

PLANT GENETIC DETERMINANTS OF ARTHROPOD COMMUNITY STRUCTURE AND DIVERSITY

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Abstract.—To test the hypothesis that genes have extended phenotypes on the community, we quantified how genetic differences among cottonwoods affect the diversity, abundance, and composition of the dependent arthropod community. Over two years, five major patterns were observed in both field and common-garden studies that focused on two species of cottonwoods and their naturally occurring F₁ and backcross hybrids (collectively referred to as four different cross types). We did not find overall significant differences in arthropod species richness or abundance among cottonwood cross types. We found significant differences in arthropod community composition among all cross types except backcross and narrowleaf cottonwoods. Thus, even though we found similar richness among cross types, the species that composed the community were significantly different. Using vector analysis, we found that the shift in arthropod community composition was correlated with percent Fremont alleles in the host plant, which suggests that the arthropod community responds to the underlying genetic differences among trees. We found 13 arthropod species representing different trophic levels that were significant indicators of the four different cross types. Even though arthropod communities changed in species composition from one year to the next, the overall patterns of community differences remained remarkably stable, suggesting that the genetic differences among cross types exert a strong organizing influence on the arthropod community. Together, these results support the extended phenotype concept. Few studies have observationally and experimentally shown that entire arthropod communities can be structured by genetic differences in their host plants. These findings contribute to the developing field of community genetics and suggest a strategy for conserving arthropod diversity by promoting genetic diversity in their host plants.

Key words.—Community genetics, composition, extended phenotype, hybrid, *Populus*.

Received January 13, 2004. Accepted October 27, 2004.

A major issue in the developing field of community genetics (Agrawal 2003; Antonovics 2003; Cavender-Bares and Wilczek 2003; Chase and Knight 2003; Collins 2003; Morin 2003; Neuhauser et al. 2003; Ricklefs 2003; Wade 2003; Whitham et al. 2003; Wilson and Swenson 2003) is the extent to which genes, especially those expressed in dominant and keystone species, have extended phenotypes (sensu Dawkins 1982) that are expressed at levels higher than the individual or population (Whitham et al. 2003). Thus, if different genes and/or alleles have extended phenotypes at the community level, two major predictions can be made. First, different genotypes of a dominant plant should support different species. Second, as genetic diversity in a dominant plant rises, so should the diversity of the associated community. If these two predictions can be demonstrated in diverse systems, it then becomes important to understand whether or not these extended phenotypes have a heritable basis. We tested the first prediction using a dominant host plant and its arthropod community. Arthropod communities are especially well suited for such studies because they account for approximately 70% of the world's species diversity (Groombridge 1992) and have numerous functional roles in communities. In studies that examined the association between host plants and

arthropod herbivores, increased plant species diversity led to increased herbivore diversity (Southwood 1961; Murdoch et al. 1972; Tscharrntke and Greiler 1995; Panzer and Schwartz 1998; Siemann et al. 1998). Similarly, at a finer scale, genetic variation among different plant clones of the same species (Fritz and Price 1988; Maddox and Root 1990), or within a hybrid swarm (Boecklen and Spellenberg 1990; Fritz et al. 1994; Floate and Whitham 1995; Dungey et al. 2000) affected the arthropod community by presenting herbivores with novel genotypes and different levels of chemical compounds than the parental species (Orians 2000). If genetic differences among plant species, within plant species, or within a hybridizing complex affect the dependent herbivore community, then these effects could “cascade up” (Hunter and Price 1992) to affect higher trophic levels. Genetic variation among different host-plant species (Pimentel 1961; Greenstone 1984), hybrid and pure parental types (Preszler and Boecklen 1994; Fritz 1995; Eisenbach 1996; Wimp and Whitham 2001), and different plant clones (Price and Clancy 1986; Clancy and Price 1987; Stiling and Rossi 1996; Hare 2002) have all been shown to affect higher trophic levels such as parasites, predators, and mutualisms.

Plant hybrid zones represent some of the most genetically diverse interbreeding systems, and thus present an excellent test of the effects of host plant genetic diversity on the arthropod community. Hybridization can result in novel host

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plant traits (Rieseberg and Ellstrand 1993) and high levels of genetic variation within the hybrid zone (Whitham et al. 1999). Previous studies have found animal population and even community responses to hybridization. This is likely because traits for host resistance and host recognition in hybrids can be quite different from the pure parental species (Fritz et al. 2003). For example, population studies of the bud gall mite (*Aceria parapopuli*) showed that mite densities were 800 times greater on F_1 type hybrids compared to pure parental species and backcross hybrids (McIntyre and Whitham 2003). In addition to arthropod species, vertebrate species such as birds respond to plant hybridization; Martinsen and Whitham (1994) found that bird nesting was twice as frequent in F_1 type hybrids compared to other tree types. Similarly, at the community level, Dungey et al. (2000) found that arthropod herbivore species richness was greater on eucalypt hybrids, and hybrids supported a compositionally distinct herbivore community.

