, is to compare the performance (growth, survival, reproduction) of an individual genotype when grown with neighbor genotypes sourced from the same site with a shared site-level evolutionary history (sympatric) compared to when grown with neighbor genotypes derived from different sites without a site-level evolutionary history (allopatric). Better performance of an individual genotype with sympatric relative to allopatric neighbor genotypes is evidence of evolution within a community context (Shuster et al. 2006), or local biotic adaptation.

We investigated the importance of local biotic adaptation among foundation woody species that dominate riparian ecosystems of the southwestern United States. In these riparian ecosystems, the trees *Populus fremontii* and *Salix gooddingii*, and the shrub *S. exigua* commonly co-occur in dense intermixed stands and comprise 90 percent or more of community plant biomass (Driebe and Whitham 2000). Given their high density and local dominance, these species are likely to have strongly interacted with each other for long periods of time. We planted multiple replicated genotypes sourced from four provenances into sympatric and allopatric treatments in a common garden (Fig. 1, 2). We tested

the hypothesis that clonally replicated genotypes would have higher average productivity and greater survivorship in sympatric compared to allopatric treatments. We used aboveground productivity as a measure of performance as it is often used as a proxy for fitness to infer local adaptation in provenance trials (Savolainen et al. 2007, Leimu and Fischer 2008, Aitken and Whitlock 2013), and is often positively correlated to reproduction (Knops et al. 2007, Satake and Bjørnstad 2007). Growth rate may be particularly important in highly productive ecosystems where competition is intense and faster growing plants are most likely to survive and reproduce.

The few previous studies of local biotic adaptation among interacting plant species have been restricted to small-statured annual and perennial forbs and grasses and generally focus on pair-wise interactions between two species (Turkington and Harper 1979, Martin and Harding 1981, Vavrek 1998, Ehlers and Thompson 2004, Proffitt et al. 2005, Fridley et al. 2007). Here, we advance the fundamental principles of evolution across plant life forms by including three foundational woody plants (i.e. organisms that are recognized as drivers of their respective communities and ecosystems; Whitham et al. 2003, Ellison et al. 2005) to better understand the importance of species interactions in community evolution through local biotic adaptation. Our findings of increased productivity of sympatric communities over allopatric communities have important implications for understanding the genetic basis of community structure and evolution.

Provenance	Number of genotypes (and total clones)		
	<i>P. fremontii</i>	<i>S. exigua</i>	<i>S. gooddingii</i>
Cibola	10 (150)	5 (338)	7 (119)
Palo Verde*	4 (100)	8 (292)	3 (37)
Verde	8 (139)	10 (416)	6 (112)
Gila	6 (70)	10 (410)	11 (209)

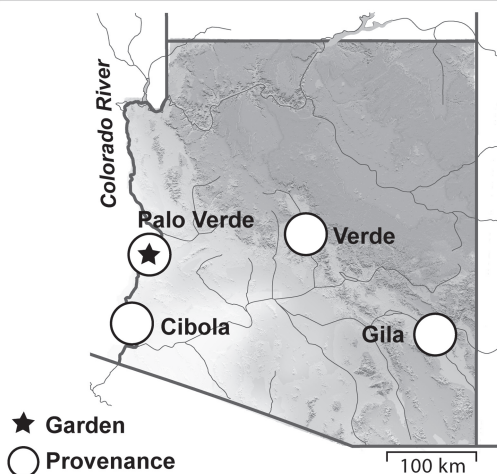


Figure 1. The number of genotypes and total number of replicated clones that were planted across sympatric and allopatric treatments for each of four provenances. The locations of each provenance collection site for sympatric treatments (white circles) are mapped for *Populus fremontii*, *Salix exigua* and *S. gooddingii*, and the location of the Palo Verde Ecological Reserve (PVER) common garden is indicated by a star. The map shading corresponds to elevations throughout Arizona; lighter colors are at lower elevation.

Methods

Site description and garden design

A 7-ha experimental common garden containing approximately 17 000 plants was established in March, 2007 at the Palo Verde Ecological Reserve (PVER), adjacent to the Colorado River, near Blythe, California (Fig. 1). The garden was flood irrigated with approximately 300 litres m⁻² (1 acre-foot) of water every two to three weeks in May through September and once every month from October through April. Soils at the garden were composed chiefly of coarse-loamy, mixed, superactive, calcareous, hyperthermic Typic Torrifluents (United States Dept of Agriculture, Natural Resources Conservation Service Soil Survey Geographic database for Arizona and California 2013: <<http://soildatamart.nrcs.usda.gov>>).

Our common garden consisted of propagated plantings from 15 *Populus fremontii*, 8 *Salix exigua*, and 14 *Salix gooddingii* populations (drawn from a total of 15 source locations separated spatially by at least ~100 km). Out of these source locations, we identified sites that included all three species and had enough healthy terminal shoots of *S. exigua* to allow propagation of > 500 vegetative cuttings to accommodate a higher proportion of *S. exigua* throughout the garden (see below). This resulted in a total of four source locations, or provenances (Fig. 1), for use in sympatric treatments. For each species, the growth rate averaged across the four provenances used in this study was similar to the mean growth rate averaged across all provenances, estimated in a prior study in this same garden using plants growing in

