Effects of pepper (*Capsicum chinense*) genotypic diversity on insect herbivores

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Abstract

1 There is growing interest on the effects of plant genotypic diversity on higher trophic levels. The present study investigated whether genotypic diversity in *Capsicum chinense* peppers influenced attack by leaf-mining fly larvae (*Lyriomyza trifolii*) and fruit-eating weevils (*Anthonomus eugenii*), as well as parasitoid attack associated with weevils.

2 We established genotypic monocultures ($n = 10$, two plots/each of five inbred lines) and polycultures ($n = 5$, random mixtures of three out of the five lines) and conducted weekly surveys of fruit number, leafmines and weevil fruit attack over a 5-month period. In addition, we collected fruits to rear weevils and estimated parasitism associated with this herbivore.

3 There was a tendency for a negative effect of diversity on leafminer attack, with polycultures exhibiting a 24% reduction in leafminer attack relative to monocultures. By contrast, diversity did not influence weevil fruit attack or the level of parasitism associated with the weevil.

4 Our findings show that plant genotypic diversity effects vary among herbivore species, presumably as a result of differences in herbivore traits (e.g. diet breadth, mobility). We also emphasize that manipulating plant genotypic diversity can be an important consideration for pest management in this commercially important crop.

Keywords *Capsicum*, diversity, genetic variation, herbivory, parasitoid.

Introduction

A fundamental goal in ecology is to understand the effects of plant diversity on ecosystem function (Hooper *et al*., 2005; Cardinale *et al*., 2011). Although a great deal of work has focused on manipulating plant species diversity and measuring effects on plant growth (Hooper, 1998; Loreau & Hector, 2001; Tilman *et al*., 2002) and higher trophic levels (Koricheva *et al*., 2000; Haddad *et al*., 2009; Scherber *et al*., 2010), there is also increasing evidence for parallel effects of within-species plant genotypic diversity on ecosystem function and consumers (Hughes *et al*., 2008; Bailey *et al*., 2009; McArt & Thaler, 2013). Both forms of plant diversity, intra- and interspecific, have been shown to

influence consumer abundance and diversity through increased producer biomass via plant–plant facilitation or reduced plant competition (Vandermeer, 1989; Hooper, 1998), as well as through increased habitat or resource heterogeneity (as a result of genotype or species trait variation) influencing consumer foraging behaviour (Hambäck *et al*., 2014).

There are important ecological implications stemming from research on plant diversity effects on higher trophic levels. One example is the frequent finding of plant diversity reducing herbivore damage (Andow, 1991; Barbosa *et al*., 2009). According to the 'Resource Concentration Hypothesis' (RCH) (Root, 1973), herbivore foraging behaviour is density-dependent and increasing plant diversity at a constant plant density reduces the chance of herbivores finding a specific host plant species (or genotype), which in turn lowers herbivore abundance and damage (Hambäck *et al*., 2014). Alternatively, the 'Enemies Hypothesis' (EH) (Root, 1973) holds that greater habitat complexity at high plant diversity results in higher predator recruitment

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(e.g. because of greater availability of shelters or prey) and thus stronger suppression of herbivores (Russell, 1989). Although both hypotheses have received much attention, not all studies are supportive (Loranger *et al.*, 2014), and these inconsistencies have been attributed at least partly to unaccounted variation in herbivore traits (Vehviläinen *et al.*, 2007; Plath *et al.*, 2012; Abdala-Roberts *et al.*, 2015). For example, the dynamics predicted by the RCH depend on herbivore dietary specialization (Root, 1973); specialist herbivores should be negatively influenced by diversity, whereas generalist herbivores should exhibit weak (or variable) responses because they are not limited to feeding on a specific host plant (Jactel & Brockerhoff, 2007; Castagneyrol *et al.*, 2013; Abdala-Roberts *et al.*, 2015). Similarly, the dynamics predicted by the EH are more likely to occur for generalist herbivores because these are more susceptible to natural enemies and frequently lack defence mechanisms present in specialist herbivores (e.g. crypsis, sequestration of plant toxic compounds) (Singer *et al.*, 2014). Finally, other traits, such as mobility and feeding mode, are also considered to be important predictors of plant diversity effects on herbivores (Bommarco & Banks, 2003).