Few studies have used plants growing in both common gardens and in the wild to quantify how the genetic differences among plants in a population might structure the arthropod community (but see Dungey et al. 2000). Our study is also the first to examine a large arthropod community that spans multiple trophic levels and feeding groups (161 species in 16 orders and 7 families). To examine how the genetic differences among trees in the plant population affected the composition of the arthropod community, we censused the arthropod community in the wild and in a common garden where the four tree cross types grew adjacent to one another (*Populus fremontii*, Fremont cottonwood; *P. angustifolia*, narrowleaf cottonwood; and their naturally occurring F_1 and backcross hybrids). We addressed four major questions: (1) Do studies of arthropod communities found on cottonwoods raised in common gardens support the findings of studies in the wild? (2) Do genetic differences among cottonwood cross types affect the abundance, diversity, and composition of their arthropod community? (3) Is the level of introgression of Fremont alleles into the narrowleaf genome associated with the changes in the arthropod community? (4) Are differences in community composition among cross types mirrored by indicator species that characterize each cottonwood cross type? Therefore, in addition to community-wide patterns in arthropod composition, do we also find individual species responses to the different cottonwood cross types? Support of these questions argues that there is a genetic component to community structure, which in turn has important evolutionary and conservation implications.

METHODS

Field Site Description and Data Collection

To address the relationship between host-plant genetics and arthropod communities, we re-analyzed the raw data of Floate and Whitham (1995) from the wild and then compared it to studies in a common garden. A complete description of arthropod collection methods is described in Floate and Whitham (1995). Hybridization in this system is unidirectional: Fremont and narrowleaf breed to form F_1 hybrids, F_1 hybrids can only breed with narrowleaf cottonwoods to form backcross hybrids, and backcross hybrids can only breed with

narrowleaf cottonwoods to form advanced generation backcrosses. At the time of the study, genetic data were not available to discriminate among backcross hybrids and narrowleaf cottonwoods and they are morphologically indistinguishable. Field studies therefore included three cross type categories: Fremont, F_1 hybrid, and a combined backcross/narrowleaf category. Within the hybrid zone where the study was conducted, trees were composed primarily of Fremont cottonwoods (51%), followed by F_1 hybrids (26%) and backcross/narrowleaf cottonwoods (23%; G. M. Wimp, unpubl. data). In the hybrid zone, genetic diversity, as measured by genetic distance, is also nearly three times greater than that found in the two pure parental zones (Whitham et al. 1999).

Common-Garden Description and Data Collection

To eliminate or reduce site effects found in the wild by Floate and Whitham (1995), we used a common garden planted in 1991. The common garden is 0.84 ha in size, and is composed of 9.6% Fremont, 18.4% F_1 hybrid, 54.4% backcross hybrid, and 17.6% narrowleaf cottonwoods. The backcross hybrids found in the garden represent the full range of backcrosses in nature; they range from trees that are genetically similar to their F_1 parents to trees that are genetically similar to their narrowleaf parents. Trees in the common garden were propagated from cuttings of trees of known genotype growing in the wild. At the time of our experiments, the trees were about 10 years old, about 10 m tall, reproductive, and represented four different cross types growing naturally along the Weber River (i.e., Fremont, F_1 hybrid, backcross hybrid, and narrowleaf cottonwoods). Pure or hybrid status of trees in the common garden was verified using restriction fragment length polymorphism analysis (Keim et al. 1989; Martinsen et al. 2001). Martinsen et al. (2001) studied 550 trees found throughout the Weber River drainage, and clones of many of these trees were represented in the common garden. Martinsen et al. (2001) used species-specific probe-restriction enzyme combinations to screen these 550 trees, and markers that demonstrated fixed polymorphisms between Fremont and narrowleaf cottonwood were used to study introgression. Although these data were used to determine the rate of introgression of different Fremont markers into the narrowleaf genome, we used the same data to make determinations about the cross type status of trees in the common garden. We conducted common-garden surveys for two years, and data were collected in a similar manner for both years. However, there was a difference in the backcross hybrids chosen in the different years. In 2000, backcross hybrids were chosen to represent a percentage of Fremont markers that was intermediate between narrowleaf and F_1 hybrids (0.088–0.37% Fremont alleles), and in 2001, backcross hybrids were chosen to represent the most common class of backcrosses found along the Weber River (0.057–0.088% Fremont alleles). Trees were blocked for age, sex, and position within the common garden to further reduce potential within-garden site effects. We examined arthropod communities by visually censusing arthropod species richness and abundance on 200 shoots from 10 trees in each of the four cross-type categories, and trees within a block were censused at approximately the same time. Visual arthropod

