

LETTER

Welcome to the neighbourhood: interspecific genotype by genotype interactions in *Solidago* influence above- and belowground biomass and associated communities

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Abstract

Intra- and interspecific plant–plant interactions are fundamental to patterns of community assembly and to the mixture effects observed in biodiversity studies. Although much research has been conducted at the species level, very little is understood about how genetic variation within and among interacting species may drive these processes. Using clones of both *Solidago altissima* and *Solidago gigantea*, we found that genotypic variation in a plant's neighbours affected both above- and belowground plant traits, and that genotype by genotype interactions between neighbouring plants impacted associated pollinator communities. The traits for which focal plant genotypic variation explained the most variation varied by plant species, whereas neighbour genotypic variation explained the most variation in coarse root biomass. Our results provide new insight into genotypic and species diversity effects in plant–neighbour interactions, the extended consequences of diversity effects, and the potential for evolution in response to competitive or to facilitative plant–neighbour interactions.

Keywords

Biotic environment, community and ecosystem genetics, genotype by genotype interactions, genotypic variation, plant–neighbour interactions, plant–plant interactions, pollination, *Solidago*.

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INTRODUCTION

Biodiversity provides key ecosystem services and yet, in over 50 years of ecological research on the causes, mechanisms and consequences of biodiversity, few generalisations can actually be made (see Hooper *et al.* 2005 for review). For example, although it is increasingly understood that variation among and within species can have extended consequences for the diversity of communities and ecosystems in which these species are embedded (e.g. Johnson & Agrawal 2005; Bailey *et al.* 2006; Crutsinger *et al.* 2006; Johnson *et al.* 2006; Whitham *et al.* 2006; Mooney & Agrawal 2008), mechanisms for understanding the community and ecosystem effects of genetic variation remain elusive. Recent research suggests that genotypic diversity (i.e. the number of unique genotypes present in a given area) in dominant plant species can structure the diversity of associated communities (e.g. Booth & Grime 2003; Crutsinger *et al.* 2006, 2008; Johnson *et al.* 2006) and influence ecosystem processes (e.g. Hughes & Stachowicz 2004; Schweitzer *et al.* 2005; Crutsinger *et al.* 2006; Madritch *et al.* 2006). The mechanism invoked for diversity effects involves either species or genotype interactions (i.e. a genotype's traits change in the presence of certain neighbour genotypes) that occur in mixture and affect community and ecosystem processes. Therefore, simple studies to understand these interactions and how they influence patterns of biodiversity can be conducted with experimental designs which are more commonly associated with research into plant–neighbour interactions (Turkington & Harper 1979; Aarssen & Turkington 1985; Cahill *et al.* 2005; Fridley *et al.* 2007; Bossdorf *et al.* 2009).

Although most work in the field of community and ecosystem genetics has been conducted within a single site or population, species are embedded in a matrix with many other species in variable environments (Whitham *et al.* 2006). Because of the constant interactions between species and their abiotic and biotic environments, understanding the community and ecosystem consequences of genotype by environment ($G \times E$) interactions is a rapidly emerging area of research. When $G \times E$ interactions have been examined, studies clearly indicate that abiotic factors such as site differences (Johnson & Agrawal 2005; Tack *et al.* 2010) and nutrient addition (Madritch *et al.* 2006; Rowntree *et al.* 2010), as well as biotic factors such as genotypic diversity (Schweitzer *et al.* 2005; Crutsinger *et al.* 2006; Johnson *et al.* 2006; Madritch *et al.* 2006) and herbivory (Schweitzer *et al.* 2005) can all influence the community and ecosystem level impacts of plant intraspecific genetic variation. Investigating the role of $G \times E$ interactions is essential to understanding the effects of species and genotypic diversity in plants, because plant–neighbour interactions are a common type of $G \times E$ interaction in which the 'biotic environment' (e.g. neighbour plant) contains genes (i.e. genotype \times genotype interactions or $G \times G$) and both participants are fixed in space and forced to interact for resources (Turkington & Harper 1979). Studies of plant–neighbour interactions have previously shown that intraspecific genetic variation in an individual's neighbours (1) can have important consequences for overall plant fitness and performance (Turkington & Harper 1979; Aarssen & Turkington 1985; Cahill *et al.* 2005; Fridley *et al.* 2007; Bossdorf *et al.* 2009; Collins *et al.* 2010) and (2) is thought to be an important part of the maintenance of species and genetic variation in

plant communities (e.g. Fridley *et al.* 2007; Lankau & Strauss 2007). Our study builds on the work of plant–neighbour interactions, genotypic diversity and coevolutionary theory to investigate how genetic variation in two naturally occurring, dominant old field plants may interact to influence above- and belowground plant traits, and associated pollinator communities.

Studying how neighbouring plants compete for pollinators or facilitate each other's pollination involves considering a system in which plant–pollinator interactions are mutualistic, but neighbouring plants can have either an antagonistic or synergistic effect on each other's sexual reproduction (reviewed in Mitchell *et al.* 2009). Exploitative competition for pollinators between neighbouring plants may reduce plant fitness when the quantity of visits to a given plant is reduced because pollinators are attracted to its co-flowering neighbours instead (e.g. Macior 1971; Pleasants 1980). Plant fitness may also be reduced due to deposition of incompatible pollen, pollen wastage, or stigma clogging; these effects may be especially important for close congeners. However, plant fitness may be increased due to facilitative interactions between neighbouring plants if pollinators are attracted to the increased floral density of species mixtures (e.g. Thomson 1982; Ghazoul 2006; Lazaro *et al.* 2009). Mitchell *et al.* (2009) highlights that both ecological and evolutionary context can affect how competition and facilitation between neighbouring plants affects plant–pollinator interactions. The ecological context includes environmental variation (i.e. variation in the presence or number of particular neighbouring species), whereas the evolutionary context includes the heritable phenotypic variation within each of the interacting plant species which scales up to determine trait variation (Mitchell *et al.* 2009). This perspective is directly relatable to the goals of $G \times G$ studies, which manipulate both the evolutionary context of focal plant phenotypic variation by including distinct genotypes of plants, and the ecological context of biotic environmental variation by manipulation of neighbour plant genotype identity.

