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PLANT-MICROBE-ANIMAL INTERACTIONS - ORIGINAL RESEARCH

Plant genetic identity of foundation tree species and their hybrids affects a litter-dwelling generalist predator

**Todd Wojtowicz · Zacchaeus G. Compson ·
Louis J. Lamit · Thomas G. Whitham ·
Catherine A. Gehring**

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Abstract The effects of plant genetics on predators, especially those not living on the plant itself, are rarely studied and poorly understood. Therefore, we investigated the effect of plant hybridization and genotype on litter-dwelling spiders. Using an 18-year-old cottonwood common garden, we recorded agelenid sheet-web density associated with the litter layers of replicated genotypes of three tree cross types: *Populus fremontii, Populus angustifolia*, and their F_1 hybrids. We surveyed 118 trees for agelenid litter webs at two distances from the trees (0–100 and 100–200 cm from trunk) and measured litter depth as a potential mechanism of web density patterns. Five major results emerged: web density within a 1-m radius of *P. angustifolia* was approximately three times higher than within a 1-m radius of *P. fremontii*, with F_1 hybrids having intermediate densities; web density responded to *P. angustifolia* and F_1 hybrid genotypes as indicated by a significant genotype × distance interaction, with some genotypes exhibiting a strong decline in web density with distance, while others did not; *P. angustifolia* litter layers were deeper than those of *P. fremontii* at both distance classes, and litter depth among *P. angustifolia* genotypes differed up to 300 %; cross type and genotype influenced web density via their effects on litter depth, and these effects were influenced by distance; web density was more sensitive to the effects of tree cross type than genotype. By influencing generalist predators, plant hybridization and genotype may indirectly impact trophic interactions such as intraguild predation, possibly affecting trophic cascades and ecosystem processes.

Keywords Agelenidae · Genotype · *Populus* · Cross type · Intraspecific plant variation

Introduction

Plant genetic identity (e.g., species, interspecific hybrids, genotypes) can influence a diverse array of associated biota. For example, plant hybrid systems can influence arthropod and understory plant species abundance and community composition (Strauss 1994; Whitham et al. 1999; Drew and Roderick 2005; Lamit et al. 2011a), while intraspecific plant variation is known to affect arthropods, understory and epiphytic plants, microbes, and epiphytic lichens (Karban 1989; Johnson and Agrawal 2005; Haloin and Strauss 2008; Schweitzer et al. 2008; Crutsinger et al. 2010; Keith et al. 2010; Lamit et al. 2011b; Zytynska et al. 2011; Whitham et al. 2012). Although species sensitivity to plant genetic identity is a widespread phenomenon (Haloin and Strauss 2008; Whitham et al. 2012), much of the arthropod research to date has focused on herbivores and other taxa that directly interact with the living plant.

Arthropod predators and parasitoids can be sensitive to interspecific plant hybrid systems (Eisenbach 1996; Wimp et al. 2005) and intraspecific variation (Johnson and Agrawal 2005; Barbour et al. 2009a, b; Crutsinger et al.

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T. Wojtowicz (✉) · Z. G. Compson · L. J. Lamit ·
T. G. Whitham · C. A. Gehring
Department of Biological Sciences, Northern Arizona University,
Flagstaff, AZ 86011-5640, USA
e-mail: tw5@nau.edu

T. G. Whitham · C. A. Gehring
Merriam-Powell Center for Environmental Research, Northern
Arizona University, Flagstaff, AZ 86011-5640, USA

2009), yet little is known about specific taxa of predators, such as spiders, which are important generalist predators in terrestrial ecosystems (Riechert and Bishop 1990; Lawrence and Wise 2000; Pringle and Fox-Dobbs 2008). Although research on this topic is almost exclusively on plant-dwelling species, Barbour et al. (2009a) reported that litter-dwelling spider abundance varied according to the race of *Eucalyptus globulus* litter. Ground-dwelling spiders are likely to be sensitive to plant genetic identity because interspecific plant hybridization and plant genotype influence litter characteristics (Schweitzer et al. 2004; Farrer and Goldberg 2009; Crutsinger et al. 2010), and ground-dwelling spiders are sensitive to litter traits (Uetz 1979; Bultman and Uetz 1982; Loeser et al. 2006).

It is necessary to better understand the influence of plant genetic identity on spiders because their direct and indirect interactions with plant- and litter-dwelling arthropods can influence plants and ecosystem processes. However, predicting the outcome of spider interactions is complicated by the fact that they prey on herbivores, detritivores, and other predators. For example, spiders can indirectly decrease plant damage by preying on herbivores (Riechert and Bishop 1990; Romero and Vasconcellos-Neto 2004); however, they can also release herbivores from predation pressure by preying on species that strongly regulate herbivore populations [e.g., intraguild predation (Finke and Denno 2006)]. Additionally, Lawrence and Wise (2000, 2004) reported that spiders can either increase or decrease litter decomposition rates. They hypothesized that litter type and/or preying on common fungivores and their predators determined if decomposition rates would increase or decrease due to spider activity. The presence of litter, which increases habitat complexity, can change the strength of intraguild predation with consequences for herbivore abundance and plant biomass (Finke and Denno 2006). However, little attention has been paid to the potential role of plant hybridization and genotype on spiders and their direct and indirect interactions with other arthropods, plants, and ecosystem processes. To begin to address this issue it is necessary to first quantify the effect plant genetic identity has on spiders. Ground-dwelling spiders may be particularly interesting to study because it is already known that an aspect of their habitat, plant litter, can influence spider abundance (Uetz 1979; Loeser et al. 2006) and intraguild predation (Finke and Denno 2006).

In this study, we used an 18-year-old cottonwood common garden to investigate the sensitivity of litter-dwelling spiders from the family Agelenidae to two scales of plant genetic identity, the genetic gradient created by the *Populus fremontii* (Fremont cottonwoods) × *Populus angustifolia* (narrowleaf cottonwoods) hybrid system and tree genotype within each *Populus* species and their F_1 hybrids. Our study addressed the following hypotheses:

1. Agelenid web abundance would be highest under narrowleaf cottonwoods compared to Fremont cottonwoods or F_1 hybrids. Field observations of litter webs and litter depth prior to conducting this study provided the impetus for this hypothesis.
2. Litter-dwelling agelenids would be sensitive to plant genotype. Past research from a variety of systems suggests that invertebrates can be sensitive to intraspecific plant variation (Haloin and Strauss 2008; Whitham et al. 2012), including litter-dwelling species (Barbour et al. 2009a).
3. Litter depth would be influenced by plant genetic identity at the hybrid and genotype scales. Narrowleaf cottonwood litter decomposes more slowly (Driebe and Whitham 2000; Schweitzer et al. 2004; LeRoy et al. 2006) and is more curled than Fremont cottonwood or F_1 hybrid litter (T. Wojtowicz, unpublished data); therefore, narrowleaf cottonwoods may be associated with the deepest litter layers. Additionally, litter depth can be influenced by intraspecific plant variation (Crutsinger et al. 2010).
4. Agelenid web density would be higher when associated with deeper litter layers. Litter-dwelling spiders generally respond positively to increased litter quantity (Uetz 1979; Bultman and Uetz 1982; Loeser et al. 2006).

Addressing these hypotheses provided insight on the sensitivity of a common family of spiders to litter systems influenced by plant genetic identity. Additionally, it is the first step to addressing how the relationship between spiders and plant genetic identity may extend to other taxa and ecosystem processes.