censuses were performed so that we could resample the same trees multiple times during the course of the growing season. Based on previous species accumulation curves, we censused 200 shoots on a tree for a minimum of 20 min, but we spent as much time as was necessary to census all species and individuals found on those 200 shoots. Arthropods were classified to species or morphospecies based on previous observations of life cycle, mating individuals, and large morphological differences among individuals within a genus or family. All individuals that had been observed to participate in the cottonwood arthropod community were recorded. We observed 118 species in 2000 and 110 species in 2001, for a total of 161 species (see Appendix available online only at <http://dx.doi.org/10-1554/04-018.1.s1>). Trees were sampled three times in 2000 and two times in 2001 during the course of the cottonwood growing season.

Statistical Analyses

Arthropod species richness and abundance.—Throughout the paper, when transformed data did not meet normality assumptions, we used the appropriate nonparametric test. Field species richness and square-root transformed arthropod abundance data were analyzed using a Kruskal-Wallis test. In 2000, common-garden species richness and double square-root transformed arthropod abundance data were analyzed using a two-way ANOVA to account for both treatment and blocking effects. In 2001, both species richness and arthropod abundance data from the common garden were analyzed using a Friedman test (Conover 1980).

Arthropod community composition.—Arthropod community composition data in both field and common-garden studies were analyzed using nonmetric multidimensional scaling (NMDS), which is a robust ordination technique for community analysis (Kruskal 1964; Minchin 1987; Clarke 1993). This technique has been used to analyze differences in community composition for both animals (Duney et al. 2000) and plants (Foster and Tilman 2000) and was chosen for its ability to handle some of the issues commonly faced with community data. It does not make any assumptions about the nature of the data; species therefore need not have normal distributions across an environmental gradient, and it can accommodate narrow and skewed distributions (Minchin 1987). Importantly, NMDS is more robust than other ordination procedures for handling data where beta diversity is high (Fasham 1977), but can still efficiently handle data where beta diversity is low (Minchin 1987). This point is critical in the cottonwood system, where beta diversity can be quite large. Analyses from previous studies (Wimp et al. 2001) show that local species turnover rates can be as high as 80% among trees of the same cross type (G. M. Wimp, unpubl. data). Nonmetric multidimensional scaling was used to create a dissimilarity matrix among the different pure species and hybrid types using the Bray-Curtis dissimilarity coefficient (Faith et al. 1987). Using stress levels obtained by fitting the dissimilarities to distance, we chose a two-dimensional solution as the best representation of the dissimilarities among tree types. Significant differences in community composition among tree types were obtained using ANOSIM (analysis of similarity), which uses 1000 random reassign-

ments of species to groups and determines whether the generated dissimilarity matrix is significantly different than chance (Warwick et al. 1990). Multiple comparisons in ANOSIM were made using a sequential Bonferroni correction (Rice 1989). Additionally, for common-garden data, we fit a vector to the ordination that represented percent Fremont alleles for each host plant. Vector analysis determined the maximum correlation between percent Fremont alleles in the host plant and the configuration of points (i.e., the arthropod community on individual trees) in the ordination. Significance was determined using 1000 random permutations of the data to determine whether the observed vector fit was significantly different than that due to chance alone (Minchin 1987; Faith and Norris 1989).

Indicator species analysis.—We also performed indicator species analysis (Dufrene and Legendre 1997) to determine whether individual arthropod species were indicators of the different cross types. This analysis is based upon the fidelity of arthropods to a particular cross type as well as their abundance on that cross type. Indicator species analysis was possible for both years of common-garden data because molecular markers allowed us to discriminate among the different cross types.

RESULTS

Arthropod Species Richness and Abundance

In re-analyzing the field arthropod data of Floate and Whitham (1995), we did not find a significant difference in species richness among cross types (see Table 1). However, we did find a significant difference in arthropod abundance among cross types (see Table 1), but this pattern was driven by a single species, the galling aphid *Pemphigus betae*. When *Pemphigus betae* was removed from the analysis, our differences in arthropod abundance among the cross types were no longer significant (see Table 1). In agreement with our findings in the wild, for the 2000 common-garden data, we did not find a significant difference in arthropod species richness or abundance among cross types (see Table 1). However, for the 2001 data, we found a significant difference in arthropod species richness (see Table 1). Using Tukey's honestly significant difference on ranks (Conover and Iman 1981), we found that species richness was significantly greater on F₁ hybrids compared to pure narrowleaf cottonwoods, but was not significantly greater than either backcross hybrids or pure Fremont cottonwoods. We did not find a significant difference in arthropod abundance among cross types in the common garden for 2001 (see Table 1).

