Importance of species interactions to community heritability: a genetic basis to trophic-level interactions

Joseph K. Bailey,[1]* Stuart C. Wooley,[2] Richard L. Lindroth[2] and Thomas G. Whitham[1]

[1]Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011, USA

[2]Department of Entomology, University of Wisconsin, Madison, WI 53706, USA

*Correspondence: E-mail: jkb22@dana.ucc.nau.edu

Abstract

Recent community genetics studies have shown that specific genotypes of a host plant support distinct arthropod communities. Building upon these findings, we examined the hypothesis that a trophic community consisting of cottonwood trees, a galling herbivore and avian predators could also be related to the genetics of the host tree. We found genetic correlations among phytochemistry of individual tree genotypes, the density of a galling herbivore, and the intensity of avian predation on these herbivores. We detected significant broad-sense heritability of these interactions that range from $H^2_B = 0.70$ to 0.83. The genetic basis of these interactions tended to increase across trophic levels suggesting that small genetic changes in the cottonwood phenotype could have major consequences at higher trophic levels affecting species interactions and energy flow. These findings show a heritable basis to trophic-level interactions indicating that there is a significant genetic basis to community composition and energy flow that is predictable by plant genotype. Our data clearly link plant genetics to patterns of avian foraging and show that species interactions are important components of community heritability and ecosystem processes. Overall, these data support the hypothesis that evolution of plant traits can alter trophic-level interactions and community composition.

Keywords

Avian predation, community genetics, condensed tannins, ecosystem processes, energy flow, herbivory, heritability, *Populus*, trophic-level interactions.

Ecology Letters (2006) **9**: 78–85

INTRODUCTION

Linking genetics to population, community and ecosystem processes is fundamental to the field of community genetics and places population, community and ecosystem interactions and processes within an evolutionary context (Whitham *et al.* 2003). Although one might think that the effects of genetic variation or specific genetically based plant traits may have little effect on higher levels of organization (i.e. community and ecosystems), recent studies have shown that specific genetically based plant traits can have direct and indirect effects that extend beyond the individual or population to affect the dependent community (Hockwender & Fritz 2004; Wimp *et al.* 2004; Johnson & Agrawal 2005), and have ecosystem consequences (Driebe & Whitham 2000; Treseder & Vitousek 2001; Madritch & Hunter 2002; Schweitzer *et al.* 2004). Together these studies suggest that

plant genetics can have strong organizational effects at the community and/or ecosystem level.

Tri-trophic-level interactions represent a model community of interacting species and ecosystem process in which to examine the direct and indirect effects of plant genetics. Since Lindeman (1942), understanding how energy availability changes across trophic groups has become a major area of ecological research at the community and ecosystem level (Odum 1957; Marquis & Whelan 1994; Price 1997). As Forkner & Hunter (2000) pointed out, since 1974 over 1000 studies have used bottom-up or top-down forces as keywords describing their research. The relative importance of bottom-up vs. top-down control of herbivore dynamics has been fundamental to trophic-level interactions (Hairston *et al.* 1960). In general, studies have shown that bottom-up factors such as productivity, phytochemistry, phenology as well as top-down impacts by predators affect herbivore

population dynamics and community structure (Price *et al.* 1980; Hunter & Price 1992; Roininen *et al.* 1996; Dyer & Letourneau 1999; Abrahamson *et al.* 2003; Rudgers 2004). For example, Forkner & Hunter (2000) showed how environmental conditions that positively affected growth of oaks, also positively affected arthropod herbivore abundance and slightly increased predation. And while the generality of these studies is strong, they generally disregard the variation in trophic-level interactions that is present at the individual plant genotype level, which is fundamental to understanding the ecology and evolution of trophic-level interactions.

There is a precedent for understanding the genetic basis of trophic-level interactions, although direct tests are few (Price & Clancy 1986; Weis & Abrahamson 1986; Preszler & Boecklen 1994; Fritz 1995; Stiling & Rossi 1996; Fritz *et al.* 1997; Wimp & Whitham 2001). Plant genes interact with the environment to produce phenotypes that affect plant resistance to herbivores (Simchuk *et al.* 1999). These phenotypes can vary dramatically from one plant genotype to another (Berenbaum *et al.* 1986; Marquis 1990; O'Reilly-Wapstra *et al.* 2002). Because predators depend on herbivores, predation could also vary by plant genotype. If plants show low within genotype variation and high among genotype variation for predation (Fritz 1995), then it could be a heritable plant trait and subject to natural selection (Falconer 1987) if predation were to feedback and affect plant fitness. Using existing quantitative genetic methods to measure the phenotypic covariance of genetically similar ecological interactions demonstrates that genetic interactions among species can produce distinct trophic-level phenotypes (Goodnight 1990a,b; Wade 2003).

