Journal of Applied Ecology

*Journal of Applied Ecology* doi: 10.1111/j.1365-2664.2012.02173.x

REVIEW

# Genotypically diverse cultivar mixtures for insect pest management and increased crop yields

**John F. Tooker[1]* and Steven D. Frank[2]**

[1]*Department of Entomology, The Pennsylvania State University, 501 ASI Building, University Park, PA, 16802, USA; and* [2]*Department of Entomology, North Carolina State University, 3318 Gardner Hall, Raleigh, NC, 27695-7613, USA*

## Summary

**1.** In modern crop production, each plant is often nearly genetically identical to its neighbours, allowing insect pests and pathogens to move easily from plant to plant and decimate crop fields. The associational resistance and enemies hypotheses predict that increasing plant diversity in agricultural fields will reduce pest abundance and damage. Ample research has supported these hypotheses by demonstrating that increased plant species diversity can improve insect pest management via bottom–up and top–down mechanisms. In spite of this support, diversification strategies that might contribute to improved pest control and yield have not been widely adopted owing to logistical and financial constraints.

**2.** Basic and applied research is increasingly demonstrating the value of intraspecific genetic diversity for improving ecosystem stability and function. Thus, a more practical way of diversifying crop fields may be to increase plant genotypic diversity by planting cultivar mixtures. Our objective is to review the literature documenting the benefits of genotypic diversity for natural and agricultural ecosystems and synthesize the evidence in support of intraspecific diversity as a viable pest management strategy for insect pests of field crops. We found strong support for wide-ranging benefits of genotypic diversity that improved plant fitness and productivity in natural and applied settings.

**3.** Multiple lines of evidence converge to support the potential of intraspecific variation to contribute to improve insect pest control. However, very little work has sought to develop empirical support or viable implementation practices in agricultural systems. Thus, implementation of this practice is limited.

**4.** *Synthesis and applications*. Intraspecific plant diversity can improve plant fitness via bottom–up and top–down effects on pest populations and niche partitioning. Further research is required to refine implementation practices and demonstrate value in terms of reduced pesticide use and increased yield. Growers can implement intraspecific crop diversity with minimal financial investment or changes in production practices. As the benefits of biodiversity for yield stability are increasingly recognized, intraspecific diversity is poised to become a prominent and sustainable management tactic.

**Key-words:** agroecosystem, bottom–up effects, diversification, intraspecific diversity, pathogen, pest control, sustainable, top–down effects

## Introduction

A goal of many integrated pest management (IPM) researchers and practitioners has been to develop sustainable management programmes that are more resilient and less reliant on synthetic pesticides (Altieri 1999; Lin 2011). Sustainable insect pest management programmes in agricultural systems often focus on using crop varieties that are more tolerant of, or resistant to, pest attack (i.e. bottom–up effects) and/or farming approaches that increase natural enemy effectiveness in controlling pest populations (i.e. top–down effects). Diverse plant species mixtures, either in crop fields (i.e. polyculture) or nearby

*Corresponding author: E-mail: tooker@psu.edu

non-crop areas, have been studied for their potential to improve both bottom–up and top–down effects in crop fields (Thomas, Wratten & Sotherton 1991; Landis, Wratten & Gurr 2000). However, despite holding potential for improving pest suppression, pest management techniques based on harnessing plant species diversity, such as non-crop plants in field borders or intercrops within fields, have not been widely implemented by conventional growers in developed countries because they are expensive, time consuming or logistically challenging for growers to plant mechanically (Lin 2011). In the light of these limitations, a logical approach is to develop IPM strategies that increase the diversity and structural complexity of agro-ecosystems, but do not require extraordinary changes in farming practices or monetary investments by growers.

A burgeoning body of literature from natural systems has demonstrated that genotypic diversity can play a large role in structuring arthropod communities and increasing plant fitness (Table 1). Less research has been conducted in agricultural settings to document the effects of intraspecific diversity on insect management (Wilhoit 1992) despite assertions to the contrary (Johnson, Lajeunesse & Agrawal 2006). Nevertheless, several lines of evidence suggest that increasing genotypic diversity in crop fields could greatly improve insect pest management and crop yield in an economically and environmentally sustainable manner. Our objective was to review literature from natural and agricultural systems in the context of a conceptual framework (Fig. 1) that presents the diverse mechanisms by which intraspecific, or genotypic, diversity could improve plant growth and yield. We define 'genotypic diversity' as genetic variation among varieties of a species and consider 'genetic diversity' to be a population-level measurement of variation or relatedness within a variety. While these terms are related, they are not interchangeable, and we focus on the former.

## Background

### CURRENT PRODUCTION PRACTICES

The great majority of crop fields in the United States and worldwide are planted with single genetic varieties. Therefore, every plant in a field is nearly genetically identical to its neighbour. These cultivars are bred to have uniform agronomic traits (i.e. limited genetic diversity), such as height, germination, development time, seed set and protein content, to facilitate farming logistics and maximize yield. However, limited genetic variation is a liability that leaves crop fields vulnerable to pest invasion and outbreaks. If all the plants in a field are susceptible to the same pest species, pest populations will spread rapidly from one plant to another once they invade a field. For example, when insect pests such as Hessian fly *Mayetiola destructor* Say overcome resistant varieties, crop fields can be quickly decimated (Gallun 1977; Gould 1986b). In other cases, crops have minimal pest resistance or resistance to only one insect or disease. Therefore, maximum crop yield is achieved with repeated insecticide applications, which have negative effects on non-target organisms and human and environmental health (Pimentel *et al.* 1992). Alternatives to single species/genotype planting are needed to reduce the intensity of pests and pesticides.

In addition to being less resistant to attack by pests, monotypic crop fields are also susceptible to pest outbreaks owing to a lack of natural enemies and the biological control services they provide (Fig. 1; Root 1973; Altieri 1999). In general, monocultures have fewer natural enemies than do polycultures (or crops set amongst non-crop vegetation) where pest outbreaks are uncommon (Root 1973; Altieri 1999). A lack of overwintering sites means natural enemies must colonize crop fields anew each year, giving pests a head start (Landis, Wratten & Gurr 2000). Moreover, crop fields are often poorly colonized by natural enemies owing to the lack of plant and prey food and other resources such as favourable microclimates and oviposition sites (Landis, Wratten & Gurr 2000). In addition, artificial selection for particular traits in some crop species has disrupted tritrophic interactions, so that natural enemies are unable to contribute as successfully to herbivore control in agricultural varieties as they do in wild relatives (Chen & Welter 2005; Rasmann *et al.* 2005). Lastly, management practices such as pesticide use, tilling and harvesting further disturb natural enemy communities in crop fields.