In the present study, we report the results obtained from a field experiment testing for the effects of genotypic diversity ('diversity' hereafter) in *Capsicum chinense* Jacq. peppers, a widely cultivated species in southern Mexico, on herbivory by two insect herbivores: the leaf-mining fly *Liriomyza trifolii* (Burgess) and the fruit-eating weevil *Anthonomus eugenii* Cano. Specifically, we considered whether *C. chinense* diversity influences herbivore attack and whether these herbivores vary in their responses to pepper diversity. *Liriomyza trifoli* is a broad dietary generalist feeding on species across more than 20 plant families, whereas *A. eugenii* has a narrower diet and it only feeds on a few species of *Capsicum* and *Solanum* (Elmore *et al.*, 1934; Tun-Dzul, 2001). Thus, in accordance with the RCH, we predicted that *A. eugenii* would be more strongly (negatively) influenced by diversity than *L. trifolii* because dietary specialists are more sensitive to changes in density of a preferred pepper genotype across levels of diversity. Alternatively, in accordance with the EH, the generalist herbivore should be more strongly affected by diversity because generalists are more susceptible to enhanced effects by natural enemies at high diversity. Accordingly, to evaluate the EH, we also tested for diversity effects on parasitism rates associated with one of these herbivores, *A. eugenii*. When considering these predictions, it is important to note that these herbivores also vary in other traits, such as mobility and feeding mode, which could influence herbivore responses to diversity. Overall, the results of the present study contribute towards a better understanding of plant genotypic diversity effects on different herbivore species coexisting on the same host plant; in this case, a commercially important crop in southern Mexico.

Materials and methods

Study system

Capsicum chinense (Solanaceae), commonly known as 'Habanero' peppers, are a major horticultural crop in southeast Mexico. In Yucatán, the state in México with the second greatest production of *C. chinense*, the total area planted with this crop

has progressively increased during the last decade (SIAP, 2014). However, yields remain low and this is largely a result of the negative impact of insect pests and pathogens. Two important insect herbivores attacking this crop in southern Mexico are the pepper weevil *A. eugenii* (Coleoptera: Curculionidae) and *L. trifolii* leafminers (Diptera: Agromyzidae). *Anthonomus eugeneii* is native to southern Mexico and Central America, although it has extended its distribution throughout the southern United States, South America and the Caribbean Islands (Bartlett *et al.*, 1978; Burke & Woodruff, 1980). This weevil has a narrower diet breadth (relative to the leafminer) because it feeds primarily on species of *Capsicum* and *Solanum* within Solanaceae (Elmore *et al.*, 1934). Adult females deposit their eggs on flower buds or immature fruits and larvae feed on seeds and placental tissues (Burke & Woodruff, 1980). Larvae pupate inside fruits and recently emerged adults make an exit cavity to then start feeding on floral buds and immature fruits (Mau & Martin, 1994). By contrast, *L. trifolii* is a broad generalist that feeds on plant species from more than 20 families, including Solanaceae (Tun-Dzul, 2001). It is originally a Nearctic and Neotropical species but now has a cosmopolitan distribution (Minkenberg & van Lenteren, 1986). Late-instar larvae drop on the ground and normally pupate in the soil (Minkenberg & van Lenteren, 1986). Adults feed and oviposit on young leaves, and larvae feed on the leaf mesophyll and produce serpentine, irregular mines (Parrella, 1987). It is important to note that these two herbivores varied not only in diet breadth, but also in traits such as mobility and feeding mode, which could also influence herbivore responses to diversity. Thus, any claim on the effects of diet breadth *per se* on herbivore responses should be made with caution.