Materials and methods

Study system

We tested our hypotheses in a common garden located at the Ogden Nature Center in Ogden, Utah, USA (latitude 41.2467, longitude –112.0095, elevation 1,299 m). The garden contains replicated genotypes of cottonwood trees from the *P. fremontii* × *P. angustifolia* hybrid system including Fremont cottonwoods, narrowleaf cottonwoods, and their natural F_1 hybrids, hereafter referred to as “cross types.” The garden was planted in 1991 using a random design with respect to tree cross type and genotype using cuttings collected from trees found along 105 km of the Weber River, Utah, including a 13-km-long hybrid zone. Thirty-five restriction fragment length polymorphism markers were used to verify the uniqueness of each tree genotype, and their cross type designation (Martinsen et al. 2001). By largely standardizing environmental factors and tree age, and using a random planting design, this 18-year-old common garden allowed us to examine the influence of plant genetic identity on a common spider family while limiting within-site variability. Additionally, previous studies showed patterns found in the garden are generally representative of those found in natural stands of *Populus* (Wimp et al. 2004; Bangert et al. 2006a, b; Lojewski et al. 2009; Busby et al. 2013, 2014).

Spider web surveys

Our study focused on webs created by agelenid spiders for several reasons. First, Agelenidae is found in a wide range of habitats from semi-arid grasslands (Riechert 1976) to tropical rainforests (Riechert et al. 1986), so patterns found in our study may be broadly applicable. Second, agelenids make conspicuous, easy to identify sheet-webs with a funnel at one end of the web (Bennett and Ubick 2005; Online Resource 1). Finally, their webs are often constructed over or on the litter layer (Riechert and Tracy 1975; Riechert 1976), so genetically based differences in plant litter traits could affect web-site choice by spiders.

We determined agelenid sheet-web density (webs m^{-2}) on cottonwood litter at two distances, 0–100 and 100–200 cm from the base of each tree. We surveyed out to 2 m from the base of the trees for several reasons. First, although arthropods can be sensitive to distance from tree trunks (Scheu and Poser 1996; Frick et al. 2007), the importance of distance to litter-dwelling arthropods has not yet been tested in the context of plant genetic identity. Second, before the study commenced, we observed a reduction in web density beyond 1 m from the base of the trees (which is supported by our data, see "Results") and noted very few webs beyond 2 m from the trees (T. Wojtowicz, personal observation). Therefore, we focused on the spatial scale that yielded the most webs. Third, it seemed reasonable to assume that, if there was an influence of tree genetic identity on agelenid spider webs, it would be detected closer to the trees rather than further away. The mixing of litter from different tree cross types occurs within 1 m of the tree trunk in the garden (T. Wojtowicz, unpublished data), and it is likely that litter mixing intensifies at further distances from the trunk, diluting the genetic identity effects of the focal tree. Finally, trees in the garden are planted 4–5 m apart north to south, and 6–7 m apart east to west, so we restricted our surveys to within 2 m of each tree to be confident that we were attributing each web to the correct tree. We felt that extending the surveys further from the tree trunk increased the probability of attributing spider webs to the wrong tree.

Every litter web was counted within each distance class around the base of each tree trunk. Because trees with larger trunk diameters and increasing distance from the base of the tree translates into more area surveyed, we used the diameter of the trunk at its base to calculate the true area surveyed, and standardized web abundance to webs per square meter for all analyses. In 2009, we surveyed webs on 10 April, 8–9 June, 6–9 July, 12–14 August, 11–12 October, and 25–26 November. The multiple survey dates allowed us to estimate peak web abundance, and to assess if webs persist for more than one growing season. We surveyed all genotypes that were replicated at least three times, which included 118 trees represented by 78 narrowleaf cottonwoods (16 replicated genotypes; three to 13 replicates per genotype), 14 Fremont cottonwoods (three replicated genotypes; four to seven replicates per genotype), and 26 F_1 hybrids (five replicated genotypes; three to six replicates per genotype).

We surveyed agelenid webs instead of the spiders themselves for two reasons. First, web placement is important to spiders. Web-building spiders engage in active web placement, construct webs non-randomly in the environment (Riechert 1974, 1976; McNett and Rypstra 2000), and web location can influence spider reproductive success (Riechert and Tracy 1975). Therefore, data on the effect of habitat on webs provide insight into how spiders respond to their environment. Second, because we conducted multiple web surveys, we were not interested in capturing or disturbing the spiders to check for their presence for every survey. Therefore, we used a non-destructive and unobtrusive approach to our surveys.

We acknowledge that by focusing only on webs, we cannot say for certain a spider inhabited every web we surveyed, or if individual spiders created multiple webs. However, there are several reasons why these are not serious limitations. First, although we did not quantify if webs were inhabited, we frequently noticed agelenid spiders on their webs early and late in the day (when there was less sunlight and lower temperatures in the garden), and the vast majority of the webs we surveyed were undamaged, a sign of web upkeep and spider habitation. Second, web construction is energetically expensive, especially for sheet-web spiders like agelenids (Prestwich 1977; Janetos 1982; Tanaka 1989) because these webs are solid sheets of dense webbing, as opposed to the more open architecture of orb weaver webs. In fact, one agelenid species, *Agelena limbata*, needs to use ~nine to 19 times its daily energetic maintenance cost to produce a single web (Tanaka 1989). Although agelenid spiders can abandon webs and create new ones (Riechert 1976), the high cost of building sheet-webs should limit how often this happens (Janetos 1982; Tanaka 1989). Third, web site choice may be influenced by the spiders' experience over time (Riechert 1976). By restricting our statistical analyses to the end of the summer (see "Statistical analyses"), we focused on the web choice of spiders that had most of the summer to find quality web sites, which should further decrease the number of spiders abandoning their webs late in the season. Therefore, the occurrence of abandoned webs should be limited, and web abundance should approximate spider abundance.

We collected 30 spiders from the garden (28 immature, two adult) between July 2008 and August 2009 for identification. Using Ubick et al. (2005) we identified all the spiders as Agelenidae, and the two mature female spiders as *Hololena* and *Agelenopsis*. All captured immature spiders were clearly one of two morphotypes, and based on morphological traits, they are likely the same genera as the adult females. However, we only had two sexually mature adults to identify to genus; therefore, it is difficult to be conclusive about the identity of the spider genera. What is clear is that the spiders were Agelenidae, and more than one agelenid species was present in the garden. Although we could readily distinguish between the two immature morphotypes in the field, there was no noticeable difference in their webs. Both morphotypes of the immature spiders were common in the garden, and have been trapped or observed in association with all tree cross types and on all survey dates when spiders were active.

Litter depth

In April 2009 we took a total of 16 litter-depth measurements beneath each web survey tree with a ruler. At each cardinal direction we measured depth at 25, 75, 125, and 175 cm from the tree trunk, and averaged the two closest and two furthest distances for each tree to represent the mean litter depth for the 0- to 100- and 100- to 200-cm distances, respectively. Litter depth was measured in April, prior to web construction (see "Results"), to avoid disruption of spider behavior, and disturbance of their habitat and webs.

