

Testing genotypic variation of an invasive plant species in response to soil disturbance and herbivory

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Abstract Herbivores, competitors, and predators can inhibit biological invasions (“biotic resistance” sensu Elton 1959), while disturbance typically promotes biological invasions. Although biotic resistance and disturbance are often considered separately in the invasion literature, these two forces may be linked. One mechanism by which disturbance may facilitate biological invasions is by decreasing the effectiveness of biotic resistance. The effects of both disturbance and biotic resistance may vary across invading genotypes, and genetic variation in the invasive propagule pool may increase the likelihood that some genotypes can overcome biotic resistance or take greater advantage of disturbance. We conducted an experimental field trial in which we manipulated soil disturbance (thatch removal and loosening soil) and the presence of insect herbivores and examined their effects on the invasion success of 44 *Medicago polymorpha* genotypes. As expected, insecticide reduced leaf damage and increased *Medicago* fecundity, suggesting that insect herbivores in this system provide some biotic

resistance. Soil disturbance increased *Medicago* fecundity, but did not alter the effectiveness of biotic resistance by insect herbivores. We found significant genetic variation in *Medicago* in response to disturbance, but not in response to insect herbivores. These results suggest that the ability of *Medicago* to invade particular habitats depends on the amount of insect herbivory, the history of disturbance in the habitat, and how the specific genotypes in the invader pool respond to these factors.

Keywords Biological invasion · Genotype-by-environment interaction · Genetic variation · Herbivory · Tolerance

Introduction

Many hypotheses have been proposed to explain the success of biological invasions (Levine et al. 2003; Catford et al. 2009; Gurevitch et al. 2011). Although many of these hypotheses have been addressed independently, there is increasing appreciation that the various mechanisms promoting invasions are not independent and that multiple mechanisms may explain the success of any one invader (e.g., Shea and Chesson 2002). Resources, natural enemies, and the physical environment (e.g., land-use change) are three main factors that influence the success of invasive species establishment, growth, and reproduction (Shea and Chesson 2002; MacDougall et al. 2014). Yet, few studies of biological invasions experimentally test mechanisms contributing to invasive species success and even fewer investigate the interactive effects or identify the relative importance of multiple mechanisms (Levine et al. 2004).

Species interactions are one of the more commonly investigated factors influencing biological invasions, as they play a dual role in invasion success. On one hand,

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invasive species may escape enemies that constrained their population growth in the native range (i.e., enemy release; Keane and Crawley 2002). On the other hand, new interactions that develop in the invaded range may limit invasion success (i.e., biotic resistance; Elton 1958). Thus, the role of species interactions in limiting invasions may depend on which species are present locally and the environmental context in which the interactions occur (Lake and O'Dowd 1991; Blumenthal 2006; Mitchell et al. 2006).

Disturbances are also commonly investigated and can facilitate invasions through three mechanisms: by altering resource availability (Davis et al. 2000; Davis and Pelsor 2001), by altering environmental conditions that favor invasives over natives (Leishman and Thomson 2005; Price et al. 2011), or by reducing the strength of antagonistic species interactions that contribute to biotic resistance (D'Antonio et al. 1999; Davis and Pelsor 2001; Seabloom et al. 2003; Hierro et al. 2006). In particular, soil disturbances can free soil nutrients for use by invading plants (Hobbs and Huenneke 1992; Leishman and Thomson 2005) or increase light availability via removal of dead or living plant biomass (Gendron and Wilson 2007) to benefit invasive species. Increased resources may benefit invasive species directly by facilitating rapid growth (Davis et al. 2000). However, it is often the change in the natural disturbance regime that increases invasion success; native species that have long-adapted to the local disturbance regime are at a disadvantage in altered disturbance regimes, whereas weedy invasive species are better able to quickly take advantage of freed resources, which often gives invaders an increased competitive advantage (Hobbs and Huenneke 1992; Seabloom et al. 2003; Leishman and Thomson 2005; Price et al. 2011).