### BENEFITS AND CHALLENGES ASSOCIATED WITH PLANT SPECIES DIVERSITY IN AGROECOSYSTEMS

A large amount of research has focused on the benefits of plant species diversity and its influence on insect diversity and herbivore suppression. Our goal is not to review this body of literature here, but we will highlight a few points on the benefits and challenges associated with plant species diversity and pest control. First, species mixtures, or polyculture, can have negative bottom–up effects on arthropod pests by reducing their ability to find preferred host plants (i.e. associational resistance; Tahvanainen & Root 1972; Root 1973; Andow 1991; Agrawal *et al.* 2006; Randlkofer *et al.*, 2010); thus, insect herbivores cannot easily move from one host to another, slowing their spread through crop fields. Second, increasing species diversity either within crop fields, in adjacent non-crop areas, or regionally via landscape-scale improvements can also improve top–down control by providing floral resources, alternative prey and suitable microclimates that increase natural enemy fitness, abundance, diversity and source habitat (Andow 1991; Landis, Wratten & Gurr 2000; Thies, Steffan-Dewenter & Tscharntke 2003; Haddad *et al.* 2009). Third, despite the benefit of significant pest suppression associated with some of these approaches to diversification, effectiveness appears inconsistent and context dependent (Andow 1991; Baggen &

**Table 1.** Examples of plant systems and ecological variables influenced by plant genotypic diversity and whether the response would be likely to have a positive, neutral or negative effect on plant productivity and crop production. Examples are arranged in the order they were published first for those showing overall positive, mixed and then negative effects

| Plant species | Ecosystem | Plot type and scale | Ecological variable | Ecological response in diverse relative to monoculture plots | Relevance of effect for plant productivity | References |
|---|---|---|---|---|---|---|
| Maize *Zea mays* L. | Tropical agricultural fields | 75-$m^2$ plots of 1 or 5 varieties | Herbivore abundance | Up to 40% less leafhoppers overall; 50% less on most preferred variety | Positive | Power (1988) |
| | | | Disease incidence | Equal | Neutral | |
| Oat *Avena sativa* L. | Temperature agricultural fields | 15-$m^2$ plots of 1 or 2 varieties | Plant productivity | Equal number of tillers | Neutral | Power (1991) |
| | | | Plant fitness | 17% less seed per plant | Negative | |
| | | | Herbivore abundance | 35% less aphids (1 of 3 years) | Positive | |
| | | | Herbivore behaviour | 380% more aphid dispersal; aphids moved 140% farther; tenure time 37% less | Positive | |
| Oat *Avena sativa* L. | Temperature agricultural fields | 8–10 $m^2$ plots | Plant productivity | 9% higher productivity under drought conditions, but no yield benefit under optimal conditions | Mixed | Peltonen-Sainioa & Karjalainen (1991) |
| Willow Salix spp. | Experimental plantation and greenhouse setting | Individual trees in 20 × 20-m plots with 1, 3 or 5 varieties | Herbivore abundance | 50% less oviposition overall; 85% fewer leaf beetles on preferred genotype | Positive | Peacock & Herrick (2000) |
| | | | Herbivore damage | 32% less damage overall; 50% less on preferred genotype | Positive | |
| Cottonwood *Populus fremontii* S. Watson, *P. angustifolia* James, and hybrids | Common garden, natural stands | Individual trees in a common garden and natural stands | Total arthropod diversity | Increased; genotypic diversity accounted for 59% of variation in arthropod diversity | Positive | Wimp *et al.* (2004) |
| Evening primrose *Oenothera biennis* L. | Common garden | 0·4-m-diameter plots with equal number of 1, 4 or 8 genotypes | Plant fitness | 27% greater fruit set | Positive | Johnson, Lajeunesse & Agrawal (2006) |
| | | | Herbivore abundance and diversity | Equal | Neutral | |
| | | | Total arthropod richness | 18% greater | Positive | |
| | | | Predator richness | Greater | Positive | |
| | | | Omnivore abundance | Up to 80% greater | Positive | |
| | | | Predator abundance | Up to 37% greater | Positive | |
| Tall goldenrod *Solidago altissima* L. | Common garden | 1-$m^2$ plots with 1, 3, 6 or 12 varieties | Net primary productivity | 36% greater in 12 genotype plots | Positive | Crutsinger *et al.* (2006) |
| | | | Total arthropod richness | 27% greater in 12 genotype plots | Positive | |
| | | | Herbivore richness | ~15% greater in 12 genotype plots | Positive | |

**Table 1.** (Continued)

| Plant species | Ecosystem | Plot type and scale | Ecological variable | Ecological response in diverse relative to monoculture plots | Relevance of effect for plant productivity | References |
|---|---|---|---|---|---|---|
| | | | Predator richness | ~20% greater in 12 genotype plots | Positive | |
| Great Lakes sea rocket *Cakile edentula* [Bigelow] Hook. var. *lacustris* | Growth chamber | 3·8 or 7·6-$cm^2$ pots with 1 or 4 genotypes | Plant productivity | Increased; Plants produced greater fine root mass when in competition with other genotypes, | Positive | Dudley & File (2007) |
| *Arabidopsis thaliana* L. Heynh. | Outdoors | 10-cm pots of 1 or 9 genotypes | Plant productivity | 17% more biomass per pot without herbivores (*Trichoplusia ni* (Hübner), 5% more biomass with herbivores; greater proportion survival | Positive | Kotowska, Cahill & Keddie (2010) |
| | | | Herbivore performance | Greater survival; 19% greater biomass per pot; 7% greater biomass per caterpillar | Negative | |
| *Lolium perenne* L. | Outdoors | 25-cm pots of 1 or 4 genotypes | 1° Parasitoid diversity | 56% more species; 88% higher Shannon index | Positive | Jones *et al.* (2011) |
| | | | 2° Parasitoid diversity | 16% more species; 26% higher Shannon index | Negative | |
| Potato, cabbage, lima bean | Temperate agricultural field | 30-$m^2$ plots with 1 or 2 varieties | Herbivore abundance | Up to 44% less potato leafhoppers, *Empoasca fabae* Harris, on most susceptible potato variety; 100% more on most resistant variety (1 of 4 experiments); 45% less oviposition by imported cabbageworm *Pieris rapae* L. on resistant cabbage variety; 110% more oviposition on susceptible variety | Mixed | Cantelo & Sanford (1984) |
| Tall goldenrod *S. altissima* L. | Outdoors | 18-cm pots of 1 or 5 genotypes | Herbivore abundance | 56% increase in aphid abundance; Observed abundance 35% greater than expected | Negative | Utsumi *et al.* (2011) |
| | | | Herbivore population growth rate | Greater | Negative | |

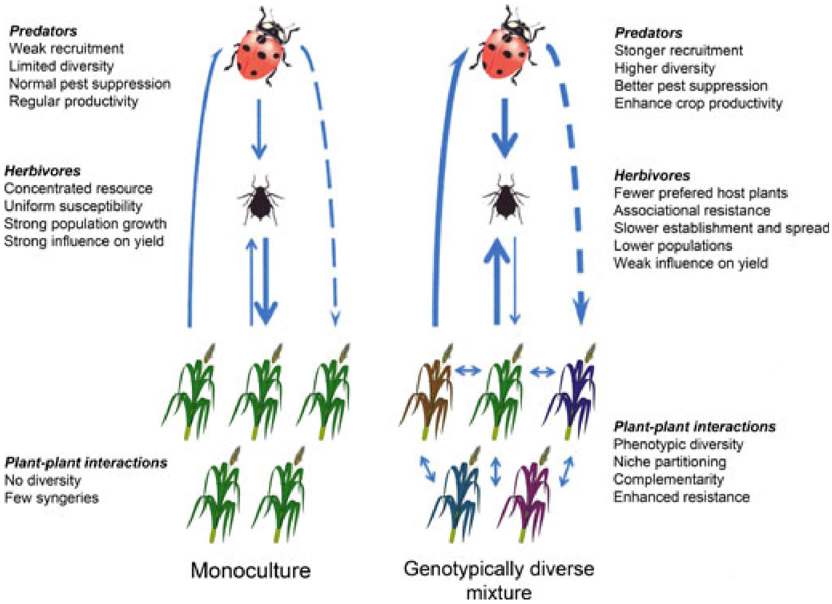


**Fig. 1.** Conceptual framework describing the hypothesized benefits of genotypic diversity for improving control of herbivorous insect pests. The left side of the panel shows anticipated interactions among plants, herbivores and natural enemies in genetically uniform monocultures and provides summaries of the influence of the interactions on each of the three trophic levels. The right panel shows the same interactions and summaries in a genotypically diverse field. The width of the arrows indicates the hypothesized relative strengths of the interactions, which were synthesized from the literature reviewed in the article, much of which is summarized in Table 1.