Pepper genotypes and experimental design

We used five inbred lines (hereafter 'genotypes') of *C. chinense* selected *a priori* to span a wide range of phenotypic variation (Berny-Mier y Terán *et al.*, 2013); namely, a typical orange habanero, a Belizean red habanero, an Antillean yellow habanero, a South American habanero of small fruits and the Cuban habanero. These genotypes differ in vegetative (e.g. plant size, architecture) and reproductive traits (flowering phenology, fruit size and yield) (Trujillo-Aguirre & Pérez-Llanes, 2004), and the data collected from plants of the present study confirmed this by showing significant variation among the selected genotypes in fruit output, fruit size and resistance to insect herbivores (Berny-Mier y Terán *et al.*, 2013) (see Supporting information, Table S1).

The field experiment was conducted at the Mococha Research Station of the Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias (INIFAP), in Yucatan, Mexico (21°6′40″N, 89°26′35″W). In July 2010, we established 15, 5×5-m² plots of *C. chinense*, of which 10 were genotypic monocultures (two plots per genotype) and five were genotypic polycultures composed of mixtures of three out of the five genotypes. In each polyculture plot, we randomly assigned positions to plants of each genotype and each genotype was planted in the soil in equal proportions. In addition, genotypes were equally represented across polyculture plots (each one planted in three plots of

this treatment level). The distance between plots was 2.5 m and, within each plot, the planting design was 30 cm between plants within rows, and 1.25 m between rows. Planting density was 2.64 plants per m^2 (66 plants/plot), for a total of 990 plants. Of these, eight plants per genotype per plot were randomly selected and monitored from July to November 2010, which represented the entire growing season. As a result, statistical analyses were based upon a sample size of 40 plants per genotype ($n = 200$ plants). The fertilization and irrigation regime was the same across all plots and followed standard agricultural practices used for *C. chinense* in southern Mexico (Tun-Dzul, 2001), with the exception that insecticides were not used. Plots were randomly located throughout the site, and plots, as well as rows between plots, were weeded periodically.

For each experimental plant, we recorded data on leaf miner and fruit weevil attack, as well as parasitoid attack rates on weevils. For leaf miners, we did this by counting the number of leaf mines of *L. trifolii* from a sample of two to six randomly chosen leaves, depending on availability of new leaves per plant; surveys were conducted every 2 weeks, from July 2010 to September 2010. We recorded leaf mines exclusively on young, fully-expanded leaves, and, during each survey, we sampled a different set of leaves. In most cases, only one leafminer was found per leaf (L. Abdala-Roberts, personal observations). For fruit weevils, from late September 2010 to mid-November 2010, we collected all the fruits produced per plant on a weekly basis and recorded how many of these were attacked by *A. eugenii*. Attacked fruits were identified based on the presence of yellowing of the fruit petiole, which is a reliable sign of weevil infestation (data from the present study). Finally, to estimate levels of parasitism associated with *A. eugenii*, at the end of the sampling season (early to mid-November), we collected a random subsample of fruits from the last two fruit harvests (two to six plants sampled per genotype, per plot depending on availability; $n = 92$ plants), and placed each fruit individually in 0.5-L plastic containers with moistened cotton to rear weevils and record parasitoid emergence based upon observations conducted every 2 days throughout a 2-week period. After 2 weeks, all fruits were dissected for further examination. We calculated the proportion of mined leaves (number of leaves with mines/total leaves sampled), the proportion of attacked fruits (number of attacked fruits/total fruits sampled) and the proportion of parasitized weevils [number of parasitoids/(number of parasitoids + number of weevils)] per plant for statistical analyses. For leafminer and weevil attack, we calculated proportions separately for each survey and then used the average across surveys for statistical analyses. For fruit output, we analyzed the total (cumulative) number of fruits sampled across surveys.

Statistical analysis

We performed general linear models with PROC GLM in (SAS, 2009; SAS Institute, Cary, North Carolina) to test for an effect of *C. chinense* genotypic diversity (fixed, two levels) on the number of fruits produced per plant, the proportion of leaves with mines per plant and the proportion of fruits attacked by the weevil per plant. In all three cases, data exhibited normally distributed residuals. In addition, we ran a generalized linear

model in PROC GENMOD (SAS, version 9.2) to test for a diversity effect on the proportion of parasitized weevils per plant, using a binomial distribution (logit link) because the data were not normally distributed after transformation. There was no evidence of overdispersion for this latter model. In all four cases, we used plot-level data.