Biotic resistance and disturbance are likely to interact to influence invasion success for several reasons. First, disturbance can increase invasion success when it reduces the strength of antagonistic interactions, such as competition or predation (Mitchell et al. 2006). Disturbance can increase resource availability and decrease the intensity of competition (Wilson and Tilman 1993; Davis and Pelsor 2001; Seabloom et al. 2003), or reduce the abundance or effect of antagonists (Hierro et al. 2006), thereby reducing the inhibitory effects of biotic resistance. For example, native red crabs (*Gecarcoidea natalis*) on Christmas Island prey on introduced giant African snails (*Achatina fulica*) and prevent invasion by snails into rainforests, but in disturbed areas of the island, red crabs are less abundant and snail invasion is more successful (Lake and O'Dowd 1991). Similarly, the Resource-Enemy Release Hypothesis (R-ERH) posits that because fast growing species adapted to high resources are typically less defended, fast growing weedy species may be more likely to benefit from enemy

release, especially in disturbed habitats (Blumenthal 2006). Alternatively, disturbance may increase apparency to antagonists, such as herbivores or predators (Castagneyrol et al. 2013; Hambäck et al. 2014; Hahn and Orrock 2015). In this case, disturbance may increase the effectiveness of biotic resistance and inhibit invasive species success. Second, increased resource availability in disturbed environments may increase invasive plant allocation to growth and reproduction, or increase tolerance to herbivory (Maschinski and Whitham 1989; Hawkes and Sullivan 2001). Increased tolerance or reproductive success may allow potential invaders to overcome biotic resistance imposed by herbivores or competitors (von Holle and Simberloff 2005; Clark and Johnston 2009; Müller et al. 2016).

The effects of disturbance and biotic resistance, as well as the capacity for an invader to overcome challenges imposed by the physical environment, may depend on traits of the invading population. As a result, genetic variation within an exotic species could change the effectiveness of biotic resistance or invader responses to disturbance if genotypes differ in their responses to negative species interactions, resource availability, or other altered abiotic conditions in disturbed environments (Lee 2002; Parker et al. 2003; Lavergne and Molofsky 2007). Functional traits, such as growth rate, competitive ability, or herbivore resistance that affect interactions between the exotic species and competitors or herbivores are often genetically variable, and thus both susceptibility to biotic resistance and invasion success could be genotype dependent (Barney et al. 2005; Stultz et al. 2009; Violle et al. 2012; ter-Horst and Lau 2015). Similarly, genetically variable traits, such as growth rate and competitive ability, may influence the response to disturbance. For example, recent hypotheses posit that adaptation to human-caused disturbances facilitate invasions, presumably because the traits that are adaptive in disturbed environments in the native range also promote reproductive success and population growth in disturbed environments in the invaded range (Orivel et al. 2009; Hufbauer et al. 2012; Foucaud et al. 2013).

Here we consider how disturbance and biotic resistance influence the size and fecundity of 44 native and invasive genotypes of *Medicago polymorpha*, a widespread invasive species. Specifically, we tested (1) the potential contribution of insect herbivory to biotic resistance, (2) whether the strength of biotic resistance depends on soil disturbance, and (3) whether the effects of herbivory and disturbance are genotype-dependent and differ between *Medicago* genotypes collected from the native versus invaded range. We hypothesized that soil disturbance would decrease the effectiveness of biotic resistance by herbivores but that the magnitude of this effect would vary across *Medicago* genotypes.

Methods

Study System and Field Site

Medicago polymorpha (hereafter, *Medicago*) is a leguminous plant native to the Mediterranean region that spread into California during the late 1800s (de Haan and Barnes 1998). *Medicago* is a small, primarily selfing, winter annual that germinates with the first rains in fall and flowers in late spring. It is commonly found in disturbed sites such as old fields, roadsides, grazed grasslands, and agricultural sites (de Haan and Barnes 1998). The Egyptian alfalfa weevil (*Hypera brunneipennis*), also an invader from the Mediterranean region, is a dominant folivore on *Medicago* (Lau and Strauss 2005). *Medicago* and *Hypera* are both abundant, and disturbance from grazing, fire, and small mammals is common at our field site located near the McLaughlin Natural Reserve in northern California, USA. Our field site had been recently used as a grazing site for cattle, but cattle were excluded during the experiment. All soil within our field area was non-saline, well-drained loam (Natural Resources Conservation Service Soil Service, United States Department of Agriculture).

