

CHAPTER TWENTY-FIVE

Plasticity and trait-mediated indirect interactions among plants

ERIK T. ASCHEHOUG and RAGAN M. CALLAWAY

Division of Biological Sciences, University of Montana

Introduction

Ecologists have long recognized the importance of phenotypic plasticity as a mechanism by which organisms acclimate and adapt to local environments. Phenotypic plasticity is commonly defined as variation in the morphological or physiological phenotype of a given genotype in response to the abiotic and biotic environment (Bradshaw 1965). Plants are particularly plastic organisms because they must solve the fundamental problems of resource acquisition, competition and herbivore attack without mobility (Sultan 1987, 2000). Plasticity has been demonstrated in the morphological, developmental, physiological and biochemical traits of plant species, with many traits showing flexibility in expression both between and within individual plant species (Novoplansky 2002; de Kroon *et al.* 2005; Valladares *et al.* 2006). The plastic responses vary not only in their form, but also in their permanence. Responses may be permanent for the lifetime of an individual, fixed for long periods of time (e.g., a growing season), or dynamic at the scale of minutes (Metlen *et al.* 2009).

Research on the nature of plasticity and its potential to broaden the ecological niches of species in shifting abiotic and biotic conditions has historically focused on the morphological responses of plants. However, morphological responses tend to be slow and are largely irreversible – two parameters that are not favoured by selection (Valladares *et al.* 2007). In contrast to changes in morphology, plants can also respond via biochemistry. These responses can be exceptionally rapid and highly ephemeral (Metlen *et al.* 2009); traits that lend themselves to adaptive value and are favoured by natural selection, but biochemical traits have been studied very little in the explicit context of plasticity.

Plasticity and trait variation have been studied extensively in plants, but the ecological consequences of such phenotypic variation are poorly understood (Miner *et al.* 2005). Experimental settings commonly overestimate the degree to which plants can exhibit plastic responses to changes in natural conditions. This may be because of the continually changing conditions in nature which

makes optimization of some plastic responses difficult, especially if plastic responses have long lag times and are largely irreversible. In addition, the diffuse nature of competition among plants within communities may limit a plant's ability to exhibit its maximum potential plasticity in response to biotic interactions. Thus there appear to be greater limits and constraints to plasticity in plants in natural systems than would be predicted from responses to controlled environments (Valladares *et al.* 2007). However, investigations that focus on trait responses that can mediate multiple environmental stimuli in plants should have a higher potential for adaptive value. For example, secondary biochemistry responses to nutrient stress may also mediate competitive or facilitative interactions (Tharayil *et al.* 2009) and therefore can potentially provide a more stable cue for plant plasticity responses in natural systems.

It is surprising that the consequences of plasticity for interactions among plants have not been more deeply explored since high phenotypic plasticity in plants is thought to be a characteristic of 'good competitors' (Grime 2001), and good competitors can have powerful effects on communities (Connell 1983). Species classified as good competitors generally show more rapid responses to variation in their environment, such as adjusting root:shoot ratios, leaf specific area, proportions of fine to coarse roots and diversity of biochemistry, than species that are poor competitors (Grime 2001; Callaway *et al.* 2003). Despite the high degree of plasticity expressed by plants, and the potential for this plasticity to affect the way a species might interact with its neighbours (known as trait-mediated interaction or TMI), very few studies have been conducted with plants that focus on plasticity and interactions. However, by re-examining earlier work with a focus on plasticity we can piece together direct evidence for TMIs.

For example, Callaway (1990) found that the root architecture of *Quercus douglasii* seedlings demonstrated plasticity to variation in water source. *Quercus douglasii* seedlings with experimentally restricted access to deep stores of water produced roughly twice as many fine lateral roots and more than 5× the lateral root mass as seedlings with access to a deep water source. This phenotypic plasticity demonstrated by seedlings in controlled experiments corresponded with apparent plasticity in the field, where mature trees without access to deep water possessed very dense surface lateral root systems while trees with deep water access did not (Callaway *et al.* 1991). Plasticity in root architecture in the field appeared to create a TMI as trees with abundant shallow roots strongly suppressed understory productivity; whereas trees without abundant shallow roots had strong facilitative effects.

More recently, ecologists have extended the view of TMIs from direct interactions between plants to indirect interactions (TMIs) among species. While we know of no studies of plant–plant interactions that test for the presence of TMIs, conceptually all of the necessary components to produce

TMIIs have been studied, making the next step ripe for empirical research. For example, in the scenario of the TMI apparently mediated by plasticity in the root architecture of *Quercus douglasii*, this plasticity also correlated with different understory community compositions. The abundance of the native *Nassella* (nee *Stipa*) *pulchra* was higher under trees with abundant shallow roots (Callaway *et al.* 1991). Simultaneously the abundance of European annuals (primarily *Avena fatua* and *Bromus diandrus*), which can competitively exclude natives such as *Nassella*, was lower. This pattern suggests the occurrence of a TMII but does not demonstrate it. However, a relatively simple experiment could explore this spatial pattern in the context of TMIIs, and similar experiments could be used to study TMII in other systems. The key would be to determine whether shallow root architecture simply promoted *Nassella* directly, or altered the competitive effects of the European annuals in ways that indirectly promoted *Nassella* (see Rice and Nagy 2000). Using *Nassella* as a target species, TMIIs would be demonstrated if experimental treatments in which European annuals were removed from around *Nassella* under trees without shallow root architecture improved the growth or fitness of *Nassella*.

This link between plastic responses to environment and its affect on plant-plant interactions (direct and indirect) represents a major gap in our understanding of how plant communities assemble. TMIs and TMIIs have the potential to create tremendous variation, or conditionality, in the outcomes of interactions among competing species, and thus have important implications for how competitors might coexist (Chesson and Rosenzweig 1991). In other words, we know that indirect interactions among groups of competitors can promote coexistence among species that would otherwise be likely to exclude each other competitively (Miller 1994; Callaway and Howard 2007), thus plasticity among species can greatly enhance the potential for indirect interactions to sustain coexistence among competing species and thus increase community diversity.

Interactions among plants

Negative direct interactions among plants appear to derive primarily from the need to acquire basic resources such as light, water and nutrients, which are often in limited supply (Goldberg 1990; Miller and Travis 1996). Because plants are sessile, resource competition between individuals can be intense, potentially making coexistence difficult when essential resources are scarce (Tilman 1982). In addition, allelopathy, the negative biochemical effects of neighbours on each other (Turlings *et al.* 1990; Williamson 1990; Mahall and Callaway 1992; Schenck *et al.* 1999), can also be a mechanism by which plant species inhibit each other.