Applicability of web density patterns beyond the common garden

To determine if the patterns we documented in the common garden may be applicable beyond the garden environment, we tested the robustness of our results using a reduced data set. Common gardens are generally small in size compared to the area in which plant material for the garden was originally collected (Tack et al. 2012), and this is the case for our study. This may result in relatively high genetic variation and low environmental variation within the garden that masks the importance of environment while enhancing the plant genetic identity effect (Hersch-Green et al. 2011; Tack et al. 2012). Therefore, we analyzed both our full data set, as well as a reduced data set that only included genotypes collected within the 13-km natural hybrid zone (all removed genotypes were narrowleaf cottonwoods) to determine if dramatically restricting the spatial scale of the genotype collection area and the concomitant decrease in genetic variation would result in different web density patterns. The reduced data set contained total of 98 trees (down from 118) from all three cross types collectively, including ten narrowleaf genotypes (down from 16). The same statistical model that was used for the full data set (see below) was also used for the reduced data set.

Statistical analyses

JMP 10.0 (SAS Institute 2012) was used for all analyses unless otherwise noted. We assessed if cottonwood genetic identity (genotype and cross type) and distance from tree base were important to litter web density or leaf litter depth. Only web density for August was statistically analyzed because surveys indicated that this was the time of peak web abundance (see "Results"). A linear mixed effects model for each response variable was fit using restricted maximum likelihood (REML) (Conner and Hartl 2004) containing the following fixed effects: tree cross type, distance from tree base, and cross type × distance interaction. The terms genotype and genotype × distance interaction were coded as random effects. Additionally, we nested the random effect of individual tree identification within genotype within cross type to account for multiple data points (i.e., the two distance classes) from each individual tree. This term was not of interest beyond preserving data structure; therefore, we did not report on the effects of individual tree. *F*-tests were used to test fixed effects and likelihood ratio tests were used for random effects. Webs per square meter data were square root transformed to address normality and homogeneity of variance issues, while litter depth data did not require transformation. When genotype was significant we used the same REML approach described above, but did so individually for each cross type within a distance class. *P* values for post hoc multiple pair-wise comparisons were adjusted by using least squares ANOVA to generate *P* values, and the false discovery rate (FDR) approach (Benjamini and Hochberg 1995; Waite and Campbell 2006) to adjust them. R version 2.15 (R Development Core Team 2012) was used to calculate FDR.

To examine the relationship between litter depth and web density, we regressed web density on litter depth for each distance class using genotype means for litter depth and web density for all tree cross types. No data transformations were necessary for the regressions.

Table 1 Effects of tree cross type, genotype, and distance (0–100 or 100–200 cm from tree base) on litter web density and litter depth using a linear mixed effects model fit with restricted maximum likelihood

Response variable	Predictor variables	*df*	χ^2- or *F*-statistic	*P*
Webs (m^{-2})	Cross type	2	$F = 5.25$	*0.02*
	Genotype (cross type)	1	$\chi^2 = 0.0$	1.0
	Distance	1	$F = 31.47$	*<0.0001*
	Cross type × distance	2	$F = 3.14$	0.07
	Genotype (cross type) × distance	1	$\chi^2 = 3.86$	*0.05*
Litter depth	Cross type	2	$F = 2.65$	0.10
	Genotype (cross type)	1	$\chi^2 = 4.74$	*0.03*
	Distance	1	$F = 4.89$	*0.05*
	Cross type × distance	2	$F = 7.56$	*0.007*
	Genotype (cross type) × distance	1	$\chi^2 = 0.057$	0.81

P values in *italic* are statistically significant

Results

Litter web abundance during the survey months

A total of 2,702 agelenid webs were found on leaf litter within 2 m of the 118 trees over the 6 months surveyed (April–November). Approximately 98 % of all observed webs were found between June and August. August was the peak month for web abundance accounting for ~60 % of all litter webs observed with approximately six and two times greater web abundance than June and July, respectively (Online Resource 2). No webs were found in April, and of the few webs found in October (58 webs) and November (one web; Online Resource 2) all were seriously damaged, suggesting that webs did not persist through the winter.

The effects of tree cross type

Web density and distance

Populus cross type and distance from tree influenced spider web density (Table 1), even with the reduced data set (Online Resource 3). At both distances from the tree trunk, narrowleaf cottonwoods were associated with more agelenid litter webs than Fremont cottonwoods, and F_1 hybrids had intermediate web densities (Fig. 1a). When averaged over both distance classes, narrowleaf cottonwoods were associated with 2.7 times and 1.5 times higher web density than Fremont cottonwoods and F_1 hybrids, respectively. Web density decreased by ~50 % at 100–200 compared to 0–100 cm from the tree (Fig. 1a). The negative effect of distance on web density partially muted the cross type effect at 100–200 cm. A decline in web density with distance was detected for narrowleaf cottonwoods (FDR corrected $P < 0.0001$) and F_1 hybrids (FDR corrected $P = 0.05$), but not for Fremont cottonwoods (FDR corrected $P > 0.1$), resulting in a trend towards a significant cross type × distance interaction ($P = 0.07$; Table 1).

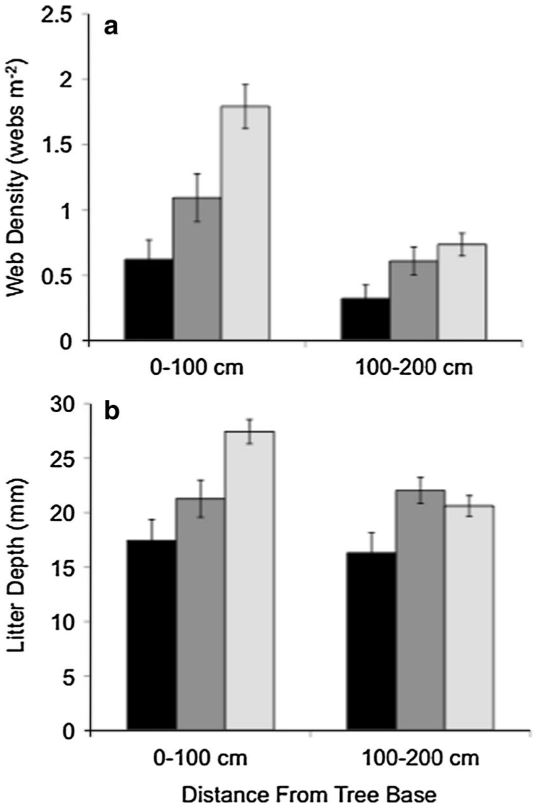

Fig. 1 The effect of tree cross type at 0–100 and 100–200 cm from tree trunk on **a** web density and **b** litter depth with Fremont cottonwood (*black bars*), F_1 hybrid (*dark gray bars*), and narrowleaf cottonwood (*light gray bars*) cross types. *Error bars* are ±1 SEM

Litter depth

Litter depth was also sensitive to tree cross type and distance. When averaged across all cross types, litter depth decreased with distance from the trunk (Table 1; Fig. 1b). However, narrowleaf cottonwoods exhibited a strong decline in litter depth with distance (FDR-corrected $P < 0.0001$) while Fremont cottonwoods and F_1 hybrids did not (FDR-corrected $P > 0.1$ for both cross types), resulting in a significant cross type × distance interaction (Table 1; Fig. 1b). Narrowleaf cottonwoods had deeper litter layers than Fremont cottonwoods (FDR-corrected $P = 0.002$) and F_1 hybrids (FDR-corrected $P = 0.005$) at 0- to 100-cm distance, but narrowleaf litter layers were not deeper than the other two cross types at the further distance (FDR-corrected $P = 0.10$ and $P = 0.44$ for Fremont cottonwoods and F_1 hybrids, respectively).