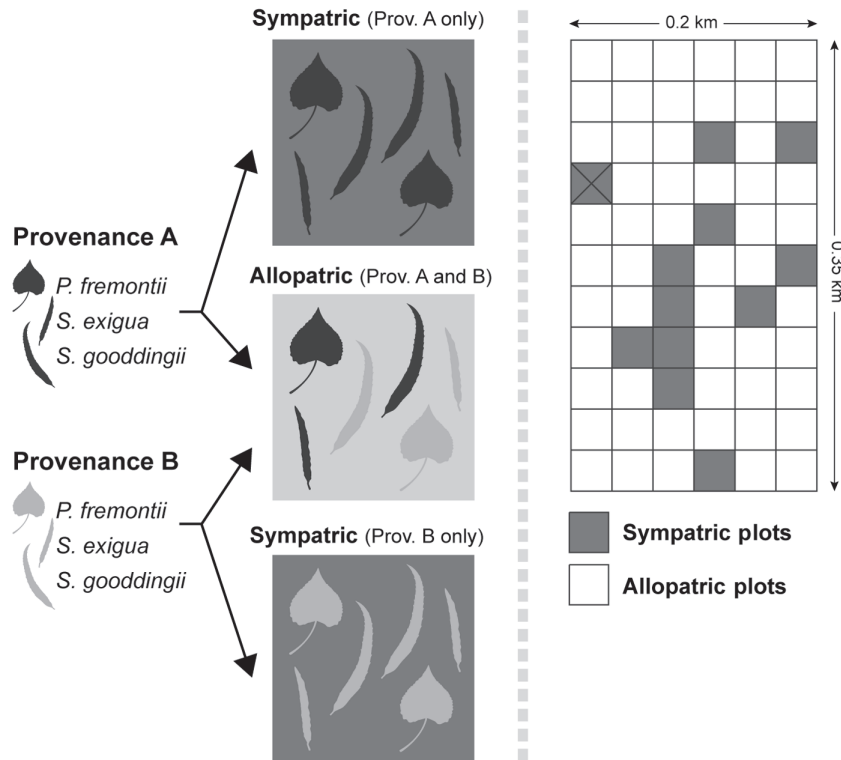


Figure 2. Experimental design showing: a general model for how sympatric and allopatric plots differed (A) and the overall treatment design of the common garden (B). For (A), we transplanted replicated genotypes of each species from four provenances into plots composed of sympatric neighbors (all genotypes from the same provenance) or allopatric neighbors (genotypes from 15 random provenances). Only two provenances are shown in this figure to reduce complexity. For (B), we created 12 sympatric plots (16 × 16 trees at 2 m spacing) and 54 allopatric plots across a 7-ha field. One of the sympatric plots was not used due to low survival of trees in the greenhouse (indicated by a X).

allopatric plots (Supplementary material Appendix 1 Fig. A1). The number of provenances used in a prior study by Grady et al. (2011) was slightly lower than the present study due to exclusion of provenances with low sample sizes (13 provenances of each of *P. fremontii* and *S. gooddingii*, and six provenances of *S. exigua*). According to Western Regional Climate Center weather stations within 10 km of collection sites, mean annual air temperature (MAT) across these provenances between 1971 and 2000 was: Cibola, 22°C; PVER, 22°C; Verde, 19.6°C, and; Gila, 17.7°C (Western Regional Climate Center 2014; <www.wrcc.dri.edu>). Individual 35 cm length cuttings were collected in December, 2007, re-cut to 20 cm in the greenhouse and grown in 655 ml root-trainers. In March, 2007, cuttings were transported from the greenhouse to PVER and planted at 2 × 2 m spacing. All cuttings were collected at randomly determined source locations from randomly selected trees within 10 m of the active flood channel of perennially flowing rivers in Arizona and California from the Colorado River watershed. Within a provenance, these collection source trees were at least 10 m distant from each other and up to a maximum of 1 km distant. Given that each provenance was at least 100 km distant from each other provenance, there were no genotypes shared among provenances.

Within the 7-ha garden, we randomly established 12 plots (16 rows × 16 columns; Fig. 2) containing 256 trees each that contained genotypes of each of three species from the same source location/provenance (sympatric plots). Across

the four source locations/provenances used in the sympatric treatment, a total of 88 genotypes across the three species were included (Fig. 1), with an average of 19 replicated genotypes in each sympatric plot. Each sympatric source location was replicated in three plots except the Verde site that was planted in only two separate plots (as a result of high mortality of *P. fremontii* cuttings in the greenhouse) resulting in a total of 11 sympatric plots.

The rest of the garden contained allopatric plots which consisted of 14 080 plants comprised of 300 genotypes (~100 per species) drawn from 15 source locations planted at random. The garden was subdivided into plots of 256 plants (16 rows × 16 columns) to simplify the planting logistics of this large-scale garden (Fig. 2) and to maintain mean species frequencies in each plot of 12.5 percent of total plants for *P. fremontii* and *S. gooddingii* and 75 percent for *S. exigua*. The percentage composition was chosen to reflect the relative abundance of these species in natural communities (Irvine and West 1979). These 256-plant plots were used for allopatric treatments with a mean of 48 genotypes per plot. Although the mean number of genotypes differed among allopatric (48) and sympatric (19) plots, the genetic diversity of the nearest neighbors for each plant in the garden (i.e. neighbor defined as the adjacent eight nearest plants within 3 m from target plant) was similar among sympatric and allopatric plots (average of 7.8 and 7.9 genotypes per focal plant, respectively) as we tried to constrain the genetic neighborhood to eight unique genotypes. Due to random

chance, the allopatric plots sometimes contained occurrences of a target plant being adjacent to a neighbor from the same source location. When this neighbor was a *P. fremontii* or *S. gooddingii* tree, the target plant was not used in statistical analyses. Due to the high proportion of *S. exigua* throughout the garden (75 percent for both sympatric and allopatric plots) and the low number of *S. exigua* provenances (i.e. eight) used in allopatric plots, it was not possible to exclude sympatric *S. exigua* neighbors from allopatric treatments during analyses of sympatric/allopatric treatments. The mean proportion of sympatric *S. exigua* neighbors out of the total of the eight nearest neighbors was less than five percent in allopatric treatments. Thus, performance benefits in sympatric plots compared to allopatric plots may have been underestimated due to the presence of a small proportion of sympatric associations in the allopatric plots.

