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Plant genotypic diversity and environmental stress interact to negatively affect arthropod community diversity

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Abstract Many studies have found positive relationships between plant diversity and arthropod communities, but the interactive effects of plant genetic diversity and environmental stress on arthropods are not well documented. In this study, we investigated the consequences of plant genotypic diversity, watering treatment, and its interaction for the ground-dwelling arthropod community in an experimental common garden of quaking aspen (*Populus tremuloides* Michx.). We found that varying plant genotypic diversity and watering treatment altered multivariate arthropod community composition and structure. Arthropod biodiversity and richness showed a distinct response to the plant diversity × watering treatment interaction, declining sharply in water-limited genotypic mixtures. Abundance of arthropod functional groups did not show any response to diversity or the plant diversity × watering treatment interaction, but varied in their response to watering treatment, with predator and detritivore abundance increasing and parasitoid abundance decreasing in well-watered blocks. Our results conflict with most previous studies, and suggest that environmental stress can substantially change the nature of the plant-arthropod diversity relationship. Additionally, we suggest that the plant-arthropod diversity relationship is dependent on the type of plant and arthropod species sampled, and that the association between tree diversity and ground-dwelling arthropods may be much different than more commonly studied grassland species and herbivorous arthropods.

Keywords Arthropod community · Ground-dwelling arthropods · Tree diversity · Genotypic diversity · Drought · Water stress · Pitfall trapping · Aspen · *Populus tremuloides*

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Introduction

With growing concerns about species extinctions, many researchers have sought to understand the community and ecosystem effects of biodiversity, particularly in plant communities (reviewed in Hooper et al. 2005). Arthropods in particular are strongly affected by the characteristics of plant communities (Murdoch et al. 1972; Southwood et al. 1979). Many plant traits are known to be important in structuring arthropod communities, from defensive chemical compounds (Hwang and Lindroth 1997; Wimp et al. 2007) to whole-plant architecture (Lawton 1983; Gardner et al. 1995; Tews et al. 2004). Additionally, plant community properties also influence arthropods, including plant species and functional diversity (Haddad et al. 2001; Wenninger and Inouye 2008), and community composition (Perner et al. 2005; Vehvilainen et al. 2008).

Although most plant-arthropod research has focused on interspecific plant variation, many recent studies have also

found strong effects of intraspecific genetic variation on arthropod communities (Hochwender and Fritz 2004; Johnson and Agrawal 2005; Wimp et al. 2005; Bangert et al. 2006). In one study, the genotype of hybrid cotton-wood trees could be predicted with 98% accuracy based on the arthropod assemblage associated with the tree (Floate and Whitham 1994), demonstrating a remarkable concordance between tree genotype and the composition of the arthropod community. The strong structuring effects of plant genotype extend to larger scales, where genetically diverse hybrid cottonwood stands harbor a greater species diversity of arthropods (Wimp et al. 2004). Additionally, experimental studies manipulating plant genotypic diversity in a common environment have shown that genetically diverse mixtures of plants harbor higher arthropod diversity and abundance than genetic monocultures (Reusch et al. 2005; Crutsinger et al. 2006; Johnson et al. 2006). In some cases, plant genotypic diversity can have even stronger structuring effects on the arthropod community than those of plant species diversity (Crutsinger et al. 2006).

Environmental conditions can dramatically alter interactions among organisms, making the environmental context in which species assemblages operate very important. For instance, there is evidence that plant–plant interactions shift from competition to facilitation as environmental stress increases (Callaway et al. 2002). Across trophic levels, drought stress can alter plant susceptibility to herbivory (Koricheva et al. 1998), and can cause widespread changes across whole food webs, such as altering biomass distribution among different trophic groups (Priesser and Strong 2004). Additionally, plant phenotypic diversity, whether at the functional, species or genetic level, can ameliorate the effects of stress through the insurance effect, where assemblages with higher trait diversity maintain a decreased probability of losing all individuals that fill a particular functional role (Yachi and Loreau 1999). If this is the case, associated arthropod communities may also be buffered against the effects of stress in more diverse plant assemblages. Drought is one of the most prevalent forms of environmental stress, and often negatively impacts arthropod communities as a whole, although individual arthropod species vary widely in their drought responses (Schowalter et al. 1999; Trotter et al. 2008).