Arthropod Community Composition

We found significant differences in arthropod community composition in the field (ANOSIM $R = 0.2951$, $n = 45$, $P < 0.0001$, see Fig. 1), with communities on all three cross types significantly different from one another. Therefore, although mean species richness and abundance were similar, the actual species that composed the arthropod community were different among cross types. For both years of common-garden data, we found that arthropod community composition was significantly different among cross types (2000: ANO-

TABLE 1. Means \pm 1 SE for the arthropod species richness and abundance on the different cross types (pure Fremont, F₁ hybrid, backcross hybrid, and pure narrowleaf cottonwoods) and results of Kruskal-Wallis, analysis of variance, and Friedman tests. Different letters indicate significant differences among cross types.

	Wild	Common garden 2000	Common garden 2001
Species richness			
Fremont	17.8 \pm 1.4967	17.9 \pm 0.948	18.3 \pm 3.07 AB
F ₁ hybrid	18 \pm 1.2536	16.5 \pm 2.034	21.6 \pm 1.61 A
Backcross hybrid	19.2667 \pm 1.2927	20.3 \pm 2.006	16 \pm 2.04 AB
Narrowleaf		23.1 \pm 1.696	13.7 \pm 1.31 B
Significance	$\chi^2 = 1.373$ $n = 45$ $P = 0.503$	Treatment F = 1.822 $n = 10$ $P = 0.171$ Block F = 2.678 $N = 10$ $P = 0.023$	$\chi^2 = 10.237$ $n = 10$ $P = 0.017$
Arthropod abundance			
Fremont	26.6087 \pm 3.4828	90.1 \pm 15.992	98.9 \pm 21.2
F ₁ hybrid	21.9573 \pm 3.7901	66.1 \pm 19.599	101.5 \pm 14.82
Backcross hybrid	87.9287 \pm 35.9862	84.6 \pm 17.424	67.2 \pm 9.84
Narrowleaf		98.3 \pm 27.66	60.1 \pm 4.86
Significance	$\chi^2 = 12.386$ $n = 45$ $P = 0.002$	Treatment F = 0.554 $n = 10$ $P = 0.65$	$\chi^2 = 6.276$ $n = 10$ $P = 0.099$
	<i>Pemphigus betae</i> removed	Block F = 1.583 $N = 10$ $P = 0.171$	

SIM $R = 0.2164$, $P < 0.0001$, see Fig. 2A, 2001: ANOSIM $R = 0.1745$, $P < 0.0001$, see Fig. 2B), with communities on all cross types significantly different from one another, except for backcross hybrid and narrowleaf cottonwoods. When we used vector analysis to examine the relationship between percent Fremont alleles in the host plant and the NMDS configuration, we found a significant correlation in both years

of study (2000: MaxR = 0.6410, $P < 0.001$, see Fig. 2A; 2001: MaxR = 0.4034, $P = 0.029$, see Fig. 2B).

When we combined all years of field and common-garden data (such that we incorporated spatial differences among field and common-garden sites as well as temporal differences among different years of study), we found that the same patterns held. We found a significant overall difference in arthropod community composition among cross types (ANOSIM $R = 0.093$, $P < 0.0001$). We found that Fremonts were significantly different from F₁ and backcross hybrids, but no other cross type comparisons were significant. When we looked strictly at patterns between years in the common garden, we found a significant difference in arthropod community composition among cottonwood cross types (ANOSIM $R = 0.1704$, $P < 0.0001$), with all cross types significantly different from one another except for backcross and narrowleaf cottonwoods.

That these patterns still hold is surprising due to the large amount of species turnover from year to year and from the field to the common garden. Within a cross type, we found a significant difference in arthropod community composition among different years of study, which included one year of field data and two separate years of common-garden data (Fremont: ANOSIM $R = 0.6279$, $P < 0.0001$; F₁ hybrid: ANOSIM $R = 0.6868$, $P < 0.0001$; backcross hybrid: ANOSIM $R = 0.7326$, $P < 0.0001$; narrowleaf, no field analog: ANOSIM $R = 0.5338$, $P < 0.0001$). This indicates that differences in arthropod community composition among cross types were robust to changes in species composition through space and time.