Experimental design

To investigate whether herbivory contributes to biotic resistance and whether that effect is dependent on disturbance, we manipulated the abundance of insect herbivores and disturbance in a factorial design. We established 24 2 m × 2 m plots separated by at least 3 m and arranged in a grid within our 100 m × 50 m field site. Each field plot was randomly assigned to one of our four factorial treatments (\pm soil disturbance crossed with ambient/reduced herbivory; $n = 6$ plots per treatment). We manipulated herbivore abundance by applying the generalist insecticide DEMAND CS (Syngenta Crop Protection, Inc., Greensboro, NC). We diluted 6 mL of insecticide per 19L of water in a tank sprayer and applied a sufficient amount directly to each plant to cover it. We applied insecticide from a distance of <10 cm on days with little wind to avoid contamination of other plots. Insecticide application began in January 2013 and was applied once per month for the duration of the experiment. The non-insecticide plots received an equal amount of water as a control. Previous work showed that application of this insecticide reduced insect herbivory on *Medicago* by 81% (terHorst and Lau 2015). We imposed soil disturbance by using a heavy rake to remove all thatch and to loosen the soil to a depth of approximately five centimeters within the plot prior to planting seedlings. This disturbance event only occurred once at the beginning of the experiment in December 2013.

The United States Department of Agriculture, National Plant Germplasm System maintains collections of *Medicago* accessions. *Medicago* is primarily selfing and the severe inbreeding quickly reduces heterozygosity in maternal lines, such that all offspring in a maternal line are effectively the same genotype (Freeman and Herron 2007). Here we refer to each accession as a genotype. We selected 38 genotypes from this collection to span a wide geographic and habitat range; 22 genotypes were from the native range, and 16 genotypes were from the invasive range (Online Resource 1). We also included 6 *Medicago* genotypes that were haphazardly collected in previous years from plants at sites separated by 0.5 km on the McLaughlin Natural Reserve (invasive range); each genotype consisted of fruits collected from the same plant and then propagated in the greenhouse. In total, we used 44 genotypes (22 native, 22 introduced). To minimize maternal effects, all genotypes were grown for a single generation in common environmental conditions in the greenhouse at the Kellogg Biological Station (Michigan, USA). We collected seeds from this common garden generation to use in our field experiment.

In December 2012, we germinated seeds of *Medicago* in cotton plugs in tissue culture trays; these seedlings were then transplanted to the field one week later. Most plots received 3–4 seedlings of each of 44 genotypes, although due to limits in seed availability, some plots received fewer seedlings (Online Resource 1). However, all genotypes were represented in all plots. Within plots, seedlings were planted in a 10 × 15 grid, with 5 cm separating each seedling. Seedlings that died within four days of transplantation were assumed to have died from transplant shock and were excluded from the analyses.

On March 17–18, 2013, we measured herbivore damage as the proportion of leaflets with signs of insect damage on each plant. We also recorded the number of fruits that were produced by each plant over the duration of the experiment, until May 2013. All fruits were collected to prevent colonization by these *Medicago* genotypes.

Statistical analyses

We performed a G-test of independence to test for the independence of our insecticide and disturbance treatments on the probability of flowering of *Medicago* genotypes that survived transplant. We developed generalized linear mixed effect models to determine the effects of insecticide and disturbance on *Medicago* traits and performance, using the “proc glimmix” function in SAS version 9.4 (SAS Institute, Cary, NC). Insecticide, disturbance, and range (native or invasive) were included as fixed factors. *Medicago* genotype (nested within range) and insecticide and disturbance interactions with genotype were included as random