Although plant diversity and stress are both important in structuring arthropod communities, the multitrophic consequences of the interaction between plant diversity and stress has received little attention. Wenninger and Inouye (2008) compared an invasive grass monoculture with native grass mixtures under differing irrigation regimes, and determined that mixtures under irrigation generally harbored the greatest abundance and diversity of arthropods. Their study manipulated both plant diversity and stress, but did not replicate species from mixtures in monocultures, making it difficult to predict the effects of native grass monocultures or intermediate diversity levels. Reusch et al. (2005) showed that arthropod abundances were higher in more genetically diverse eelgrass plots during a heat wave. In their study, plant genotypic diversity appeared to ameliorate the effects of high temperatures that may have otherwise negatively affected the arthropod community, but the study lacked a cooler control to simultaneously test for the interactive effects of genotypic diversity and stress.

To examine the effects of plant genotypic diversity, water limitation, and their interaction on the arthropod community, we established an experimental common garden with genotypes of quaking aspen (*Populus tremuloides*), a deciduous tree species common throughout western North America. Aspen genotypes exhibit high levels of variation in morphological and physiological traits (Kanaga et al. 2008) and defense against herbivores (Stevens et al. 2007), traits that can have important ecological effects on the arthropod community (Bangert et al. 2006). In this study, arthropods were collected from pitfall traps, which primarily sample ground-dwelling arthropods. We expected that plant genotypic diversity would indirectly influence ground-dwelling arthropods, either via plant architecture, which can modify the environment on the ground, or through plant nutritional quality and chemical composition, which influences grazer and decomposer food chains.

Methods

Common garden experiment

We collected aspen genotypes from a 40 km² area in Utah, USA, and shoots were propagated clonally (described in Kanaga et al. 2008). Trees were planted in a flat agricultural field in northern Utah, and four experimental blocks were set up: two with high levels of irrigation (referred to as well-watered blocks) and two with low irrigation (referred to as water-limited blocks). Within each block, trees were planted in plots of two diversity levels: monocultures planted with replicates of a single genotype, and mixtures planted with a combination of genotypes. Six genotypes were originally planted across both well-watered and water-limited environments, but five genotypes were used in this study, as all individuals of one genotype died prior to sampling in 2007. Each of the five genotypes was planted in one-genotype monocultures in each of the four blocks, for a total of 20 monocultures. Six replicates of the mixture of all five genotypes were planted, with two replicates represented in each of the well-watered blocks and one replicate planted in each of the water-limited blocks. Each diversity plot (genotypic monoculture or mixture) was set up as a 2.5 m² hexagonal-shaped group of 19 trees,

all placed 50 cm apart on a diagonal grid in which each tree had six equidistant neighbors. Monoculture plots consisted of 19 genetically identical trees, and mixture plots contained between two and four individuals of each of the five genotypes, configured so no two replicates of the same genotype were adjacent. A single row of border trees of other non-experimental genotypes was placed between all plots and around the outside of each block at 50 cm spacing to minimize edge effects. A thin layer of wood chips was placed on the ground in all plots to simulate a litter layer, and weeds were removed manually. Arthropods were allowed to naturally colonize the site for 1 year following planting and prior to collection.

Watering treatments

The experimental site is located at an elevation of 1,400 m, lower than most native aspen forest, and thus the site experiences hotter, drier summers than adjacent upland forests. An irrigation system was installed, and from June through September of 2007 well-watered blocks were given approximately 58 cm of water and water-limited blocks 37 cm. All trees were watered equally in the first year of the study (2006) to allow establishment of saplings.