The effects of tree genotype

Web density and distance

Narrowleaf cottonwood and F_1 hybrid web densities were influenced by tree genotype as illustrated by a genotype × distance interaction (Table 1; Online Resource 4a, b). However, genotype alone was not significant (Table 1). Some genotypes within these two cross types exhibited strong declines in web density with distance, while other genotypes exhibited little change in web density with distance (Fig. 2a). However, neither genotype nor the genotype × distance interaction term was significant in the reduced model (Online Resource 3).

Litter depth

There was significant genotype variation in litter depth among narrowleaf cottonwoods (Table 1). This variation among narrowleaf cottonwoods was exhibited at both distance classes (0–100 cm, $\chi^2 = 5.78$, $P = 0.02$; 100–200 cm, $\chi^2 = 5.78$, $P = 0.02$; Fig. 2b, c). In contrast, there was no significant genotype variation in litter depth among Fremont cottonwoods or F_1 hybrids ($\chi^2 < 0.05$, $P > 0.50$ for both Fremont cottonwoods and F_1 hybrids).

Relationship between litter depth and web density

There was a significant positive linear relationship between litter depth and web density. Across all genotypes and cross types, litter depth alone accounted for 24 and 20 % of the variation in web density at the 0- to 100-cm ($P = 0.02$) and 100- to 200-cm ($P = 0.03$) distance, respectively (Fig. 3a, b). The most shallow litter layers and lowest agelenid web densities were almost exclusively associated with Fremont cottonwood and F_1 hybrid genotypes at the 0- to 100-cm distance. In contrast, the trees associated with the deepest litter layers and highest web densities at 0–100 cm were almost completely dominated by narrowleaf cottonwood genotypes (Fig. 3a). At 100- to 200-cm distance from the tree, Fremont cottonwood genotypes were again associated with some of the most shallow litter depths and lowest agelenid web densities, with F_1 hybrid genotypes being associated with deeper litter depths and higher agelenid web densities. Narrowleaf cottonwood genotypes, however, were

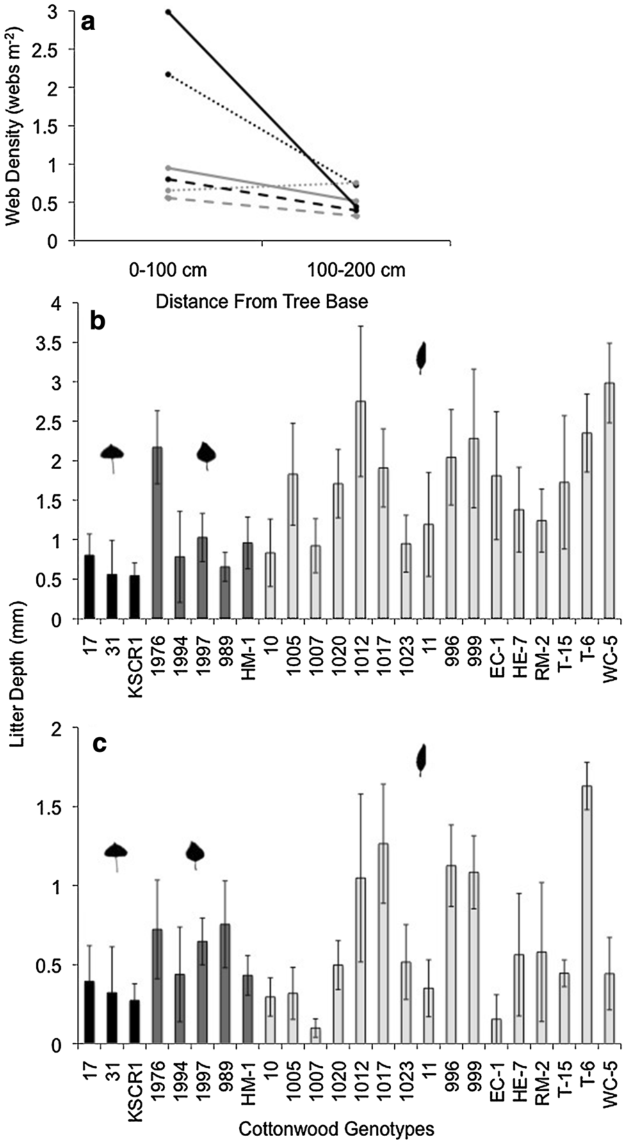

Fig. 2 The effect of **a** genotype × distance interactions on mean agelenid web density and genotype variation in litter depth at **b** 0–100 cm and **c** 100–200 cm from the base of the trees. Fremont cottonwood (*solid lines*), F_1 hybrid (*dotted lines*), and narrowleaf cottonwood (*dashed lines*) genotypes with the lowest (*gray lines*) and highest (*black lines*) web density are depicted. Only the two most disparate genotypes per cross type are presented in **a** to make it easier to see the general patterns across all cross types. Fremont cottonwood (*black bars*), F_1 hybrid (*dark gray bars*), and narrowleaf cottonwood (*light gray bars*) genotypes in **b** are represented by their respective leaf icons. Untransformed data are presented for ease of viewing. *Error bars* are ±1 SEM

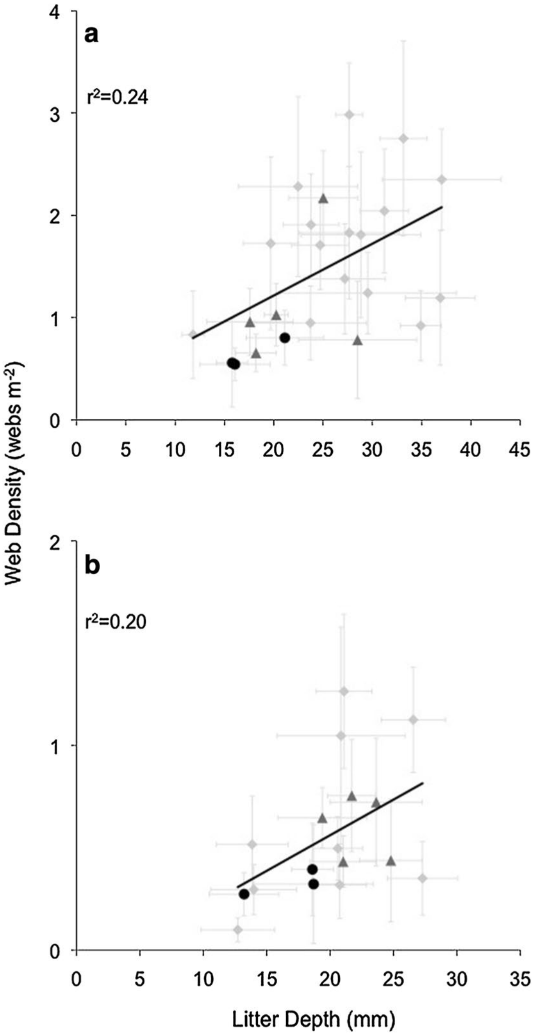

Fig. 3 Relationship between litter depth and web density at **a** 0- to 100-cm and **b** 100- to 200-cm distance from tree base. Genotype means (±1 SE; *light grey error bars*) of Fremont (*black circles*), narrowleaf (*light gray diamonds*), and F_1 hybrid (*dark gray triangles*) cottonwoods are presented

well represented along the entire gradient of litter depth and web densities at 100–200 cm, including genotypes with some of the deepest litter layers and highest web densities (Fig. 3b).