Growth rates and survivorship

Growth rate was estimated from measurements on at least three replicates of each genotype in each sympatric/allopatric treatment (Fig. 1, Supplementary material Appendix 1 Table A1). This included measurements on every tree in the garden from the four provenances tested for sympatric effects and every shrub from the same provenances in 14 plots selected at random from the total number of plots immediately adjacent to sympatric plots. We used only 14 plots for shrubs as shrubs represented 75 percent of total plants and 14 plots provided adequate replication for allopatric *S. exigua* genotypes. The number of replicates per genotype and total number of genotypes per provenance varied because of differences in the availability of initial collection material from provenance origins, and mortality of plants both in the greenhouse and subsequent to transplanting. We measured diameter at breast height (DBH; 1.4 m height) between 2 and 27 May 2009, when trees were approximately 2.2 years old. We predicted aboveground biomass (wood and foliage) from DBH using previously published allometric equations for the same or closely related species (Grady et al. 2013). An index of aboveground net primary productivity (ANPP kg tree⁻¹ year⁻¹) was estimated using the following equation: ANPP = wood biomass/tree age + foliar biomass. For each tree used in our estimate of ANPP, we counted the number of neighbors of each species out of the eight nearest neighbors. Mean survivorship, the ratio of live trees to total planted trees, was determined for each genotype of each species in both sympatric and allopatric treatments. We excluded individual trees from survivorship analyses per the same rules for growth rate determination.

Genetic analyses

Genotype identification was based initially on spatial discreteness of genets and a minimum distance of 10 m between individuals and a maximum distance of 1 km between individuals at source collection sites. Genotype identification was confirmed for every genotype in the garden with genetic-based analyses using simple sequence repeat (SSR) markers. For each genotype, total genomic DNA was extracted from dried leaf material using DNeasy Plant Mini Kits, spectrophotometrically quantified, and standardized to 12.5 ng μl^{-1}

(NanoDrop ND-1000). After screening of various marker loci to insure repeatability, we selected and amplified 15 SSR loci from *P. fremontii* (Tuskan et al. 2004), 13 SSR loci from *S. gooddingii*, and 14 SSR loci from *S. exigua* (Barker et al. 2003). All loci were amplified using polymerase chain reaction (PCR) and standard touchdown protocols. The PCR products were resolved on an automated sequencer using GENESCAN-600 LIZ as an internal size standard. Genotypes were scored using GeneMapper ver. 4.0 software. For each of the three species, genetic differentiation among populations, and among individuals within populations was analyzed using an analysis of molecular variation (AMOVA; Excoffier et al. 1992) with 1000 permutations, as implemented in Arlequin 3.5 (Excoffier and Lischer 2010). For *P. fremontii*, AMOVA indicated significant variation among populations ($p < 0.0001$) but not among individuals within populations ($p = 0.988$). We found significant variation among populations of *S. exigua*, and among individuals within populations ($p < 0.0001$) which is consistent with populations composed of distinct genets. For *S. gooddingii*, we found significant variation among populations ($p < 0.0001$) but not among individuals within populations ($p = 0.1378$). Taken together, a high degree of genetic differentiation among populations confirms that our treatments are composed of genetically distinct groups. To determine among population differentiation, inter-site F_{ST} values were calculated for each pairwise comparison between all provenances used in both sympatric and allopatric treatments (Rousset 1997; Supplementary material Appendix 1 Table A2) with 1000 permutations of Mantel tests for significance, as implemented in GENEPOP ver. 4.0 (Raymond and Rousset 1995).

Statistical design

We evaluated differences in tree performance between the sympatric and allopatric plots. First, for each species separately, we compared ANPP between sympatric and allopatric treatments using a restricted maximum likelihood (REML) linear mixed model approach with genotype nested within provenance and the interaction between genotype and sympatric/allopatric treatment as a random effects and the following fixed effects: sympatric/allopatric treatment, provenance, and the interaction between provenance and the sympatric/allopatric treatment. The REML approach accounts for uneven sample sizes among treatments. Data were log-transformed when the residuals of the statistical model violated assumptions of normality or homogeneity of variance.

If an interaction between provenance and the sympatric/allopatric treatment was significant, we ran an ANOVA for each provenance separately to compare ANPP between sympatric and allopatric treatments, and we ran an ANOVA for each treatment separately to compare ANPP between provenances. For each species, to evaluate interactions between genotype (nested within provenance) and the sympatric/allopatric treatment, we compared the number of genotypes out of the total number of genotypes for each provenance ($n = 4$ provenances) that increased in growth in sympatry to those that did not increase in growth using a generalized linear model (GLM) for binary data (e.g. either a

positive or non-positive outcome). This approach allowed us to examine if the response to sympatry was driven by broad congruence among genotypes or by only a few genotypes responding strongly to sympatry.

We also used a GLM to compare survivorship between sympatric and allopatric treatments by comparing the total number of trees surviving to the total number of trees planted for each provenance ($n = 4$ provenances). For both GLM tests, we used a χ^2 test to evaluate the null hypothesis that patterns were random. If significance of the χ^2 test was less than 0.05, we rejected the null hypothesis and attributed patterns to treatment effects.

Last, we used analysis of covariance (ANCOVA) to assess if growth was impacted by the number of conspecific versus heterospecific neighbors (out of the eight nearest neighbors) for each species separately (e.g. model parameters included the number of neighbors of each species, the sympatric/allopatric treatment, and their interaction). The number of neighbors of *P. fremontii* and *S. gooddingii* was limited to a range of 0–3 due to few samples with more than three, and was limited to a range of 3–8 *S. exigua* neighbors due to limited samples with less than three. All analyses were performed using JMP 11.0 statistical software (SAS Inst.) using $\alpha = 0.05$ significance level.

Data deposition

Data available from the DataTurbine repository (Grady et al. 2016).