Gurr 1998). Fourth, it must be recognized that increasing plant species diversity often entails considerable logistical and/or economic challenges. For example, growing more than one crop in a single field is not compatible with modern agricultural equipment, and diversification via non-crop areas can reduce land available for production. Thus, with questionable economic benefits and considerable challenges, techniques to increase plant diversity for better pest control are rarely implemented by growers (Letourneau *et al*. 2011; Lin 2011).

### *Benefits associated with genotypic diversity in non-crop systems*

A more practical and increasingly supported approach to increase diversity in agriculture systems is to increase the genotypic diversity of plants within species. This approach runs counter to large-scale monotypic plantings that dominate agriculture. However, basic evolutionary theory predicts that there is great value in intraspecific diversity (aka genotypic variation; Bolnick *et al*. 2011). After all, genetic variation is the basis of evolution by natural selection and without it populations would risk going extinct because they would not be able to survive the range of challenges they face in their environment (Fisher 1930; Hughes *et al*. 2008; Bolnick *et al*. 2011). Furthermore, it is clear that lack of genetic diversity (i.e. low heterozygosity) can lead to some problematic population-level phenomena, such as bottlenecks and inbreeding depression (Hedrick & Kalinowski 2000). Perhaps it is not surprising then, that a growing body of animal- and plant-based empirical studies are demonstrating the value of increased levels of intraspecific diversity.

For years, it has been recognized that intraspecific diversity provides populations flexibility to succeed under a range of conditions (Berenbaum, Zangerl & Nitao 1986). However, a newer body of literature has revealed emergent effects of genotypic diversity on system productivity and resiliency (Hughes *et al*. 2008). For example, colonies of honeybees established by multiply mated queens are far more productive (more waggle dances, greater foraging rates, foragers exploited more distant food sources) than colonies produced from singly mated queens (Mattila & Seeley 2007; Mattila, Burke & Seeley 2008). Similar effects have been found for autotrophs. Genotypically diverse mixtures of the alga *Chlamydomonas reindhartii* Dangeard grew to a 10% greater density in laboratory studies than genetic monocultures of the same species (Bell 1991). Pots sown with genetic mixtures of *Arabidopsis thaliana* (L.) Heynh under semi-natural conditions were 17% more productive than monocultures (Kotowska, Cahill & Keddie 2010). Similarly, higher levels of intraspecific diversity in field plots increased production of above-ground biomass of *Solidago altissima* L. by 36% (Crutsinger *et al*. 2006). In these cases of greater plant productivity, genotypically diverse plantings were able to exploit more of the available resources than the monocultures perhaps due to varietal complementarity (i.e. niche partitioning or facilitation; Crutsinger *et al*. 2006; Kotowska, Cahill & Keddie 2010). Importantly, recent work has demonstrated that the influence of genotypic diversity on primary production can be equivalent to that of plant species diversity (Cook-Patton *et al.* 2011). The mechanism(s) behind similar influences of plant species and genotypic diversity on plant productivity remain(s) to be clarified, but arthropods appear to be among the contributory factors (Cook-Patton *et al.* 2011).

Genotypically diverse populations are also known to better resist disease. This is because more diverse populations will contain a greater range of genotypes that have reduced susceptibility to pathogens; therefore, diseases will not spread as easily through the population (Mundt 2002). This increased resistance to disease has been empirically demonstrated for a wide range of organisms, including vertebrates (e.g. frogs), invertebrates (e.g. honeybees) and plants (e.g. willow) (Peacock & Herrick 2000; Tarpy 2003; Pearman & Garner 2005; Hughes *et al.* 2008; Bailey *et al.* 2009; Bolnick *et al.* 2011).

A developing body of literature also illustrates that intraspecific diversity in natural plant systems can strongly influence arthropod populations and herbivory, often extending to plant productivity (Table 1). Similar to effects of plant species diversity, genotypic diversity plays an important role in structuring insect communities and driving ecological interactions at multiple trophic levels (Table 1, Fig. 1; Peacock & Herrick 2000; Wimp *et al.* 2004; Crutsinger *et al.* 2006; Johnson, Lajeunesse & Agrawal 2006; Cook-Patton *et al.* 2011). In fact, some of this work has even led to the conclusions that 'plant genotype can be one of the most important ecological factors shaping tritrophic communities' (Johnson 2008) and that plant genotypic diversity most strongly influences arthropod communities, including natural enemy species, relative to soil microbes, fungi and the plants themselves (Bailey *et al.* 2009). For instance, genotypically diverse plantings of willow received as much as 50% less damage from leaf beetles than willow monocultures because beetles preferentially fed in patches of more suitable hosts (i.e. resource concentration hypothesis) and had difficulty finding palatable willow varieties when they were grown in mixtures (i.e. associational resistance; Peacock & Herrick 2000).

Similarly, work with two plant species native to the United States (the goldenrod *S. altissima* and evening primrose *Oenothera biennis* L.) has demonstrated that plant genotypic diversity can also result in less herbivory, but via a different mechanism. In these cases, increased phenotypic diversity associated with higher levels of genotypic diversity enhanced arthropod species diversity, including that of natural enemies, which suppressed populations of herbivorous insects, resulting in greater production of above-ground biomass (Table 1, Fig. 1; Crutsinger *et al.* 2006; Johnson, Lajeunesse & Agrawal 2006). Genotypic diversity can strongly affect natural enemy abundance and behaviour (Fig. 1; Starks, Muniappan & Eikenbary 1971; Price *et al.* 1980; Bottrell, Barbosa & Gould 1998; Glinwood *et al.* 2009; Lundgren *et al.* 2008). These effects tend to be driven by phenotypic diversity that accompanies genotypic diversity and can influence natural enemy abundance even when herbivore populations are similar (Bottrell, Barbosa & Gould 1998).

There are examples of genotypic diversity fostering larger populations of insect herbivores. Caterpillars feeding upon genotypically diverse plantings of *Arabidopsis* developed total biomass 19% higher than caterpillars reared on monocultures (Kotowska, Cahill & Keddie 2010). While the mechanism driving large caterpillar biomass was not explicitly explored, it may be that a mixture of food items with varying nutritional quality improved caterpillar growth rates (Kotowska, Cahill & Keddie 2010). Similarly, diverse plots of *S. altissima* increased aphid population growth rate compared to monotypic plots (Utsumi *et al.* 2011). In this study, aphids moved from highly populated, less resistant genotypes to less populated but more resistant genotypes where population growth could increase; thus, aphid movement between hosts with high and low competition contributed to their results, among other mechanisms (Utsumi *et al.* 2011).

In addition to bottom–up and top–down effects on herbivore abundance and plant fitness, research has demonstrated that increasing genotypic diversity in plant communities increases resistance to abiotic stress and stochastic events such as increased temperatures or disturbance (Hughes & Stachowicz 2004; Reusch *et al.* 2005; Hughes *et al.* 2008). For example, in the face of extreme temperatures, eelgrass biomass increased as much as 30% as diversity of plantings increased from one to six genotypes. This suggests that more genotypically diverse populations can maintain productivity better than monocultures when confronted with abiotic stress. Genetically diverse populations can also recover more quickly from disturbance, such as vertebrate grazing (Hughes & Stachowicz 2004), and even better resist invasion (Crutsinger, Souza & Sanders 2008). In this latter case, weed biomass was 32% lower in plots with twelve genotypes of *S. altissima* than in monotypic plots owing to a combination of genotype diversity and identity effects (Crutsinger, Souza & Sanders 2008). This evidence suggests that genotypically diverse populations might be more stable and resilient in the face of increased stress as can be expected under several scenarios of global climate change (Brouder & Volenec 2008).