We used *Solidago* spp. as a model system to examine the role of $G \times G$ interactions in affecting above- and belowground plant traits and arthropod pollinator visitation. We hypothesised that $G \times G$ interactions would affect plant–plant interactions and provide a mechanism for understanding effects that occur when species and genotypes co-occur in natural systems. We established a common garden experiment using clonally replicated individuals (i.e. genotypes) of both *Solidago altissima* and *Solidago gigantea*, with each genotype planted alone in monoculture treatments and with all possible interspecific combination of genotypes. We examined how intraspecific genotypic variation (i.e. 'focal genotype') and genotypically based biotic environmental variation (i.e. 'neighbour genotype') affected a range of population and community traits. Specifically, we addressed the following questions: (1) Does focal plant genotypic variation influence above- and belowground productivity, floral biomass, and pollinator visitation? (2) Does the biotic environment affect these same traits, either through the effects of neighbour plant genotype or $G \times G$ interactions? Our results indicate that the genotype identity of a plant's neighbour affected both above- and belowground biomass, and that interspecific indirect genetic effects can drive patterns of pollinator visitation. Across species, the genotype identity of a plant's neighbour had more consistent effects on coarse root biomass than did the focal plant's genotype identity, which suggests that genetic variation in a plant's neighbours may be an important, but less frequently considered mechanism explaining population and community trait variation in ecological communities.

MATERIAL AND METHODS

Study species

Solidago altissima is a dominant species in abandoned agricultural fields where it can have large impacts on biodiversity and ecosystem function (Maddox & Root 1987; Crutsinger *et al.* 2006). Intraspecific genetic variation in *S. altissima* has been shown to affect herbivores (e.g. Maddox & Root 1987; Crutsinger *et al.* 2006), flowering phenology (e.g. Gross & Werner 1983), as well as floral visitor abundance (Genung *et al.* 2010). *Solidago gigantea* is less common than *S. altissima* in southeastern old fields, but these two species are among the most frequently co-occurring species pairs in the genus *Solidago* (Abrahamson *et al.* 2005). Although the two species are ecologically similar, they differ in life-history traits (Abrahamson & Weis 1997), allocation of resources to different growth forms, and tolerance for variation in soil moisture (Abrahamson *et al.* 2005). Specifically, *S. altissima* allocates relatively more biomass belowground and is more capable of tolerating broad variation in soil moisture than is *S. gigantea* whereas *S. gigantea* allocates relatively more biomass into flowers (Abrahamson *et al.* 2005). Both *S. altissima* and *S. gigantea* are gynodioecious, self-incompatible, and rely on insect pollination for fertilisation (Wise *et al.* 2008). Each capitulum contains 10–15 pistillate ray flowers surrounding 3–7 hermaphroditic disc flowers (Abrahamson & Weis 1997); the ray flowers mature and become receptive to pollen before the disc flowers (Gross & Werner 1983). Each ray and disc flower produces a single seed (Wise *et al.* 2008).

Garden description

In April 2008, a common garden experiment was established at Freels Bend on the reservation of Oak Ridge National Laboratory to examine the community and ecosystem level impacts of genotype-based plant–neighbour interactions in *Solidago*. This common garden includes three locally collected genotypes (i.e. clonal families) of both *S. altissima* and *S. gigantea*. The *S. altissima* and *S. gigantea* clones we utilised were originally propagated by G.M. Crutsinger and clones were maintained at the University of Tennessee and Freels Bend. The genotypes were collected from random locations around the study site at Freels Bend; sampled individuals from both species were carefully collected from unique connected genets that were at least 50–150 m apart (Crutsinger *et al.* 2006; Supplementary Material). Rhizomes were collected from connected ramets to ensure they were from the same genet. The three *S. altissima* genotypes were originally collected and determined as unique genotypes using AFLP (Crutsinger *et al.* 2006, Supplementary Material); however, molecular data is unavailable for the *S. gigantea* genotypes.

The experimental treatments included genotype monocultures as well as all possible interspecific combinations of *S. altissima* and *S. gigantea* genotypes, planted together in 95 L pots ($n =$ three replicates per genotype-neighbour genotype combination, six monoculture treatments and nine genotype mixture combinations, a total of 45 pots). All plants were propagated from cloned stocks of genotypes. A 3-cm rhizome of each species and genotype were grown in a greenhouse in flats in standard potting media for 8 weeks; the plants received regular water. Rooting hormones (Hormodin, OHP Inc., Mainland, PA, USA) were applied to each rhizome. When the plants were ≈ 10 cm in height they were transplanted into the pots at the field site. Each pot initially included four individuals, but variation in

plant density occurred due to clonal production of new ramets beginning during the initial growing season (2008) that continued throughout the experiment. In monocultures, all four individuals were clones of the same genotype. In genotype mixtures, each pot initially contained two individuals of each genotype (four plants total/pot). The pots were randomly placed in a grid formation within an old field with *c.* 3 m separating each pot from its neighbours. The field was not mown during the course of the experiment, creating an aboveground environment which closely mimicked that which the plants would experience in natural systems. Supplementary water was pumped to each pot in equal amounts when conditions required. The pots were filled with Fafard Growing Mix #1 (Conrad Fafard Inc, Agawam, MA, USA), and invading plants were removed throughout the experiment. Approximately 10 g of fertilizer (24/8/16, Miracle-Gro, Marysville, OH, USA) was applied once to each pot in April 2008.