Cottonwoods are recognized as a dominant riparian forest tree that commonly hybridizes across many rivers in the western United States. Along the Weber River, Utah, the ranges of Fremont cottonwood (*Populus fremontii*) and narrowleaf cottonwood (*P. angustifolia*) overlap in a 13-km zone where the two species naturally hybridize and introgress unidirectionally towards narrowleaf cottonwoods (Martinsen *et al.* 2001). Because of this unidirectional genetic introgression, hybridization represents a genetic continuum between Fremont and narrowleaf cottonwoods that results in a large amount of genetic variation (Martinsen *et al.* 2001). Within this naturally hybridizing complex, Whitham (1989) showed a strong genetic basis to the resistance and susceptibility of backcross hybrids and narrowleaf cottonwoods to a common gall-forming aphid, *Pemphigus betae* (Aphidae, Homoptera). Dickson & Whitham (1996) also demonstrated that *P. betae* is an important food item for insectivorous birds, and phytochemistry has also been shown to be an important mechanistic link affecting herbivores (Bangert *et al.* 2005b) making this an ideal

system to examine the genetic basis of tri-trophic-level interactions.

Based upon the above studies, we addressed three basic hypotheses: (1) phytochemistry, aphid gall density, avian predation and tri-trophic-level interactions differ among genotypes in a common garden; (2) phytochemistry, aphid gall density and avian predation are related; (3) tri-trophic-level interactions exhibit broad-sense heritability. Our results show that there is heritable genetic variation in plants for tri-trophic-level interactions. These findings contribute to the growing field of community genetics (Goodnight 1990a,b; Dungey *et al.* 2000; Hockwender & Fritz 2004; Johnson & Agrawal 2005) by suggesting that phytochemistry and genetically based species interactions are important components of community heritability and ecosystem processes.

MATERIALS AND METHODS

Common garden and surveys

We examined the genetic basis of tri-trophic-level interactions in a 13-year-old common garden with replicated clones of cottonwood genotypes whose genetic makeup had been quantified using RFLP analyses (Martinsen *et al.* 2001). Genotypes planted in the common garden were randomly selected from multiple populations of trees which show distinct population structure (Wimp *et al.* 2004) growing throughout the entire 201 km long Weber River drainage and planted in a random design. We randomly selected 11 genotypes of backcross hybrids and *P. angustifolia*. At least three replicates of each genotype were surveyed for a total of 41 replicates. F_1 hybrids and *P. fremontii* do not host *P. betae* and were not used in this study.

To determine potential mechanistic relationships among cottonwoods, galls and birds we measured phytochemistry, gall density and avian predation. Concentrations of the principal secondary metabolites (phenolic glycosides and condensed tannin; Palo 1984; Lindroth & Hwang 1996) were quantified from the randomly selected replicate genotypes (see above). Leaves were collected on dry ice, lyophilized and ground to pass a 40-mesh screen in a Wiley Mill. The phenolic glycosides, salicortin and HCH-salicortin, were quantified using high-performance thin layer chromatography (Lindroth *et al.* 1993), using purified salicortin and HCH-salicortin as standards. Condensed tannin levels were measured on 70% acetone extracts of the leaf samples using the butanol-HCl method of Porter *et al.* (1986). Narrowleaf cottonwood condensed tannins purified by the method of Hagerman & Butler (1980) were used as the reference standard. Total nitrogen and carbon analyses were performed by combustion on a Carlo Erba CNS analyzer (Carlo Erba, Milan, Italy).

Pemphigus betae gall density was surveyed on 25 shoots of two randomly selected branches per replicate genotype for a total of 50 shoots per replicate (total of 2050 shoots). To determine the relationship between galls and birds we surveyed all *P. betae* galls on these shoots for avian predation. From these data we calculated predation pressure by dividing the number of galls attacked by the total number of galls. Avian predation of galls can be easily identified as a detectable peck mark, and/or slice of the gall (see also Dickson & Whitham 1996). Thus predation was characterized as the number of galls attacked. Feeding by Black-Headed Grosbeaks (*Pheucticus melanocephalus*), American Robin (*Turdus migratorius*) and Black-capped Chickadees (*Poecile atricapilla*) were observed making these conspicuous marks on the gall.

We considered phytochemistry, gall density and predation on cottonwood genotypes as quantitative traits because they are likely to arise from genetic and environmental factors similar to that which produces other plant phenotypes displaying quantitative inheritance (Bradshaw & Stettler 1995; Bailey *et al.* 2004b). When these estimates are generated according to standard breeding designs (e.g. among lineages of clones grown in a common environment), standard quantitative genetic methods are appropriate for relating the observable components of phenotypic variance to the measurable components of genetic variance (Falconer 1987).

Statistical analysis

In order to examine how the presence and interactions among galls and birds varied by cottonwood genotype we used Non-metric Multidimensional Scaling ordination (NMDS; Minchin 1987). NMDS is a robust multivariate statistical approach that places samples with similar phenotypes close together in ordination space and dissimilar samples far away in ordination space based on the standard Bray–Curtis distance (Faith *et al.* 1987). We used two traits from each replicate clone for our data matrix: gall density and avian predation. Each NMDS score represents the combined cottonwood gall density, and avian predation for each clonal replicate of each tree genotype. Because tri-trophic-level interactions represent a simple community of interacting 'species' in a particular location and by definition is concerned with how energy flows among organisms in an ecosystem (Lindeman 1942; Odum 1957; Marquis & Whelan 1994; Price 1997), these analyses are important because they address three major questions: (1) is there genetically based variation in community composition? (2) Are species interactions important components of community heritability? (3) Is there genetically based variation in the way energy flows among organisms in an ecosystem?