Discussion

Effects of a *Populus* hybrid system on associated taxa and their habitat

Our data suggest that the litter layer associated with narrowleaf cottonwoods is a relatively high-quality habitat for agelenid spiders compared to the habitats found beneath Fremont cottonwoods or F_1 hybrids. Higher quality habitats attract more spiders (Riechert and Bishop 1990; Halaj et al. 2000; Schmidt and Rypstra 2010), and we found almost three times and 1.5 times the web density within 200 cm of narrowleaf cottonwoods compared to Fremont cottonwoods and F_1 hybrids, respectively. The higher density of webs associated with narrowleaf cottonwoods, especially within 100 cm of the tree (Fig. 1a), indicates that there is, on average, less space between webs beneath this cross type compared to Fremont cottonwoods and F_1 hybrids. This is important because agelenid spiders can be territorial and do not tolerate encroachment into their territory by other agelenids (Riechert 1981). However, territory size can change with habitat quality. Agelenid territory size decreases with increased habitat quality (Riechert 1979, 1981), suggesting that narrowleaf cottonwoods are associated with a higher agelenid web density because they offer a higher quality habitat for these spiders.

The cross type effect on web density was still significant when only using genotypes originally collected from the natural hybrid zone. This indicates that the cross type patterns we detected in the common garden may also be found beyond the garden environment. Although we know of no other studies investigating the response of litter-dwelling arthropods to plant hybridization, Bangert et al. (2006a, b) reported that arthropod herbivores responded to *Populus* cross type at the scales of the common garden, tree stands, individual rivers, and region. In other words, the effects of tree cross type were detected even at very large spatial scales, where environmental factors were expected to be strong. Given the extremely large spatial scale over which herbivores can respond to tree hybridization in the *Populus* system [up to 720,000 km^2 (Bangert et al. 2006b)], it seems likely that litter taxa, even if they are less sensitive than herbivores, will also be responsive to plant hybridization in habitats that differ from the common garden in size and tree genetic variation. Although the natural hybrid zone is still larger than the common garden, we decreased the collection area by almost 90 % (linear distance) and reduced the number of narrowleaf genotypes by almost 40 %, and still detected a significant cross type effect. The results of Bangert et al. (2006a, b) and others that have investigated multiple spatial scales found significant effects of *Populus* cross types on associated organisms (e.g., Busby et al. 2013, 2014). Similarly, the congruent results from our full and reduced data sets suggest that the effect of tree cross type on web density is likely applicable beyond the confines of the common garden environment.

Although we have data on web density and not spider density, these data should be indicative of how agelenid spiders are interpreting the environment beneath the different cottonwood cross types. Agelenid spiders are highly mobile. Therefore, if some spiders eventually determined that their web sites needed to be abandoned in favor of a higher quality sites, they could have easily and quickly relocated beneath another tree. Additionally, agelenid spiders can become more discriminating in their web site choice over time (Riechert 1976). Therefore, by the time we conducted our August survey, the spiders had had most of the summer to locate, and if necessary, relocate to higher quality web site locations. In addition, agelenid webs are easily damaged or destroyed by wind, rain, animals, and debris, suggesting that webs that are not constantly maintained by a spider will not last very long. Finally, web site location is not trivial for web-building spiders as it can strongly influence spider reproductive success (Riechert and Tracy 1975). Although we cannot be certain that spiders inhabited 100 % of the webs, for the aforementioned reasons it seems likely that the vast majority of them were active webs inhabited by spiders, and that narrowleaf cottonwood litter is a relatively high-quality habitat for agelenids.

Litter depth appears to be an important habitat trait influencing agelenid web density, and there are several lines of evidence suggesting a link between tree cross type, web density, and litter depth:

1. Web density and litter depth responded to tree cross type (Fig. 1a, b), although the effect of cross type on litter depth must be interpreted in the context of distance. Additionally, there was also a strong trend towards a significant cross type × distance interaction affecting web density ($P = 0.07$; Table 1). In fact, the cross type × distance relationship for web density and litter depth was expressed in the same way; they both declined with distance under narrowleaf cottonwoods. This may be the result of narrowleaf cottonwoods being generally smaller trees (Lojewski et al. 2009), and having smaller canopies compared to the other two cross types.
2. When averaged over all tree cross types, both web density and litter depth followed the same pattern, decreasing with increasing distance (Fig. 1a, b).
3. At the 0- to 100-cm distance, web density and litter depth again followed the same pattern—highest under narrowleaf cottonwoods, lowest under Fremont cottonwoods, and intermediate under F_1 hybrids (Fig. 1a, b). However, this pattern did not extend to the 100- to 200-cm distance.
4. Higher web densities were generally associated with deeper litter layers (Fig. 3a, b).

The relationship between web density and litter depth in our study supports previous research indicating that spiders respond positively to plant litter. For example, an agelenid spider species found in semi-arid systems prefer the presence of litter when selecting web sites (Riechert and Tracy 1975; Riechert 1976). Additionally, spider abundance and diversity generally increases with increased litter quantity (Uetz 1979; Loeser et al. 2006). The positive response of web density to litter depth in our study could be because deeper litter layers can decrease soil temperature and increase soil moisture (Uetz 1979; Beatty and Sholes 1988), which can create a more favorable microclimate for ground-dwelling spiders (Uetz 1979), including agelenids (Riechert and Tracy 1975). Additionally, deeper litter depths may be associated with more interstitial space in the litter layer (Uetz 1979). More interstitial space in the litter layer may offer more quality sites to place the escape end of an agelenid web funnel, and may enhance the ability of a spider to safely escape if necessary. Our original hypotheses regarding the effects of cross type on web density and litter depth were generally supported, but appear to have been too simplistic. Although web density and litter depth were linked via tree cross type, the relationship is more complex and context dependent than we originally hypothesized, and the cross type-litter depth relationship did not extend to the 100- to 200-cm distance.

Distance from tree also influenced web density beneath cottonwood cross types. Narrowleaf cottonwoods and F_1 hybrids drove this pattern, while Fremont cottonwood web density was not influenced by distance. Several factors may have contributed to these distance effects. Tree canopies may be less able to provide shade further from the tree trunk, and this could negatively affect spiders due to increased thermal stress (Riechert and Tracy 1975). This may be particularly important for narrowleaf cottonwoods in the garden because they are generally smaller trees (Lojewski et al. 2009), and experienced the largest decline in webs with distance. The lack of a distance effect for Fremont cottonwoods may be because litter nearest to these trees appeared to be periodically disturbed by strong stemflow during rainstorms, as indicated by evidence of water-related disturbance of the soil and litter near their trunks and shallow or non-existent litter layers within ~10–25 cm of their trunks (T. Wojtowicz, personal observations). This was not observed for narrowleaf cottonwoods, possibly as a result of these trees having more branches on the lower reaches of their trunks (T. Wojtowicz, unpublished data), which may decrease stemflow velocity. Therefore, the cumulative effects of litter disturbance via stemflow near Fremont cottonwood trunks, combined with any decrease in shade further from their trunks, may have kept web densities relatively low at both distance classes beneath Fremont cottonwoods.