Collection and identification of arthropod samples

To sample the arthropod community, three 7 cm diameter × 8 cm deep pitfall traps were installed in each plot. Traps were filled with ethylene glycol (1:1 diluted antifreeze) for a 5 day sampling period once a month in July, August, and September of 2007. Arthropods caught in pitfall traps were sorted to order and counted. Orders represented in pitfall traps included Collembola, Archaeognatha, Dermaptera, Orthoptera, Hemiptera, Coleoptera, Diptera, Lepidoptera, Hymenoptera, Araneae, Lithobiomorpha and Isopoda. Arthropods of the order Hemiptera were divided into two suborders: Heteroptera and Auchenorryncha/Sternorryncha, corresponding to the traditional classification of these suborders as orders Hemiptera and Homoptera. Collembola and Acarina (mites, in the order Araneae) were not included in analyses due to extremely large numbers and difficult detection in samples, resulting in inaccurate counts. Collembola and Acarina were found in every sample, and thus their exclusion is unlikely to alter our comparisons of arthropod taxonomic richness.

We also identified all arthropods to a sufficient taxonomic level to place them into feeding functional groups. We placed orders Orthoptera, Hemiptera, and Lepidoptera (both suborders; see above), along with Coleoptera families Chrysomelid, Curculonid, Cerambycid, and Elaterid in the herbivore functional group. Orders Araneae and Lithobiomorpha, along with Coleoptera families Carabid,

Coccinelid, and Dyticid, were considered predators. Arthropods of the order Hymenoptera, family Vespidae (wasps) were placed in the parasitoid functional group. Omnivores included Hymenoptera of the family Formicidae (ants) and Dermaptera. Lastly, arthropod orders Archaeognatha and Isopoda, along with Coleoptera families Tenebrionid and Scarabid were considered detritivores. The majority of the dipterans caught in pitfall traps belonged to the family Chironomidae, and were not included in functional group analyses because adults rarely feed (Armitage 1995) and the order is extremely functionally diverse. Lepidopterans were also omitted from functional group analyses, as all individuals caught were adults, and nectar sources for feeding were not present in our experimental plots.

Categorization of foliage density, plant biomass and survivorship

Foliage density and biomass were quantified based on structural traits of the trees in September 2007, and were summed across all trees in each plot. Foliage density was quantified as: $BL \times LA_s$, where BL is the estimated length of all branches (average branch length multiplied by branch number, for primary, secondary and tertiary branches), and LA_s is average single leaf area (calculated as: $\pi (L_l/2) \times (L_w/2)$, where L_l is average leaf length and L_w is average leaf width). Our foliage density metric provides a relative measure of cover or shading experienced by ground-dwelling arthropods. Woody biomass of each tree was estimated by the volume of a cone: $1/3\pi r^2_{stem}h_{stem} + 1/3\pi r^2_{branch}h_{branch}$, where h_{stem} and h_{branch} are stem height and estimated total branch length, and r_{stem} and r_{branch} are basal radius measurements of the stem and branches. Survivorship was calculated as the percentage of trees alive in each plot at the end of the 2007 growing season.

Plant physiological measures

Mature leaves from throughout the plant canopy were collected for stable isotope analysis, leaf nutrient content, and phytochemistry in August 2007. Plant water use was inferred from $\delta^{13}C$ stable isotope ratios of leaf tissue, which provides a long-term indicator of stomatal conductance and plant water use (Farquhar and Richards 1984). $\delta^{13}C$ values were generated from desiccated leaf tissue of 93 trees using an isotope ratio mass spectrometer. Leaf carbon and nitrogen content were determined with a Thermo Finnigan Flash 1112 elemental (CN) analyzer. High-performance thin layer chromatography was used to quantify levels of the phenolic glycosides salicortin and tremulacin, compounds produced by plants to deter insect

herbivory, using purified aspen phenolic glycoside standards (Lindroth et al. 1993). Condensed tannins were extracted from leaf tissue with 70% acetone at 4°C, and quantified using acid butanol (Porter et al. 1986) and purified aspen tannin standards. Assays for leaf carbon and nitrogen were generated from 35 trees, and concentration of tremulacin, salicortin and condensed tannins from 20 trees.