These various lines of evidence strongly suggest that increased genotypic diversity can increase productivity and resiliency in a wide range of systems. And while much remains to be learned about the role of genotypic diversity in ecological interactions and ecosystem function, the existing evidence is particularly tantalizing for agriculture because productivity, resistance to herbivores and resiliency to abiotic stress are essential features of sustainable crop production. Moreover, genotypic diversity could be implemented with relatively minor changes to agricultural practice. If theory and empirical results continue to support the strong effects of genotypic diversity for plant productivity, a simple new approach to farming may transform planting strategies and agricultural productivity.

In the following paragraphs, we provide examples that support the successful use of intraspecific variation to help manage diseases in large-scale row-crop production, followed by studies that suggest the potential of genotypic diversity to help control populations of insect herbivores in crop systems.

## GENOTYPIC DIVERSITY OF RESISTANCE TRAITS IN AGRICULTURAL PLANTS

It has long been clear that populations benefit from higher levels of variation because genetic variation provides a basis for selection to act upon. In plants, this notion has been illustrated very well by classic research exploring trade-offs between growth and defence by non-crop plant species (Berenbaum, Zangerl & Nitao 1986). In this work, genetically based levels of toxic secondary metabolites were positively associated with plant fitness in the presence of herbivores, but negatively related to fitness in absence of herbivores (Berenbaum, Zangerl & Nitao 1986). In agricultural systems, similar work would appear challenging because crop species appear to have limited genetic diversity. In fact, the genetic diversity of some crop species appears to be so low that it is a source of national and international concern (National Research Council 1972; FAO 1998). The fear is that genetic uniformity could leave crops vulnerable to an epidemic like the corn blight *Helminthosporium maydis* outbreak of 1970 that destroyed about 15% of the US corn crop (National Research Council 1972). In some crops, the decrease in genetic diversity has been quantified. In soybeans, for example, the genetic bottleneck imposed by domestication resulted in the loss of *c*. 50% of genetic diversity, but it does not seem as though subsequent artificial selection has further limited diversity (Hyten *et al*. 2006). In contrast, other crop species, such as *Brassica oleracea* L. (i.e. cole crops), have experienced during domestication heavy artificial selection for desirable agronomic traits, and this selection has significantly reduced concentrations of toxic secondary metabolites compared to their wild relatives, leaving crop plants more vulnerable to pest species (Gols *et al*. 2008a, b).

While domestication and subsequent artificial selection have reduced genetic diversity of crop species, it is clear that significant useful, genetic variation remains. This is evident from research efforts and breeding programmes that have identified crop genotypes showing resistance to myriad pathogen and herbivore species (Painter 1951; Gallun 1977; Wilhoit 1992; McIntosh 1998; Mundt 2002; Thomas *et al*. 2002). For example, research with wheat has detected resistance to at least 28 bacterial, fungal and viral pathogens, four species of nematodes and nine species of insect (McIntosh 1998). Importantly, many of these resistant varieties are available and form the basis of IPM programmes worldwide. For pathogen control, plant resistance is particularly vital, and the available genotypic variation in resistance to pathogens has been harnessed for improved pest control and will be discussed next.

### *Genotypically diverse mixtures and disease management*

Monocultures were developed to maximize growth potential of superior genotypes, and the associated genetic uniformity (e.g. similar plant height, maturity) facilitates harvesting and processing of the crop; however, genetic uniformity also provides disadvantages because of uniform vulnerability to pests. Vulnerability associated with uniformity can be mitigated by increasing the number of cultivars in fields to increase genotypic diversity. The resulting 'cultivar mixtures' are defined as mixtures of genotypes (i.e. cultivars) 'that vary for many characters including disease resistance, but have sufficient similarity to be grown together' (Wolfe 1985). Close to 50% of wheat fields in Europe and tens of thousands of hectares of rice in China have been sown as cultivar mixtures (Zhu *et al*. 2000; Mundt 2002). In the United States, 18% of soft winter wheat planted in Washington State in 2000 and 7% of Kansas wheat planted in 2001 were cultivar mixtures (Bowden *et al*. 2001; Mundt 2002). These mixtures are typically constructed as random mixtures of five cultivars that vary in susceptibility to important diseases (e.g. rusts, powdery mildew), and yield nearly 30% better than monocultures when disease is present while maintaining yield, or even slightly improving it when disease is absent (Wolfe 1985; Martinelli, Brown & Wolfe 1993; Mundt 1994, 2002; Smithson & Lenne 1996; Garrett & Mundt 1999). Importantly, logistics associated with mixtures (i.e. mixing seeds, harvesting, marketing) have not hindered production, particularly with small grains where cultivar mixtures have been most popular (Mundt 2002).

### *Genotypic diversity and arthropod pest management*

In contrast to well-established benefits of using genotypic diversity to combat plant pathogens, limited applied research has explored the influence of intraspecific diversity on insect pests and/or arthropods in agricultural systems. Nevertheless, cultivar mixtures have improved insect pest suppression in some crop studies (Cantelo & Sanford 1984; Power 1988, 1991). For example, in separate experiments, mixtures of two oat varieties or five corn varieties were found to harbour significantly fewer pests (aphids and leafhoppers, respectively) than monotypic stands, but this effect was only detected when pest populations were large (Table 1; Power 1988, 1991). Similarly, mixing a susceptible variety of potato with more resistant varieties lead to a reduction in numbers of potato leafhoppers (Table 1; Cantelo & Sanford 1984). A comparable effect was found for eggs of imported cabbageworms on cabbage, perhaps because more preferred plant varieties were masked from ovipositing moths by less preferred varieties (i.e. associational resistance; Table 1; Cantelo &

Sanford 1984; Hamback, Agren & Ericson 2000). Genotypically diverse mixtures can also increase movement of insect herbivores, decreasing acquisition and transmission of persistent viruses, which require longer bouts of feeding to be acquired and transmitted to new host plants (Kennedy & Kishaba 1977; Power 1991). Genotypic diversity can also foster plant–plant interactions that may lead to improved resistance of plants. For example, fewer aphids settled on barley varieties that had been previously exposed to volatile organic compounds (VOCs) emitted by other undamaged varieties (Glinwood *et al.* 2009). Moreover, this effect extended to parasitoids and generalist predators, which were more attracted to VOCs from mixtures of varieties rather than monocultures (Glinwood *et al.* 2009). Other work has found that parasitoids were 56% more abundant and 88% more diverse in mixtures of four cultivars than in monocultures and that these effects occurred independently from herbivore populations (Jones *et al.* 2011). These results strongly suggest some trophic interactions in genetically uniform monocultures may not be optimized and could be improved by mixing cultivars together.

In contrast, while some evidence suggests that genotypic diversity may improve top–down control, it must be acknowledged that habitats with more genotypes and associated phenotypes may inhibit the efficacy of some natural enemy species as can occur with plant species diversification (Araj *et al.* 2009; Jonsson *et al.* 2009). Some natural enemies provide better control on plants that are morphologically less complex (Carter, Sutherland & Dixon 1984; Legrand & Barbosa 2003). Genotypically diverse mixtures are likely to provide a mosaic of plant morphologies, some of which may decrease the efficacy of some of the natural enemy species, weakening the influence of top–down control (Araj *et al.* 2009; Jonsson *et al.* 2009). Furthermore, in at least one instance, hyperparasitoids were found to be 16% more abundant and 26% more diverse in four-variety mixtures than in monocultures (Jones *et al.* 2011), suggesting that potentially disruptive species could cause problems for top–down control if they respond to diversity in significant numbers.