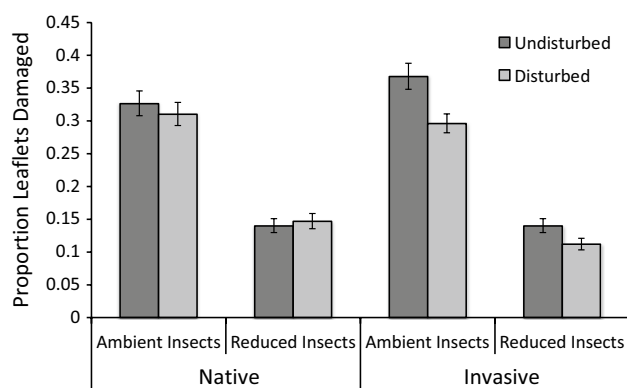


Fig. 1 *Medicago* leaf damage (% of leaflets damaged; backtransformed LS mean \pm SE) with ambient insects and reduced insects in undisturbed and disturbed environments. Disturbance decreases damage on invasive genotypes to a greater extent

factors. We included fruit number and proportion of damaged leaves as dependent variables. We used Laplace's method to approximate log likelihoods and used Likelihood Ratio Tests to determine the significance of random factors. We compared various error distributions and used a gamma distribution for leaf damage and a poisson distribution for fruit number, because they produced the lowest AIC values. We used Pearson Chi-Square/DF to examine overdispersion; both models produced values less than 1 (leaf damage = 0.53; fruit number = 0.32). Random effects that did not result in a lower AIC value were excluded from the final model.

Results

Insecticide and disturbance reduced leaf damage by 57 and 10%, respectively, although the magnitude of disturbance effect differed for native range versus invasive range genotypes ($F_{1,1059} = 4.06$, $P = 0.044$; Online Resource 2, Fig. 1). Disturbance reduced damage on genotypes collected from the invasive range by 12%, but had virtually no effect on damage on genotypes collected from the native range. All interactions of treatment effects with *Medicago* genotypes were non-significant and dropped from the model.

Most of the 3444 seedlings (~98%) survived transplant. 51% of the plants survived through at least February 2013. By the end of the experiment in May 2013, 700 *Medicago* plants (~21%) had survived and produced flowers. Disturbance had little effect on the likelihood of flowering when insects were reduced, but in the ambient insect treatment, disturbance doubled the likelihood of flowering relative to the control treatment ($G_{df=1} = 22.5$, $p < 0.005$). Overall, 44% of the flowering *Medicago* survived to produce

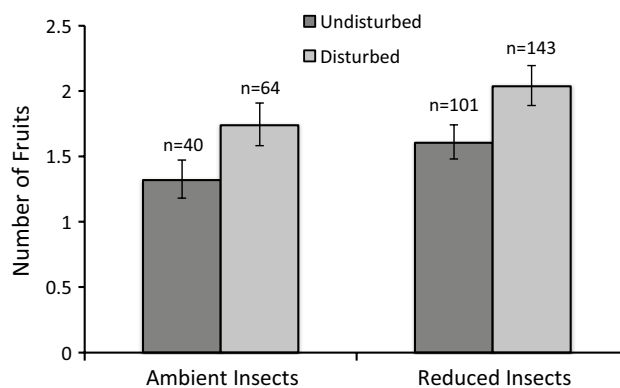


Fig. 2 *Medicago* fruit production (backtransformed mean \pm SE) with ambient insects in undisturbed and disturbed environments ($N = 40$, $N = 64$), and reduced insects in undisturbed and disturbed environments ($N = 101$, $N = 143$)

fruits. Plants produced a maximum of 12 fruits, and only two genotypes produced no fruits. Insecticide increased fruit production by 19% ($F_{1,263} = 6.39$, $P = 0.012$), independent of disturbance (Insecticide \times Disturbance: $F_{1,263} = 0.08$, $P = 0.784$), *Medicago* range (Insecticide \times Range: $F_{1,263} = 1.09$, $P = 0.298$), and genotype (Insecticide*Genotype not part of the final model) (Online Resource 2, Fig. 2). Disturbance increased fruit production by 68%, on average ($F_{1,36} = 8.19$, $P = 0.007$), but genotypes responded to disturbance differently (genotype \times disturbance $\chi^2 = 6.42$, $P = 0.011$). The positive effects of disturbance were realized in many, but not all, *Medicago* genotypes; some genotypes even responded negatively to disturbance (Fig. 3).