Whenever a diversity effect was significant ($P < 0.05$) or marginally significant ($0.05 < P < 0.10$) in the above models, we determined whether such effect was additive (i.e. the result of the presence of one or more resistant or susceptible genotypes in mixtures; the 'sampling' effect; Houston, 1997) or non-additive where diversity results in higher or lower values as a consequence of emergent, patch-level properties because of interactive effects among genotypes (Johnson *et al*., 2006). In accordance with Johnson *et al*. (2006), we calculated pepper genotype means for each variable in monoculture (i.e. expected values) and compared these values with the mean of each genotype in polyculture (i.e. observed values). For a given response variable, we compared observed and expected values with a one-way general linear model using PROC MIXED in SAS, version 9.2. These models also included the effects of plot and genotype nested within plot, making them similar to a paired test comparing observed versus expected values for each genotype (Johnson *et al*., 2006). A significant difference between observed and expected values is necessarily a result of non-additivity because the comparison is performed by specifying the monoculture values of each genotype (i.e. sampling effects are accounted for by including genotype-specific expected values).

In all cases, we report results for Type III sums of squares (for general linear models) and Type III analyses (for generalized linear models), and use the mean ± SE as descriptive statistics.

Results

Effects of plant diversity on leafminer attack

There was a tendency for a negative effect of *C. chinense* diversity on the number of leaves mined by *L. trifolii*, although this effect was marginally significant ($P = 0.07$) (Table 1). Genotypic polycultures exhibited a lower percent of leaves with mines ($22.98 \pm 2.26\%$) relative to monocultures ($30.21 \pm 2.34\%$) (Fig. 1A). This decrease in leafminer attack was lower than would be expected based upon sampling effects alone ($F_{1,14} = 13.28$, $P = 0.003$), showing that the negative effect of diversity on leafminers was non-additive.

Table 1 Results (*F*- or χ^2 statistics, with *P*-values in parenthesis) from general (or generalized in the case of parasitism) linear models testing for the effects of *Capsicum chinense* genotypic diversity on fruit number, the proportion of leaves mined by the fly *Liriomyza trifolii*, the proportion of fruits attacked by the weevil *Anthonomus eugenii* and the proportion of parasitized weevils (weevil parasitism)

Response	Diversity effect
Number of fruits	$F_{1,13} = 0.33$ (0.571)
Leaf miner attack	$F_{1,13} = 3.80$ (0.073)
Fruit weevil attack	$F_{1,13} = 0.15$ (0.703)
Weevil parasitism	χ^2 (d.f. = 1,7) = 0.01 (0.950)

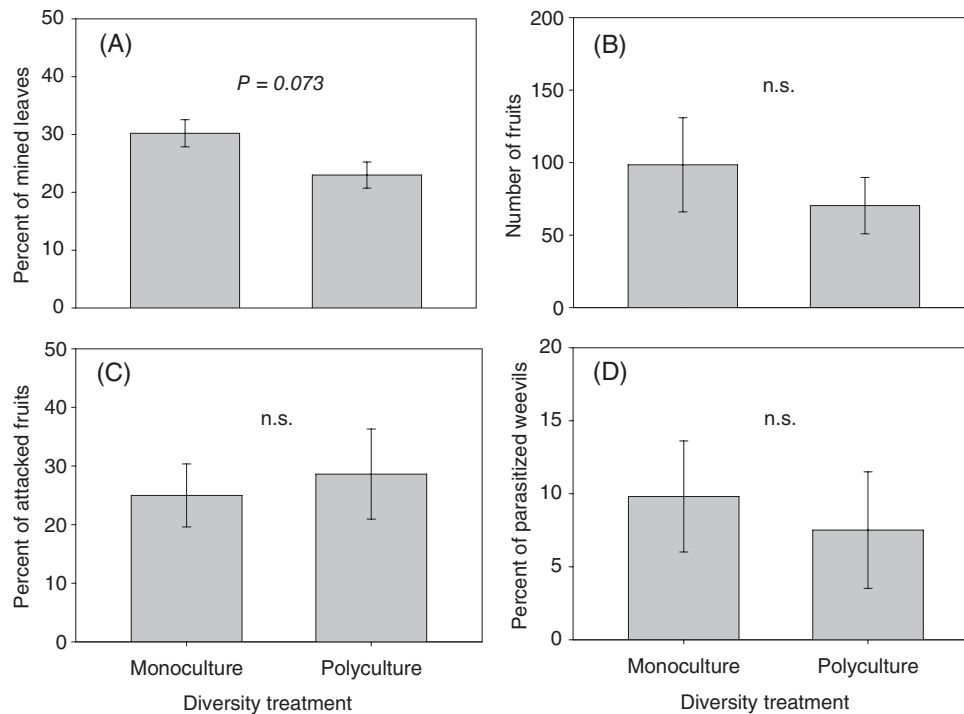Marginally significant ($0.05 < P < 0.10$) effects are shown in italics.