These NMDS scores, as well as the independent surveys for phytochemistry, gall abundance and avian predation, were analysed using a one-way ANOVA model with genotype as a random effect. All data were transformed to meet assumptions of normality and homogeneity of variance. We used simple linear regression for genetic correlations to relate genotype means of phytochemistry, gall density and predation. Regression was used because we were interested in whether host plant genotype predicted the associated gall density and predation. Additionally, we used a multiple regression approach to specifically examine if the effects of plant genotype on avian predation were direct or indirect. We used a standard least squares model with partial (type III sums of squares) error structure and genotype and the number of galls attacked as our factors.

We calculated the broad-sense heritability (H_{B}^2) of tree phytochemistry, gall density, bird predation, and their interaction as the among-lineage component of variation in the phenotype, H_{S}^2, divided by the total variance in the phenotype for all trees, H_{total}^2, or

$$H_{\mathrm{B}}^2 = H_{\mathrm{S}}^2 / H_{\mathrm{total}}^2.$$

Calculations of mean squares and methods for partitioning within-, among- and total phenotypic variance from ANOVA results are described in detail (Falconer 1987). Broad-sense heritability measurements were made for backcross hybrids, *P. angustifolia*, and both tree classes together.

RESULTS

Because phytochemistry is often associated with a plants' resistance to herbivory and herbivore density is commonly related to predator abundance we examined how these traits varied by plant genotype. In agreement with our hypothesis that phytochemistry, aphid gall density, avian predation, predation pressure and tri-trophic interactions vary within and among genotypes in a common garden, we found significant differences among cottonwood genotypes in all traits examined except % foliar nitrogen and % foliar carbon (Table 1). Average gall density on individual tree genotypes ranged from 0 to 44 galls per 50 shoots, and avian predation of these galls varied from 0 to 36 galls attacked.

Because galls were virtually absent from some genotypes, we conducted a separate more conservative survey of predation to confirm that insectivorous birds were visiting all trees and tracking gall density. We searched trees that were low in gall density for 10 galls and randomly selected 10 galls on genotypes where they were common. We found that similar to the first survey these data also showed that avian predation differed by cottonwood genotype (d.f.$_{(10,40)}$, $F = 5.56$, $P < 0.0001$), which confirmed that insectivorous birds visited all trees.

Table 1 Plant genotype effects on phytochemistry and trophic-level interactions and broad-sense heritability of these traits

| Genotype/Trait | Tree class | | | | | | | | | | | | |
| | Backcross hybrids | | | | | | *Populus angustifolia* | | | | | Overall | |
	1979	1012	1017	11	10	18	1008	T15	RM2	WC5	1020	$F_{\text{(d.f.)}}$	P
Nitrogen	2.04	2.02	1.73	1.96	2.07	2.08	2.06	1.83	1.79	2.11	1.79	$1.01_{(10,40)}$	0.45
H_B^2			0.11 $\pm$ 0.34						0.0 $\pm$ 0.49			0.00 $\pm$ 0.27	
Carbon	43.8	44.4	45.0	46.2	44.6	42.1	46.0	43.7	44.1	45.7	45.6	$1.14_{(10,40)}$	0.37
H_B^2			0.06 $\pm$ 0.35						0.0 $\pm$ 0.53			0.04 $\pm$ 0.27	
Condensed tannin	1.91	11.9	14.3	11.2	15.4	5.57	7.86	8.14	5.63	15.5	5.86	$3.17_{(10,40)}$	**0.0069**
H_B^2			**0.43 $\pm$ 0.33**						**0.52 $\pm$ 0.42**			**0.37 $\pm$ 0.25**	
Salicortin	8.37	8.69	6.70	8.67	3.71	5.67	14.8	15.3	14.3	8.74	12.0	$4.69_{(10,40)}$	**0.0005**
H_B^2			0.16 $\pm$ 0.34						0.18 $\pm$ 0.45			**0.50 $\pm$ 0.25**	
HCH-salicortin	2.12	0.0	0.38	0.0	0.0	3.06	0.0	1.33	0.0	0.0	4.63	$9.55_{(10,40)}$	**0.0001**
H_B^2			**0.62 $\pm$ 0.32**						**0.79 $\pm$ 0.34**			**0.70 $\pm$ 0.23**	
Gall density	0.0	43.67	21.3	10.75	4.8	0.0	0.0	12.3	7.33	3.0	0.0	$15.49_{(10,40)}$	**0.0002**
H_B^2			**0.81 $\pm$ 0.27**						**0.60 $\pm$ 0.41**			**0.80 $\pm$ 0.20**	
Galls attacked	0.0	35.67	14.0	8.5	2.4	0.0	0.0	7.0	4.67	1.0	0.0	$17.88_{(10,40)}$	**0.0001**
H_B^2			**0.83 $\pm$ 0.25**						**0.53 $\pm$ 0.42**			**0.82 $\pm$ 0.19**	
Galls attacked/total	0.0	0.83	0.67	0.71	0.41	0.0	0.0	0.55	0.34	0.40	0.0	$6.67_{(10,40)}$	**0.0001**
H_B^2			**0.80 $\pm$ 0.28**						0.30 $\pm$ 0.48			**0.62 $\pm$ 0.24**	
Galls removed	0.0	8.0	7.33	2.25	2.40	0.0	0.0	5.33	2.67	2.0	0.0	$3.14_{(10,40)}$	**0.039**
H_B^2			**0.62 $\pm$ 0.32**						**0.82 $\pm$ 0.32**			**0.37 $\pm$ 0.25**	
NMDS score	−1.08	1.72	1.05	0.53	−0.07	−1.08	−1.08	0.69	0.07	−0.38	−1.08	$16.39_{(10,40)}$	**0.0001**
H_B^2			**0.83 $\pm$ 0.25**						**0.70 $\pm$ 0.38**			**0.80 $\pm$ 0.20**	