While a limited set of research provides evidence that intraspecific diversity can contribute to insect pest control, there are further reasons to be optimistic that this effect occurs. These reasons fall into six categories. First, four conditions have been recently described under which intraspecific diversity will have the strongest ecological effects (Hughes *et al.* 2008). Three of these conditions – community dominated by one species, diversity which influences predator [i.e. keystone] species and environments subject to human disturbance (Hughes *et al.* 2008) – clearly apply to agricultural systems because crop fields are dominated by single plant species, disturbed regularly, and the dominant predator species often respond to plant traits (e.g. hymenopteran parasitoids or predaceous beetles; Bottrell, Barbosa & Gould 1998). The fourth – ample variation occurs within the focal species (Hughes *et al.* 2008) – requires consideration. As mentioned earlier, genetic variation in crop species is often considered to be limited (NRC 1972; FAO 1998; Hyten *et al.* 2006), but variation in pathogen resistance is high enough to provide benefit in diverse wheat crops, and resistant crop varieties with a variety of mechanisms have been isolated for many herbivore species (Painter 1951; Gallun 1977; Wilhoit 1992; McIntosh 1998; Mundt 2002; Thomas *et al.* 2002). Interestingly, genetically modified crop resistance to insect herbivory (e.g. maize varieties that encode insecticidal proteins from *Bacillus thuringiensis*) is expanding available crop genetic diversity, and the current trend being imposed by agricultural industry is to have growers plant two-variety mixtures comprising resistant and susceptible varieties because mixes can simultaneously protect crops while maintaining the durability of the transgenic technology (Onstad *et al.* 2011). This application of mixtures provides one more example of the utility of intraspecific diversity in managing insect pests.

A second reason to believe that intraspecific diversity can improve insect pest control is that many insect species, chiefly hemipterans, like aphids, whiteflies and similar taxa, share attributes of pathogens. These attributes include patterns of short- and long-range dispersal, size of populations first colonizing a field, the narrow degree of host–plant specialization, short generation times and induction of similar host–plant defences, often triggered by salicylic acid (Orlob 1961; Wilhoit 1992; Garrett & Mundt 1999; Walling 2000; Castro 2001; Merrill, Holtzer & Peairs 2009). While this generalization has obvious exceptions, the point is that insect species that share more characteristics with pathogens may be more sensitive to the influence of genotypic diversity. Third, because genotypic diversity has helped control disparate taxa (lepidopterans, dipterans and hemipterans; Cantelo & Sanford 1984; Gould 1986b; Power 1988, 1991), it seems likely to increase control of a wider range of species. Fourth, natural enemies can be effective regulators of herbivore populations in crop fields (e.g. Costamagna, Landis & Difonzo 2007) and are clearly influenced by intraspecific variation (Bottrell, Barbosa & Gould 1998). In some systems, they provide improved control of herbivorous insect populations with higher levels of genotypic diversity (Crutsinger *et al.* 2006), suggesting that they may be more useful providers of pest control services in genetically diverse crop fields. The final two reasons have already been addressed above. Fifth, plant genotypic diversity influences 'natural' arthropod populations. Finally, the strategy of mixing cultivars within fields already works for disease management in grain production and has been adopted by growers worldwide with few apparent limitations.

### *Other benefits of genotypic diversity in agroecosystems*

In addition to arthropod and disease management, other ecological mechanisms are at work in genotypically diverse plantings that could improve yield and provide other agronomic benefits. Increased levels of genotypic diversity can translate into greater floral abundance and greater diversity and abundance of floral visitors, suggesting genotypic diversity may improve pollination services (Genung *et al.* 2010). Similar to species-rich plant communities (Elton 1958; Knops, Tilman & Haddad 1999), genotypically diverse plant populations are better able to resist invasion by other plant species (Crutsinger, Souza & Sanders 2008; Kaut *et al.* 2009). Wheat varieties differ significantly in how well they compete against weeds, and combining varieties of differing competitive ability can significantly improve weed suppression and yield (Hucl 1998; Mason, Goonewardene & Spaner 2006; Kaut *et al.* 2009).

Relative to single-line fields, genetically diverse fields tend to have small but significant yield increases resulting from intergenotypic interactions for light, soil and water resources (Trenbath 1974; Smithson & Lenne 1996; Cowger & Weisz 2008). For wheat and soybeans, this yield advantage has been estimated at 5·4% and 11%, respectively (Schutz & Brim 1967; Schweitzer *et al.* 1986; Smithson & Lenne 1996). This effect results in part because of *cultivar complementarity,* where the blend as a whole is better able to exploit in-field resources because the cultivars exploit slightly different microniches when in direct competition owing to various mechanisms (Sarandon & Sarandon 1995; Mundt 2002; Ninkovic 2003; Cowger & Weisz 2008). Some wheat mixtures also had higher yield under low input organic conditions (Kaut *et al.* 2009). Some oat mixtures had yield advantages as high as 9% in the face of drought stress (Peltonen-Sainioa & Karjalainen 1991), suggesting that genotypic diversity may help buffer agricultural fields against the extremes of climate change.

Another important benefit derived from cultivar mixtures is yield stability, allowing growers to better predict their annual production and reduce risk (Finckh *et al.* 2000). In any given year, a particular monoculture may or may not be the best-yielding variety because of various biotic and abiotic factors, but these factors are likely to be different the next year (Kaut *et al.* 2009). A cultivar mixture decreases this annual uncertainty because stability results from complementary fluctuations among cultivars that tend to balance each other out (Smithson & Lenne 1996; Mundt 2002). Thus, the 'portfolio' or 'insurance' effects of biodiversity can stabilize crop yield under diverse biotic and abiotic conditions (Tilman, Lehman & Bristow 1998; Yachi & Loreau 1999; Haddad *et al.* 2011).

## Conclusions

Increasing the diversity of genotypes within crop fields holds great promise to reduce disease, decrease pest abundances and increase crop yield. Reliance on synthetic pesticides has created a cycle of resistance development that is unsustainable and fraught with repercussions involving degradation of human and environmental health (Pimentel *et al.* 1992). Therefore, farmers need alternative pest management strategies to protect plants and profits and decrease reliance on pesticides. In addition, consumer demand for agricultural products grown more sustainably with little or no insecticide residue has created a rapidly expanding market for organic crops for human and animal consumption. These farmers have limited pest management options and could benefit greatly by planting cultivar mixtures.

Planting fields with more than one variety of seed makes sense from an evolutionary perspective because mixed fields would be less vulnerable to biotic or abiotic perturbation. Genotypically diverse cultivar mixtures reduce pathogen transmission from one plant to another, reducing pathogen abundance and increasing yield in wheat and other field crops; therefore, diverse cultivar mixtures are a popular and effective way to manage pathogens of wheat, rice and other crops in Europe, Asia and a few pockets of the United States (Wolfe 1985; Garrett & Mundt 1999; Mundt 2002). Moreover, research from natural systems indicates that populations of insect herbivores can be strongly influenced by intraspecific plant diversity. We now need applied research to determine whether these multiple lines of evidence can translate to improved insect pest control via cultivar mixtures. To help direct this research, we offer a conceptual framework (Fig. 1), which is based on interactions featured in some of the literature we have reviewed here and tabulated (Table 1). The framework presents interactions among plants, herbivores and natural enemies that are expected to be influenced by genotypic diversity as well as some of the mechanisms that may be driving these interactions (Fig. 1). This vision is presented to stimulate hypothesis-driven research into how these interactions influence insect pest control in crop systems. We would hypothesize that these interactions could also help buffer crop systems against abiotic extremes like those expected to be imposed by climate change, as has been demonstrated in at least one crop species (Peltonen-Sainioa & Karjalainen 1991) and a marine grass (Reusch *et al.* 2005).