Results

With *Populus fremontii*, three lines of evidence support our hypothesis that productivity and survival are greater in sympatric than allopatric plots. First, aboveground net primary productivity (ANPP) of *P. fremontii* was 44 percent greater in sympatric than allopatric plots ($p < 0.0001$; Fig. 3A), and this difference was consistent across all four provenances, as shown by a non-significant provenance by treatment interaction ($p = 0.162$; Fig. 3A). Second, we found that a majority of *P. fremontii* genotypes (21 of 28; 75 percent) showed a positive growth response to sympatry (Fig. 4A; probability $> \chi^2 = 0.007$; Fig. 5A). Third, survival of genotypes was non-random (probability $> \chi^2 = 0.024$) with survivorship of 91 percent of total planted trees in sympatry compared to 84 percent in allopatry (Fig. 6A).

A similar, but more complex, pattern was observed for the shrub *Salix exigua*. First, ANPP was 15 percent higher in sympatric than allopatric plots ($p = 0.021$, Fig. 3B). A significant interaction between sympatric/allopatric treatment and provenance ($p < 0.0001$) indicated that the Gila River provenance benefited the most from sympatric associations (Fig. 3B). Second, while we found a significant interaction between sympatric/allopatric treatment and genotype ($p < 0.003$, Fig. 3B), reaction norms indicated that a significant majority (23 of 33; 70 percent) of *S. exigua* genotypes had higher ANPP in sympatry than allopatry (Fig. 4B; probability $> \chi^2 = 0.022$; Fig. 5B). The survivorship of *S. exigua* was higher in sympatric than allopatric treatments as indicated by a marginally statistically

significant rejection of the null hypothesis that survivorship was random ($\chi^2 = 0.057$; Fig. 6B).

Also supporting our hypothesis, we found that ANPP was 33 percent higher with sympatric than with allopatric neighbors for *Salix gooddingii* (Fig. 3C). We also found significant interactions between treatment and both provenance and genotype (Fig. 3C). Overall, a majority of genotypes (18 of 27; 67 percent) responded positively to sympatry (Fig. 4C; probability $> \chi^2 = 0.080$; Fig. 5C). Although this pattern was only marginally significant, the trend is consistent with results for the other two species. We did not detect a difference between sympatric and allopatric treatments in survivorship for *S. gooddingii* (Fig. 6D). Although the effect of the sympatric treatment on performance of *S. gooddingii* was less consistent than the other two species, the overall response was positive.

To investigate if performance benefits in sympatry were driven by conspecific or heterospecific interactions, we evaluated whether the number of conspecifics in the neighborhood impacted growth rate and if this impact differed among sympatric and allopatric treatments. We did not find an effect of the number of conspecific neighbors on growth rate (Fig. 7). However, we found a categorical neighbor effect related to growth form: as the total number of trees increased (and conversely, the proportion of the shrub, *S. exigua*, decreased), *P. fremontii* grew faster and *S. gooddingii* slower (Fig. 7). This result was significant in both sympatric and allopatric treatments suggesting that this pattern does not explain the observed study-wide advantage of sympatry. However, we suggest that this result should be interpreted cautiously as our experimental design did not include a well-balanced approach in which neighborhood species proportions were carefully controlled among species and provenances within species.

Discussion

Evidence for local biotic adaptation

Our results provide evidence to support our hypothesis that plant interactions can result in biotic adaptation of foundation woody species. We found that enhanced performance (growth and survival) in sympatric compared to allopatric treatments is broadly congruent across two tree and one shrub species, indicating that neighbor genotypic identity (sympatric or allopatric) was an important determinant of plant performance. We recognize that we cannot determine conclusively if this pattern is driven by heterospecific or conspecific interactions. However, using analysis of covariance, we did not find any evidence of variation between sympatric and allopatric treatments in the effect of the number of conspecific neighbors on growth rate (Fig. 7). We acknowledge that our study was not explicitly designed to test the influence of a particular species on growth of another species and we recommend such testing in the future to validate the importance of hetero- versus conspecific interactions in driving sympatric benefits. Further, given that all three species responded positively to sympatry, and that the vast majority of interactions were interspecific for *Populus fremontii* and *Salix gooddingii* (e.g. an average of