Figure 1 Effects of *Capsicum chinense* genotypic diversity on fruit number (A), the proportion of leaves with mines by *Liriomyza trifolii* (B), the proportion of fruits attacked by the pepper weevil *Anthonomus eugenii* (C) and the proportion of parasitized *A. eugenii* weevils (D) from a field experiment in southern Mexico (Yucatan). Bars are the mean ± SE. n.s., nonsignificant difference ($P > 0.05$); the diversity effect on leafminer attack was marginally significant ($0.05 < P < 0.10$).

Effects of plant diversity on fruit output and weevil attack

Plant diversity did not influence fruit output as indicated by no significant difference in total fruit number between *C. chinense* genotypic monocultures (98.48 ± 32.49 fruits) and polycultures (70.36 ± 19.42 fruits) (Fig. 1B and Table 1). In addition, we found no significant difference in the proportion of fruits attacked by *A. eugenii* between monocultures ($24.97 \pm 5.38\%$) and polycultures ($28.61 \pm 7.69\%$) (Fig. 1C and Table 1).

Effect of plant diversity on parasitism associated with the fruit weevil

Overall, 18.6% of the sampled weevils were parasitized. Plant diversity did not influence weevil parasitism as the generalized linear model indicated no significant difference in the proportion of parasitized weevils between *C. chinense* genotypic monocultures ($9.81 \pm 3.81\%$) and polycultures ($7.51 \pm 3.99\%$) (Fig. 1D and Table 1).

Discussion

We found contrasting effects of diversity on each herbivore; there tended to be a negative effect of diversity on *L. trifolii* leafminer attack but no effect whatsoever on *A. eugenii* fruit attack. In addition, diversity did not influence the amount of parasitism associated with *A. eugenii*, suggesting that natural enemies did not mediate effects of plant genotypic diversity on the recruitment patterns of this herbivore.

Our results showed a 24% reduction in leaf miner attack for *C. chinense* genotypic polycultures relative to monocultures. Although this result was not statistically significant ($P = 0.07$), we consider that the effect size observed is biologically meaningful and that it was likely burdened by low statistical power. Although sampling effects cannot be entirely ruled out (e.g. a higher incidence of resistant pepper genotypes in mixtures), our analyses indicated that this result was driven by non-additive dynamics from interactions among genotypes in mixtures (Johnson *et al*., 2006). Similarly, a number previous studies have also reported negative effects of plant diversity on insect herbivores (Andow, 1991; Barbosa *et al*., 2009) driven by habitat heterogeneity interfering with herbivore foraging (Björkman *et al*., 2010; Hambäck *et al*., 2014) or changes in plant traits reducing herbivore recruitment or damage (e.g. higher leaf defences; McArt & Thaler, 2013; Moreira *et al*., 2014). However, our finding that *L. trifolii* was negatively influenced by *C. chinense* genotypic diversity, despite being a broad dietary generalist herbivore, runs counter to the RCH, which predicts that specialist (rather than generalist) herbivores should be negatively influenced by diversity (Jactel & Brockerhoff, 2007). This suggests that diet breadth did not mediate diversity effects on this herbivore and that, instead, other traits such as dispersal ability or feeding mode were responsible for this finding (Bommarco & Banks, 2003). For example, adult *Liriomyza* females exhibit high dispersal rates (Jones & Parrella, 1986) and highly mobile herbivores are expected to respond more strongly to plant diversity than sedentary herbivores because they can disperse more readily and choose among plant patches of varying