Effects of tree genotype on associated taxa and their habitat

When all narrowleaf genotypes were used, we found that agelenid web abundance was influenced by intraspecific plant variation, but this effect was not as straightforward as the effect of tree cross type. Agelenid litter web abundance was influenced by tree genotype, but this response was affected by distance from tree (Table 1). Our findings generally support those of Barbour et al. (2009a) who reported that spider abundance was affected by intraspecific variation of *Eucalyptus globulus* litter systems. Additionally, our data support studies that indicate terrestrial litter invertebrate communities can respond to intraspecific plant variation (Classen et al. 2006; Barbour et al. 2009a; Zytynska et al. 2011). An important difference between our study and the aforementioned ones is that our study incorporated distance from tree. Other studies investigating the influence of intraspecific plant variation on terrestrial litter arthropods sampled at a single distance from the plant, which was usually directly adjacent to the base of the tree. Our study indicates that, in the garden, there was a complex spatial mosaic of relatively high and low agelenid web densities as a result of spiders differentially responding to cottonwood genotypes (and cross types) at different distances from the tree, which may influence prey abundance across this spatial mosaic of webs.

The significant genotype × distance interaction in our study occurred because some narrowleaf cottonwood and F_1 hybrid genotypes exhibited a strong decline in web density with distance, while other genotypes within these two cross types did not. Decreased amounts of litter can decrease spider abundance (Loeser et al. 2006). However, this does not seem to be the case for the narrowleaf genotypes as the genotype with most and least dramatic declines in web density with distance experienced a similar decline in litter depth with distance (data not shown). Additionally, the F_1 hybrid genotype that experienced the strongest decline in web density had very similar litter depth at both distances. However, the F_1 hybrid genotype that exhibited a slight increase in web density with distance also had a slightly deeper litter layer at the further distance (data not shown), which probably contributed to the significant interaction term for hybrid genotypes. Alternatively, it may be that some genotypes allow for more litterfall from neighboring genotypes and cross types at the 100- to 200-cm distance due to genotypic variation in canopy size or aboveground productivity (Lojewski et al. 2009). Tree genotypes with relatively large canopies will extend the reach of their litter-drop zones while genotypes with higher aboveground productivity will produce more leaf litter than those of lower productivity. Variation in these traits could result in differential litter mixing from different tree cross types and genotypes beneath individual trees influencing the physical complexity of the litter layer. This could be particularly important if there was differential mixing of the relatively flat litter of Fremont cottonwoods or the F_1 hybrids with the relatively curled narrowleaf cottonwood litter. Ground-dwelling spiders respond positively to habitat complexity (Uetz 1979; Bultman and Uetz 1982; Schmidt and Rypstra 2010), and intraspecific plant variation can affect physical features of plants (Bailey et al. 2004) influencing associated biota (Fritz and Price 1988; Barbour et al. 2009b; Crutsinger et al. 2010).

In contrast to the results using all the narrowleaf genotypes (Table 1), neither genotype nor the genotype × distance interaction term were significant when only using the genotypes from the natural hybrid zone (Online resource 3). This could be because the excluded narrowleaf genotypes were collected from higher elevations, and may have contained unique genetic variation compared to the narrowleaf genotypes collected in the hybrid zone. However, a confounding factor is that the reduced data set decreased the number of narrowleaf genotypes by almost 40 %, and reduced the total number of narrowleaf trees by ~25 %, which might have made it more difficult to detect potential genotype effects. Whatever the case, it is clear that agelenid spiders can be affected by tree genotype if there is enough plant genetic variation present.

Litter depth was also influenced by *Populus* intraspecific variation, but only among narrowleaf cottonwoods. Litter depth was influenced by narrowleaf genotype, but not by a significant genotype × distance interaction (Table 1). This might be explained by genotype variation in aboveground productivity among narrowleaf cottonwoods (Lojewski et al. 2009); the more productive genotypes probably create more litter than less productive genotypes. Although litter chemistry has often been investigated in the context of plant genotype (e.g., Madritch and Hunter 2005; LeRoy et al. 2007; Crutsinger et al. 2009), we know of only one other study that investigated the effects of intraspecific variation on litter depth, and that study reported that genetically based plant architectural phenotypes can influence litter depth (Crutsinger et al. 2010).

Other potential mechanisms of genetic effects on spiders

Although investigating the role of prey on agelenid web density was beyond the scope of this study, prey abundance is important to spiders (Riechert and Tracy 1975; Uetz 1975; Chen and Wise 1999). The cottonwood cross types in our study have different foliar arthropod communities (Wimp et al. 2005, 2007), and ground-dwelling spiders can intercept those prey if they fly or fall from the tree (Pringle and Fox-Dobbs 2008). Additionally, potential litter-dwelling prey species may be affected by litter layer characteristics such as depth and litter architecture (Uetz 1979; Stevenson and Dindal 1982), and intraspecific plant variation (Barbour et al. 2009a). Thus, litter-dwelling spiders beneath different cross types likely feed on different prey communities from the litter or from the trees themselves, contributing to the patterns we have documented here.

The amount of sunlight the litter layer receives could impact microclimate variables, such as temperature and moisture, which in turn, can also influence spiders (Riechert and Tracy 1975). In the Ogden Nature Center garden, photosynthetically active radiation is highest beneath narrowleaf canopies, lowest beneath Fremont canopies, with F_1 hybrids having intermediate levels (Lamit et al. 2011a), probably as a result of narrowleaf cottonwoods generally having smaller canopies. This suggests that the litter layer beneath narrowleaf cottonwoods is warmer and drier than Fremont cottonwoods' or F_1 hybrids' litter layers, and thus a more stressful environment for spiders. However, we found the highest agelenid web density associated with narrowleaf cottonwoods, the cross type that may be associated with the warmest and driest conditions. A possible explanation for this apparent contradiction is the deeper litter layer beneath narrowleaf cottonwoods. The deeper litter may mitigate the stresses brought on by more sunlight striking the litter layers beneath narrowleaf cottonwoods (Uetz 1979; Beatty and Sholes 1988) while offering a more structurally complex habitat for the spider (Uetz 1979).

Plant genetic identity and generalist predators: potential consequences for trophic interactions

By influencing the abundance of a generalist predator, plant genetic identity may also indirectly influence trophic interactions (Riechert and Bishop 1990). For example, our study suggests that the arthropod communities associated with the litter layer, and possibly the understory plant community (mostly grasses and forbs), experienced the most intense predation pressure by agelenid spiders beneath narrowleaf cottonwoods due to these trees having 2.7 and 1.5 times higher web density compared to Fremont and F_1 hybrid cottonwoods, respectively. It is also possible that there was differential predation pressure among narrowleaf and F_1 hybrid cottonwood genotypes, as per the significant genotype × distance interaction term. It is important to note that spider abundance and richness tend to increase with increased litter quantity (Uetz 1979; Bultman and Uetz 1982; Loeser et al. 2006), so it is likely that other spider taxa also responded to plant genetic identity in our study via its effects on litter depth, elevating predation pressure beneath narrowleaf cottonwoods even more.