Arthropod Indicators of Cottonwood Cross Types

We found 13 arthropod species that were significant indicators of the different cross types (see Table 2). There were

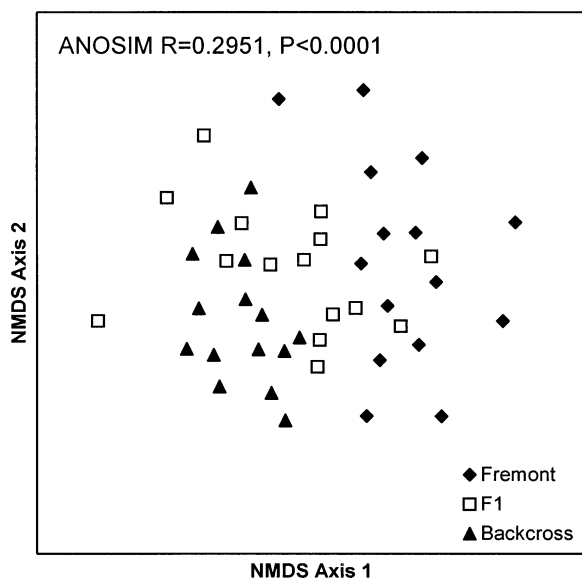


FIG. 1. Two-dimensional representation of the arthropod community found on 45 trees (15 in each of the following categories: Fremont, F₁ hybrid, and backcross hybrid) based on global, non-metric multidimensional scaling (NMDS). In the wild, arthropod community composition was significantly different among different cottonwood cross types. Compositional dissimilarity was based on the presence or absence of 82 species of arthropods.

significant indicator species for all four cross types. Arthropods that modified cottonwood leaves or stems constituted a majority of the indicator species and were significant indicators for both years of study. Although we did not find an overall community-wide difference in arthropods between backcross hybrid and narrowleaf cottonwoods, individual arthropod species distinguished between these cross types.

DISCUSSION

Effect of Plant Genetics on Arthropod Community Composition

Three lines of evidence argue that genetic differences among cross types affect arthropod community structure. First, in two years of common-garden studies, all cross types were significantly different from one another in arthropod community composition, with the exception of backcross and narrowleaf cottonwoods. Importantly, our results in the common garden agreed with findings in the wild and largely eliminated environmental or site effects. We predicted that different cross types would support communities that were compositionally different and our results supported this hypothesis. Furthermore, we found robust support for the compositional differences in the arthropod community among cross types. Even when we analyzed data from different years and in both field and common-garden studies, we found the same significant differences in arthropod community composition among cross types. Thus, in spite of changes in the arthropod community from one year to the next, which has been observed in many systems, these findings argue that the genetic differences among cross types exert a strong organizing influence on the arthropod community. Due to these consistent differences, we would therefore expect overall arthropod diversity to be greatest where Fremont, F₁ hybrid, and backcross hybrid/narrowleaf cottonwoods occur in combination. These findings agree with those of Dungey et al. (2000), who found that arthropod herbivore communities on hybrid and pure parental species of eucalypts were all significantly different from one another in composition. Similarly, Fritz et al. (1994) found that interspecific hybridization led to differences in insect herbivore community structure among hybrids and their parents.

Second, vector analyses suggested even finer levels of discrimination at the individual plant level. Vector analysis showed that there was a significant correlation between percent Fremont alleles in the host plant and the NMDS configuration. From an evolutionary standpoint, this suggests that the shift in arthropod community composition among cross types coincides with patterns of Fremont introgression into the narrowleaf cottonwood genome. Our study did not elucidate the specific genetic mechanisms responsible for a change in community composition. However, previous work in a hybridizing willow system by Fritz et al. (2003) has shown host plant susceptibility to herbivores to be the result of additive, dominant, and epistatic genetic effects. Genetic changes in hybrids affected their resistance or susceptibility to herbivores, as well the herbivore's ability to recognize hybrids as hosts (Fritz et al. 2003).

Third, indicator species analysis demonstrated that individual species from different trophic levels and feeding