Plant trait measurements

We measured a series of plant and community traits over the course of a growing season; these included rhizome biomass, coarse root biomass, vegetative biomass, floral biomass, and arthropod pollinator visitation. To determine vegetative biomass, we measured the aboveground height of the plants during peak productivity in early August and used an allometric equation to estimate aboveground biomass (Appendix S1 in Supporting Information). To estimate floral biomass, we used a representative panicle of *S. altissima* with known floral biomass as a unit of measurement. We chose a panicle which was smaller than average, *c.* ½ the size of an average panicle, and estimated floral biomass as the number of replicates of the representative panicle required to equal the floral abundance of the pot (*sensu* Genung *et al.* 2010). We measured floral biomass for each plant at the time when floral abundance was at its peak; this ranged from late August through late October 2009.

Belowground plant structures were sampled after the plants had senesced in December 2009, by carefully removing all plant structures intact from the soil. Aboveground differences allowed us to differentiate *S. altissima* and *S. gigantea* belowground structures in species mixture pots. We did not assess fine roots (< 2 mm in diameter) which became disconnected from the larger root structure during the excavation process, because we could not identify which *Solidago* species had produced the roots. We separated all rhizomes (i.e. horizontal underground stems) from coarse roots (> 2 mm in diameter) by hand in the laboratory. All belowground structures were air-dried for 2 weeks before weighing; a subsample was dried (70 °C for 48 h) such that all final biomass is presented on a dry mass basis. Although we were careful to excavate entire rhizome systems, in some cases rhizomes were severed during the excavation process; these pots were excluded from our analysis of belowground traits because we could no longer be certain which genotype had produced the rhizomes in question. One rhizome biomass sample and one coarse root biomass sample were excluded due to labelling errors.

Pollinator visitation was assessed using visual surveys of the pots, performed ten times beginning in early August and continuing through mid-November (approximately every 10 days). We summed pollinator visitation across all 10 surveys for our analyses; this sum is referred to as 'pollinator visitation'. During each survey, each pot was observed for five min from a distance of *c.* 3 m and the abundance of insects which visited flowers was counted (*sensu* Genung *et al.* 2010 and references therein). A pollinator visit was recorded if an insect

contacted a reproductive portion of the plant (Lazaro *et al.* 2009). Pollinators were grouped into taxa based on differences the surveyor (MAG) could consistently identify from a range of 3 m. The most common pollinator taxa on *S. gigantea* were halictid bees, especially *Agapostemon* species, and the most common pollinator taxa on *S. altissima* were *Apis* species and *Bombus* species (see Appendix S2 for a complete list of observed pollinator taxa). Following the visual survey, flowering panicles were shaken onto a sheet of white paper to assess pollinators which had not moved between plants during the survey time; by far the most common pollinator recorded in this way was *Chauliognathus pennsylvanicus*. We also estimated pollinator visitation per unit floral biomass per unit time (hereafter 'per-flower visitation'), where time included the total length of surveys during which plants were flowering.

Statistical analyses

To determine the effects of focal plant genotype, neighbour plant genotype, and the interaction of focal genotype and neighbour genotype, we selected only the pots which contained one genotype of both *S. altissima* and *S. gigantea* and tested which factors explained variation in our measured plant and community traits. We used a generalised linear model with a normal distribution and an identity link function to test for the effects of plant and neighbour genotypic variation. This approach excluded monoculture pots because including these pots would confound the effects of neighbour species identity and pot-level species and genotypic diversity with neighbour genotype identity effects. We separated our analyses by species such that our data points remained independent within each analysis. However, the two analyses themselves are not independent. For each species, our analysis included the following terms: focal genotype, neighbour genotype, and focal genotype × neighbour genotype. Focal genotype and neighbour genotype were entered as fixed factors. To determine the percentage of variation accounted for by each experimental factor, we repeated this analysis, with the same factors and responses, as a general linear model. Variances were calculated with the following equation: (treatment sum of squares)/(total sum of squares) × 100% (Johnson 2008).

To determine whether neighbour trait values, as opposed to neighbour genotype identity, could explain variation in focal plant traits, we repeated the above analysis and substituted the neighbour plant's trait value in place of neighbour genotype identity. The trait value (i.e. rhizome biomass, coarse root biomass, aboveground vegetative biomass, floral biomass, pollinator visitation, per-flower visitation) used was always the same as the response variable in the focal plant. Again, we separated our analyses by species such that our data points remained independent. Our analysis included the following terms: species identity, focal genotype, neighbour trait value, and focal genotype × neighbour trait value. Focal genotype was entered as a fixed factor. Variances were calculated for each factor as described in the preceding paragraph.

To determine which plant traits were most important to pollinator visitation, we used generalised linear models to examine how pollinator visitation and per-flower visitation were affected by plant traits. Again, we separated our analyses by species and neighbour species such that our data points remained independent. Focal genotype was entered as a fixed factor. Floral biomass was not used as a predictor for per-flower visitation. Although factorial combinations of plant traits may be important for predicting pollinator visitation, we

were unable to include these factors because of sample size limitations.

RESULTS

Consistent with the hypothesis that genotypic variation in a plant's neighbour would affect plant traits, we found that neighbour genotype affected both above- and belowground biomass (Table 1, Fig. 1). In addition, consistent with the hypothesis that $G \times G$ interactions would affect the response of plants in mixture, we detected a $G \times G$ interaction affecting pollinator visitation (Table 1, Fig. 1). The traits for which focal genotype explained the most variation varied by plant species (Table 1). The per cent of variation explained by focal plant genotype ranged between 6 and 21% for *S. altissima* focal plants, and 12 and 65% for *S. gigantea* focal plants. We detected weaker effects (i.e. not consistently significant across focal species, and less proportion variance explained) of focal genotype on per-flower pollinator visitation.