Positive interactions among plants, or facilitation, occur when the presence of one plant enhances the growth, survival or reproduction of a neighbour

(Callaway 2007). But it is important to note that facilitation by one species on another may correspond with reciprocal negative, positive or neutral responses. Direct positive interactions may incorporate a wider range of mechanisms than direct negative interactions (Callaway 2007). Like competition, facilitation may occur through resource effects, one species increasing nutrient, water or light availability to another, or through chemical effects (Metlen *et al.* 2009). However, facilitation can also be driven by non-resource processes. Most commonly, species that are physically tolerant to stresses such as cold, heat, wind, salinity and disturbance buffer other species from these abiotic conditions.

Indirect interactions among plants can be derived from direct resource competition, allelopathy or facilitation (Pages and Michalet 2003; Callaway 2007; Callaway and Howard 2007), but these have received far less attention than the direct impacts that plants have on one another. This may be because plants are generally embedded within a matrix of many other plants, all of which require the same basic resources of light, water and nutrients; thereby creating an environment in which direct interactions appear to be assured. However, the highly aggregate nature of plant communities also sets the stage for common and strong indirect interactions – situations in which the direct interaction between two species is caused or altered by simultaneous interactions with additional species (Miller 1994; Levine 1999; Callaway and Pennings 2000; Callaway and Howard 2007; Cuesta *et al.* 2010).

Ecological consequences of plant interactions

Competition and facilitation among plants are the basic processes through which TMIs and TMIs can operate, and these interactions can be powerful organizing forces in structuring plant communities (Allen and Forman 1976; Grime 1977; Connell 1983; Tilman 1985; Ortega and Pearson 2005; Callaway 2007; Cavieres and Badano 2009). Because of this, evaluating species' inherent competitive abilities can likely provide some insight into how they will perform in a community context. However, assessing the relative competitive strengths of species is difficult in anything other than simple pairwise or 'bioassay' experiments; and it now is becoming apparent that such experiments do not accurately predict how individuals may respond when subjected to the diffuse nature of interactions found in plant communities (Callaway and Howard 2007; Perkins *et al.* 2007; Engel and Weltzin 2008; Schmidtke *et al.* 2010; Aschehoug 2011). Even more, rankings of competitive effects and responses may not be complete indicators of individual competitive abilities when plants are in real communities (Wang *et al.* 2010). Thus theory for how plant communities assemble that fails to incorporate indirect interactions is probably incomplete, and this has very important implications for studying TMIs.

There are two general, but contrasting, theories for how plant species may assemble into communities under equilibrium conditions as a result of

competition among plants. The first does not incorporate indirect interactions, and thus does not have the potential to integrate TMIs, and poses that plant communities are competitively transitive in nature (Goldsmith 1978; Mitchley and Grubb 1986; Keddy and Shipley 1989). In other words, all species in a given pool, or community, can be ranked in a linear competitive hierarchy. The strict 'pecking order' that results from hierarchical competitive abilities provides a predictive tool for community organization. A transitive, or hierarchical, perspective on assembly rules assumes that communities will consistently move towards dominance by the best competitor in the hierarchy in a homogeneous abiotic environment, and this can potentially lead to the development of monocultures. An important theoretical consequence of not allowing TMIs among plants in such transitive or hierarchical communities is that weak competitors will be competitively excluded given enough time and the absence of non-equilibrium processes. In this paradigm only non-equilibrium forces, such as fire, herbivory (which can establish TMIs) or abiotic heterogeneity, can prevent the dominance of a small number of species or the formation of monocultures in a local community.

In contrast to hierarchical assembly rules is the theory that plants exhibit non-transitive or non-hierarchical competitive properties as they form communities (Jackson and Buss 1975; May and Leonard 1975; Petraitis 1979). Whereas hierarchical organization is best described mathematically as $A > B > C$, non-hierarchical organization occurs when loops form in the hierarchy such as $A > B$, $B > C$, but $C > A$. In other words, species C indirectly benefits species B by having a direct negative impact on species A, which creates the opportunity for TMIs to be included in conceptual models. Given the right starting point, a simple loop within a suite of competing species can result in a perpetually shifting state in which all three species coexist indefinitely (Buss and Jackson 1979). This coexistence is based entirely on the balance of direct competitive interactions, but leads to the formation of complex networks of species interactions which may be mediated directly or indirectly via plant plasticity. Proponents of non-transitive competitive processes note that because plants interact with many other species simultaneously, clear pecking orders are likely rare. In addition, sporadic reversals of dominance among species can create powerful and facilitative indirect effects among competitors which can transform overall community structure.

When community members interact in complex 'networks' of interactions, competitive exclusion is much less likely. In addition, coexistence may be maintained among large pools of species in the absence of abiotic heterogeneity or non-equilibrium processes. Mathematical evaluations of such interactions predict that such indirect interactions among competitors can allow large communities of species to coexist (Karlson and Jackson 1981; Laird and Schamp 2006; Laird and Schamp 2008).

Non-transitive theory requires quite specific combinations or sequences of interactions among species to produce indirect interactions, and thus TMIs. However, groups of plant species appear to compete in ways that produce indirect interactions, but without the competitive ‘loops’ required for non-transitive theory. In other words, some species appear to ‘modify’ interactions among other species without establishing the classic non-transitive combinations of competitive dominance (Callaway and Pennings 2000; Metlen 2010).

A key commonality of the transitive and non-transitive theories of plant community assembly is the requirement of strong, species-specific, direct negative effects. In a hierarchical system, the direct effect of each species on another is linear; a single dominant species that exerts primary control of community wide species diversity via competitive interactions, and subdominant species that exert lesser degrees of control in direct proportion to their place in the hierarchy. In non-hierarchical systems, there is the requirement of at least one of the weaker competitors directly outcompeting a species of higher competitive ranking. In other words, a species that loses most of its interactions with other community members must be able to outcompete a species that wins most of its interactions in the community, an unlikely scenario without the presence of TMIs. In fact, the conditionality of competitive outcomes may be explained in large part by the plastic response of plants to competition (Cahill *et al.* 2010).