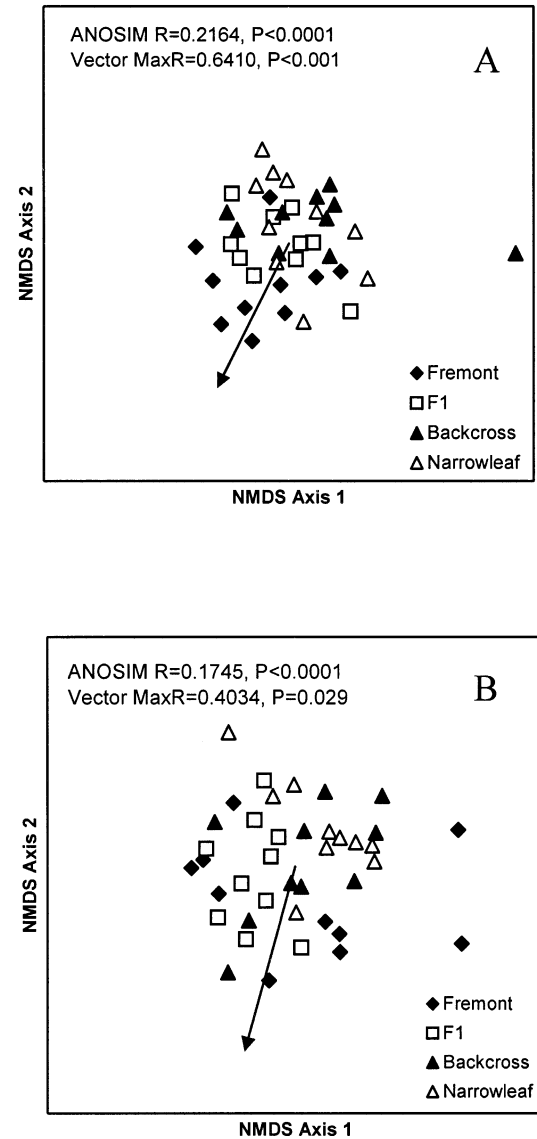


FIG. 2. Two-dimensional representations of the arthropod community found on 40 trees for each year (10 in each of the following categories: pure Fremont, F₁ hybrid, backcross hybrid, and pure narrowleaf) based on global, nonmetric multidimensional scaling (NMDS). For both the 2000 (A) and 2001 (B) common-garden experiments, arthropod community composition was significantly different among all cross types except backcross hybrids and narrowleaf cottonwoods. Compositional dissimilarity was based on the presence or absence of 118 species of arthropods in 2000 and 110 species in 2001. Vector analyses indicated that differences in arthropod community composition were correlated with percent Fremont alleles in the host plant.

groups discriminated among individual cross types, including complex backcrosses and pure narrowleaf cottonwoods. That some arthropods discriminated between these latter two categories was particularly impressive because morphology is not sufficient and molecular techniques are required to distinguish between these two cross types. Indicator species analysis (Dufrene and Legendre 1997) has previously been used to characterize habitats; in this study we found that individual arthropod species could be used to distinguish

TABLE 2. Significant indicator species (Dufrene and Legendre 1997) of the different cottonwood cross types.

Indicator of:	Leaf and stem-modifying herbivores	Free-feeding herbivores	Predators	Parasites
Fremont	<i>Paraleucoptera albella</i> * <i>Phyllocnistis</i> sp.* <i>Thecabius populicondupifolius</i> * <i>Pemphigus populitransversus</i> *			
F ₁ hybrid	<i>Aceria parapopuli</i> *	<i>Chaitophorus popullellus</i> * <i>Brochymena</i> sp.1 Cicadellidae sp.1 Cicadellidae sp.2	Saiticidae sp.1	
Backcross hybrid	<i>Pemphigus betae</i>		<i>Scymnus</i> sp.1	
Narrowleaf	<i>Pemphigus populiglobuli</i> *			
Percent indicator species/ total species within a feeding group	54% (2000) 33% (2001)	5% (2000) 12% (2001)	3% (2000) 3% (2001)	0% (2000) 0% (2001)

* Significant indicator for 2000 and 2001.

among cottonwood cross types that can only be differentiated using molecular analyses (Martinsen et al. 2001). These results agree with the findings of Floate and Whitham (1995) who found that arthropod communities were as reliable as plant morphological traits in distinguishing among cross types.

Additionally, community responses to cross types were not limited to a single group; diverse feeding groups and trophic levels were affected. The group of arthropods that was most specific to cross type was the leaf and stem-modifying herbivores. Because of their specialized and close association with their host plant, we predicted that these species would exhibit the highest fidelity to a particular cross type. This feeding group is likely using specific phenological and chemical cues to make decisions about oviposition and to stimulate gall formation (Abrahamson et al. 1993). Mopper et al. (1995) and Stiling and Rossi (1996) also found very close associations between galling insects and their host plants because genetic changes in the host plant affected gall size and mortality. Our study showed that some species of galling aphids were able to distinguish between complex backcrosses and narrowleaf cottonwoods, even though the arthropod community as a whole did not.