Although focal plant genotype was a significant factor affecting above- and belowground productivity, floral biomass, pollinator visitation and per-flower visitation when in mixture, the genotype of the interacting neighbour plant was a consistent predictor of coarse root biomass and also affected *S. altissima* vegetative biomass (Table 1). The per cent of variation explained by the genotype of the neighbouring plant ranged between 1 and 36% for *S. altissima* focal plants, and 0 and 14% for *S. gigantea* focal plants. The traits for which neighbour genotype explained the most variation varied by plant species, but for both species the most consistently explanatory effects of neighbour genotype were on belowground traits (Table 1). Importantly, we also detected an interspecific $G \times G$ interaction affecting pollinator visitation to *S. altissima* (Table 1). This result demonstrates that the extended effects on pollinator visitation found in plant–plant mixtures are a consequence of interactions amongst individual genotypes. In other words, the pollinators which visited an individual depended upon the genotypically based variation in the

individual's biotic environment. We found no neighbour genotype effects or $G \times G$ interactions for per flower pollinator visitation. We also found that neighbour plant traits (as opposed to neighbour genotype) could explain variation in focal plant traits. We found that neighbour biomass affected focal plant biomass for the following traits: rhizome biomass, coarse root biomass and aboveground vegetative biomass (Table 2). For floral biomass, pollinator visitation, and per flower visitation we found no effect of neighbour traits on the focal plant (Table 2).

We also found species level effects with respect to which plant and community traits were influenced by each of the model factors. In general, focal genotype was the most significant predictor of plant traits in *S. gigantea*, whereas neighbour genotype was the most significant predictor of plant traits in *S. altissima* (Table 1). These results demonstrate that there is little phenotypic plasticity in the response of *S. gigantea* to the genetic environment of *S. altissima*. In contrast, *S. altissima* demonstrated significant plasticity in their response to *S. gigantea*, particularly in belowground traits (Conner & Hartl 2004). For both species, the only plant trait which consistently predicted pollinator visitation was floral biomass, whereas coarse root biomass predicted per flower visitation to *S. gigantea*, but not *S. altissima* (Table 3).

Averaging across species, focal genotype explained the most variation in aboveground plant biomass and pollinator visitation, and the least variation in belowground plant biomass, whereas the opposite pattern was observed for neighbour genotype. However, the proportion of variation explained by focal genotype and neighbour genotype varied by plant species (Fig. 2a,b). Focal genotype and neighbour genotype explained roughly the same amount of variation in belowground plant traits, whereas focal genotype explained more variation in aboveground plant and pollinator visitation than did neighbour genotype. This result suggests that processes (which may be competitive or facilitative) related to coarse root and rhizome biomass may be strongly influenced by genetically based biotic environmental variation.

Table 1 The results of generalised linear models testing the effects of focal genotype, neighbour genotype, and focal genotype by neighbour genotype interactions shown for six traits. Per flower visitation refers to the number of pollinators visits a plant received, per unit floral biomass, per unit time. To ensure independence within each analysis, data were only analysed for pots containing one genotype of both *S. altissima* and *S. gigantea*, and the analysis was run separately for each species. The most significant effects of focal genotype are found for *S. gigantea* focal plants and the pollinator visitation trait. The most significant effects of neighbour genotype were found for *S. altissima* focal plants and the coarse root biomass trait. A significant $G \times G$ interaction was detected for pollinator visitation to *S. altissima*. Bold values are significant at $\alpha = 0.05$

| Trait | Focal genotype | | | Neighbour genotype | | | $G \times G$ | | |
|--------------------------------------|----------------|----------------|-------------------------|--------------------|--------------|-------------------------|--------------|--------------|-------------------------|
| | d.f. | <i>P</i> | * <i>r</i> ² | d.f. | <i>P</i> | * <i>r</i> ² | d.f. | <i>P</i> | * <i>r</i> ² |
| (a) <i>Solidago altissima</i> | | | | | | | | | |
| Rhizome biomass | 2, 25 | 0.026 | 0.170 | 2, 25 | 0.001 | 0.354 | 4, 25 | 0.902 | 0.022 |
| Coarse root biomass | 2, 24 | 0.060 | 0.137 | 2, 24 | 0.005 | 0.285 | 4, 24 | 0.413 | 0.093 |
| Vegetative biomass | 2, 27 | 0.290 | 0.055 | 2, 27 | 0.002 | 0.358 | 4, 27 | 0.782 | 0.039 |
| Floral biomass | 2, 27 | 0.076 | 0.127 | 2, 27 | 0.066 | 0.135 | 4, 27 | 0.152 | 0.170 |
| Pollinator visitation | 2, 27 | 0.012 | 0.210 | 2, 27 | 0.492 | 0.029 | 4, 27 | 0.027 | 0.272 |
| Per flower visitation | 2, 27 | 0.124 | 0.106 | 2, 27 | 0.841 | 0.008 | 4, 27 | 0.104 | 0.209 |
| (b) <i>Solidago gigantea</i> | | | | | | | | | |
| Rhizome biomass | 2, 24 | 0.206 | 0.116 | 2, 24 | 0.842 | 0.012 | 4, 24 | 0.784 | 0.062 |
| Coarse root biomass | 2, 25 | 0.003 | 0.286 | 2, 25 | 0.042 | 0.136 | 4, 25 | 0.161 | 0.141 |
| Vegetative biomass | 2, 27 | < 0.001 | 0.421 | 2, 27 | 0.663 | 0.016 | 4, 27 | 0.676 | 0.047 |
| Floral biomass | 2, 27 | < 0.001 | 0.645 | 2, 27 | 0.926 | 0.002 | 4, 27 | 0.732 | 0.023 |
| Pollinator visitation | 2, 27 | < 0.001 | 0.616 | 2, 27 | 0.379 | 0.023 | 4, 27 | 0.483 | 0.043 |
| Per flower visitation | 2, 27 | 0.045 | 0.186 | 2, 27 | 0.212 | 0.089 | 4, 27 | 0.737 | 0.056 |

d.f., degrees of freedom.