Statistical analyses

We conducted permutational multivariate analyses of variance (MANOVA) using the Adonis function in the Vegan package of Program R (Anderson 2001; McArdle and Anderson 2001; Oksanen et al. 2008) to test for the effects of genotypic diversity, water limitation, the diversity × watering treatment interaction, sampling date, and experimental block on the multivariate arthropod community. The Adonis function takes a dissimilarity matrix describing the multivariate community and statistically tests for experimental effects by identifying relevant centroids and calculating the squared deviations from those points. Two forms of community data were used for MANOVA analyses: a presence/absence community matrix describing community composition, and a community matrix incorporating abundance of arthropod groups, describing community structure (Table 1). Distance matrices for use in MANOVA were constructed using the Bray-Curtis index, and P-values were generated using F-tests based on sequential sums of squares from 1000 permutations of the raw data. Note that MANOVA analyses produced P-values and R^2 for each factor, but indicated only whether or not there were differences among experimental treatments, not the directionality of any changes.

To assess the directionality of change due to experimental treatments, arthropod order data was used to generate three diversity metrics: the Shannon-Weiner diversity index based on richness and evenness of arthropod orders (hereafter termed "biodiversity" to differentiate arthropod diversity from plant genotypic diversity), taxonomic richness (number of arthropod orders), and total arthropod abundance (Table 1). Because multivariate analyses

showed that sample date explained the greatest proportion of the data, each sample date (July, August, and September) was analyzed separately for all diversity metrics. Three-factor ANOVA was conducted using proc mixed in SAS v. 9.1 (SAS Institute, 2003) to test for fixed effects of plant diversity, watering treatment and experimental block (nested within watering treatment), and the diversity × watering treatment interaction. Functional group analyses were conducted for arthropod abundance within each of the five functional groups, using a four-factor ANOVA model with plant diversity, watering treatment, block, and the diversity × watering treatment interaction as fixed effects, and month as a random effect in proc mixed (SAS Institute 2003). We did not assess diversity or richness within functional groups due to low numbers of arthropod orders in most functional groups.

To determine the effects of plant diversity, watering treatment and the diversity × watering treatment interaction on plant phenotype (foliage density, biomass, and survivorship) and physiological measures (water use, leaf nutrients, and leaf phytochemical content), we used the same three-factor ANOVA as described above, with treatment, diversity and experimental block as fixed effects. We further examined the relationship between plant structure and arthropods by regressing foliage density, biomass and survivorship against arthropod biodiversity, richness and abundance in separate simple linear regressions. When necessary, response variables were square root transformed to meet the assumption of normality of residual distribution.

Results

Effects of plant diversity and watering treatment on plant phenotype

Trees in the experiment averaged 1.2 m tall with 22 cm average primary branch lengths at the end of the 2007 growing season. Genotypic mixture plots had slightly lower foliage density than monocultures across watering treatments ($F = 3.59$, df = 1, $P = 0.062$), but there were

Table 1 Definitions of terms used to characterize the arthropod community

Term	Definition
Community composition	Multivariate measure of the arthropod community using presence/absence of orders
Community structure	Multivariate measure of the arthropod community incorporating abundance of orders
Biodiversity	Shannon-Weiner diversity index calculated for arthropod orders
Taxonomic richness	Number of arthropod orders
Abundance	Total arthropod abundance

no other significant main effects of genotypic diversity on plant phenotype or physiology. Watering treatments did not significantly affect foliage density, biomass or survivorship, but several physiological traits showed significant effects of watering treatment. Well-watered trees had a significantly more negative $\delta^{13}C$ stable isotope ratio (mean $-27.54‰$) than water-limited trees (mean $-27.06‰$; $F = 12.07$, df $= 1$, $P < 0.001$). Leaf tissue concentrations of tremulacin and salicortin, phenolic glycoside compounds that deter herbivory, were on average 28 and 18% higher, respectively, among trees in water-limited blocks compared to well-watered blocks, although the change in salicortin was not statistically significant (tremulacin: $F = 7.76$, df $= 1$, $P = 0.015$; salicortin: $F = 2.56$, df $= 1$, $P = 0.132$). Leaf carbon content was 1% higher among plants in water-limited blocks ($F = 4.18$, df $= 1$, $P = 0.050$), but leaf nitrogen and condensed tannins showed no significant treatment effects ($P > 0.2$). The plant diversity × watering treatment interaction did not affect any aspect of plant phenotype or physiology except leaf carbon concentrations, with water-limited mixtures maintaining the highest levels of leaf carbon ($F = 4.60$, df $= 1$, $P = 0.040$).