Plant genetic identity may also influence more complex trophic interactions such as intraguild predation, which occurs when predators kill other predators who are also competitors for the same prey species (Polis and McCormick 1987; Gangon et al. 2011). Understanding intraguild predation is important because it is thought be a widespread interaction among many taxa, is considered important in structuring communities (Arim and Marquet 2004), and results in outcomes not predicted by simple predator–prey models. For example, simple trophic interactions can result in predators indirectly limiting plant damage by controlling herbivore populations as predicted by the Hairston-Smith-Slobodkin model (Hairston et al. 1960). Alternately, intraguild predation can yield the opposite result with generalist predators indirectly increasing herbivory by preying on species that are superior in controlling some herbivore taxa (Rosenheim et al. 1993; Snyder and Wise 2001). Although intraguild predation is common, it has not been studied in the context of plant genetic identity; however, there are several reasons to think that plant genetic identity may influence intraguild predation. First, it is known that plant genetic identity affects the abundance of generalist predators and potential prey species (e.g., Wimp et al. 2005; Barbour et al. 2009a, b). In fact, predators may be surprisingly sensitive to plant genetic identity because they can strongly respond to architectural traits of their habitat (Bultman and Uetz 1982; Barbour et al. 2009b), which can be strongly influenced by plant hybridization (Bailey et al. 2004) and intraspecific variation (Barbour et al. 2009b). Second, our study illustrates that plant genetic identity can influence litter depth, an important habitat characteristic for both spiders and their prey (Uetz 1979), and habitat characteristics can impact intraguild predation (Finke and Denno 2006; Schmidt and Rypstra 2010). For example, Finke and Denno (2006) reported that the presence of litter limited the influence of intraguild predation and enhanced the effects of a trophic cascade because predators who are fed upon by other predators were able to more effectively hide in the structurally complex habitat provided by litter, and thus contributed to controlling herbivore abundance, which ultimately resulted in an increase in plant biomass. Finally, intraguild predation is a common phenomenon that occurs on living plants, in the litter, and in soil (Polis and McCormick 1987; Polis et al. 1989; Rosenheim et al. 1993; Arim and Marquet 2004; Gangon et al. 2011), so it is likely that it often occurs in systems where plant genetic identity could influence the outcome of this important trophic interaction. The ubiquity and ecological importance of plant genetic identity effects and generalist predators necessitate a better understanding of how they interact and the consequences of these interactions.

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References

Arim M, Marquet PA (2004) Intraguild predation: a widespread interaction related to species biology. Ecol Lett 7:557–564

Bailey JK, Bangert RK, Schweitzer JA, Trotter T III, Shuster SM, Whitham TG (2004) Fractal geometry is heritable in trees. Evolution 58:2100–2102

Bangert RK, Allan GJ, Turek RJ, Wimp GM, Meneses N, Martinsen GD, Keim P, Whitham TG (2006a) From genes to geography: a genetic similarity rule for arthropod community structure at multiple geographic scales. Mol Ecol 15:4215–4228

Bangert RK, Turek RJ, Rehill B, Wimp GM, Schweitzer JA, Allan GJ, Bailey JK, Martinsen GD, Keim P, Lindroth RL, Whitham TG (2006b) A genetic similarity rule determines arthropod community structure. Mol Ecol 15:1379–1391

Barbour RC, Baker SC, O'Reilly-Wapstra JM, Harvest TM, Potts BM (2009a) A footprint of tree-genetics on the biota of the forest floor. Oikos 118:1917–1923

Barbour RC, Forster LG, Baker SC, Steane DA, Potts BM (2009b) Biodiversity consequences of genetic variation in bark characteristics within a foundation tree species. Conserv Biol 23:1146–1155

Beatty SW, Sholes ODV (1988) Leaf litter effect on plant species composition of deciduous forest treefall pits. Can J For Res 18:553–559

Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. J R Stat Soc B 57:289–300

Bennett RG, Ubick D (2005) Agelenidae. In: Ubick D, Paquin P, Cushing PE, Roth V (eds) Spiders of North America: an identification manual. Am Arachnol Soc, pp 56–59

Bultman TL, Uetz GW (1982) Abundance and community structure of forest floor spiders following litter manipulation. Oecologia 55:34–41

Busby PE, Newcombe G, Dirzo R, Whitham TG (2013) Genetic basis of pathogen community structure for foundation tree species in a common garden and in the wild. J Ecol 101:867–877

Busby PE, Newcombe G, Dirzo R, Whitham TG (2014) Differentiating genetic and environmental drivers of plant–pathogen community interactions. J Ecol 102:1300–1309. doi:10.1111/1365-2745.12270

Chen B, Wise DH (1999) Bottom-up limitation of predaceous arthropods in a detritus-based terrestrial food web. Ecology 80:761–772

Classen AT, DeMarco J, Hart SC, Whitham TG, Cobb NS, Koch GW (2006) Impacts of herbivorous insects on decomposer communities during the early stages of primary succession in a semi-arid woodland. Soil Biol Biochem 38:972–982

Conner JK, Hartl DL (2004) A primer of ecological genetics. Sinauer, Sunderland

Crutsinger GM, Sanders NJ, Classen AT (2009) Comparing intra- and inter-specific effects on litter decomposition in an old-field ecosystem. Basic Appl Ecol 10:535–543

Crutsinger GM, Strauss SY, Rudgers JA (2010) Genetic variation within a dominant shrub species determines plant species colonization in a coastal dune ecosystem. Ecology 91:1237–1243

Drew AE, Roderick GK (2005) Insect biodiversity on plant hybrids within the Hawaiian silversword alliance (Asteraceae: Heliantheae-Madiinae). Environ Entomol 34:1095–1108

Driebe EM, Whitham TG (2000) Cottonwood hybridization affects tannin and nitrogen content of leaf litter and alters decomposition. Oecologia 123:99–107

Eisenbach J (1996) Three-trophic-level interactions in cattail hybrid zones. Oecologia 105:258–265

Farrer EC, Goldberg DE (2009) Litter drives ecosystem and plant community changes in cattail invasion. Ecol Appl 19:398–412

Finke DL, Denno RF (2006) Spatial refuge from intraguild predation: implications for prey suppression and trophic cascades. Oecologia 149:265–275

Frick H, Nentwig W, Kropf C (2007) Influence of stand-alone trees on epigeic spiders (Araneae) at the alpine timberline. Ann Zool Fenn 44:43–57

Fritz RS, Price PW (1988) Genetic variation among plants and insect community structure: willows and sawflies. Ecology 69:845–856

Gangon A, Heimpel GE, Brodeur J (2011) The ubiquity of intraguild predation among predatory arthropods. PLoS ONE 6:1–7

Hairston NG, Smith FE, Slobodkin LB (1960) Community structure, population control, and competition. Am Nat 94:421–425

Halaj J, Cady AB, Uetz GW (2000) Modular habitat refugia enhance generalist predators and lower plant damage in soybeans. Biol Control 29:383–393

Haloin JR, Strauss SY (2008) Interplay between ecological communities and evolution: review of feedbacks from microevolutionary to macroevolutionary scales. Ann N Y Acad Sci 1133:87–125

Hersch-Green EL, Turley NE, Johnson TJ (2011) Community genetics: what have we accomplished and where should we be going? Philos Trans R Soc B 366:1453–1460

Janetos AC (1982) Foraging tactics of two guilds of web-spinning spiders. Behav Ecol Sociobiol 10:19–27

Johnson MTJ, Agrawal AA (2005) Plant genotype and environment interact to shape a diverse arthropod community on evening primrose (*Oenothera biennis*). Ecology 86:874–885

Karban R (1989) Fine-scale adaptation of herbivorous thrips to individual host plants. Nature 340:60–61

Keith AR, Bailey JK, Whitham TG (2010) A genetic basis to community repeatability and stability. Ecology 91:3398–3406