Discussion

We found that insect herbivory reduced *Medicago* fecundity, providing some degree of biotic resistance to invasion. Conversely, disturbance increased fecundity, likely facilitating invasion. However, we found that the effects of disturbance and insect herbivory on the reproductive success of this invasive plant species were largely independent and additive. Importantly, the effects of disturbance were largely dependent on *Medicago* genotype; some genotypes responded positively to disturbance, but other genotypes responded weakly or negatively to disturbance. In contrast, we failed to detect genetic variation in response to insecticide in direct contrast to our previous experiments in this system (terHorst and Lau 2015).

Our finding that herbivory and disturbance affect invaders negatively and positively, respectively, is consistent with many other studies documenting the negative effects of antagonistic species interactions and positive effects of

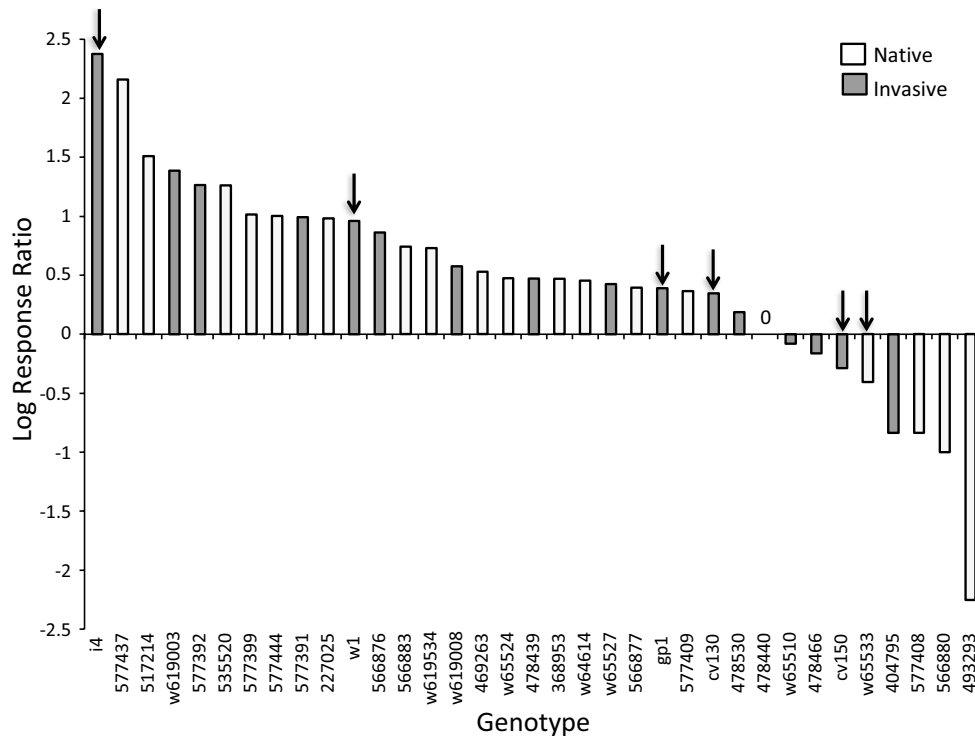


Fig. 3 The response of each *Medicago* genotype to disturbance, measured as the log response ratio between disturbed and undisturbed treatments. Native range genotypes are shown in white and invasive range genotypes are in gray. Arrows indicate genotypes collected

disturbance on invasion success (reviewed in D'Antonio et al. 1999; Levine et al. 2004; Hierro et al. 2006). Few studies investigate the interactive effects of multiple invasion mechanisms despite reason to expect that such mechanisms are not independent (Levine et al. 2004). However, in this case, these processes indeed act independently; for *Medicago*, the effectiveness of biotic resistance is independent of disturbance. By examining both processes simultaneously, we were able to determine that the relative effect of disturbance on fecundity was roughly three times as great as the effect of biotic resistance from insect herbivores. For *Medicago*, disturbance is more important for increasing invasion success than insect herbivores are for resisting invasion, although we have not considered other important agents of biotic resistance to *Medicago* invasion, such as competition (terHorst and Lau 2015) or lack of mutualists (terHorst et al., in review).