Interactive effects of plant genotypic diversity and water limitation on the arthropod community

Arthropod community composition based on presence/ absence of arthropod orders showed marginally significant effects of plant genotypic diversity and significant effects of watering treatment (Table 2). Community structure based on abundance was significantly altered by both plant diversity and watering treatment. The multivariate genotypic diversity × watering treatment interaction also significantly affected arthropod community composition, but not community structure. Community composition and structure varied widely across months, as evidenced by the highly significant terms and highest R^2 values for sample date in both models.

Across the three sample dates, average arthropod biodiversity declined by roughly 25% in water-limited genotypic mixtures (Fig. 1a). The interaction between plant genotypic diversity and watering treatment was significant in July and September, whereas in August the effects of water limitation decreased arthropod biodiversity in both monocultures and mixtures. Arthropod taxonomic richness showed a similar trend in July and September, with richness values roughly 30% lower in water-limited genotypic mixtures (Fig. 1b). August samples showed little difference among plant diversity or watering levels. Arthropod abundance did not change with plant genotypic diversity or watering treatment level throughout the summer, but declined across the three months to half the number of arthropods caught at the beginning of the study (Fig. 1c).

None of the five arthropod functional groups responded to changes in plant genotypic diversity or the diversity × watering treatment interaction (Table 3). However, three functional groups showed responses to watering treatment but differed in the directionality of their response. Detritivores and predators reached 28 and 4.6% higher abundances, respectively, in well-watered blocks, although predator response to watering treatment was only marginally statistically significant ($P = 0.026$ and $P = 0.063$). Conversely, parasitoids reached higher abundances in water-limited blocks, increasing their average abundance by 27% ($P = 0.051$).

Effects of plant structure on the arthropod community

There was no significant relationship between foliage density, biomass or survivorship and arthropod biodiversity, richness or abundance ($P > 0.169$).

Discussion

A long-standing body of theory predicts that more diverse plant assemblages should provide a greater diversity of resources (both food and shelter), which should increase the diversity of associated herbivores as well as their natural enemies (Andow 1991). In contrast, our study found that aspen genotypic diversity and its interaction with water stress negatively affected the arthropod community. Arthropod biodiversity and richness declined substantially

Table 2 R^2 and *P*-values from MANOVA analysis of arthropod community composition (based on presence/absence) and community structure (incorporating abundance)