All phytochemical trait values are expressed as mean % dry weight ($\mu g\ mg^{-1}$). HCH-salicortin is hydroxy-hexenoyl-ene-one salicortin. Items in bold show significant differences among genotypes as well as significant broad-sense heritability.

In support of the hypothesis that phytochemistry, aphid gall density, avian predation and tri-trophic interactions are related, we found that average % foliar condensed tannins was significantly related to gall density (Fig. 1a; d.f.$_{(1,10)}$, $F = 6.86$, $r^2 = 0.43$, $P < 0.05$) the number of galls attacked by birds (Fig. 1b; d.f.$_{(1,10)}$, $F = 5.74$, $r^2 = 0.39$, $P < 0.05$) and the interaction of galls and birds (Fig. 1c; d.f.$_{(1,10)}$, $F = 5.74$, $r^2 = 0.39$, $P < 0.05$). As mean foliar condensed tannins among tree genotypes increased from 5% to 16% dry weight, gall density also increased from 0 to 15 galls per 50 shoots. Foliar condensed tannins also indirectly affected avian predators through this galling herbivore. As condensed tannins increased, avian predation also increased from 0 to 10 galls being attacked. When genotype 1012 is removed from the analysis, condensed tannins were still positively related to gall density (Fig. 1a; d.f.$_{(1,9)}$, $F = 5.66$, $r^2 = 0.42$, $P = 0.045$) and avian predation (Fig. 1b; d.f.$_{(1,9)}$, $F = 5.44$, $r^2 = 0.40$, $P = 0.048$). These genetic correlations show that phytochemistry affects gall density, avian predation, and demonstrate a genetically based bottom-up organizing effect in this system.

When the relationship between gall density and avian predation was examined, there was a strong positive relationship where birds selectively foraged on tree genotypes where aphid gall densities were greatest (d.f.$_{(1,10)}$, $r^2 =$ 0.98, $F = 621.7$, $P < 0.0001$, Fig. 2). Cottonwood genotypes with low gall density had low avian predation, whereas genotypes with high gall density had high avian predation. These data strongly suggest that the effects of plant genotype on avian predation are indirect.

To test this hypothesis that host plant genetic effects on avian predators are indirect we used a multiple regression approach with plant genotype and gall density to predict the number of galls attacked. Overall, genotype was not a significant predictor of avian predation when gall density was included in the model (Table 2). When gall density was removed from the model, genotype emerged demonstrating that the effects of plant genetics on avian predators are indirect (Table 2). Because genetically based resistance to dominant herbivores can extend to the next trophic level, these data suggest that this interaction may be heritable.

In agreement with our hypothesis that phytochemistry, aphid gall density, avian predation and tri-trophic interactions show heritable variation, there was significant broad-sense heritability of all traits examined except % foliar nitrogen and % foliar carbon (Table 1). Overall, 37% of the variation in foliar condensed tannins, 80% of the variation in gall density, 82% of the variation in avian predation, and 80% of the variation in tri-trophic interactions was related to host plant genetics. Even when the backcross hybrid or
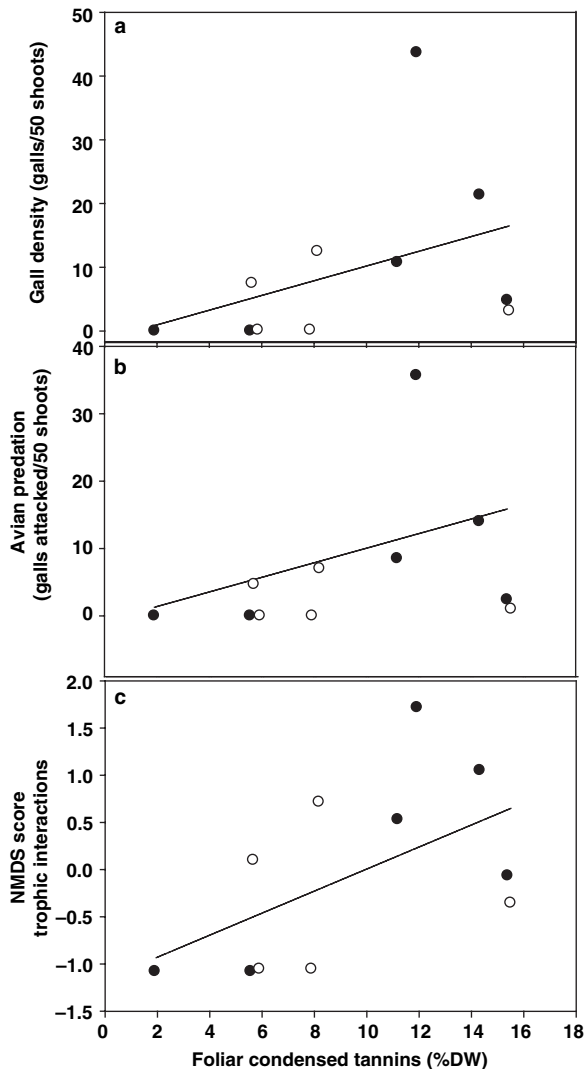
Figure 1 In a 13-year-old common garden, foliar condensed tannins were related to gall density (a), avian predation (b) and their interaction (c). Genetic correlations showed that as foliar condensed tannins increased from 2% dry weight to 15% dry weight gall abundance and avian predation also increased. Black dots are backcross hybrids and white dots are pure narrowleaf. All data are square root transformed for statistical purposes however the actual data are shown.
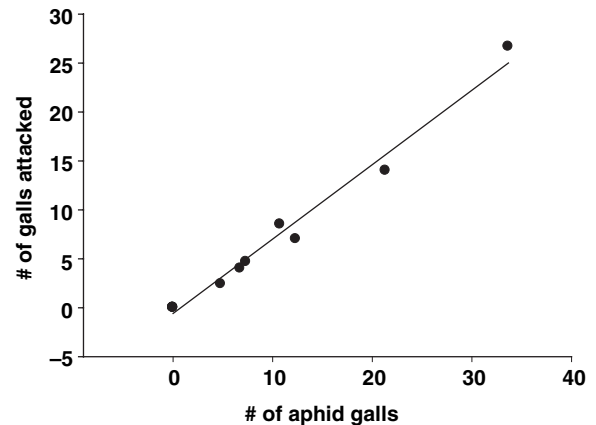