Transitive and non-transitive processes occur in communities but plants also experience ‘diffuse’ competition in a community context. Instead of a distinct interaction with another single species, for which ranks might be determined, a plant experiences the additive effects (positive or negative) of many species interacting in space and time. Such diffuse interactions may have profound impacts on the species composition of plant communities (Davidson 1980; Vandermeer 1980; Wilson and Keddy 1986; Miller 1994; Li and Wilson 1998; Levine 1999; Callaway and Pennings 2000) and provide tremendous potential, conceptually if not logistically, to study TMIs.

There is a substantial escalation in the complexity of assembly rules as we move from transitive to non-transitive models and as we add interaction modifications and diffuse interactions to competitive loops. And this complexity increases again once we consider that most current thinking is built on the construct, or at least the implicit assumption, that plants are fixed in their competitive abilities. However, we know that plants vary in their competitive abilities both within and between populations. For example, Grøndahl and Ehlers (2008) found that genotypic variation in the production of different terpenes by ecotypes of *Thymus pulegioides* and *T. serpyllum* altered the effects of the *Thymus* species on co-occurring plant species. The ecological effects demonstrated for *Thymus* species (also see Ehlers and Thompson 2004; Jensen and Ehlers 2010) corresponded with selective effects of *Thymus* on their

neighbours. Plants that came from sites where they co-occurred naturally with a carvacrol (a terpene)-producing ecotype of *Thymus* also performed better on soil treated with carvacrol. This example of how genotypic variation can affect the competitive effects of a species derives from at least two general ways that plants interact directly, facilitation and allelopathy. If relatively subtle differences in 'fixed' competitive interactions can have such a large impact on community formation, then *phenotypic* shifts that lead to changes in interaction outcomes (TMIs and TMIs) have the potential to be very powerful in determining how plant communities assemble.

Plasticity and direct interactions

In both transitive and non-transitive models, the intensity of direct interactions determines the degree to which plants can coexist. Therefore understanding how plasticity affects interaction intensities can greatly improve our ability to predict plant coexistence in communities. Much is known about how plant traits such as morphology, growth rates, final size, reproduction, qualitative and quantitative biochemical traits, and biomass allocation can vary widely for a given genotype (Sultan 1987, 2000; Metlen *et al.* 2009), which creates exceptional opportunities for exploring how phenotypic plasticity within an individual species can influence interactions with other species and the subsequent effects on the structure of plant communities.

A substantial component of the way that plants affect each other (either negatively or positively) is based on plant size and growth rate. For example, Brooker *et al.* (2005) reanalysed data from Reader *et al.* (1994) to compare the intensity of the competitive effect of neighbours on *Poa pratensis* to the importance of the competitive effect. Among grasslands that varied in productivity, both components of competition were significantly affected by total neighbour biomass. Plant size can also affect facilitative interactions. Tewksbury and Lloyd (2001) found that larger *Olneya tesota* trees in the Sonoran Desert supported higher numbers of beneficiary species and larger beneficiary perennials than small canopies. Because of the importance of the size of individual plants for competitive and facilitative effects, phenotypic plasticity in size may have substantial effects on interaction outcomes.

Morphological plasticity as a response to abiotic conditions, however, is often slow and costly, which may limit the ability of plants to respond when subjected to intense competition (Novoplansky 2002). Biochemical responses, such as the release of secondary metabolites that increase nutrient availability in the rhizosphere, are less costly and more ephemeral responses that can have immediate impacts on plant performance (Metlen *et al.* 2009) and potentially effects on neighbouring competitors. Li *et al.* (2007) found that the cluster root forming species *Vicia faba* increased phosphorus availability in the soil rhizosphere via the release of acidifying chemicals (citrate and

malate). The biochemical response of *V. faba* to phosphorus deficiency is also exceptionally fast; laboratory tests show it reducing the pH of nutrient agar by ~2 units in 6 hours. Such changes in soil acidity can result in 10-fold changes in phosphorus availability. In field experiments, the increase in phosphorus availability resulted in an overyielding of 26% for *V. faba*. In addition, *V. faba* directly facilitated *Zea mays* through the shared increase in phosphorus availability leading to an overyielding of 43% by *Z. mays*. This example demonstrates the strong potential for biochemical plasticity to be a model system for understanding how TMIs and TMIs can impact both competitive and facilitative interactions and the organization of communities.

Plasticity and indirect interactions

We know of no examples in which phenotypic plasticity in a plant trait has been shown to alter *indirect* interactions among other plant species. Conceptually, however, all of the component pieces of TMIs can be examined from existing empirical studies. What is lacking is a comprehensive set of experiments that explicitly link plasticity and indirect interactions. Ideally, such studies would entail an experiment in which species 'A' demonstrated two or more phenotypes (e.g., A_{Ph1} and A_{Ph2}), and then the indirect effects of these two phenotypes would be tested in experiments involving two or more other neighbours (Fig. 25.1). For example, in Fig. 25.1a, the hypothetical A_{Ph1} has weak competitive effects on species B, and species B has strong competitive effects on species C. Thus the indirect effects of A_{Ph1} on C are weak. In contrast, the hypothetical A_{Ph2} has strong competitive effects on species B, and thus strong indirect facilitative effects on species C. Figure 25.2 illustrates how TMIs might occur when there is plasticity in a facilitative benefactor (species A) or a beneficiary (species B).

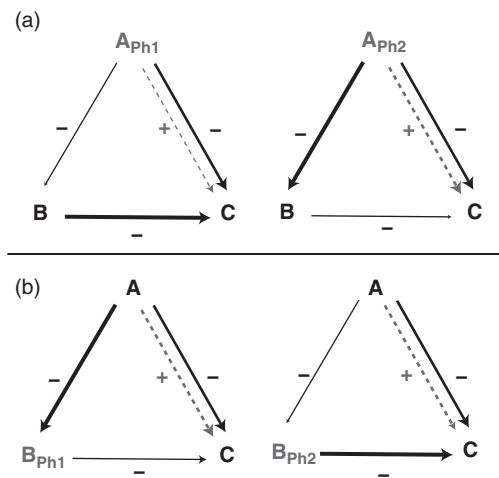


Figure 25.1 (a) A conceptual model of how a phenotypic shift in species A can alter the competitive effect (solid line) of species A on species B, resulting in an increase in indirect (dashed line) benefit to species C. (b) A model of how a phenotypic change in species B in response to competition by species A can result in a change in the indirect effect of species A on species C. Both models represent TMIs as a result of competitive interactions. See colour plate section.