Previous studies have found significant interactions between biotic resistance and disturbance, resource availability, or abiotic stress (Dethier and Hacker 2005; Clark and Johnston 2009; Going et al. 2009; Maron et al. 2012), but these studies focused on competition as the mechanism of biotic resistance. The contrast between our results and previous work may be that we examined herbivory as the mechanism of biotic resistance. Although disturbance and

from the McLaughlin Natural Reserve. We were unable to calculate log response ratios for nine genotypes because they produced no fruits in one or both treatments

herbivory may interact to influence invasion success when disturbance alters the abundance or likelihood of attack by herbivores or tolerance to herbivory, we detected little evidence that these mechanisms influence invasion success in this system. Disturbance reduced herbivory slightly, but ultimately did not alter fitness effects of herbivory (no disturbance \times insecticide effect on fitness). It is possible that disturbance frees resources for *Medicago* and increases tolerance of herbivory (Hawkes and Sullivan 2001), potentially counteracting the increased herbivory we observed in disturbed environments. However, that is not likely the case in our experiment. We quantified tolerance as the covariance between herbivore damage and fruit production and found no difference in tolerance between disturbance treatments ($F_{1,235} = 1.56$, $P = 0.213$; Online Resource 3).

Similarly, the Resource Enemy Release Hypothesis would predict that the effects of enemy removal would be the greatest in disturbed, more resource-rich treatments. Our results are inconsistent with this hypothesis as well, as enemy removal increased fitness similarly in both disturbed and undisturbed environments. A lack of enemy release in our study could also be explained by the evolutionary history that the primary herbivore (a co-invader, *H. brunneipennis*) shares with *Medicago*. It is possible that the lack of a range effect in our model is because all

genotypes, regardless of range, were exposed to similar selection pressures over the course of a shared evolutionary history.

Importantly, we also examined genotypic variation in response to disturbance and biotic resistance. In contrast to previous work on this system (terHorst and Lau 2015), we detected little evidence for genotypic variation in the ability to overcome biotic resistance by herbivores. This might be because studies were conducted in different years and at different field sites, with potential differences in soil types, herbivores, and disturbance histories. However, we found significant genotypic variation in response to disturbance. Of our 44 genotypes, 31 responded positively to disturbance, 10 responded negatively to disturbance, one had similar fitness in both environments, and two had no fitness in either environment. Previous work suggests that the genetic composition of the invasion pool is likely to affect invader fitness and success (Barney et al. 2005; Sthultz et al. 2009; Violle et al. 2012; terHorst and Lau 2015), and our results demonstrate that disturbance affects which genotypes are the most successful. Although *Medicago* is common in disturbed environments in California (de Haan and Barnes 1998), it is also successful in less disturbed grassland environments (terHorst et al., in review). Our results suggest that invasion success in a particular habitat depends both on the local disturbance regime and the genetic composition on the invasion pool.

The variation in genotype response to disturbance was not related to the collection range (native vs. invasive) of *Medicago* (Fig. 3). This is in contrast to a similar study that showed the significance of plant response to disturbance differed between natives and invasives dependent upon herbivore and pathogen presence (Müller et al. 2016). Further, we found no evidence that our six genotypes collected from both disturbed and undisturbed areas near the McLaughlin Reserve performed any better or worse than genotypes from other invaded ranges (Fig. 3). This suggests that invasion into nearby environments does not pre-dispose genotypes for success. Nor does this indicate that invasive range genotypes have evolved in ways that make them more likely to invade novel habitats. However, the genotypic variation in fruit production in response to disturbance we observed independent of collection range indicates a potential for contemporary evolution that could affect invasion success of *Medicago* (Fig. 3, ESM2).

Collectively, these results suggest that biotic resistance by insect herbivores can decrease invasion success, but that these effects may be outweighed by the positive effects of disturbance. However, invasion success in this system can be predicted by the additive effects of biotic resistance and disturbance. Invasion success will also depend on the interactive effects of the genetic composition of the invader pool and the history of disturbance in a particular habitat.

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Author contribution CPT and JAL conceived, designed, and performed the experiments. SLJB entered and analyzed data, and wrote the manuscript. CPT and JAL provided editorial advice.

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