diversity (Bommarco & Banks, 2003). Finally, although speculative because we did not measure parasitism associated with the leafminer, it is worth noting that our finding agrees with the EH, which predicts negative effects of diversity on generalist herbivores such as *L. trifolii* because these are highly susceptible to enhanced effects of natural enemies in species or genotype mixtures. Nonetheless, further work is necessary to test this hypothesis and to determine whether natural enemies mediate *C. chinense* genotypic diversity effects on *L. trifolii*.

Pepper genotypic diversity had no overall effect on fruit attack by the relatively more diet-specialized herbivore *A. eugenii*, which is unsupportive of the RCH, which predicts negative effects of plant diversity on specialist herbivores. Thus, it appears that this herbivore it is not strongly influenced by changes in density or traits of specific genotypes across levels of genotypic diversity, at least for *C. chinense*. However, we caution that predictions of plant genotypic diversity based upon herbivore diet breadth alone may not be straightforward in this case because *A. eguenii* is not a strict specialist on *C. chinense* or even the genus *Capsicum*. In addition, it is also possible that other traits such as dispersal ability could have limited the response of this herbivore to genotypic diversity in *C. chinense*. For example, previous studies have shown that *A. eugenii* exhibits low dispersal and highly clumped distributions (Riley *et al.*, 1992) and herbivores with low mobility may exhibit weaker responses to plant diversity (Bommarco & Banks, 2003). Thus, to test for effects of diet breadth, we should ideally examine responses to diversity by multiple herbivore species located at different points along a continuum of dietary specialization, at the same time as controlling for other traits (e.g. dispersal ability, feeding guild; Ali & Agrawal, 2012). At the same time, our result could be interpreted as supportive of the EH, which predicts weaker effects of diversity on specialist (relative to generalist) herbivores because these are better defended against natural enemies. Accordingly, there was no effect of diversity on parasitism associated with this specialist weevil, which supports the idea that natural enemies did not mediate diversity effects on this herbivore (for similar findings, see Langer, 1996; Björkman *et al.*, 2010).

Taken together, the results of the present study reveal contrasting effects of plant genotypic diversity on different species of insect herbivores. Such effects are likely dependent upon herbivore species-specific traits (e.g. diet breadth, mobility, feeding mode), as well as plant genetically-based variation in key traits influencing consumers. Accordingly, a predictive understanding of plant genotypic diversity effects on higher trophic levels will be achieved only to the extent that we identify which genetically-based plant traits underlie such dynamics (Mooney & Singer, 2012; Barbour *et al.*, 2015) and how such traits interact with herbivore traits (Hambäck *et al.*, 2014). Finally, our findings suggest that, by reducing the abundance of generalist herbivores (i.e. leafminers), genotypic mixtures can serve as a pest control strategy in *C. chinense*, a commercially important crop that is usually planted in genotypic monocultures throughout southern Mexico.

Acknowledgements

Supporting information

Additional Supporting information may be found in the online version of this article under the DOI reference: 10.1111/afe.12125

Table S1. Variation in reproductive traits and resistance to insect herbivores and virus infection among habanero pepper (*Capsicum chinense*) inbred lines used in the present study (from Berny-Mier y Terán *et al.*, 2013). We present the magnitude of variation (fold variation among the two most extreme lines for each variable) and test of genetic variation among lines for fruit weight, fruit output, attack by *Liriomyza trifolii* leaf miners (proportion of attacked leaves), attack by *Anthonomus eugenii* fruit weevils (proportion of attacked fruits) and severity of symptoms of co-infection by viruses transmitted by the whitefly *Bemisia tabaci* (scale of 1–9).

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