Research to optimize the efficacy of intraspecific crop diversity as an insect management tactic ranges from basic ecology to grower implementation. For example, research is needed to determine the number of cultivars that maximizes yield and stability and whether this number can be generalized across crop species and management systems (e.g. organic vs. conventional). Research is also needed to determine how different pests and natural enemies respond to intraspecific diversity and whether guilds of pests, such as aphids, all respond similarly. In addition, research conducted in natural systems has been in very small plots (<1 m; Table 1), so conducting large-scale experiments in field crops would be essential to determine efficacy for growers but would also contribute greatly to our understanding of how intraspecific diversity affects food web and trophic dynamics.

Research on cultivar mixtures for insect control is also relevant because incorporating resistant and non-resistant varieties in the same field should slow the evolution of resistance to resistant varieties (i.e. improve durability of resistance; Gould 1986a). This approach is credited, in part, with minimizing resistance to transgenic Bt crops wherein susceptible varieties are planted alongside insect-resistant Bt varieties as a refuge for Bt-susceptible pests (Onstad *et al.* 2011; Sanahuja *et al.* 2011). Because plant resistance traits are often among the few tools available for managing some pest species (e.g. Hessian fly; Gould 1986a, b), research is needed to characterize levels, or new forms, of resistance to insect herbivores in various crop species. New resistant varieties can then be developed and incorporated into cultivar mixtures, which will help maintain the efficacy and durability of such tools (Gould 1986a).

Cultivar mixtures appear to have many benefits and, as long as varieties have similar agronomic characteristics, should not require farmers to change production practices such as planting and harvesting time and do not require any economic investment in new equipment (Wilhoit 1992). This is important because logistical and economic concerns are the primary roadblock to implementation of new, sustainable pest-farming practices. Using cultivar mixtures do not appear to pose major economic or logistical challenges and, indeed, may provide economic and production benefits. By wisely increasing genotypic diversity, growers stand a good chance of decreasing pest problems while stabilizing or even increasing yield. Such ecologically sound pest management strategies should be studied in depth.

## Acknowledgements

Many thanks to F. Gould, N. Haddad and G. Crutsinger and three anonymous reviewers for providing comments that improved the quality of our manuscript. Thanks also to M. W. Tooker for assistance with Fig. 1.

## References

Agrawal, A.A., Lau, J.A. & Hamback, P.A. (2006) Community heterogeneity and the evolution of interactions between plants and insect herbivores. *The Quarterly Review of Biology*, **81**, 349–376.

Altieri, M. (1999) The ecological role of biodiversity in agroecosystems. *Agriculture, Ecosystems & Environment*, **74**, 19–31.

Andow, D.A. (1991) Vegetational diversity and arthropod population response. *Annual Review of Entomology*, **36**, 561–586.

Araj, S.-E., Wratten, S., Lister, A. & Buckley, H. (2009) Adding floral nectar resources to improve biological control: Potential pitfalls of the fourth trophic level. *Basic and Applied Ecology*, **10**, 554–562.

Baggen, L.R. & Gurr, G.M. (1998) The influence of food on *Copidosoma koehleri* (Hymenoptera: Encyrtidae), and the use of flowering plants as a habitat management tool to enhance biological control of potato moth, *Phthorimaea operculella* (Lepidoptera: Gelechiidae). *Biological Control*, **11**, 9–17.

Bailey, J.K., Schweitzer, J.A., Ubeda, F., Koricheva, J., LeRoy, C.J., Madritch, M.D., Rehill, B.J., Bangert, R.K., Fischer, D.G., Allan, G.J. & Whitham, T.G. (2009) From genes to ecosystems: a synthesis of the effects of plant genetic factors across levels of organization. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **364**, 1607–1616.

Bell, G. (1991) The ecology and genetics of fitness in *Chlamydomonas*. IV. The properties of mixtures of genotypes of the same species. *Evolution*, **45**, 1036–1046.

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

Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M., Rudolf, V.H.W., Schreiber, S.J., Urban, M.C. & Vasseur, D.A. (2011) Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution*, **26**, 183–192.

Bottrell, D.G., Barbosa, P. & Gould, F. (1998) Manipulating natural enemies by plant variety selection and modification: a realistic strategy? *Annual Review of Entomology*, **43**, 347–367.

Bowden, R., Shroyer, J., Roozeboom, K., Claassen, M., Evans, P., Gordon, B., Heer, B., Janssen, K., Long, J., Martin, J., Schlegel, A., Sears, R. & Witt, M. (2001) Performance of wheat variety blends in Kansas. Keeping Up with Research 128, Kansas State University Agricultural Experiment Station and Cooperative Extension Service Manhattan, Kansas.

Brouder, S.M. & Volenec, J.J. (2008) Impact of climate change on crop nutrient and water use efficiencies. *Physiologia Plantarum*, **133**, 705–724.

Cantelo, W. & Sanford, L.L. (1984) Insect population response to mixed and uniform plants of resistant and susceptible plant material.pdf. *Environmental Entomology*, **13**, 1443–1445.

Carter, M.C., Sutherland, D. & Dixon, A.F.G. (1984) Plant structure and the searching efficiency of coccinellid larvae. *Oecologia*, **63**, 394–397.

Castro, A. (2001) Cultivar Mixtures. *The Plant Health Instructor*. Available online doi: 10.1094/PHI-A-2001-1230-01.

Chen, Y. & Welter, S. (2005) Crop domestication disrupts a native tritrophic interaction associated with the sunflower, *Helianthus annuus* (Asterales: Asteraceae). *Ecological Entomology*, **30**, 673–683.

Cook-Patton, S.C., McArt, S.H., Parachnowitsch, A.L., Thaler, J.S. & Agrawal, A.A. (2011) A direct comparison of the consequences of plant genotypic and species diversity on communities and ecosystem function. *Ecology*, **92**, 915–923.

Costamagna, A.C., Landis, D.A. & Difonzo, C.D. (2007) Suppression of soybean aphid by generalist predators results in a trophic cascade in soybeans. *Ecological Applications*, **17**, 441–451.

Cowger, C. & Weisz, R. (2008) Winter wheat blends (mixtures) produce a yield advantage in North Carolina. *Agronomy Journal*, **100**, 169–177.

Crutsinger, G.M., Souza, L. & Sanders, N.J. (2008) Intraspecific diversity and dominant genotypes resist plant invasions. *Ecology Letters*, **11**, 16–23.

Crutsinger, G.M., Collins, M.D., Fordyce, J.A., Gompert, Z., Nice, C.C. & Sanders, N.J. (2006) Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science*, **647**, 966–968.

Dudley, S.A. & File, A.L. (2007) Kin recognition in an annual plant. *Biology Letters*, **3**, 435–438.

Elton, C.S. (1958) *The Ecology of Invasions by Animals and Plants*. Methuen, London.

FAO. (1998) *The State of the World's Plant Genetic Resources for Food and Agriculture*. A Report from the Food and Agriculture Organization of the United Nations. Available online http://www.fao.org/agriculture/crops/core-themes/theme/seeds-pgr/sow/en/. Assessed February 2012.

Finckh, M.R., Gacek, E.S., Goyeau, H., Lannou, C., Merz, U., Mundt, C.C., Munk, L., Nadziak, J., Newton, A.C., de Vallavieille-Pope, C. & Wolfe, M.S. (2000) Cereal variety and species mixtures in practice, with emphasis on disease resistance. *Agronomie*, **20**, 813–837.

Fisher, R.A. (1930) *The Genetical Theory of Natural Selection*. Oxford University Press, Oxford.