Figure 2 In a 13-year-old common garden, total gall abundance on cottonwood genotypes is highly related to avian predation. Using genotype means from 11 randomly selected clones, gall abundance explained 98% of the variation in avian predation.

Table 2 Effects of plant genotype, phytochemistry and gall density on avian predation

Trait	With galls included		With galls excluded	
	F-ratio	*P*	*F*-ratio	*P*
Genotype	0.87	0.57	5.40	< 0.0001
Gall density	190.95	< 0.0001		
Full model	302.12	< 0.0001	5.40	< 0.0001

DISCUSSION

Recent studies have shown that there are genetic components that can determine community structure (e.g. Dungey *et al.* 2000; Wade 2003; Hockwender & Fritz 2004; Wimp *et al.* 2004, 2005, Bangert *et al.* 2005a,b; Johnson & Agrawal 2005). Johnson & Agrawal (2005) showed that intraspecific genetic differences in the evening primrose (*Oenothera biennis*) accounted for as much as 41% of the variation in arthropod diversity. Although the community is small, our data also show relatively high levels of phenotypic variation for tri-trophic-level interactions (i.e. cottonwoods, an aphid herbivore and avian predators; $H_{\mathrm{B}}^2 = 0.70–0.83\%$) and demonstrates the importance of species interactions to community heritability and ecosystem processes such as energy flow. For example, our data show that the direct and indirect interactions among species result in distinct community composition that is predictable by cottonwood genotype. Because there is variation in the interactions among cottonwoods, galls and avian predators that does result in functionally organized communities, our results also show that 'populations of communities' can persist on the

P. angustifolia tree class were analysed separately there was significant broad-sense heritability for all traits measured except % foliar salicortin (Table 1). This is important because it demonstrates that heritability is not driven by the mixing of hybrids and a pure parental species; heritable variation is observed within a pure species as well as a hybridizing complex. Thus, our findings are important for understanding tri-trophic-level interactions in individual species of plants as well as in hybridizing complexes.

landscape (*sensu* Wilson 1997) and that how these interactions vary affects energy flow in this forest ecosystem.

It has been proposed that associated communities can change as a result of natural selection that acts on plants (Whitham *et al.* 2003) if there are genetic correlations between those plant traits and associated communities. Our data showed genetic correlations among condensed tannins, gall density and avian predation and support the hypothesis that the evolution of *Populus* could result in changes to community composition by altering the interactions among species. Condensed tannins have also been shown to impact microbial communities (Bailey *et al.* 2005) and mammalian herbivores (Bailey *et al.* 2004a; O'Reilly-Wapstra *et al.* 2004). Although we showed that condensed tannins can affect avian predators, it is clear that the effects of plant genetics on avian predation are indirect (see Table 2). Gall density explained 98% of the variation in attack by avian predators demonstrating that the effects of plant genetics are indirect and strongly mediated through the effects of herbivory.

These results support previous data (Dickson & Whitham 1996) demonstrating that *P. betae* is an important food resource for birds and show that direct and indirect genetically based species interactions are important components of community heritability. Because animals tend to accumulate in shelters, predators such as insectivorous birds may identify them as an easy and reliable food resource (Bailey & Whitham 2003). For example, Heinrich & Collins (1983) showed that birds used leaf morphology (including leaf-folds) as foraging clues. Dickson & Whitham (1996) showed a positive association between Black-capped chickadees and *P. betae*. Still, very few studies have linked bird foraging to plant quality. Mäntylä *et al.* (2004) found that birds may use olfaction or UV vision to detect their prey after plants induce phytochemical compounds to defend against herbivores. Bailey & Whitham (2003) showed that elk browsing on aspen negatively affected plant quality, herbivore abundance and avian predation. When the direct effects of genetically based plant traits on dominant herbivores are predictable, they may also extend to the next trophic level indirectly impacting predators and parasitoids.