Lamit LJ, Bowker MA, Holeski LM, Næsborg RR, Wooley SC, Zinkgraf M, Lindroth RL, Whitham TG, Gehring CA (2011a) Genetically-based trait variation within a foundation tree species influences a dominant bark lichen. Fungal Ecol 4:103–109

Lamit LJ, Wojtowicz T, Kovacs Z, Wooley SC, Zinkgraf M, Whitham TG, Lindroth RL, Gehring CA (2011b) Hybridization among foundation tree species influences the structure of associated understory plant communities. Botany 89:165–174

Lawrence KL, Wise DH (2000) Spider predation on forest-floor Collembola and evidence for indirect effects on decomposition. Pedobiologia 44:33–39

Lawrence KL, Wise DH (2004) Unexpected indirect effect of spiders on the rate of litter disappearance in a deciduous forest. Pedobiologia 48:149–157

LeRoy CJ, Whitham TG, Keim P, Marks JC (2006) Plant genes link forests and streams. Ecology 87:255–261

LeRoy CJ, Whitham TG, Wooley SC, Marks JC (2007) Within-species variation in foliar chemistry influences leaf-litter decomposition in a Utah river. J N Am Benthol Soc 26:426–438

Loeser MR, McRae BH, Howe MM, Whitham TG (2006) Litter hovels as havens for riparian spiders in an unregulated river. Wetlands 26:13–19

Lojewski NR, Fischer DG, Bailey JK, Schweitzer JA, Whitham TG, Hart SC (2009) Genetic basis of aboveground productivity in two native *Populus* species and their hybrids. Tree Physiol 29:1133–1142

Madritch MD, Hunter MD (2005) Phenotypic variation in oak litter influences short- and long-term nutrient cycling through litter chemistry. Soil Biol Biochem 37:319–327

Martinsen GD, Whitham TG, Turek RJ, Keim P (2001) Hybrid populations selectivity filter gene introgression between species. Evolution 55:1325–1335

McNett BJ, Rypstra AL (2000) Habitat selection in a large orb-weaving spider: vegetational complexity determines site selection and distribution. Ecol Entomol 25:423–432

Polis GA, McCormick SJ (1987) Intraguild predation and competition among desert scorpions. Ecology 68:332–343

Polis GA, Myers CA, Holt RD (1989) The ecology and evolution of intraguild predation: potential competitors that eat each other. Annu Rev Ecol Syst 20:297–330

Prestwich KN (1977) The energetics of web-building in spiders. Comp Biochem Physiol 57A:321–326

Pringle RM, Fox-Dobbs K (2008) Coupling of canopy and understory food webs by ground-dwelling predators. Ecol Lett 11:1328–1337

R Development Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Riechert SE (1974) The pattern of local web distribution in a desert spider: mechanisms and seasonal variation. J Anim Ecol 43:733–746

Riechert SE (1976) Web-site selection in the desert spider *Agelenopsis aperta*. Oikos 27:311–315

Riechert SE (1979) Games spider play. II. Resource assessment strategies. Behav Ecol Sociobiol 6:121–128

Riechert SE (1981) The consequences of being territorial: spiders, a case study. Am Nat 117:871–891

Riechert SE, Bishop L (1990) Prey control by and assemblage of generalist predators: spiders in garden test systems. Ecology 71:1441–1450

Riechert SE, Tracy CR (1975) Thermal balance and prey availability: bases for a model relating web-site characteristics to spider reproductive success. Ecology 56:265–284

Riechert SE, Roeloffs R, Echternacht AC (1986) The ecology of the cooperative spider *Agelena consociata* in equatorial Africa (Araneae, Agelenidae). J Arachnol 14:175–191

Romero GQ, Vasconcellos-Neto J (2004) Beneficial effects of flower-dwelling predators on their host plant. Ecology 85:446–457

Rosenheim JA, Wilhoit LR, Armer C (1993) Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. Oecologia 96:439–449

SAS Institute (2012) JMP version 10.0. SAS Institute, Cary

Scheu S, Poser G (1996) The soil macrofauna (Diplopoda, Isopods, Lumbricidae and Chilopods) near tree trunks in a beechwood on limestone: indications for stem flow induced changes in community structure. Appl Soil Ecol 3:115–125

Schmidt JM, Rypstra AL (2010) Opportunistic predator prefers habitat complexity that exposes prey while reducing cannibalism and intraguild encounters. Oecologia 164:899–910

Schweitzer JA, Bailey JK, Rehill BJ, Martinsen GD, Hart SC, Lindroth RL, Keim P, Whitham TG (2004) Genetically based trait in a dominant tree affects ecosystem processes. Ecol Lett 7:127–134

Schweitzer JA, Bailey JK, Fischer DG, LeRoy CJ, Lonsdorf EV, Whitham TG, Hart SC (2008) Plant–soil–microorganism interactions: heritable relationships between plant genotype and associated soil microorganisms. Ecology 89:773–781

Snyder WE, Wise DH (2001) Contrasting trophic cascades generated by a community of generalist predators. Ecology 82:1571–1583

Stevenson BG, Dindal DL (1982) Effect of leaf shape on forest litter Collembola: community organization and microhabitat selection of two species. J Ga Entomol Soc 17:363–369

Strauss SY (1994) Levels of herbivory and parasitism in host hybrid zones. Trends Ecol Evol 9:209–214

Tack AJM, Johnson MTJ, Roslin T (2012) Sizing up community genetics: it's a matter of scale. Oikos 121:481–488

Tanaka K (1989) Energetic cost of web construction and its effect on web relocation in the web-building spider *Agelena limbata*. Oecologia 81:459–464

Ubick D, Paquin P, Cushing PE, Roth V (eds) (2005) Spiders of North America: an identification manual. American Arachnological Society

Uetz GW (1975) Temporal and spatial variation in species diversity of wandering spiders (Araneae) in deciduous forest litter. Environ Entomol 4:719–724

Uetz GW (1979) The influence of variation in the litter habitats on spider communities. Oecologia 40:29–42

Waite TA, Campbell LG (2006) Controlling the false discovery rate and increasing statistical power in ecological studies. Ecoscience 13:439–442

Whitham TG, Martinsen GD, Floate KD, Dungey HS, Potts BM, Keim P (1999) Plant hybrid zones affect biodiversity: tools for a genetic-based understanding of community structure. Ecology 80:416–428

Whitham TG, Gehring CA, Lamit LJ, Wojtowicz T, Evans LM, Keith AR, Smith DS (2012) Community specificity: life and afterlife effects of genes. Trends Plant Sci 17:271–281

Wimp GM, Young WP, Woolbright SA, Martinsen GD, Keim P, Whitham TG (2004) Conserving plant genetic diversity for dependent animal communities. Ecol Lett 7:776–780

Wimp GM, Martinsen GD, Floate KD, Bangert RK, Whitham TG (2005) Plant genetic determinants of arthropod community structure and diversity. Evolution 59:61–69

Wimp GM, Wooley S, Bangert RK, Young WP, Martinsen GD, Keim P, Rehill B, Lindroth RL, Whitham TG (2007) Plant genetics predicts intra-annual variation in phytochemistry and arthropod community structure. Mol Ecol 16:5057–5069

Zytynska SE, Fay MF, Penney D, Preziosi RF (2011) Genetic variation in a tropical tree species influences the associated epiphytic plant and invertebrate communities in a complex forest ecosystem. Philos Trans R Soc B 366:1329–1336