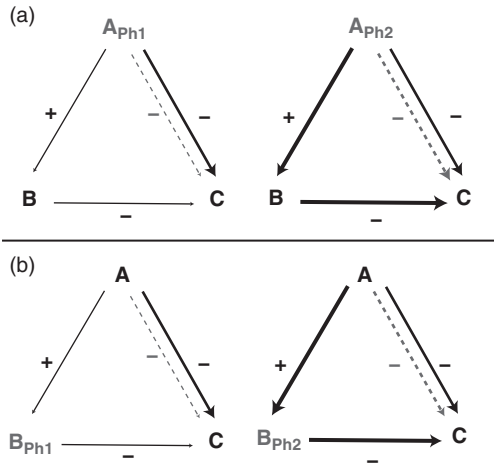


Figure 25.2 (a) A conceptual model of how a phenotypic shift in species A can alter the facilitative effect (solid line) of species A on species B, resulting in an increase in indirect (dashed line) negative effect on species C. (b) A model of how a phenotypic change in species B in response to facilitation by species A can result in a change in the indirect effect of species A on species C. Both models represent TMIIs as a result of facilitative interactions. See colour plate section.

Next we suggest potential scenarios in nature in which these TMIIs might occur, with the goal of stimulating ideas for how such studies might be approached in the future. An intriguing scenario may exist for *Q. agrifolia*, the native perennial herb *Pholistima auritum*, and European annual grasses in California grasslands. *Pholistima* can form near monocultures directly beneath the canopies of some *Q. agrifolia* trees, but is much less abundant in the grassland directly adjacent to the canopies where European annuals dominate (Parker and Muller 1982). However, if *Pholistima* is not present under the oaks, European grass species are intensely facilitated (as *Pholistima* itself appears to be) by *Q. agrifolia* which suggests that the low abundance of annual grass species in the understory is not due to the direct effects of the oaks. Instead, it appears that once facilitated, *Pholistima* excludes the European annual grasses through the inhibitory effects of its litter and leachates. In field experiments, fresh *Pholistima* litter reduced *Bromus* germination by 73% and *Avena* by 96%. However, when experiments were conducted with *Pholistima* litter that had been leached, at least 92% of seeds germinated in every treatment. *Q. agrifolia* appears to have powerful negative indirect effects on grasses, and the stage is set for the next necessary step for TMIIs – if *Q. agrifolia* demonstrates plasticity in some way that affects its facilitative effect on *Pholistima*, the indirect effects of the tree on annual grasses are likely to change as well.

Q. douglasii and *Q. agrifolia* may help us understand the effects of plasticity on indirect interactions (Fig. 25.2a), but plants show a great deal of plasticity in response to neighbours as well (Callaway *et al.* 2003; Cahill *et al.* 2010). We know of no examples in which plastic responses have been connected to cascading indirect interactions with other species, but much like the *Quercus* example above, we can speculate about how the plastic response to competition may lead to indirect interactions.

Cahill *et al.* (2010) found that plants altered their root foraging strategies based on the amount and distribution of resources in the soil and the presence of competitors. When grown alone, *Abutilon theophrasti* had broadly developed root systems regardless of whether resources were uniformly or patchily distributed within the soil. However, when in competition with a conspecific, *A. theophrasti* was highly plastic in root distribution and distance from stem depending on the distribution of resources, suggesting that plants are capable of altering the plastic response of roots to nutrients depending on the presence or absence of a competitor, a good example of a TMI. While this example highlights the plastic response of *A. theophrasti* to competition, this particular set of experiments was limited to pairwise competition, which does not test TMIs. Nevertheless, the alteration of root system morphology based on the presence of competitors and variable resources suggests that when placed in a multispecies context, the intensity of competition that *A. theophrasti* experiences (stronger or weaker) is highly dependent on the plastic response. A test of this TMII response could easily be carried out by replicating the experiments with multiple competitors. TMIs would be demonstrated if competition intensities differed between single and multiple competitor experiments.

Plasticity and exotic invaders

Plasticity expressed by any plant species provides an opportunity to explore TMIs in novel ways, but exotic invaders might provide unusually good opportunities because they are thought to be unusually plastic (Richards *et al.* 2006; Hulme 2008) and unusually strong competitors (Maron and Marler 2008). High phenotypic plasticity has been suggested as a good predictor of invasiveness (Mal and Lovett-Doust 2005; Chun *et al.* 2007, but see Bossdorf *et al.* 2005; Hulme 2008). Unlike our focus here on plasticity and TMII, both Richards *et al.* (2006) and Hulme (2008) focus on the potential role of plasticity in allowing an invader to express advantageous phenotypes as they colonize a broad range of environments (Bradshaw 1965; Van Valen 1965; Whitlock 1996; Sultan *et al.* 1998a, b; Donohue *et al.* 2001; Richards *et al.* 2005). While likely true, exotic 'invasion' is only defined in part by colonization by exotic species. Callaway and Maron (2006) and Hierro *et al.* (2005) note that exotic 'invasions' involve biogeographic shifts in the fundamental ecology of a species; generally much higher abundances and stronger apparent impacts in non-native ranges than

in native ranges. Thus the essence of an 'invader' as opposed to an 'exotic' is not just in the processes involved in colonization, but in the processes involved in the attainment of very high densities, biomass and impacts on other species. It is in the context of plasticity within these processes and impacts that invaders provide the best opportunities to study TMIs.

Strong competitive interactions are likely to play an important role in establishing the dominance of some invaders (D'Antonio and Mahall 1991; Levine *et al.* 2003; Vila and Weiner 2004; Maron and Marler 2008; Munshaw and Lortie 2010). Release from specialist herbivores or pathogens may allow plants to be more competitive in non-native ranges (Keane and Crawley 2002), or successful invaders may possess competitive advantages because they come from a more competitive species pool, or happen to possess inherent traits that give them an advantage relative to their new neighbours. Invaders may have strong competitive effects in their non-native ranges through their ability to attain higher biomass, or because of novel traits that confer more subtle competitive advantages (Callaway and Pennings 2000; Callaway and Ridenour 2004). There have been quantitative biogeographic comparisons of productivity, biomass or density in both the native and non-native ranges of invasive plant species (Woodburn and Sheppard 1996; Grigulis *et al.* 2001; Paynter *et al.* 2003; Jakobs *et al.* 2004; Beckmann *et al.* 2009), and many studies have clearly documented strong negative impacts of invaders in their non-native ranges; apparently much stronger than most if not all native species (e.g., Bruce *et al.* 1997; Ridenour and Callaway 2001; Lu and Ma 2005; Ortega and Pearson 2005; Hejda *et al.* 2009). One study has quantified the impact of an invasive species on the productivity or diversity of its neighbours in the field in both its native and non-native ranges. Inderjit *et al.* (2011) found that the canopies of *Ageratina adenophora*, a widespread and aggressive subtropical invader, had facilitative effects on other species in its native Mexico but highly inhibitory effects in its non-native ranges in China and India.