We found moderate to large estimates of broad-sense heritability for many phytochemical traits, gall density and avian predation. In general, genetically based phenotypic variation was lowest in the plant phenotype ($H_B^2 = 0.37$), and greatest at the second ($H_B^2 = 0.80$) and third trophic levels ($H_B^2 = 0.82$). Because heritability is an estimate of the amount of variation in a trait that is explained by underlying genetic factors, and genetic variation is related to the evolutionary potential of a trait, these data suggest that small evolutionary changes in *Populus* could result in large changes in community composition and species interactions. If small evolutionary changes in plant phenotype do result in strong selection on associated community members, then relatively tight ecological associations and functionally organized communities could emerge (Wilson 1997).

Our data showed that predation of aphid galls was a predictable consequence of plant genetics. Evolutionarily these data suggest that if reductions in herbivore density lead to an increase in plant fitness, then genes that negatively affect herbivores may be less likely to introgress from *P. fremontii* into *P. angustifolia* than genes that are neutral or positively affect herbivores. For example, backcrossed hybrids carrying resistance genes effective at reducing aphid density would have lower fitness relative to non-resistant genotypes, suggesting that there may be benefits to susceptibility and that avian predators may represent a 'low cost' defence for plants (Kearsley & Whitham 1992). Other studies have shown linkages between bird foraging, herbivore density and plant traits that in some cases do affect plant growth (Heinrich & Collins 1983; Greenberg 1987; Atlegrim 1992; Marquis & Whelan 1994; Dickson & Whitham 1996; Sipura 1999; Bailey & Whitham 2003). For example, Marquis & Whelan (1994) showed that predation of herbivorous insects by insectivorous birds resulted in a one-third increase in biomass of white oak relative to plants where birds were excluded. If the effects of predators are related to the indirect effects of host plant genetics then predators could provide a general selective force affecting herbivore resistance in these systems. Our study provides results consistent with this idea, but does not provide a definitive test of whether predators are acting as extended defensive traits of the plant.

Plant genetics also affect how energy flows from one trophic level to another and clearly link genetically based plant traits to the foraging patterns of vertebrates. Eighty percent of the variation in how energy flowed from plants to galls to avian predators was explained by underlying genetic factors in this common garden (Table 1). Because energy flow is related to the laws of thermodynamics (Price 1997), and there is high genetic variation in this trait, *Fisher's fundamental theorem* suggests then that natural selection and evolution may act easily on those traits that affect energy flow in forest ecosystems. With the rapid loss of biodiversity and unknown consequences of genetically modified crop, pulp, and lumber species on communities and ecosystem processes these data expose our need for a genetic perspective in conservation policy, particularly in light of recent studies showing that host plant genetic factors impact terrestrial and aquatic arthropod (Bangert *et al.* 2005a,b; LeRoy *et al.* 2005) and microbial communities (Bailey *et al.* 2005), mammalian foraging (Bailey *et al.* 2004a), leaf litter decomposition (Driebe & Whitham 2000; Schweitzer *et al.* 2004, 2005a,b) and soil nitrogen mineralization rates (Schweitzer *et al.* 2004).

REFERENCES

Abrahamson, W.G., Blair, C.P., Eubanks, M.D. & Morehead, S.A. (2003). Sequential radiation of unrelated organisms: the gall fly *Eurosta solidaginis* and the tumbling flower beetle *Mordellistena convicta*. *J. Evol. Biol.*, 16, 781–789.

Atlegrim, O. (1992). Mechanisms regulating bird predation on a herbivorous larva guild in boreal coniferous forests. *Ecography*, 15, 19–24.

Bailey, J.K. & Whitham, T.G. (2003). Interactions among elk, aspen, galling sawflies, and insectivorous birds. *Oikos*, 101, 127–134.

Bailey, J.K., Schweitzer, J.A., Rehill, B., Lindroth, R. & Whitham, T.G. (2004a). Beavers as molecular geneticist: a genetic basis to the foraging of an ecosystem engineer. *Ecology*, 85, 603–608.

Bailey, J.K., Bangert, R.K., Schweitzer, J.A., Trotter, R.T., III, Shuster, S.M. & Whitham, T.G. (2004b). Broad sense heritability of fractal architecture in trees. *Evolution*, 58, 2100–2102.

Bailey, J.K., Deckert, R., Schweitzer, J.A., Rehill, B.J., Lindroth, R.L., Gehring, C. *et al.* (2005). Host-plant genetics affect hidden ecological players: links among *Populus*, condensed tannins and fungal endophyte infection. *Can. J. Bot.*, 83, 350–355.

Bangert, R.K., Turek, R.J., Martinsen, G.D., Wimp, G.M., Bailey, J.K. & Whitham, T.G. (2005a). Benefits of conservation of plant genetic diversity on arthropod diversity. *Conserv. Biol.*, 19, 379–390.

Bangert, R.K., Turek, R.J., Rehill, B., Wimp, G.M., Schweitzer, J.A., Allen, G.J. *et al.* (2005b). A genetic similarity rule determines arthropod community structure. *Mol. Ecol.*, in press.