Gallun, R.L. (1977) Genetic basis of Hessian fly epidemics. *Annals of the New York Academy of Science*, **287**, 223–229.

Garrett, K.A. & Mundt, C.C. (1999) Epidemiology in mixed host populations. *Phytopathology*, **89**, 984–990.

Genung, M.A., Lessard, J.-P., Brown, C.B., Bunn, W.A., Cregger, M.A., Reynolds, W.M.N., Felker-Quinn, E., Stevenson, M.L., Hartley, A.S., Crutsinger, G.M., Schweitzer, J.A. & Bailey, J.K. (2010) Non-additive effects of genotypic diversity increase floral abundance and abundance of floral visitors. *PLoS ONE*, **5**, e8711.

Glinwood, R., Ahmed, E., Qvarfordt, E., Ninkovic, V. & Pettersson, J. (2009) Airborne interactions between undamaged plants of different cultivars affect insect herbivores and natural enemies. *Arthropod–Plant Interactions*, **3**, 215–224.

Gols, R., Bukovinszky, T., Dam, N.M.V., Dicke, M., Bullock, J.M. & Harvey, J.A. (2008a) Performance of generalist and specialist herbivores and their endoparasitoids differs on cultivated and wild Brassica populations. *Journal of Chemical Ecology*, **34**, 132–143.

Gols, R., Wagenaar, R., Bukovinszky, T., van Dam, N.M., Dicke, M., Bullock, J.M. & Harvey, J.A. (2008b) Genetic variation in defense chemistry in wild cabbages affects herbivores and their endoparasitoids. *Ecology*, **89**, 1616–1626.

Gould, F. (1986a) Simulation models for predicting durability of insect-resistant germ plasm: a deterministic diploid, two-locus model. *Environmental Entomology*, **15**, 1–10.

Gould, F. (1986b) Simulation models for predicting durability of insect-resistant germ plasm: hessian fly (Diptera: Cecidomyiidae)-resistant winter wheat. *Environmental Entomology*, **15**, 11–23.

Haddad, N.M., Crutsinger, G.M., Gross, K., Haarstad, J., Knops, J.M.H. & Tilman, D. (2009) Plant species loss decreases arthropod diversity and shifts trophic structure. *Ecology Letters*, **12**, 1029–1039.

Haddad, N.M., Crutsinger, G.M., Gross, K., Haarstad, J. & Tilman, D. (2011) Plant diversity and the stability of foodwebs. *Ecology Letters*, **14**, 42–46.

Hamback, P.A., Agren, J. & Ericson, L. (2000) Associational resistance: insect damage to purple loosestrife reduced in thickets of sweet gale. *Ecology*, **81**, 1784–1794.

Hedrick, P.W. & Kalinowski, S.T. (2000) Inbreeding depression in conservation biology. *Annual Review of Ecology and Systematics*, **31**, 139–162.

Hucl, P. (1998) Response to weed control by four spring wheat genotypes differing in competitive ability. *Canadian Journal of Plant Science*, **78**, 171–173.

Hughes, A.R. & Stachowicz, J.J. (2004) Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. *Proceedings of the National Academy of Sciences, USA*, **101**, 8998–9002.

Hughes, A.R., Inouye, B.D., Johnson, M.T.J., Underwood, N. & Vellend, M. (2008) Ecological consequences of genetic diversity. *Ecology letters*, **11**, 609–623.

Hyten, D.L., Song, Q., Zhu, Y., Choi, I.Y., Nelson, R.L., Costa, J.M., Specht, J.E., Shoemaker, R.C. & Cregan, P.B. (2006) Impacts of genetic bottlenecks on soybean genome diversity. *Proceedings of the National Academy of Sciences, USA*, **103**, 16666–16671.

Johnson, M.T.J. (2008) Bottom-up effects of plant genotype on aphids, ants, and predators. *Ecology*, **89**, 145–154.

Johnson, M.T.J., Lajeunesse, M.J. & Agrawal, A.A. (2006) Additive and interactive effects of plant genotypic diversity on arthropod communities and plant fitness. *Ecology letters*, **9**, 24–34.

Jonsson, M., Wratten, S.D., Robinson, K.A. & Sam, S.A. (2009) The impact of floral resources and omnivory on a four trophic level food web. *Bulletin of Entomological Research*, **99**, 275–285.

Jones, T.S., Allan, E., Härri, S.A., Krauss, J., Müller, C.B. & van Veen, F.J.F. (2011) Effects of genetic diversity of grass on insect species diversity at higher trophic levels are not due to cascading diversity effects. *Oikos*, **120**, 1031–1036.

Kaut, A.H.E.E., Mason, H.E., Navabi, A., O'Donovan, J.T. & Spaner, D. (2009) Performance and stability of performance of spring wheat variety mixtures in organic and conventional management systems in western Canada. *Journal of Agricultural Science*, **147**, 141–153.

Kennedy, G.G. & Kishaba, A.N. (1977) Response of alate melon aphids to resistant and susceptible muskmelon lines. *Journal of Economic Entomology*, **70**, 407–410.

Knops, J.M.H., Tilman, D. & Haddad, N.M. (1999) Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecology Letters*, **2**, 26–293.

Kotowska, A.M., Cahill Jr, J.F. & Keddie, B.A. (2010) Plant genetic diversity yields increased plant productivity and herbivore performance. *Journal of Ecology*, **98**, 237–245.

Landis, D.A., Wratten, S.D. & Gurr, G.M. (2000) Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology*, **45**, 175–201.

Legrand, A. & Barbosa, P. (2003) Plant morphological complexity impacts foraging efficiency of adult *Coccinella septempunctata* L. (Coleoptera: Coccinellidae). *Environmental Entomology*, **32**, 1219–1226.

Letourneau, D.K., Armbrecht, I., Rivera, B.S., Lerma, J.M., Carmona, E. J., Daza, M.C., Escobar, S., Galindo, V., Gutierrez, C., López, S.D., Mejia, J.L., Rangel, A.M.A., Rangel, J.H., Rivera, L., Saavedra, C.A., Torres, A.M. & Trujillo, A.R. (2011) Does plant diversity benefit agroecosystems? A synthetic review. *Ecological Applications*, **21**, 9–21.

Lin, B.B. (2011) Resilience in agriculture through crop diversification: adaptive management for environmental change. *BioScience*, **61**, 183–193.

Lundgren, J.G., Hesler, L.S., Tilmon, K., Dashiell, K. & Scott, R. (2008) Direct effects of soybean varietal selection and Aphis glycines-resistant soybeans on natural enemies. *Arthropod–Plant Interactions*, **3**, 9–16.

Martinelli, J.A., Brown, J.K.M. & Wolfe, M.S. (1993) Effects of barley genotype on induced resistance to powdery mildew. *Plant Pathology*, **42**, 195–202.

Mason, H.E., Goonewardene, L. & Spaner, D. (2006) Competitive traits and the stability of wheat cultivars in differing natural weed environments on the northern Canadian Prairies. *Journal Agricultural Science*, **146**, 21–33.

Mattila, H.R., Burke, K.M. & Seeley, T.D. (2008) Genetic diversity within honeybee colonies increases signal production by waggle-dancing foragers. *Proceedings of the Royal Society B: Biological Sciences*, **275**, 809–816.

Mattila, H.R. & Seeley, T.D. (2007) Genetic diversity in honey bee colonies enhances productivity and fitness. *Science*, **317**, 362–364.

McIntosh, R.A. (1998) Breeding wheat for resistance to biotic stresses. *Euphytica*, **100**, 19–34.