Despite the wealth of information on the plasticity of invaders and the powerful impacts they have in their non-native ranges, we know nothing about the phenotypic plasticity of invaders within the context of TMIs or TMIs. We can only speculate again on likely scenarios and ways in which we might experimentally explore TMIs produced by the phenotypic plasticity expressed by exotic invasive species. For example, when the California native shrubs *Haplopappus ericoides* and *H. venetus* var. *seloides* grow in the absence of competition their root systems are concentrated near the soil surface (D'Antonio and Mahall 1991). However, when competing with the exotic *Carpobrotus edulis* the root systems of *Haplopappus* shift to a much deeper morphology as they are displaced by the mat-forming exotic (D'Antonio and Mahall 1991). This change in rooting depth by *Haplopappus* suggests that neighbouring species can exert strong control over the phenotype of

competitors – in this case inducing a change that may result in a trade-off in access to nutrients and water (Ho *et al.* 2005). Further, a change in *Haplopappus* rooting depth may decrease the intensity of competition between *Haplopappus* and *Carpobrotus* but may increase the intensity of competition with other species that utilize deeper soil sections, which would represent a TMII.

Carpobrotus invades different abiotic habitats (D'Antonio 1993) which is likely to elicit plastic responses by *Carpobrotus* (Weber and D'Antonio 1999). Plasticity expressed by *Carpobrotus* may change its effects on the root architecture of *Haplopappus*, creating a complex suite of plastic effects and responses between the two species. It would be intriguing to explore the next step by experimentally subjecting *Haplopappus* to competition with other species while it is experiencing at least two different manifestations of plasticity in *Carpobrotus*.

Chemically mediated interactions among plants, such as allelopathy, can also have strong impacts on the organization of communities and represent a promising area in the search for TMIs. *Centaurea stoebe*, an European invader in North America, exudes the compound (\pm)-catechin from its roots (Tharayil and Triebwasser 2010), which can inhibit the growth of neighbouring competing plants (Callaway *et al.* 2005; Inderjit *et al.* 2008a, b; Simoes *et al.* 2008; He *et al.* 2009; Pollock *et al.* 2009; but see Blair *et al.* 2006; Duke *et al.* 2009). In addition to inhibiting neighbour performance, (\pm)-catechin is also a chelator, the addition of which makes phosphorus available in soils where it is bound by calcium (Thorpe *et al.* 2006; Tharayil *et al.* 2008, 2009) which can improve the performance of *C. stoebe* in phosphorus deficient soils. Native species vary a great deal in their susceptibility to (\pm)-catechin (Thorpe *et al.* 2009). Weir *et al.* (2006) found that two good competitors with *C. stoebe*, *Lupinus sericeus* and *Gaillardia grandiflora*, produced levels of oxalate in their root exudates that were more than an order of magnitude higher than that of three poor competitors. They also found that oxalic acid reduces the oxidative damage generated by (\pm)-catechin. Furthermore, exposure to (\pm)-catechin increased the exudation of oxalate by *G. grandifolia* four-fold and *L. sericeus* by 50-fold. This suggests that some native plants may respond to competition with *C. stoebe* in a plastic way, which is a demonstration of a TMI. This response creates the opportunity for a TMII involving the amelioration of (\pm)-catechin effects on co-occurring species. Interestingly, native grasses are highly spatially associated with *L. sericeus* in communities invaded by *C. stoebe* and field experiments show that *L. sericeus* indirectly facilitates native grasses in vegetation dominated by *C. stoebe*. This facilitation was correlated with the presence of oxalic acid in the soil in the field. When oxalic acid was applied to the roots of native grasses it alleviated the allelopathic effects of (\pm)-catechin, indicating that root secreted oxalic acid may act as a chemical facilitator for plant species that do not produce the

chemical. Again, this example is not an explicit test of TMIs, but it does suggest that the chemically mediated suite of indirect interactions derives from the plastic response of some species to the presence of a novel chemical in the soil rhizosphere.

Conclusion

Although we know of no examples in which researchers have specifically investigated the effects of plasticity on indirect interactions among plants, the requisite component pieces of TMIs in plants are well understood. Because of both the highly plastic nature of plants and a myriad of probable indirect interactions in plant communities, TMIs among plants are clearly an important future research direction. But beyond linking existing ideas about plasticity and interactions, we also have considered how to use TMIs to provide fundamental insight into broader ecological questions, such as how plant communities assemble, or how invasive species can act as powerful reorganizing forces in communities.

Among the more promising lines of research, the biochemical plasticity of plants (Metlen *et al.* 2009) has the potential to provide highly dynamic and inducible phenotypic shifts in plants that may also have strong allelopathic effects on some, but not all, neighbours (e.g., Thorpe *et al.* 2009), and in some, but not all abiotic contexts (Pollock *et al.* 2009). Because plant secondary biochemistry can also be specialized in purpose and unique to a family, genus, or even an individual species, the potential for plasticity, and thus TMIs, via plant biochemistry is nearly endless. In addition, the cascading effects of induced biochemical plasticity could also be facilitative as it can provide associational defence (Pfister and Hay 1988) and possibly alert other species to the presence of herbivores (Karban *et al.* 2006).

The absence of studies of TMIs among plants may be due in part to the daunting matter of experimenting with highly diffuse interactions occurring among multiple species. But diffuse interactions are the product, in part, of the immobility of plants, and immobility in multispecies complexes may be why plants are so unusually plastic and provide such exceptional opportunities for studying TMIs and TMIs. Exploring how shifts in phenotypes respond to changing abiotic and biotic conditions, and in turn affect interactions with multispecies complexes, may yield major advances towards a more mechanistic understanding of the distributions and abundances of plant species.