Berenbaum, M.R., Zangerl, A.R. & Nitao, J.K. (1986). Constraints on chemical coevolution: wild parsnips and the parsnip webworm. *Evolution*, 40, 1215–1228.

Bradshaw, H.D., Jr & Stettler, R.F. (1995). Molecular genetics of growth and development in Populus, IV. Mapping QTL's with large effects on growth, form, and phenology traits in a forest tree. *Genetics*, 139, 963–973.

Dickson, L.L. & Whitham, T.G. (1996). Genetically-based plant resistance traits affect arthropods, fungi, and birds. *Oecologia*, 106, 400–406.

Driebe, E. & Whitham, T.G. (2000). Cottonwood hybridization affects tannin and nitrogen content of leaf litter and alters decomposition. *Oecologia*, 123, 99–107.

Dungey, H.S., Potts, B.M., Whitham, T.G. & Li, H.F. (2000). Plant genetics affects arthropod community richness and composition: evidence from a synthetic Eucalypt hybrid population. *Evolution*, 54, 1938–1946.

Dyer, L.A. & Letourneau, D.K. (1999). Relative strengths of top-down and bottom-up forces in a tropical forest community. *Oecologia*, 119, 265–274.

Faith, D.P., Minchin, P.R. & Belbin, L. (1987). Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio*, 69, 57–68.

Falconer, D.S. (1987). *Introduction to Quantitative Genetics*, 3rd edn. Longman, New York and London.

Forkner, R.E. & Hunter, M.D. (2000). What goes up must come down? Nutrient addition and predation pressure on oak herbivores. *Ecology*, 81, 1588–1600.

Fritz, R.S. (1995). Direct and indirect effects of plant genetic variation on enemy impact. *Ecol. Entomol.*, 20, 18–26.

Fritz, R.S., McDonough, S.E. & Rhoads, A.G. (1997). Effects of plant hybridization on herbivore–parasitoid interactions. *Oecologia*, 110, 360–367.

Goodnight, C.J. (1990a). Experimental studies of community evolution. I: The response to selection at the community level. *Evolution*, 44, 1614–1624.

Goodnight, C.J. (1990b). Experimental studies of community evolution. II: The ecological basis of the response to community selection. *Evolution*, 44, 1625–1636.

Greenberg, R. (1987). Seasonal foraging specialization in the worm-eating warbler. *Condor*, 89, 158–168.

Hagerman, A.E. & Butler, L.G. (1980). Condensed tannin purification and characterization of tannin-associated protein. *J. Agr. Food Chem.*, 28, 947–952.

Hairston, N.G., Smith, F.E. & Slobodkin, L.B. (1960). Community structure, population control, and competition. *Am. Nat.*, 44, 421–425.

Heinrich, B. & Collins, S.L. (1983). Caterpillar leaf damage, and the game of hide-and-seek with birds. *Ecology*, 64, 592–602.

Hockwender, C.G. & Fritz, R.S. (2004). Plant genetic differences influence herbivore community structure: evidence from a hybrid willow system. *Oecologia*, 138, 547–557.

Hunter, M.D. & Price, P.W. (1992). Playing chutes and ladders: heterogeneity and the relative role of bottom-up and top-down forces in natural communities. *Ecology*, 73, 724–732.

Johnson, M.T. & Agrawal, A.A. (2005). Plant genotype and the environment interact to shape a diverse arthropod community on evening primrose (*Oenothera biennis*). *Ecology*, 86, 874–885.

Kearsley, M.J.C. & Whitham, T.G. (1992). Guns and butter: a no cost defense against predation for *Chrysomela confluens*. *Oecologia*, 92, 556–562.

LeRoy, C.J., Whitham, T.G., Keim, P. & Marks, J.C. (2005). Plant genes link forests and streams. *Ecology*, in press.

Lindeman, R.L. (1942). The trophic dynamic aspect of ecology. *Ecology*, 23, 399–418.

Lindroth, R.L. & Hwang, S.-Y. (1996). Diversity, redundancy and multiplicity in chemical defense systems of aspen. In: *Recent Advances in Phytochemistry*, Vol. 33 (ed. Romeo, J.). Plenum Press, New York, pp. 25–56.

Lindroth, R.L., Kinney, K.K. & Platz, C.L. (1993). Responses of deciduous trees to elevated atmospheric CO_2: productivity, phytochemistry and insect performance. *Ecology*, 74, 763–777.

Madritch, M.D. & Hunter, M.D. (2002). Phenotypic diversity influences ecosystem functioning in oak sandhills community. *Ecology*, 83, 2084–2090.

Mäntylä, E., Klemola, T. & Haukioja, E. (2004). Attraction of willow warblers to sawfly-damaged mountain birches: novel function of inducible plant defences? *Ecol. Lett.*, 7, 915–918.

Marquis, R.J. (1990). Genotypic variation in leaf damage in *Piper arieianum* (Piperaceae) by a multispecies assemblage of herbivores. *Evolution*, 44, 104–120.

Marquis, R.J. & Whelan, C.J. (1994). Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. *Ecology*, 75, 2007–2014.

Martinsen, G.D., Whitham, T.G., Turek, R.J. & Keim, P. (2001). Hybrid populations selectively filter gene introgression between species. *Evolution*, 55, 1325–1335.