Merrill, S.C., Holtzer, T.O. & Peairs, F.B. (2009) *Diuraphis noxia* reproduction and development with a comparison of intrinsic rates of increase to other important small grain aphids: a meta-analysis. *Environmental Entomology*, **38**, 1061–1068.

Mundt, C.C. (1994) Use of host genetic diversity to control cereal diseases: implications for rice blast. *Rice Blast Disease* (eds R.S. Zeigler, S.A. Leong & P.S. Teng), pp. 293–308. CAB International, London.

Mundt, C.C. (2002) Use of multiline cultivars and cultivar mixtures for disease management. *Annual Review of Phytopathology*, **40**, 381–410.

National Research Council. (1972) *Genetic Vulnerability of Major Crops*. National Academy of Sciences, Washington, District of Columbia, USA.

Ninkovic, V. (2003) Volatile communication between barley plants affects biomass allocation. *Journal of Experimental Botany*, **54**, 1931–1939.

Onstad, D.W., Mitchell, P.D., Hurley, T.M., Lundgren, J.G., Porter, R.P., Krupke, C.H., Spencer, J.L., DiFonzo, C.D., Baute, T.S., Hellmich, R. L., Buschman, L.L., Hutchison, W.D. & Tooker, J.F. (2011) Seeds of change: corn seed mixtures for resistance management and integrated pest management. *Journal of Economic Entomology*, **104**, 343–352.

Orlob, G.B. (1961) Host plant preference of cereal aphids in the field in relation to the ecology of barley yellow dwarf virus. *Entomologia Experimentalis et Applicata*, **4**, 62–72.

Painter, R.H. (1951) *Insect Resistance in Crop Plants*. Macmillan, New York, New York, USA.

Peacock, L. & Herrick, S. (2000) Responses of the willow beetle *Phratora vulgatissima* to genetically and spatially diverse Salix spp. plantations. *Journal of Applied Ecology*, **37**, 821–831.

Pearman, P.B. & Garner, T.W.J. (2005) Susceptibility of Italian agile frog populations to an emerging strain of Ranavirus parallels population genetic diversity. *Ecology Letters*, **8**, 401–408.

Peltonen-Sainioa, P. & Karjalainen, R. (1991) Agronomic evaluation of growing oat cultivar mixtures under various stress conditions in Finland. *Acta Agriculturae Scandinavica*, **41**, 47–53.

Pimentel, D., Acquay, H., Biltonen, M., Rice, P., Silva, M., Nelson, J., Lipner, V., Giordano, S., Horowitz, A. & Damore, M. (1992) Environmental and economic costs of pesticide use. *BioScience*, **42**, 750–760.

Power, A.G. (1988) Leafhopper response to genetically diverse maize stands. *Entomologia Experimentalis et Applicata*, **219**, 213–219.

Power, A.G. (1991) Virus spread and vector dynamics in genetically diverse plant populations. *Ecology*, **72**, 232–241.

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

Randlkofer, B., Obermaier, E., Hilker, M. & Meiners, T. (2010) Vegetation complexity—The influence of plant species diversity and plant structures on plant chemical complexity and arthropods. *Basic and Applied Ecology*, **11**, 383–395.

Rasmann, S., Köllner, T.G., Degenhardt, J., Hiltpold, I., Toepfer, S., Kuhlmann, U., Gershenzon, J. & Turlings, T.C.J. (2005) Recruitment of entomopathogenic nematodes by insect-damaged maize roots. *Nature*, **434**, 732–737.

Reusch, T.B.H., Ehlers, A., Hämmerli, A. & Worm, B. (2005) Ecosystem recovery after climatic extremes enhanced by genotypic diversity. *Proceedings of the National Academy of Sciences, USA*, **102**, 2826–2831.

Root, R.B. (1973) Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecological Monographs*, **43**, 95–124.

Sanahuja, G., Banakar, R., Twyman, R.M., Capell, T. & Christou, P. (2011) *Bacillus thuringiensis*: a century of research, development and commercial applications. *Plant Biotechnology Journal*, **9**, 283–300.

Sarandon, S.J. & Sarandon, R. (1995) Mixture of cultivars: pilot field trial of an ecological alternative to improve production or quality of wheat (*Triticum aestivum*). *The Journal of Applied Ecology*, **32**, 288.

Schutz, W.M. & Brim, C.A. (1967) Inter-genotypic competition in soybean. I. Evaluation of effects and proposed field plot design. *Crop Science*, **7**, 371–376.

Schweitzer, L.E., Nyquist, W.E., Santini, J.B. & Kimes, T.M. (1986) Soybean cultivar mixtures in a narrow-row, noncultivatable production system. *Crop Science*, **26**, 1043–1046.

Smithson, J.B. & Lenne, J. (1996) Varietal mixtures: a viable strategy for sustainable productivity in subsistence agriculture. *Annals of Applied Biology*, **128**, 127–158.

Starks, K.J., Muniappan, R. & Eikenbary, R. (1971) Interaction between plant resistance and parasitism against the greenbug on barley and sorghum. *Annals of the Entomological Society of America*, **65**, 650–655.

Tahvanainen, J.O. & Root, R.B. (1972) The influence of vegetational diversity on the population ecology of a specialized herbivore, *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae). *Oecologia*, **10**, 321–346.

Tarpy, D.R. (2003) Genetic diversity within honey bee colonies prevents severe infections and promotes colony growth. *Proceedings of the Royal Society B: Biological Sciences*, **270**, 99–103.

Thies, C., Steffan-Dewenter, I. & Tscharntke, T. (2003) Effects of landscape context on herbivory and parasitism at different spatial scales. *Oikos*, **101**, 18–25.

Thomas, M.B., Wratten, S.D. & Sotherton, N.W. (1991) Creation of 'island' habitats in farmland to manipulate populations of beneficial arthropods: predator densities and emigration. *Journal of Applied Ecology*, **28**, 906–917.

Thomas, J., Hein, G., Baltensperger, D., Nelson, L. & Haley, S. (2002) Managing the Russian wheat aphid with resistant wheat varieties. *NebFact*, Nebraska Cooperative Extension NF96-307.

Tilman, D., Lehman, C.L. & Bristow, C.E. (1998) Diversity-stability relationships: statistical inevitability or ecological consequence? *American Naturalist*, **151**, 277–282.

Trenbath, B.R. (1974) Biomass productivity of mixtures. *Advances in Agronomy*, **26**, 177–210.

Utsumi, S., Ando, Y., Craig, T.P. & Ohgushi, T. (2011) Plant genotypic diversity increases population size of a herbivorous insect. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 3108–3115.

Walling, L.L. (2000) The myriad plant responses to herbivores. *Journal of Plant Growth Regulation*, **19**, 195–216.

Wilhoit, L.R. (1992) Evolution of herbivore virulence to plant resistance: influence of variety mixtures. *Plant Resistance to Herbivores and Pathogens: Ecology, Evolution and Genetics* (eds R.S. Fritz & E.L. Simms), pp. 91–119. University of Chicago Press, Chicago, Illinois, USA.

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

Wolfe, M.S. (1985) The current status and prospects of multiline cultivars and variety mixtures for disease resistance. *Annual Review of Phytopathology*, **23**, 251–273.

Yachi, S. & Loreau, M. (1999) Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proceedings of the National Academy of Sciences, USA*, **96**, 1463–1468.

Zhu, Y., Chen, H., Fan, J., Wang, Y., Li, Y., Chen, J., Yang, S., Hu, L., Leung, H., Mew, T.W., Teng, P.S., Wang, Z. & Mundt, C.C. (2000) Genetic diversity and disease control in rice. *Nature*, **406**, 718–722.

*Received 19 March 2012; accepted 15 June 2012*
*Handling Editor: Ingolf Steffan-Dewenter*