**r*² estimate obtained from ordinary least square analysis, and represents the percentage of variation explained by a given factor in the full model.

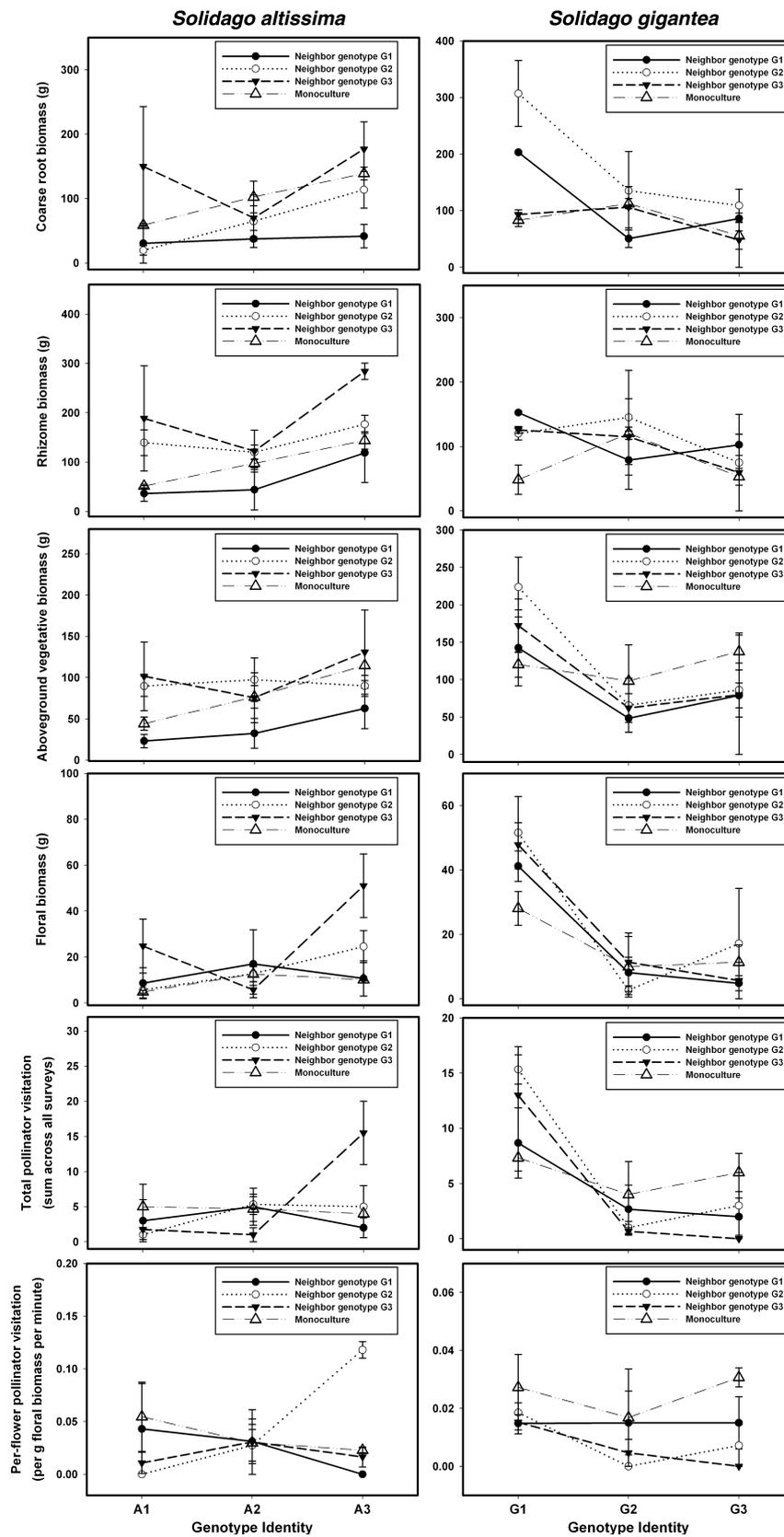


Figure 1 The relative importance of focal genotype, neighbour genotype, and G × G interactions varies across plant traits and by focal species. Per flower visitation refers to the number of pollinators visits a plant received, per unit floral biomass, per unit time. Mean trait values for plant traits and pollinator visitation are presented for each focal genotype of each species depending on the neighbour genotype with which they were grown. *S. altissima* (left panels) or *S. gigantea* (right panels) focal genotype identity is listed along the x-axis and each connected set of points represents the genotype identity of the neighbouring plants.

Table 2 The results of an ANCOVA generalised linear model testing the effects of focal genotype, neighbour trait, and focal genotype by neighbour trait interactions shown for six plant traits. 'Neighbour trait' was always the same as the response variable for the focal plant. To ensure independence of data points within each analysis, data were only analysed for pots containing one genotype of both *S. altissima* and *S. gigantea*, and the analysis was run separately for each species. For rhizome biomass, coarse root biomass, and aboveground vegetative biomass, the biomass produced by a plant's neighbour influenced the biomass of the focal plant. For floral biomass, pollinator visitation and per flower visitation, we found no effect of neighbour traits on the focal plant. Bold values are significant at $\alpha = 0.05$