Acknowledgements

E. T. Aschehoug thanks the NSF Graduate Research Fellowship Program for support and R. M. Callaway thanks the NSF (DEB 0614406) and the Andrew W. Mellon Foundation for support.

References

- Allen, E. and Forman, R. (1976) Plant species removals and old-field community structure and stability. *Ecology*, **57**, 1233–1243.
- Aschehoug, E. T. (2011) Indirect interactions and plant community structure. PhD Thesis, University of Montana.
- Beckmann, M., Erfineier, A. and Bruelheide, H. (2009) A comparison of native and invasive populations of three clonal plant species in Germany and New Zealand. *Journal of Biogeography*, **36**, 865–878.
- Blair, A., Nissen, S., Brunk, G. and Huffbauer, R. (2006) A lack of evidence for an ecological role of the putative allelochemical (\pm)-catechin in spotted knapweed invasion success. *Journal of Chemical Ecology*, **32**, 2327–2331.
- Bossdorf, O., Auge, H., Lafuma, L. *et al.* (2005) Phenotypic and genetic differentiation between native and introduced plant populations. *Oecologia*, **144**, 1–11.
- Bradshaw, A. (1965) Evolutionary significance of phenotypic plasticity in plants. In E. Caspari, ed., *Advances in Genetics*. London: Academic Press, pp. 115–151.
- Brooker, R., Kikvidze, Z., Pugnaire, F. I. *et al.* (2005) The importance of importance. *Oikos*, **111**, 208–208.
- Bruce, K., Cameron, G., Harcombe, P. and Jubinsky, G. (1997) Introduction, impact on native habitats, and management of a woody invader, the Chinese tallow tree, *Sapium sebiferum* (L.) roxb. *Natural Areas Journal*, **17**, 255–260.
- Buss, L. W. and Jackson, J. B. C. (1979) Competitive networks: nontransitive competitive relationships in cryptic coral reef environments. *American Naturalist*, **113**, 223–234.
- Cahill Jr, J., McNickle, G., Haag, J. *et al.* (2010) Plants integrate information about nutrients and neighbors. *Science*, **328**, 1657.
- Callaway, R. and Howard, T. (2007) Competitive networks, indirect interactions, and allelopathy: a microbial viewpoint on plant communities. In U. L. K. Esser, W. Beyschlag and Jin Murata, eds., *Progress in Botany*. Berlin: Springer, pp. 317–335.
- Callaway, R., Ridenour, W., Laboski, T., Weir, T. and Vivanco, J. (2005) Natural selection for resistance to the allelopathic effects of invasive plants. *Ecology*, **93**, 576–583.
- Callaway, R. M. (1990) Effects of soil-water distribution on the lateral root development of three species of California oaks. *American Journal of Botany*, **77**, 1469–1475.
- Callaway, R. M. (2007) *Positive Interactions and Interdependence in Plant Communities*. Dordrecht, The Netherlands: Springer.
- Callaway, R. M. and Maron, J. L. (2006) What have exotic plant invasions taught us over the past 20 years? *Trends in Ecology and Evolution*, **21**, 369–374.
- Callaway, R. M. and Pennings, S. C. (2000) Facilitation may buffer competitive effects: indirect and diffuse interactions among salt marsh plants. *American Naturalist*, **156**, 416–424.
- Callaway, R. M. and Ridenour, W. M. (2004) Novel weapons: invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and the Environment*, **2**, 436–443.
- Callaway, R. M., Nadkarni, N. M. and Mahall, B. E. (1991) Facilitation and interference of *Quercus douglasii* on understory productivity in central California. *Ecology*, **72**, 1484–1499.
- Callaway, R. M., Pennings, S. C. and Richards, C. L. (2003) Phenotypic plasticity and interactions among plants. *Ecology*, **84**, 1115–1128.
- Cavieres, L. A. and Badano, E. I. (2009) Do facilitative interactions increase species richness at the entire community level? *Journal of Ecology*, **97**, 1181–1191.
- Chesson, P. and Rosenzweig, M. (1991) Behavior, heterogeneity, and the dynamics of interacting species. *Ecology*, **72**, 1187–1195.
- Chun, Y. J., Collyer, M. L., Moloney, K. A. and Nason, J. D. (2007) Phenotypic plasticity of native vs. invasive purple loosestrife: a two-state multivariate approach. *Ecology*, **88**, 1499–1512.