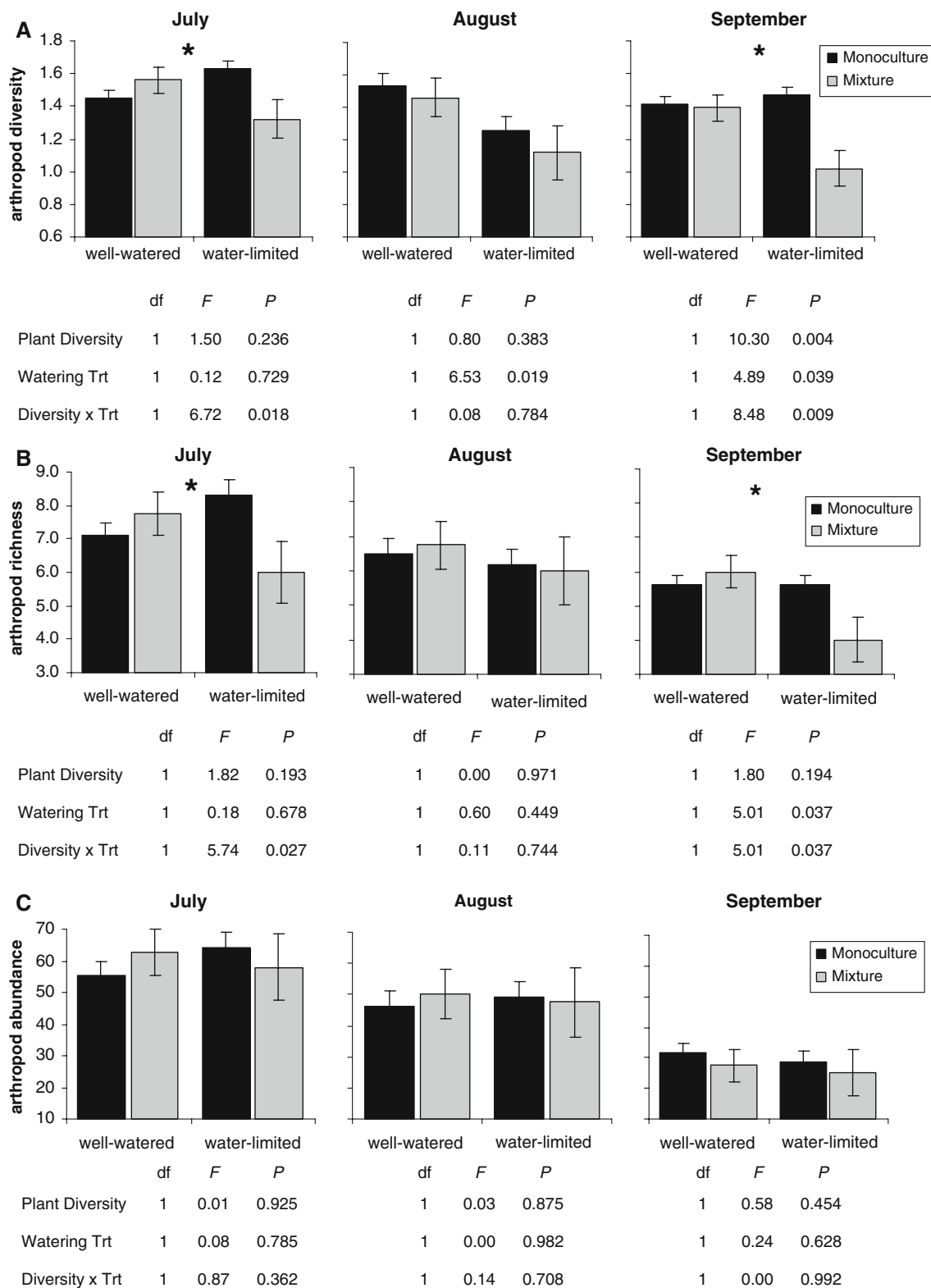|	Community Composition		Community Structure	
	R^2	*P*	R^2	*P*
Plant genotypic diversity	0.020	0.081	0.020	0.042
Watering treatment	0.057	0.001	0.030	0.007
Diversity × watering treatment	0.025	0.043	0.002	0.927
Sample date	0.151	<0.001	0.389	<0.001
Experimental block	0.032	0.133	0.025	0.124

Fig. 1 Arthropod biodiversity (**a**), richness (**b**) and abundance (**c**) compared between plant diversity levels (genotypic monocultures and mixtures) and watering treatments (well-watered and water-limited). Error bars represent 1 SE. Tables below each graph report *F* values and *P*-values for each experimental treatment, and asterisks in the graphs denote significant plant diversity × watering treatment interactions

Table 3 Degrees of freedom, *F*-statistics and *P*-values for effects of experimental treatments and interactions on the abundance of arthropod functional groups

	df	Plant diversity		Watering treatment		Diversity × treatment	
		F	P	F	P	F	P
Herbivores	1	0.24	0.625	1.55	0.218	2.49	0.120
Predators	1	0.40	0.531	3.57	0.063	2.19	0.143
Parasitoids	1	0.03	0.858	3.96	0.051	0.00	0.972
Omnivores	1	0.36	0.551	1.66	0.202	0.08	0.782
Detritivores	1	2.30	0.134	5.16	0.026	1.93	0.169

in genotypic mixtures under water limitation, particularly in the months of July and September. This interaction is driven by a decline in the number of arthropod groups, not a change in their abundances (Table 2; Fig. 1). Our results contrast with many other studies showing positive relationships between plant and arthropod diversity in experiments manipulating both plant species diversity (Siemann et al. 1998; Knops et al. 1999; Wenninger and Inouye 2008) and plant genotypic diversity (Crutsinger et al. 2006; Johnson et al. 2006).