| Trait | Focal genotype | | | Neighbour trait | | | G × Neighbour trait | | |
|--------------------------------------|----------------|-------------------|-------------------------|-----------------|--------------|-------------------------|---------------------|----------|-------------------------|
| | d.f. | <i>P</i> | * <i>r</i> ² | d.f. | <i>P</i> | * <i>r</i> ² | d.f. | <i>P</i> | * <i>r</i> ² |
| (a) <i>Solidago altissima</i> | | | | | | | | | |
| Rhizome biomass | 2, 24 | 0.142 | 0.117 | 1, 24 | 0.010 | 0.214 | 2, 24 | 0.617 | 0.027 |
| Coarse root biomass | 2, 24 | 0.773 | 0.015 | 1, 24 | 0.005 | 0.259 | 2, 24 | 0.230 | 0.088 |
| Vegetative biomass | 2, 27 | 0.500 | 0.033 | 1, 27 | 0.001 | 0.294 | 2, 27 | 0.986 | 0.001 |
| Floral biomass | 2, 27 | 0.248 | 0.085 | 1, 27 | 0.106 | 0.080 | 2, 27 | 0.245 | 0.086 |
| Pollinator visitation | 2, 27 | 0.110 | 0.141 | 1, 27 | 0.534 | 0.011 | 2, 27 | 0.502 | 0.042 |
| Per flower visitation | 2, 27 | 0.077 | 0.150 | 1, 27 | 0.296 | 0.030 | 2, 27 | 0.101 | 0.132 |
| (b) <i>Solidago gigantea</i> | | | | | | | | | |
| Rhizome biomass | 2, 24 | 0.507 | 0.036 | 1, 24 | 0.004 | 0.250 | 2, 24 | 0.050 | 0.178 |
| Coarse root biomass | 2, 24 | 0.275 | 0.076 | 1, 24 | 0.219 | 0.044 | 2, 24 | 0.609 | 0.028 |
| Vegetative biomass | 2, 27 | 0.084 | 0.100 | 1, 27 | 0.046 | 0.079 | 2, 27 | 0.738 | 0.011 |
| Floral biomass | 2, 27 | < 0.001 | 0.469 | 1, 27 | 0.420 | 0.007 | 2, 27 | 0.702 | 0.008 |
| Pollinator visitation | 2, 27 | < 0.001 | 0.637 | 1, 27 | 0.935 | 0.000 | 2, 27 | 0.244 | 0.037 |
| Perflower visitation | 2, 27 | 0.079 | 0.169 | 1, 27 | 0.298 | 0.034 | 2, 27 | 0.656 | 0.026 |

d.f., degrees of freedom.

**r*² estimate obtained from ordinary least square analysis, and represents the percentage of variation explained by a given factor in the full model.

Table 3 The results of a generalised linear model analysis linking plant traits to pollinator visitation, grouped by species and neighbour species (represented by the first and second names, respectively, at the top of each column). Per flower visitation refers to the number of pollinator visits a plant received, per unit floral biomass, per unit time. All listed traits and response variables were measured on focal plants, and not neighbouring plants. Only data from pots containing both species are presented here. Floral biomass is not used to predict per flower visitation. Floral biomass is the only trait which consistently predicts total pollinator visitation. In contrast, several traits predict per flower pollinator visitation, but only for *S. gigantea* focal plants with *S. altissima* neighbours. Bold values are significant at $\alpha = 0.05$

| Trait | Response = Total pollinator visitation | | Response = Per-flower visitation | |
|---------------------|----------------------------------------|----------------------------------|----------------------------------|----------------------------------|
| | <i>S. altissima/ S. gigantea</i> | <i>S. gigantea/ S. altissima</i> | <i>S. altissima/ S. gigantea</i> | <i>S. gigantea/ S. altissima</i> |
| | <i>P</i> | <i>P</i> | <i>P</i> | <i>P</i> |
| Rhizome biomass | 0.070 | 0.506 | 0.734 | 0.253 |
| Coarse root biomass | 0.271 | 0.390 | 0.152 | 0.009 |
| Vegetative biomass | 0.675 | 0.897 | 0.100 | 0.418 |
| Floral biomass | < 0.001 | < 0.001 | NA | NA |

NA, not applicable.

DISCUSSION

We examined whether (1) genotypic variation in a plant's neighbours and (2) indirect genetic effects (i.e. effects on an individual's phenotype due to genes in an interacting individual; Wolf *et al.* 1998) between plants and their neighbours influenced above- and belowground productivity, floral biomass, and pollinator visitation. Our results indicate that genotypic variation in a plant's neighbours affected both above and belowground plant traits, and that G × G interactions between neighbouring plants extended to associated communities (specifically pollinators visiting *S. altissima*). The neighbour genotype effects and G × G interactions we detected are both

types of indirect genetic effects, because the focal plant's traits are altered due to the genotype identity of its neighbour; however, the indirect genetic effect in G × G interactions is contingent on the genotype identity of the focal plant. In addition, the strongest effects of focal genotype and neighbour genotype varied by plant species. For example, focal genotype explained the most variation in pollinator visitation and rhizome biomass for *S. altissima* focal plants, and the most variation in pollinator visitation and floral biomass for *S. gigantea* focal plants.

Indirect genetic effects in community and ecosystem genetics

We found that genotypic variation in a plant and its neighbour affected a wide range of plant traits, and we also found that G × G interactions between neighbouring plants extended to affect pollinator communities (Table 1). These results align with those from across a wide range of plant systems which have shown that intraspecific genetic variation affects traits at the population and community level (Schweitzer *et al.* 2004, 2008; Crutsinger *et al.* 2006; Johnson *et al.* 2006; Whitham *et al.* 2006). Although a smaller collection of studies have examined how genetically based plant-neighbour interactions affect population-level responses (e.g. Aarssen & Turkington 1985; Fridley *et al.* 2007; Bossdorf *et al.* 2009), our data suggest that these interactions can also affect belowground biomass and associated communities. Although we did not detect an effect of species diversity (Appendix S3, Supporting Information) our results emphasise the fact that species interactions (which may be genotype-based) can occur in mixture even without consistently increasing or decreasing a given trait value relative to monoculture. Importantly, the most consistent effects of genetically-based biotic environmental variation (i.e. 'neighbour genotype') were on coarse root biomass, suggesting that studies which solely examine aboveground biomass may not detect the effects of species or genotypic variation in a plant's neighbour.