- Connell, J. H. (1983) On the prevalence and relative importance of interspecific competition: evidence from field experiments. *American Naturalist*, **122**, 661–696.
- Cuesta, B., Villar-Salvador, P., Puertolas, J., Benayas, J. M. R. and Michalet, R. (2010) Facilitation of *Quercus ilex* in Mediterranean shrubland is explained by both direct and indirect interactions mediated by herbs. *Journal of Ecology*, **98**, 687–696.
- D'Antonio, C. (1993) Mechanisms controlling invasion of coastal plant communities by the alien succulent *Carpobrotus edulis*. *Ecology*, **74**, 83–95.
- D'Antonio, C. M. and Mahall, B. E. (1991) Root profiles and competition between the invasive, exotic perennial, *Carpobrotus edulis*, and two native shrub species in California coastal scrub. *American Journal of Botany*, **78**, 885–894.
- Davidson, D. W. (1980) Some consequences of diffuse competition in a desert ant community. *American Naturalist*, **116**, 92–105.
- de Kroon, H., Huber, H., Stuefer, J. F. and van Groenendael, J. M. (2005) A modular concept of phenotypic plasticity in plants. *New Phytologist*, **166**, 73–82.
- Donohue, K., Pyle, E. H., Messiqua, D., Heschel, M. S. and Schmitt, J. (2001) Adaptive divergence in plasticity in natural populations of *Impatiens capensis* and its consequences for performance in novel habitats. *Evolution*, **55**, 692–702.
- Duke, S., Blair, A., Dayan, F. et al. (2009) Is (-)-catechin a novel weapon of spotted knapweed (*Centaurea stoebe*)? *Journal of Chemical Ecology*, **35**, 141–153.
- Ehlers, B. K. and Thompson, J. (2004) Do co-occurring plant species adapt to one another? The response of *Bromus erectus* to the presence of different *Thymus vulgaris* chemotypes. *Oecologia*, **141**, 511–518.
- Engel, E. C. and Weltzin, J. F. (2008) Can community composition be predicted from pairwise species interactions? *Plant Ecology*, **195**, 77–85.
- Goldberg, D. E. (1990) Components of resource competition in plant communities. In J. Grace and D. Tilman, eds., *Perspectives on Plant Competition*. San Diego, CA: Academic Press, pp. 27–50.
- Goldsmith, F. B. (1978) Interaction (competition) studies as a step towards the synthesis of sea-cliff vegetation. *Journal of Ecology*, **66**, 921–931.
- Grigulis, K., Sheppard, A. W., Ash, J. E. and Groves, R. H. (2001) The comparative demography of the pasture weed *Echium plantagineum* between its native and invaded ranges. *Journal of Applied Ecology*, **38**, 281–290.
- Grime, J. P. (1977) Evidence for existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist*, **111**, 1169–1194.
- Grime, J. P. (2001) *Plant Strategies, Vegetation Processes, and Ecosystem Properties*. Chichester, UK: John Wiley and Sons.
- Grøndahl, E. and Ehlers, B. K. (2008) Local adaptation to biotic factors: reciprocal transplants of four species associated with aromatic *Thymus pulegioides* and *T. serpyllum*. *Journal of Ecology*, **96**, 981–992.
- He, W., Feng, Y., Ridenour, W. et al. (2009) Novel weapons and invasion: biogeographic differences in the competitive effects of *Centaurea maculosa* and its root exudate (\pm)-catechin. *Oecologia*, **159**, 803–815.
- Hejda, M., Pysek, P. and Jarosik, V. (2009) Impact of invasive plants on the species richness, diversity and composition of invaded communities. *Journal of Ecology*, **97**, 393–403.
- Hierro, J. L., Maron, J. L. and Callaway, R. M. (2005) A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. *Journal of Ecology*, **93**, 5–15.
- Ho, M., Rosas, J., Brown, K. and Lynch, J. (2005) Root architectural trade-offs for water and phosphorus acquisition. *Functional Plant Biology*, **32**, 737–748.
- Hulme, P. E. (2008) Phenotypic plasticity and plant invasions: is it all jack? *Functional Ecology*, **22**, 3–7.

- Inderjit, Evans, H., Crocoll, C. *et al.* (2011) Volatile chemicals from leaf litter are associated with invasiveness of a neotropical weed in Asia. *Ecology*, **92**, 316–324.
- Inderjit, Pollock, J. L., Callaway, R. M. and Holben, W. (2008a) Phytotoxic effects of (±)-catechin in vitro, in soil, and in the field. *PLoS ONE*, **3**, e2536.
- Inderjit, Seastedt, T. R., Callaway, R. M. and Kaur, J. (2008b) Allelopathy and plant invasions: traditional, congeneric, and biogeographical approaches. *Biological Invasions*, **10**, 875–890.
- Jackson, J. B. C. and Buss, L. (1975) Allelopathy and spatial competition among coral-reef invertebrates. *Proceedings of the National Academy of Sciences of the United States of America*, **72**, 5160–5163.
- Jakobs, G., Weber, E. and Edwards, P. (2004) Introduced plants of the invasive *Solidago gigantea* (Asteraceae) are larger and grow denser than conspecifics in the native range. *Diversity and Distributions*, **10**, 11–19.
- Jensen, C. G. and Ehlers, B. K. (2010) Genetic variation for sensitivity to a thyme monoterpene in associated plant species. *Oecologia*, **162**, 1017–1025.
- Karban, R., Shiojiri, K., Huntzinger, M. and McCall, A. (2006) Damage-induced resistance in sagebrush: volatiles are key to intra- and interplant communication. *Ecology*, **87**, 922–930.
- Karolson, R. H. and Jackson, J. B. C. (1981) Competitive networks and community structure: a simulation study. *Ecology*, **62**, 670–678.
- Keane, R. M. and Crawley, M. J. (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution*, **17**, 164–170.
- Keddy, P. A. and Shipley, B. (1989) Competitive hierarchies in herbaceous plant communities. *Oikos*, **54**, 234–241.
- Laird, R. A. and Schamp, B. S. (2006) Competitive intransitivity promotes species coexistence. *American Naturalist*, **168**, 182–193.
- Laird, R. A. and Schamp, B. S. (2008) Does local competition increase the coexistence of species in intransitive networks? *Ecology*, **89**, 237–247.
- Levine, J. M. (1999) Indirect facilitation: evidence and predictions from a riparian community. *Ecology*, **80**, 1762–1769.
- Levine, J. M., Vila, M., D'Antonio, C. M. *et al.* (2003) Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society of London, Series B*, **270**, 775–781.
- Li, L., Li, S.-M., Sun, J.-H. *et al.* (2007) Diversity enhances agricultural productivity via rhizosphere phosphorus facilitation on phosphorus-deficient soils. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 11192–11196.
- Li, X. D. and Wilson, S. D. (1998) Facilitation among woody plants establishing in an old field. *Ecology*, **79**, 2694–2705.
- Lu, Z. J. and Ma, K. P. (2005) Scale dependent relationships between native plant diversity and the invasion of croftonweed (*Eupatorium adenophorum*) in southwest China. *Weed Science*, **53**, 600–604.
- Mahall, B. E. and Callaway, R. M. (1992) Root communication mechanisms and intracommunity distributions of two Mojave desert shrubs. *Ecology*, **73**, 2145–2151.
- Mal, T. K. and Lovett-Doust, J. (2005) Phenotypic plasticity in vegetative and reproductive traits in an invasive weed, *Lythrum salicaria* (Lythraceae) in response to soil moisture. *American Journal of Botany*, **92**, 819–825.
- Maron, J. L. and Marler, M. (2008) Field-based competitive impacts between invaders and natives at varying resource supply. *Journal of Ecology*, **96**, 1187–1197.
- May, R. M. and Leonard, W. J. (1975) Nonlinear aspects of competition between three species. *Siam Journal on Applied Mathematics*, **29**, 243–253.
- Metlen, K. L. (2010) Using patchy plant invasions to understand how diffuse interactions modify facilitation and competition.