In addition to leaf and stem-modifying herbivores, we also found free-feeding herbivores and predators that were significant indicators of the different cross types. However, there were fewer species in these groups that showed specificity to a cross type than leaf and stem-modifying herbivores. Because specificity of arthropods to a cross type extends all the way to the primary consumer trophic level, these differences argue that the genetic differences among cross types affect more than just herbivores, and are likely to ripple throughout the community.

The Extended Host-Plant Phenotype

Where population genetics considers the effects of genes at the level of individuals and populations, from a community perspective we define the extended phenotype (sensu Dawkins 1982) as the effects of genes at levels higher than the population (Whitham et al. 2003). Two major community-level predictions emerge from this concept. First, different genotypes—and in the case of our study, different cross types—should support different communities of organisms.

This prediction at the higher level of cross types was clearly supported with three lines of evidence. (1) We found that genetic differences between cross types of cottonwoods affect both individual arthropod species and the composition of an entire community of arthropods. (2) This response to genetic diversity in the host plant was not restricted to a single trophic level, but extended all the way to the primary consumer level. We found 13 different species of herbivores and predators that tracked genetic differences in their host plants and were reliable indicators of specific cross types. Importantly, these 13 species made up 54% of the total arthropod abundance in 2000 and 47% in 2001. Because several of these species are known to affect other diverse species ranging from fungi to vertebrates, their presence or absence could directly or indirectly affect a much larger community (Larson and Whitham 1991; Dickson and Whitham 1996). (3) Not only did individual species respond to genetic differences among host plants, but also vector analysis showed that the degree of Fremont introgression into narrowleaf cottonwood was strongly associated with a compositional shift in the arthropod community. This finding suggests that arthropods may discriminate among host plants at even finer levels than the cross type, which warrants further investigation at the genotype level.

The idea that arthropod communities are closely associated with the genetic structure of their host-plant population is not surprising when we consider the array of host-plant traits that can affect arthropods. Arthropods are sensitive to differences in host-plant chemistry (Rosenthal and Berenbaum 1991; Dungey et al. 2000; Osier and Lindroth 2001), resistance (Moran and Whitham 1990; Mopper et al. 1991; Fritz et al. 2003), trichomes (Turnipseed 1977; Walters et al. 1989; Lambert et al. 1995), and phenology (Hunter et al. 1997), all of which are in part genetically controlled (e.g., plant secondary metabolites; Hamilton et al. 2002). Because of this sensitivity to the traits of their hosts, Floate and Whitham (1995) found 98% agreement in cottonwood cross-type identity based on either traditional morphological traits or their arthropod communities.

A second major prediction of the extended phenotype concept is that genetic variation at the stand level should be associated with greater diversity in the arthropod community. In other words, greater genetic diversity in a dominant plant

provides greater niche diversity for the dependent community, which in turn allows more species to be supported. This prediction has been observationally and experimentally supported in studies of the same system we studied here. In the wild, Wimp et al. (2004) used amplified fragment length polymorphism molecular markers to quantify the genetic diversity of 11 different stands of cottonwoods that were isolated from one another by natural and man-made barriers, and were all located along a 13 km stretch of the Weber River. Importantly, genetic variation at the stand level accounted for nearly 60% of the variation in the arthropod community. Thus, genetic variation in a dominant riparian tree appears to have major community consequences.

In combination, the confirmation of these two predictions supports the extended phenotype concept and the importance of a community genetics perspective. It is now important to demonstrate these effects in other systems to understand their generality. Furthermore, the validity of an extended phenotype approach to understanding community structure and biodiversity will be enhanced if future studies demonstrate that extended phenotypes are heritable. The demonstration of such community heritability in the wild would represent a major advance in community genetics. For example, research on laboratory populations has demonstrated genetically based interactions among species that have contributed to the among-community component of phenotypic variance, that is, community heritability (Goodnight 1990a,b; Goodnight and Craig 1996; Swenson et al. 2000). Large field trials show that *Eucalyptus* genotypes of known pedigree predictably affect the composition and richness of their arthropod communities (Dungey et al. 2000). Thus, offspring communities on *Eucalyptus* trees resemble the parent communities that produced them: initial evidence that community heritability exists in the wild (Whitham et al. 2003).

Our findings that plant genetics structures the associated arthropod community also argue that it is important to consider how host-plant genotype and associated arthropod communities may drive each other's evolution. Consistent with this hypothesis, Moran and Whitham (1988) found that life cycle of *P. betae* has apparently been affected by the pattern of resistance resulting from hybridization in cottonwoods. In the hybrid zone where susceptible hosts are common, *P. betae* annually alternates between cottonwoods and herbaceous plants. In the adjacent narrowleaf zone where trees are more resistant and aphid survival is reduced, *P. betae* has abandoned its cottonwood host to remain on its herbaceous hosts. Reciprocal aphid transfer experiments in the field, and the performance of aphid clones in the lab, showed that the differences between the simple and complex life cycles are, in part, genetically based (Moran and Whitham 1988; Moran 1991). Such different life cycles argue that hybridization and genetic variation in cottonwoods can affect insect fitness, evolution, and perhaps even speciation (see also Floate and Whitham 1993; McIntyre and Whitham 2003).