The effects of focal genotype varied by species, and explained the most variation in floral biomass and pollinator visitation for *S. gigantea*

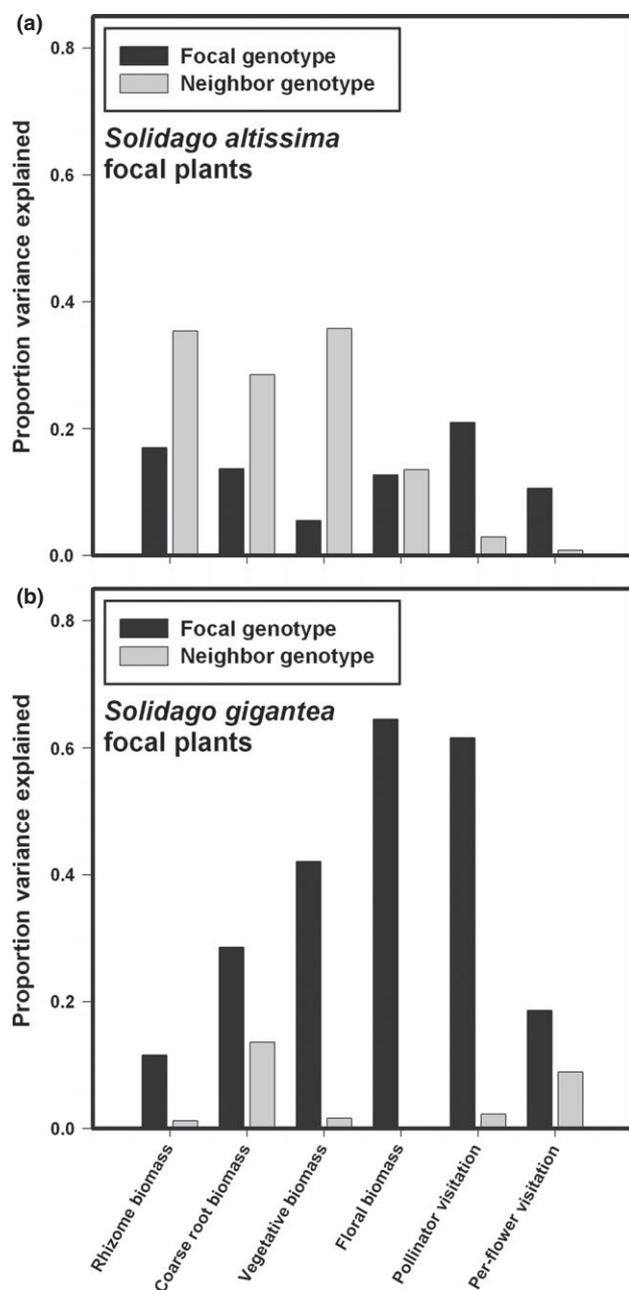


Figure 2 The proportion of variation explained by focal genotype and neighbour genotype vary across six plant and community traits. Per flower visitation refers to the number of pollinators visits a plant received, per unit floral biomass, per unit time. The proportion variance explained by focal genotype and neighbour genotype varies depending on whether the focal plant is an individual of *S. altissima* (a) or *S. gigantea* (b). Proportion variation in plant and community traits (along x-axis), as explained by focal plant genotype identity (black bars) and neighbour genotype identity (grey bars), is shown. Belowground traits (rhizome biomass, root biomass), aboveground traits (vegetative biomass, floral biomass) and community traits (pollinator visitation and per flower visitation) are included.

focal plants, and pollinator visitation and rhizome biomass for *S. altissima* focal plants (Table 1). The effects of neighbour genotype also varied by plant species, and explained the most variation in coarse root biomass for *S. gigantea* focal plants, and rhizome biomass and aboveground biomass for *S. altissima* focal plants. The effects of neighbour genotype were largest on *S. altissima* focal plants, and this

pattern appears to be driven by an especially vigorous *S. gigantea* genotype 'G1' which suppresses the production of rhizome, root, and aboveground biomass in its *S. altissima* neighbours (Fig. 1). As competition is likely to be more intense belowground in nitrogen limited environments (Tilman 1988; Wilson & Tilman 1993), the observation that neighbour genotype is important to belowground productivity suggests that intraspecific variation for traits related to nitrogen acquisition are responsible. This idea is also supported by data showing that, for *S. gigantea* focal plants, the only significant effect of neighbour genotype was on coarse root biomass (Table 1). As the total belowground biomass of focal plants was negatively correlated with neighbour plant belowground biomass, the mechanism for our observed neighbour effects probably involves neighbouring plants directly competing for space and resources. Other pathways, such as chemical inhibition (i.e. allelopathy) between neighbouring plants, or indirect interactions in which one genotype impacts its neighbour by altering associated communities cannot be ruled out as also contributing to neighbour effects.