Arthropod functional groups show little response to diversity or the diversity × watering treatment interaction, but three of the five functional groups responded to watering treatment main effects. Predators and detritivores responded positively to irrigation, reaching higher abundances in well-watered blocks, whereas parasitoids attained higher abundances in water-limited blocks. This variation in response to water stress is consistent with some previous studies that have found that many arthropod species respond differently to water stress, but the majority tend to perform better under conditions of low water stress (Schowalter et al. 1999; Trotter et al. 2008). Interestingly, the only effects of experimental treatments on arthropod abundance appear at the functional group level, with no significant effects of any treatments on overall abundance (Fig. 1c). The striking diversity × treatment interaction effects only become apparent when analyzing the community based on diversity indices of arthropod orders, not at the functional group level.

Our results conflict with the insurance hypothesis, which predicts a buffering effect of plant diversity under conditions of stress. In our study, water limitation negatively impacted the arthropod community, mostly through its interaction with plant diversity in water-limited genotypic mixtures. The differences in water use, defensive compound production, and leaf nutritional quality between watering treatments indicate that water-limited trees were subjected to enough water stress to affect their physiology, although they maintained similar growth patterns to well-watered trees. Less negative carbon stable isotope ratios indicate that photosynthesis in trees planted in water-limited blocks was likely limited by availability of CO_2 due to smaller stomatal apertures during times of water stress (Farquhar and Richards 1984). Higher levels of leaf tremulacin, a phenolic glycoside compound that deters herbivory, were detected in water limited blocks, indicating that water-stressed plants contained better defended tissue. However, rather than diversity providing a buffer against environmental stress, arthropods in plots with higher genotypic diversity were more adversely affected by water stress.

Few previous studies have reported negative relationships between plant diversity and arthropod biodiversity or abundance. In a grassland experiment manipulating plant species diversity, Koricheva et al. (2000) found that the abundance of predators caught in pitfall traps decreased with increasing plant species diversity, a trend they attributed to higher temperatures in monoculture plots and thus greater arthropod activity. However, in our study, plant diversity affected only arthropod biodiversity and richness, with no significant changes in arthropod abundance. In another experimental manipulation of grassland species diversity, Siemann (1998) found that arthropod species richness decreased with increasing plant species richness, although in their study species richness was not directly manipulated but was created by varying historical fertilization treatments. Neither of these studies investigated the interaction of plant diversity and water stress, but they show that negative relationships between plant diversity and arthropod communities have been documented.

We also found no significant relationships between the arthropod community and foliage density, biomass or survivorship, despite many studies (Lawton 1983; Gardner et al. 1995; Tews et al. 2004) that have shown plant architecture to be important in structuring arthropod communities. However, several trends in the data suggest that plant traits may affect the arthropod community. Genotypic mixture plots had marginally significantly lower foliage density than monocultures across watering treatments, and water-limited mixtures had the lowest foliage density of all combinations of diversity and watering treatment. This finding runs counter to previous studies that have found increasing plant productivity in diverse mixtures, particularly under water stress (Tilman and Downing 1994; Tilman 1996). The discrepancy in our results may stem from high levels of variation in the response of aspen genotypes to conspecifics, where different aspen genotypes show a diversity of positive, neutral and negative responses to genotypic diversity and watering treatment (Kanaga et al., manuscript in preparation). A high level of response variation among genotypes could produce an overall weak negative effect of genotypic diversity on plant

cover, as found in our study. Leaf carbon also showed a significant plant diversity × watering treatment interaction in which water-limited mixtures had the highest levels of leaf carbon, possibly indicating lowered nutritional quality. Leaf tremulacin and salicortin concentration also showed the same nonsignificant trend, with the highest levels of defensive compounds found in water-limited genotypic mixtures. Although many of these patterns are not statistically significant, they suggest that the decline in arthropod biodiversity and richness may have been partially explained by lower foliage density and heightened levels of defensive compounds in trees found in water-limited genotypic mixtures. We do not have data on the nutrient or phytochemical content of leaf litter, and therefore it is unknown whether the same leaf quality patterns apply to leaf litter on the ground.