For these differences in aphid life cycles to evolve as a result of the patterns of hybridization in cottonwoods would likely require that these interactions are relatively stable. Two lines of evidence support this requirement. (1) Hybrid cottonwoods have been found in the fossil record that are 12 million years old (Eckenwalder 1984, 1996), hybrid zones

can be 100 km or more in size (Martinsen et al. 2001), and molecular studies show that hybridization has been important in *Populus* speciation (Smith and Sytsma 1990). In combination, these traits provide the opportunity for organisms to genetically covary with *Populus* and perhaps even coevolve with their hosts via *Populus* hybridization and speciation (Floate and Whitham 1993). (2) The same pattern of *P. betae* being positively associated with cottonwood hybrid zones was found across seven different river systems from Arizona to Alberta, Canada (Floate et al. 1997). The consistency of this association across a 1600 km north/south gradient argues that the relationship is stable and likely to enhance the probability that *P. betae* will genetically covary with its host plants. Because these hybrid zones occur in different geographical drainages and are isolated from one another, the inception of simple or complex life cycles could have occurred multiple times.

At the community level, Bangert et al. (2005) found the same general community patterns we report in Figure 1, for 25 galling arthropod species on two different host-plant hybridizing systems across 21 rivers in Arizona, Utah, Colorado, and New Mexico. The consistency of these patterns in common gardens and from local to regional levels suggests that patterns of hybridization in a dominant plant have the potential to affect the evolution of taxonomically diverse organisms and warrants further investigation into the genetic structuring of these arthropod populations.

Similarly, selective herbivory by arthropods has the potential to affect the evolution of hybrids and hybridizing species. In a review of 152 case studies of taxa associated with diverse hybridizing systems, hybrids were more susceptible than their parent species in 43 (28%) cases, and more resistant in seven (5%); and exhibited additivity in 35 (23%), dominance in 35 (23%), and no difference in 32 (21%) (Strauss 1994; Whitham et al. 1999). Thus, across diverse taxa, most exhibit significant responses to hybridization in their hosts. However, we are aware of no studies that have demonstrated how such selective feeding has shaped the evolution of their hosts other than polymorphisms of resistance.

Conservation Implications

If arthropod species respond to genetic differences among host plants, as our studies argue, then to conserve the diversity of the dependent arthropod community, it is important to conserve genetic diversity in the host plant population. Although conservation biology recognizes that there is a minimum viable population size (MVP; Shaffer 1981) needed to maintain the existence of a species (especially rare and threatened species), this population size may not be adequate to support the rest of the community. Our findings argue that it is also important to conserve genetic diversity in very common species to support their dependent communities. We refer to the population size necessary to support these community interactions as the minimum viable interacting population (MVIP; Whitham et al. 2003). Rather than preserving the minimum amount of diversity necessary to sustain a species, the concept of MVIP seeks to maximize genetic diversity in a host plant population to increase diversity in the dependent community, thereby maximizing the number of

potentially interacting species. Such conservation of genetic diversity may be especially important for dominant plants that are community and ecosystem drivers (Wimp et al. 2004; Bangert et al. 2005).

Conclusions

In this study we have shown that genetic differences between cottonwoods result in extended phenotypes that structure the composition of the dependent arthropod community. Through both observational field studies and experimental common-garden studies, we have shown that pure species of cottonwoods (*Populus fremontii* and *P. angustifolia*) and their F₁ hybrids supported arthropod communities that were compositionally different from one another. Individual arthropod species and the community at large appeared to track the level of introgression among trees in the population. These results demonstrate a host-plant genetic basis for arthropod community structure and the need for conserving host-plant genetic diversity as a means for maintaining arthropod diversity.

ACKNOWLEDGMENTS

We would like to thank M. Howe, N. Collins Johnson, M. Kearsley, P. Keim, P. McIntyre, S. Page, P. Price, J. Schweitzer, S. Shuster, L. Stevens, A. Thompson, R. Williams, and two anonymous reviewers for assistance in the field, statistical support, and/or comments on the manuscript. This research was supported by National Science Foundation grants DEB-9726648 and DEB-0078280. We also thank C. Palmer, E. Gause, and the staff of the Ogden Nature Center for supporting our cottonwood plantations.

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