Most community genetics studies have focused on interactions across trophic levels, and those studies which have examined within trophic level interactions have focused on competition and allelopathy (Booth & Grime 2003; Fridley *et al.* 2007; Lankau & Strauss 2007; Bossdorf *et al.* 2009); however, interspecific genetic variation may also affect facilitative interactions within the same trophic level (Michalet *et al.* 2011). Facilitation within a trophic level has particular importance for plant–pollinator interactions, because co-flowering neighbouring plants can compete for pollinators or facilitate each other's pollination (Thomson 1982; Callaway 1995). Both variation in the presence or number of particular neighbouring species and the heritable phenotypic variation within the interacting plant species can affect pollinator visitation to neighbouring plants (Mitchell *et al.* 2009). Our results indicate that pollinator visitation to *S. gigantea* was not affected by the genotype identity of (Table 1) or pollinator visitation to (Table 2) neighbouring *S. altissima* plants, but rather by genotypic variation for the floral biomass trait (Tables 1 and 3). This result emphasises the evolutionary context of plant–pollinator interactions by indicating that natural selection can act on genotypic variation for floral biomass in *S. gigantea* focal plants, regardless of the genotype identity of those plants' *S. altissima* neighbours. In contrast, pollinator visitation to *S. altissima* was affected by both focal genotype and an interspecific $G \times G$ interaction with a neighbouring *S. gigantea* genotype (Table 1). This result appears to be due to an increase in the performance of genotype 'A3' when planted with 'G3' relative to other *S. gigantea* neighbours. This pattern is visible across all measured traits (Fig. 1), although it is especially pronounced for pollinator visitation. This $G \times G$ interaction emphasises the ecological context of plant–neighbour interactions affecting pollinator visitation by showing that genotypic variation in an individual's biotic environment may exert fitness effects on a focal plant, and that these biotic environmental effects depend upon the genotype of the focal plant. As a $G \times G$ interaction was not detected for per flower visitation, floral abundance and flowering duration are likely to be at least partially responsible for the $G \times G$ interaction observed for total pollinator visitation. Although ecologists have spent over a century researching how neighbouring plants of different species compete for pollinators or facilitate each other's pollination (Robertson 1895; Clements & Long 1923; Macior 1971; Pleasants 1980; Thomson 1982; Callaway 1995; review Mitchell *et al.* 2009), our results extend this perspective by including the effects of intraspecific genotypic variation

and interspecific $G \times G$ interactions on pollinator visitation to neighbouring plants. The significant effects of focal plant and neighbour plant genotypic variation show that plant–pollinator interaction studies conducted at the species level may overlook the importance of considering finer genetic scales. In addition, because natural selection operates on the genetic variation present in populations, the results of $G \times G$ studies have implications for whether plant–neighbour interactions affect the rate and direction of evolutionary change, given that the trait being measured has an impact on fitness. These $G \times G$ interactions create the opportunity for individuals to adapt to fine-scale genetic variation in their environment (Fridley *et al.* 2007) and may also support the idea that plant–neighbour interactions are responsible for the maintenance of high levels of genetic variation which are displayed over small areas by many plant populations (Linhart & Grant 1996) because of the fitness consequences of intransitive (i.e. rock-paper-scissors) competitive relationships between interacting genotypes (Fridley *et al.* 2007; Lankau & Strauss 2007). Similarly, neighbouring conspecific plants can also influence each other's pollination success through the effects of genotypic variation and diversity (Genung *et al.* 2010), perhaps due to increased aboveground productivity in patches containing multiple genotypes (e.g. Crutsinger *et al.* 2006).

Plant response to the genetic environment of neighbours

Incorporating the effects of plant–neighbour interactions into the field of community and ecosystem genetics will lend more insight into our understanding of how genetic variation within species scales up to affect patterns and processes above the population level. Our results demonstrate that focal genotype and neighbour genotype can affect plant and community traits independently of each other, or in combination, and that neglecting to consider the influences of genotypic variation in a plant's neighbours can lead to an incomplete understanding of patterns and processes in natural systems. In particular, belowground plant traits may be especially affected by plant–neighbour interactions in the nitrogen-limited environments (Tilman 1988; Wilson & Tilman 1993) which occur world-wide (LeBauer & Treseder 2008). This suggests that a better understanding of how much carbon plants are investing into belowground biomass requires considering species and genetic variation in neighbouring plants which are also competing for belowground resources. Most studies of plant–neighbour interactions in a $G \times G$ context may have underestimated the importance of biotic environmental variation (but see Collins *et al.* 2010) by not including belowground trait measurements. Although some studies have found that root biomass is not related to plant competitive ability (Cahill 2003), belowground productivity represents an important part of net primary production and contributes organic carbon which can be sequestered or used by soil microorganisms (Bessler *et al.* 2009), reinforcing the importance of including measurements of belowground biomass. As belowground biomass in *Solidago* species has a genotypic basis (Table 1), the genotype identity of a plant's neighbours will determine the belowground environment in which the plant has to compete.

It remains to be seen whether focal genotype and neighbour genotype influence associated communities in natural settings, when moisture, soil texture, and other factors which affect plant productivity and pollinator visitation may vary along gradients. In fact, quantifying the importance of intraspecific genetic variation relative to other ecological factors remains a major issue in the field of

community and ecosystem genetics (Johnson *et al.* 2008; Bailey *et al.* 2009). Future studies should (1) investigate whether genotype-based plant–neighbour interactions scale up to affect associated communities in natural systems or (2) manipulate other ecological factors (i.e. density, nutrient availability, competition) alongside intraspecific genetic variation. These approaches will allow for a better determination of the importance of “community and ecosystem genetics” questions to broad ecological and evolutionary dynamics. Although the importance of genotype-based plant–neighbour interactions in natural systems remains unclear, results from our common garden experiment show that biotic environmental variation and $G \times G$ interactions can have important effects on belowground biomass production in plants and also extend to affect associated pollinator visitation. These findings reinforce the idea that organisms cannot be solely studied at the species level or as individuals, but rather a full understanding of ecological patterns must incorporate intraspecific genetic variation both within a focal species and the neighbours with which it interacts.

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AUTHOR CONTRIBUTIONS

MG collected and analysed data. All authors contributed to designing the study, as well as writing and revising the manuscript.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Allometric equation used to determine aboveground biomass estimates.

Appendix S2 Taxonomic groups used for visual surveys of pollinator visitation.

Appendix S3 Species diversity effects.

Appendix S4 Genotype contrasts for each trait grouped by neighbour genotype.

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