We use our measure of foliage density as a surrogate for shade or cover experienced by ground-dwelling arthropods, but many other abiotic factors may differ between experimental treatments, including temperature, moisture and humidity. We measured ground-level humidity at several locations across all blocks using a Kestrel 3000, but variance among measurements was too high to make any robust conclusions about the effects of experimental treatments or plant structure on humidity levels. Our lack of reliable abiotic environmental data weakens our power to test mechanistic hypotheses about the how the effects of tree characteristics on arthropods may be mediated by changes in the abiotic environment. However, we were able to test more indirectly for potential abiotic effects mediated through plant phenotype using regressions of plot-level plant biomass, foliage density and survivorship. The positive regression between foliage density and arthropod biodiversity, although only marginally significant, suggests that plant traits are affecting the arthropod community, either by modifying the abiotic environment or providing greater habitat structure for foraging and/or predator avoidance.

We collected arthropods by pitfall trapping, which primarily samples ground-dwelling arthropods, and the discrepancy in our results compared to other diversity studies may partially stem from sampling methods and differences in focal arthropod groups. Pitfall traps sample arthropods based on both their abundance and their mobility (Southwood 1978), and therefore highly mobile taxa are overrepresented in pitfall catches compared to less mobile taxa. If pitfall catches actually reflect arthropod activity more than abundance, the expected relationships between plant diversity and arthropod communities may not hold. Previous studies using multiple methods of arthropod collection found that trends observed based on pitfall trap catches can differ substantially from the results of sweep net and suction sampling methods (Koricheva et al. 2000, and

references therein). This suggests that either ground-dwelling arthropods show fundamentally different relationships with plant diversity, or that pitfall trapping methods may cause significant biases that could alter the plant-arthropod diversity relationship. However, we primarily detected effects of experimental treatments on arthropod biodiversity and richness, not on arthropod abundance (except the effects of watering treatment on abundance of some functional groups), suggesting that our results are not explained solely by pitfall trapping biases. Additionally, tree species have very different growth, morphology and life history patterns than more commonly studied herbaceous species (Scherer-Lorenzen et al. 2007), and the effects of diversity may be quite different for different groups of plants. These previous studies suggest that the expectation for the relationship between plant diversity and arthropods may depend on both the type of plants and the type of arthropods under consideration (Vehvilainen et al. 2008).

The community effects of plant diversity that we detected in this study are of a smaller magnitude than many previous studies. We expected that the effects of plant diversity on ground-dwelling arthropods would be more diffuse than previous studies of phytophagous arthropods because interactions between plants and ground-dwelling arthropods are indirectly mediated through trophic dynamics and/or physical characteristics of the plant. Consistent with our expectations, the R^2 values for community composition and structure are low for plant diversity and watering treatment when pooled across the three sample dates, and the amount of variation explained by sample date is much larger (Table 2). We were not able to generate reliable R^2 values for each separate month due to small sample sizes, but the amount of variation explained by plant diversity and watering treatment is likely to be substantially higher for each individual month.

Due to small plot sizes and continuous planting of trees between plots, some of the more mobile arthropods were almost certainly able to move between plots and may have experienced multiple diversity or watering treatment levels. Although we recognize this as a possible source of error, we maintain that it will only result in a dampening of experimental effects, causing our estimates of experimental treatment effects to be more conservative rather than overestimating effect sizes or generating spurious results. Also, our sampling encompassed the middle and late portions of the growing season, from July through September, and therefore may have missed important dynamics between plant diversity and arthropods in the early season. Vehvilainen et al. (2007) found that effects of tree species diversity on arthropod herbivores were more pronounced in older trees, early season sampling, larger plot sizes and low planting density, suggesting that our study design and

sampling dates may have biased against finding a relationship between plants and arthropods. Despite these experimental biases, we still detected significant effects of plant genetic diversity and water limitation, suggesting that diversity and water limitation have important effects on the arthropod community.

In this study, we add to the existing literature showing that intraspecific plant genotypic diversity can have important community-level effects, and we extend previous knowledge by showing that the plant-arthropod diversity relationship can vary dramatically across environmental stress levels. Few studies have investigated the environmental dependence of the plant-arthropod diversity relationship, and our results show that there is a greater need for studies across varying environments, particularly across stress gradients. We also suggest that the types of plant and arthropod species used in biodiversity experiments can greatly impact the nature of the plant-arthropod diversity relationship, and that the generalities suggested by grassland studies may not extend across all types of ecological systems.

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