Minchin, P.R. (1987). An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio*, 69, 89–107.

O'Reilly-Wapstra, J.M., McArthur, C. & Potts, B.M. (2002). Genetic variation in *Eucalyptus globulus* to marsupial browsers. *Oecologia*, 130, 289–296.

O'Reilly-Wapstra, J.M., McArthur, C. & Potts, B.M. (2004). Linking plant genotype, plant defensive chemistry and mammal browsing in a *Eucalyptus* species. *Func. Ecol.*, 18, 677–684.

Odum, H.T. (1957). Trophic structure and productivity of Silver Springs, Florida. *Ecol. Monogr.*, 27, 55–112.

Palo, R.T. (1984). Distribution of birch (*Betula* spp.), willow (*Salix* spp.), and poplar (*Populus* spp.) secondary metabolites and their potential role as chemical defense against herbivores. *J. Chem. Ecol.*, 10, 499–520.

Porter, L.J., Hrstich, L.N. & Chan, B.G. (1986). The conversion of procyanidins and prodelphinidins to cyaniding and delphinidin. *Phytochemistry*, 25, 223–230.

Preszler, R.W. & Boecklen, W.J. (1994). A three-trophic-level analysis of the effects of plant hybridization on a leaf-mining moth. *Oecologia*, 100, 66–73.

Price, P.W. (1997). *Insect Ecology*, 3rd edn. Wiley, New York.

Price, P.W. & Clancy, K.M. (1986). Interactions among three trophic levels: gall size and parasitoid attack. *Ecology*, 67, 1593–1600.

Price, P.W., Bouton, C.E., Gross, P., McPheron, B.A., Thompson, J.N. & Weiss, A.E. (1980). Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Annu. Rev. Ecol. Syst.*, 11, 41–65.

Roininen, H., Price, P.W. & Tahvanainen, J. (1996). Bottom-up and top-down influences in the trophic system of a willow, a galling sawfly, parasitoids and inquilines. *Oikos*, 77, 44–50.

Rudgers, J.A. (2004). Enemies of herbivores can shape plant traits: selection in a facultative ant–plant mutualism. *Ecology*, 85, 192–205.

Schweitzer, J.A., Bailey, J.K., Hart, S.C., Woolbright, S.A. & Whitham, T.G. (2004). A genetic component to ecosystem processes: the role of genetic variation, and condensed tannins on soil nitrogen dynamics. *Ecol. Lett.*, 7, 127–134.

Schweitzer, J.A., Bailey, J.K., Hart, S.C., Wimp, G.M., Chapman, S. & Whitham, T.G. (2005a). The interaction of plant genotype and herbivory decelerate leaf litter decomposition and alter nutrient dynamics. *Oikos*, 110, 133–145.

Schweitzer, J.A., Bailey, J.K., Hart, S.C. & Whitham, T.G. (2005b). Synergistic effects of plant genotype and herbivory alter litter decomposition and nutrient flux. *Ecology*, 86, 2834–2840.

Simchuk, A.P., Ivashov, A.V. & Companiytsev, V.A. (1999). Genetic patterns as possible factors causing population cycles in oak leafroller moth, *Tortrix viridana*, L. *For. Ecol. Manage.*, 113, 35–49.

Sipura, M. (1999). Tri-trophic interactions: willows herbivorous insects and insectivorous birds. *Oecologia*, 121, 537–545.

Stiling, P. & Rossi, A.M. (1996). Complex effects of genotype and environment on insect herbivores and their enemies. *Ecology*, 77, 2212–2218.

Treseder, K.K. & Vitousek, P.M. (2001). Potential ecosystem level effects of genetic variation among populations of *Metrosideros polymorpha* from a soil fertility gradient in Hawaii. *Oecologia*, 126, 266–275.

Wade, M.J. (2003). Community genetics and species interactions. *Ecology*, 84, 583–585.

Weis, A.E. & Abrahamson, W.G. (1986). Evolution of host-plant manipulation by gall makers: ecological and genetic factors in the Solidago-Eurosta system. *Am. Nat.*, 127, 681–695.

Whitham, T.G. (1989). Plant hybrid zones as sinks for pests. *Science*, 244, 1490–1493.

Whitham, T.G., Young, W., Martinsen, G.D., Gehring, C.A., Schweitzer, J.A., Shuster, S.M. *et al.* (2003). Community and ecosystem genetics: a consequence of the extended phenotype. *Ecology*, 84, 559–573.

Wilson, D.S. (1997). Biological communities as functionally organized units. *Ecology*, 78, 2018–2024.

Wimp, G.M. & Whitham, T.G. (2001). Biodiversity consequences of predation and host plant hybridization on an aphid-ant mutualism. *Ecology*, 82, 440–452.

Wimp, G.M., Young, W.P., Woolbright, S., Martinsen, G.D., Keim, P. & Whitham, T.G. (2004). Conserving plant genetic diversity for dependent animal communities. *Ecol. Lett.*, 7, 776–780.

Wimp, G.M., Martinsen, G.D., Floate, K.D., Bangert, R.K. & Whitham, T.G. (2005). Plant genetic determinants of arthropod community structure and diversity. *Evolution*, 59, 61–69.