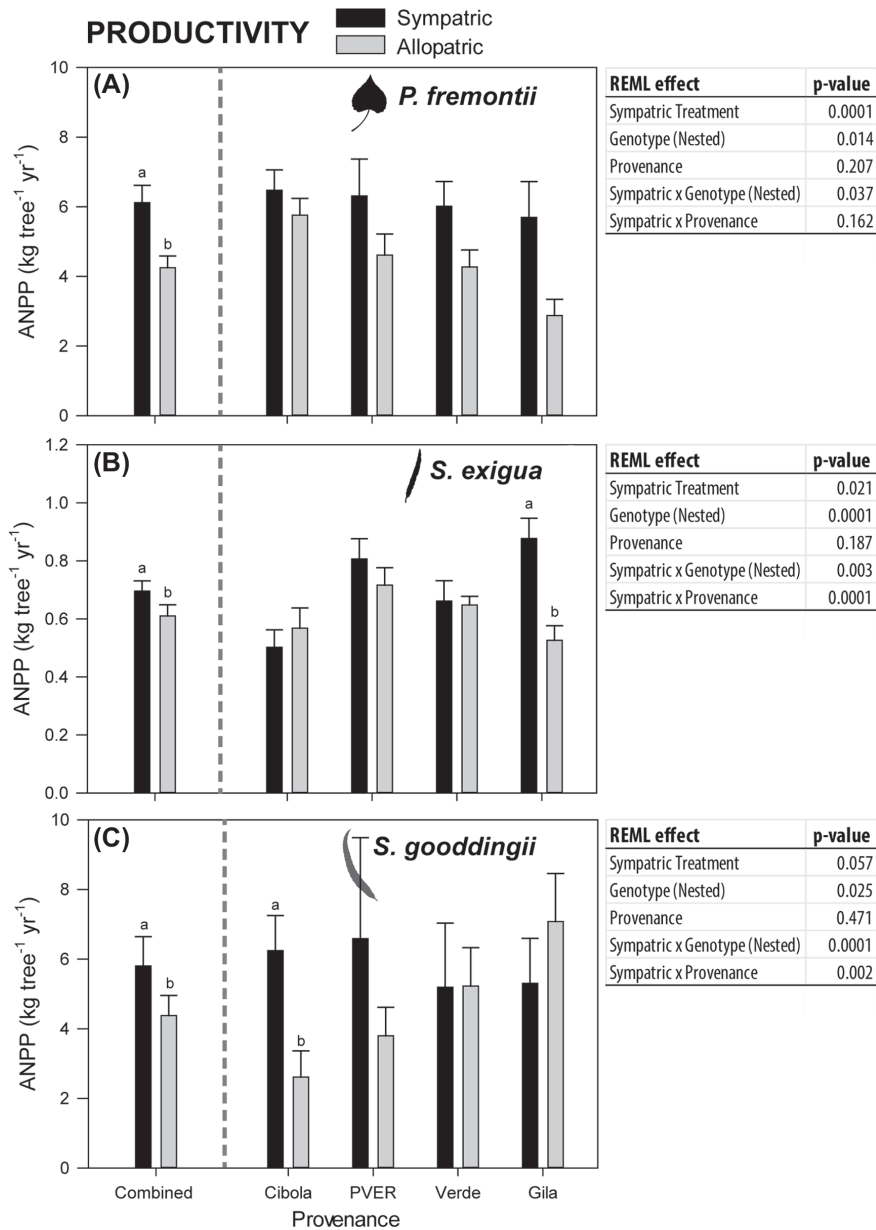


Figure 3. Mean annual aboveground net primary productivity (ANPP) of three species (*Populus fremontii* (A), *Salix exigua* (B), and *S. gooddingii* (C)) from four provenances compared between sympatric and allopatric treatments. For each species, we used a REML analysis with genotype nested in provenance (random effect), provenance, the sympatric/allopatric treatment, and their interactions as model parameters. If an interaction occurred, differences in ANPP between treatments were evaluated for each provenance separately using genotype means. Vertical lines denote one standard error of the mean.

1.1 and 1.0 conspecific neighbors versus 6.9 and 7.0 heterospecific neighbors, respectively out of the eight nearest neighbors), we suggest that it is likely that interspecific interactions played a role in the observed performance increases in sympatry compared to allopatry. Our finding of local biotic adaptation in riparian woody plant taxa builds upon prior studies of local biotic adaptation in experimental studies of herbaceous species (Turkington and Harper 1979, Martin and Harding 1981, Ehlers et al. 2016) thereby advancing fundamental principles of evolution in a community context across life forms.

Co-evolutionary theory predicts the potential for natural selection to act on strongly interacting species (Thompson

2005). Empirical evidence for biotic adaptation has been demonstrated across interacting species from different trophic groups (Erlach and Raven 1964, Thompson 2005) with only few studies evaluating how interacting species from the same trophic level, such as between different plant taxa, can impact evolution (Turkington and Harper 1979, Martin and Harding 1981, Ehlers et al. 2016). Results of these few prior studies have demonstrated potential for plant interactions to be under selection. For example, genotypes of clover *Trifolium repens* were collected from fields that varied in species composition and propagated in a greenhouse (Turkington and Harper 1979). These same genotypes were subsequently planted in both of the fields from which they

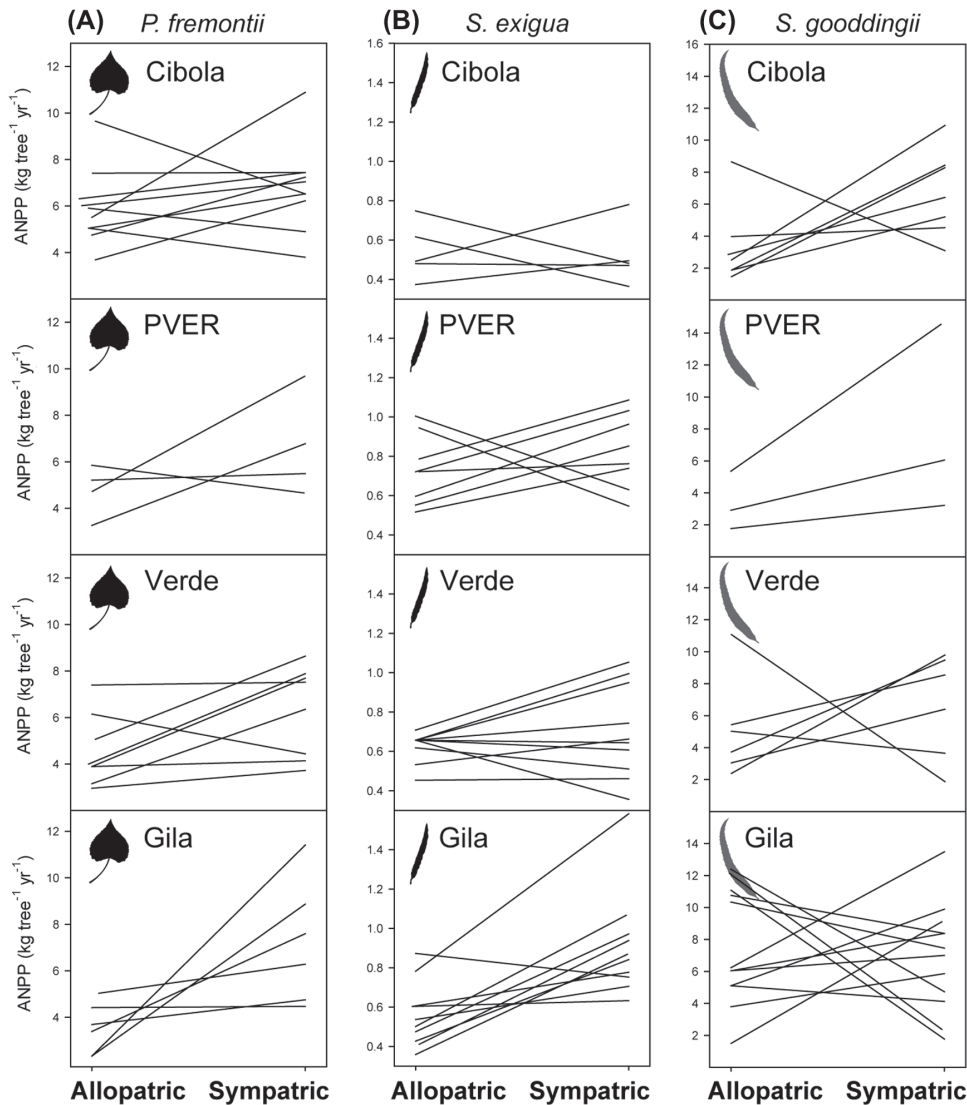


Figure 4. Reaction norms of annual aboveground net primary productivity (ANPP) between genotypes paired in sympatric and allopatric treatments of three species (*Populus fremontii* (A), *Salix exigua* (B) and *S. gooddingii* (C)) for each of four provenances (Cibola, PVER, Verde, and Gila) growing in a common garden. Each line corresponds to an individual genotype replicated clonally ($n = 3-16$). Error bars were omitted for clarity.

were collected and growth rates were highest when genotypes were planted back into their native site. The authors attributed this home-site advantage to co-adaptation among species. In a later study at the same location, investigators found that the home-site advantage of *T. repens* was influenced by the interaction of the bacterial endophytic *Rhizobium* sp. with a native grass, *Lolium perenne* (Chanway et al. 1989). When *Rhizobium* sp. was excluded from the community interaction the home-site advantage was not apparent. In our study, although we did not explicitly address the role of soil organisms, consistent benefits in sympatric treatments across both locally and non-locally derived genotypes suggests that our results were chiefly driven by direct ecological interactions among plants.

In another study, sympatric community plots composed of the annual forbs *Erodium obtusifolium* and *E. cicutarium* had higher reproductive rate (measured by seed yield) and equivalent mortality than allopatric communities

(Martin and Harding 1981). This increase in reproduction was attributed to adaptation of *E. cicutarium* in response to selection imposed by *E. obtusifolium*, and not co-adaptation, because most of the seed yield increase occurred in *E. cicutarium*. Other examples indicate that strongly asymmetric competition (i.e. competition between a strongly and a weakly competitive species) can select for more competitive genotypes of the weaker species (Vavrek 1998, Proffitt et al. 2005, Fridley et al. 2007, Rowe and Leger 2011). This response has been repeatedly demonstrated in experiments that include an invasive exotic competing with native species illustrating that rapid evolutionary change is possible when species interact (Vavrek 1998, Proffitt et al. 2005, Fridley et al. 2007, Lankau 2012). The majority of these past studies focus on contrasting performance between one species that occurs with (sympatric) or without (allopatric) one other species in common transplanted environments. Character displacement resulting

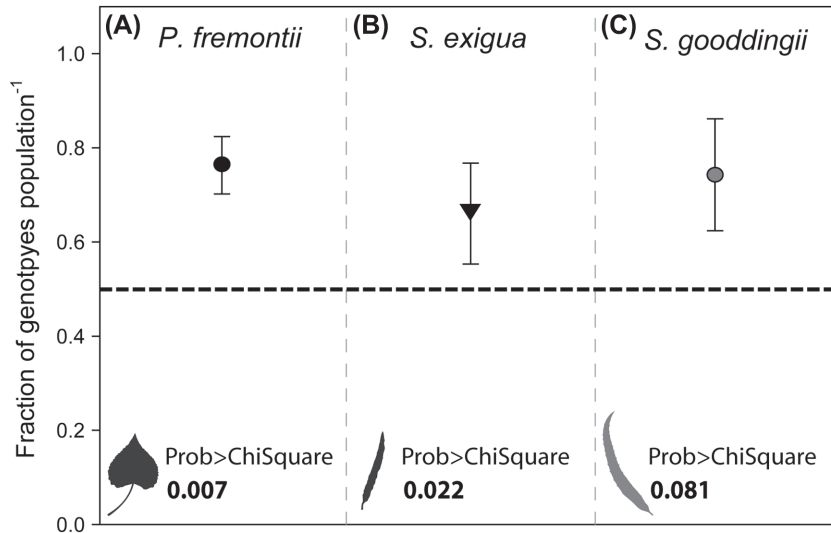


Figure 5. The mean fraction of genotypes out of total genotypes from four provenances ($n = 4$) that showed a positive response to sympatry for each of three species (*Populus fremontii* (A), *Salix exigua* (B) and *S. gooddingii* (C)). Vertical lines denote one standard error of the mean. The null hypothesis that results were random was tested using a generalized linear model with a χ^2 -test.

from asymmetric competition is the most frequently suggested mechanism of biotic adaptation (Martin and Harding 1981, Vavrek 1998, Proffitt et al. 2005, Fridley et al. 2007, Lankau 2012). Our experimental design builds on the sympatric/allopatric treatment used in prior studies but is unique in contrasting communities of three co-occurring woody species in sympatry and allopatry. Although, given our experimental design, we cannot determine if character displacement drives biotic adaptation, the consistency in sympatric benefits across provenances suggests that a similar, albeit unidentified, evolutionary mechanism is involved at all source locations.

Although competition has traditionally been considered the most important selective agent driving the evolution of plant interactions, recent work has demonstrated that facilitation among conspecific (Dudley and File 2007, Biedrzycki and Bais 2011) and heterospecific plants (Proffitt et al. 2005, Michalet et al. 2011) can also result in evolution. In addition, a growing body of research demonstrates that kinship recognition and facilitation among close relatives can lead to outcomes that differ from the traditional view (Dudley and File 2007, Biedrzycki and Bais 2011). Facilitative interactions can be mediated by chemical signaling among plants such as when related plants recognize roots or root

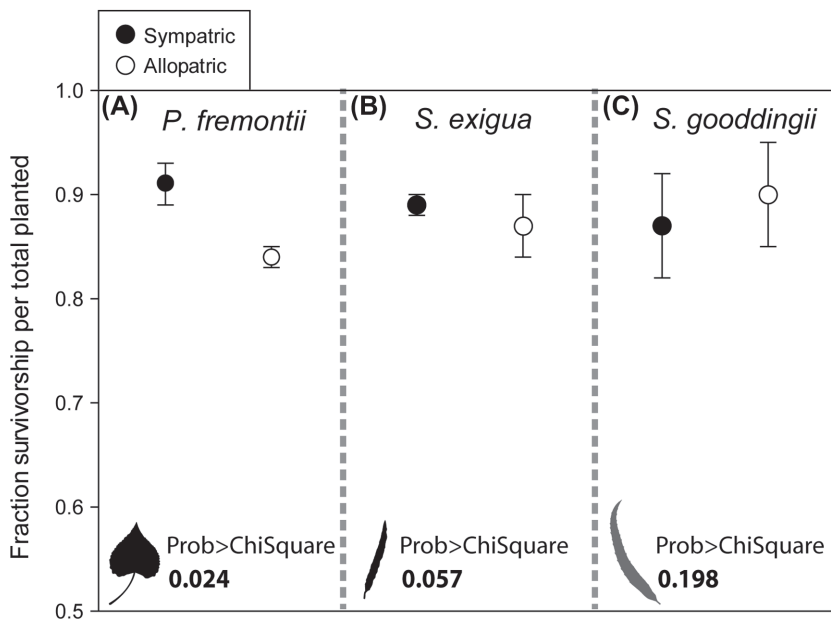


Figure 6. The mean fraction of genotypes surviving out of total genotypes planted from four provenances ($n = 4$) in both sympatric and allopatric treatments for each of three species (*Populus fremontii* (A), *Salix exigua* (B) and *S. gooddingii* (C)). Vertical lines denote one standard error of the mean. The null hypothesis that results were random was tested using a generalized linear model with a χ^2 -test.

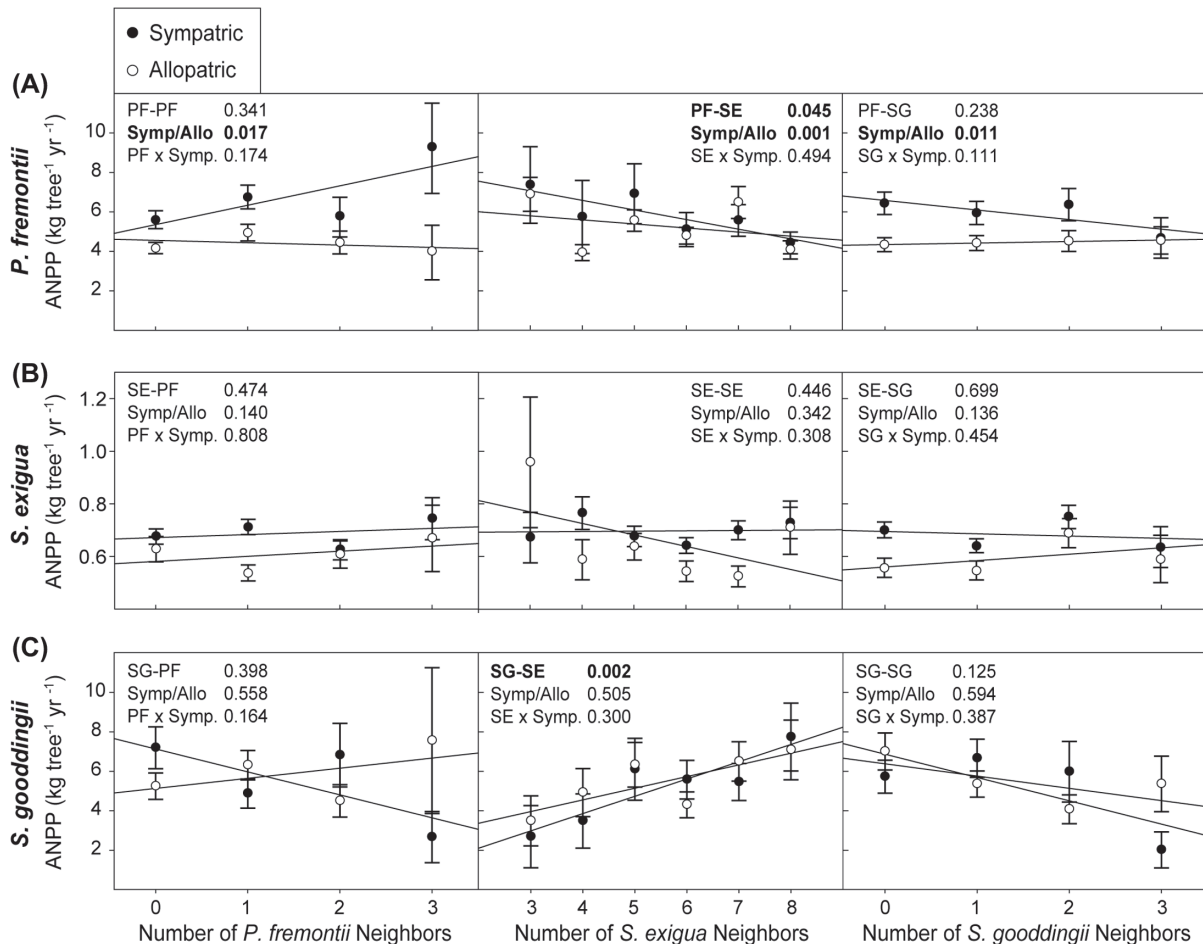


Figure 7. The effect of each plant's immediate neighborhood (eight nearest neighbors) on growth rate in both sympatric (black circles) and allopatric (white circles) treatments for *P. fremontii* (A), *S. exigua* (B), and *S. gooddingii* (C). For each species combination, we performed an analysis of covariance (ANCOVA) that included the following terms: number of each target neighbor species; the sympatric/allopatric treatment (Symp/Allo); and the interaction between the number of neighbors and the sympatric/allopatric treatment (Species \times Symp.). For instance, for *P. fremontii* (A) the number of *P. fremontii* (PF) neighbors is evaluated on the left panel (PF-PF), the number of *S. exigua* in the center (PF-SE), and the number of *S. gooddingii* on the right (PF-SG). Vertical lines denote one standard error of the mean.

exudates of their kin and reduce root growth or alter their morphology (Mahall and Callaway 1996, Dudley and File 2007, Biedrzycki and Bais 2011). Other examples include when native plant roots produce chemical compounds in response to invasion that promote native plant growth (Callaway et al. 2005, Weir et al. 2006) or when herbivores elicit volatile production in leaves that stimulates production of defensive secondary metabolites in genetically-related neighboring plants (Karban and Shiojiri 2010). In our study, we could not differentiate whether observed performance advantages in sympatry over allopatry were due to reduced competition or facilitation. However, faster growth of all three species in sympatry in our common garden should increase opportunities for competition, suggesting that facilitative mechanisms are most likely and should be further explored. Growing evidence for local biotic adaptation of plant species (Ehlers et al. 2016), together with empirical and theoretical studies demonstrating potential for the evolution of plant facilitation (Bertness and Callaway 1994, Brooker et al. 2008, Vellend 2008) indicates a need to examine the relative importance of facilitation and competition in plant community dynamics and evolution.

Alternative hypotheses

The consistent effect of the sympatric treatment across genotypes and provenances allows us to rule out the alternative hypothesis that local adaptation was driven by other selection pressures such as local adaptation to temperature (Grady et al. 2011, 2013, 2015). However, if adaptation was in response to an abiotic factor, we would have expected the impact of sympatry to be apparent in plants locally adapted to the abiotic conditions of the garden site. However, the positive effects of sympatry on plant performance were observed across multiple provenances (Fig. 3) and from multiple genotypes from each provenance (Fig. 4, 5). The consistency of increased ANPP in sympatric treatments, especially for *P. fremontii*, supports the inference that high productivity in sympatric plots is influenced by local *biotic* adaptation. For the shrub, *S. exigua*, we did not find evidence of local abiotic adaptation to temperature using this same garden site (Grady et al. 2011); the moderate growth and survival advantages in sympatry are not likely influenced by temperature variation among provenances. We acknowledge the potential for abiotic and biotic factors to simultaneously drive local

adaptation. For instance, adaptation of one species to the abiotic environment may, in turn, impact that species facilitative or competitive relationship with another species. Such multi-factor adaptation could account for a pattern of convergent biotic evolution across provenances.

Because previous studies of *P. fremontii* and *S. gooddingii* have demonstrated that provenances with climates more similar to common garden sites have higher growth rates than those from less similar climates (Grady et al. 2011, 2013), it is important to consider if the probability of more frequently encountering a faster growing, more locally adapted neighbor genotype in allopatry is itself able to explain increased growth in sympatry. While we cannot completely rule out the contribution of such an effect here, consistent, positive responses among multiple provenances and genotypes to sympatry indicate that sympatric performance is not wholly contingent on abiotic adaptation (Fig. 3, 4, 5). Further, the mean growth rates of the four provenances used in this study were similar to the mean growth rate averaged across all provenances for each species (Supplementary material Appendix 1 Fig. A1), suggesting equal opportunities for competition in allopatric treatments. For a competitive bias to drive variation in performance between sympatry and allopatry, we would first need to show evidence of competition. If we assume that a high proportion of fast-growing trees (*P. fremontii* and *S. gooddingii*) relative to slower growing shrub (*S. exigua*) represents a highly competitive environment, we would expect to find slower growth of all species as the proportion of trees increases. We found that as tree number increased (and conversely, shrub number decreased), *P. fremontii* grew faster, *S. gooddingii* slower, and *S. exigua* was not impacted (Fig. 7). However, the impact of increasing number of neighboring trees had a similar impact across species in both sympatry and allopatry as indicated by similar slopes (i.e. lack of significant interaction; Fig. 7).

Systematic differences in genetic diversity across the treatment groups, rather than genotype origin, may also account for our findings, but the effect would be expected to be opposite of what we observed (Crutsinger et al. 2006, Hughes and Stachowicz 2011). Indeed, an artifact of our experimental design was a higher total genotypic diversity, measured by numbers of genotypes, in allopatric plots (mean of 48 genotypes per plot) relative to sympatric plots (mean of 19 genotypes per plot). However, we suggest that the strongest interactions occurred between the eight nearest neighbors (which were within 3 m) of the focal tree and genotypic diversity of these eight neighbors was similar in both sympatry and allopatry. Other studies with *Solidago altissima* and *Zostera marina* have shown that genotypic diversity is positively correlated to growth rates (Crutsinger et al. 2006, Hughes and Stachowicz 2011) which could have reduced the direct positive effect of sympatry on growth rate in our study. Given this potential bias, we may have underestimated the effect of sympatry on productivity, and our results are likely conservative.

Conclusions

Although the benefits of sympatry were observed in just the first few years following establishment of long-lived species, the rapid growth rate of these species in this environment

had already resulted in canopy closure, a characteristic state of a maturing forest stand (Oliver and Larson 1996). Rapidly growing and interacting plants compete for resources that limit growth, survival, and reproduction, and consequently, there is potential for natural selection to occur as a result of plant interactions. We tested the hypothesis that plant species are locally adapted to each other and that individuals genotypes grown with plant neighbor genotypes from their native site would grow faster and have higher survival than those grown with neighboring genotypes collected from foreign sites. Our results provide broad support for the hypothesis that foundational woody plants can adapt to one another in nature, and that this adaptation enhances growth rate.

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Supplementary material (available online as Appendix oik-3240 at <www.oikosjournal.org/appendix/oik-03240>). Appendix 1.