- PhD Thesis, The University of Montana, Missoula, MT, USA.
- Metlen, K. L., Aschehoug, E. T. and Callaway, R. M. (2009) Plant behavioural ecology: dynamic plasticity in secondary metabolites. *Plant Cell and Environment*, **32**, 641–653.
- Miller, T. E. (1994) Direct and indirect species interactions in an early old-field plant community. *American Naturalist*, **143**, 1007–1025.
- Miller, T. E. and Travis, J. (1996) The evolutionary role of indirect effects in communities. *Ecology*, **77**, 1329–1335.
- Miner, B. G., Sultan, S. E., Morgan, S. G., Padilla, D. K. and Relyea, R. A. (2005) Ecological consequences of phenotypic plasticity. *Trends in Ecology and Evolution*, **20**, 685–692.
- Mitchley, J. and Grubb, P. (1986) Control of relative abundance of perennials in chalk grassland in southern England: I. Constancy of rank order and results of pot- and field-experiments on the role of interference. *Journal of Ecology*, **74**, 1139–1166.
- Munshaw, M. and Lortie, C. (2010) Back to the basics: using density series to test regulation versus limitation for invasive plants. *Plant Ecology*, **211**, 1–5.
- Novoplansky, A. (2002) Developmental plasticity in plants: implications of non-cognitive behavior. *Evolutionary Ecology*, **16**, 177–188.
- Ortega, Y. K. and Pearson, D. E. (2005) Weak vs. strong invaders of natural plant communities: assessing invasibility and impact. *Ecological Applications*, **15**, 651–661.
- Pages, J. P. and Michalet, R. (2003) A test of the indirect facilitation model in a temperate hardwood forest of the northern French Alps. *Journal of Ecology*, **91**, 932–940.
- Parker, V. T. and Muller, C. H. (1982) Vegetational and environmental-changes beneath isolated live oak trees (*Quercus agrifolia*) in a California annual grassland. *American Midland Naturalist*, **107**, 69–81.
- Paynter, Q., Downey, P. O. and Sheppard, A. W. (2003) Age structure and growth of the woody legume weed *Cytisus scoparius* in native and exotic habitats: implications for control. *Journal of Applied Ecology*, **40**, 470–480.
- Perkins, T. A., Holmes, W. R. and Weltzin, J. F. (2007) Multi-species interactions in competitive hierarchies: new methods and empirical test. *Journal of Vegetation Science*, **18**, 685–692.
- Petraitis, P. S. (1979) Competitive networks and measures of intransitivity. *American Naturalist*, **114**, 921–925.
- Pfister, C. A. and Hay, M. E. (1988) Associational plant refuges: convergent patterns in marine and terrestrial communities result from differing mechanisms. *Oecologia*, **77**, 118–129.
- Pollock, J., Callaway, R., Thelen, G. and Holben, W. (2009) Catechin-metal interactions as a mechanism for conditional allelopathy by the invasive plant *Centaurea maculosa*. *Journal of Ecology*, **97**, 1234–1242.
- Reader, R. J., Wilson, S. D., Belcher, J. W. *et al.* (1994) Plant competition in relation to neighbor biomass: an intercontinental study with *Poa pratensis*. *Ecology*, **75**, 1753–1760.
- Rice, K. and Nagy, E. (2000) Oak canopy effects on the distribution patterns of two annual grasses: the role of competition and soil nutrients. *American Journal of Botany*, **87**, 1699.
- Richards, C. L., Bossdorf, O., Muth, N. Z., Gurevitch, J. and Pigliucci, M. (2006) Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecology Letters*, **9**, 981–993.
- Richards, C. L., Pennings, S. C. and Donovan, L. A. (2005) Habitat range and phenotypic variation in salt marsh plants. *Plant Ecology*, **176**, 263–273.
- Ridenour, W. M. and Callaway, R. M. (2001) The relative importance of allelopathy in interference: the effects of an invasive weed on a native bunchgrass. *Oecologia*, **126**, 444–450.
- Schenck, J., Mahall, B. and Callaway, R. (1999) Spatial segregation of roots. *Advances in Ecology*, **28**, 145–180.

- Schmidtke, A., Rottstock, T., Gaedke, U. and Fischer, M. (2010) Plant community diversity and composition affect individual plant performance. *Oecologia*, **164**, 1–13.
- Simoes, K., Du, J., Kretzschmar, F. S. *et al.* (2008) Phytotoxic catechin leached by seeds of the tropical weed *Sesbania virgata*. *Journal of Chemical Ecology*, **34**, 681–687.
- Sultan, S. E. (1987) Evolutionary implications of phenotypic plasticity in plants. *Evolutionary Biology*, **21**, 127–178.
- Sultan, S. E. (2000) Phenotypic plasticity for plant development, function and life history. *Trends in Plant Science*, **5**, 537–542.
- Sultan, S. E., Wilczek, A. M., Bell, D. L. and Hand, G. (1998a) Physiological response to complex environments in annual *Polygonum* species of contrasting ecological breadth. *Oecologia*, **115**, 564–578.
- Sultan, S. E., Wilczek, A. M., Hann, S. D. and Brosi, B. J. (1998b) Contrasting ecological breadth of co-occurring annual *Polygonum* species. *Journal of Ecology*, **86**, 363–383.
- Tewksbury, J. and Lloyd, J. (2001) Positive interactions under nurse-plants: spatial scale, stress gradients and benefactor size. *Oecologia*, **127**, 425–434.
- Tharayil, N. and Triebwasser, D. (2010) Elucidation of a diurnal pattern of catechin exudation by *Centaurea stoebe*. *Journal of Chemical Ecology*, **36**, 200–204.
- Tharayil, N., Bhowmik, P., Alpert, P. *et al.* (2009) Dual purpose secondary compounds: phytotoxin of *Centaurea diffusa* also facilitates nutrient uptake. *New Phytologist*, **181**, 424–434.
- Tharayil, N., Bhowmik, P. and Xing, B. (2008) Bioavailability of allelochemicals as affected by companion compounds in soil matrices. *Journal of Agricultural and Food Chemistry*, **56**, 3706–3713.
- Thorpe, A., Archer, V. and DeLuca, T. (2006) The invasive forb, *Centaurea maculosa*, increases phosphorus availability in Montana grasslands. *Applied Soil Ecology*, **32**, 118–122.
- Thorpe, A. S., Thelen, G. C., Diaconu, A. and Callaway, R. M. (2009) Root exudate is allelopathic in invaded community but not in native community: field evidence for the novel weapons hypothesis. *Journal of Ecology*, **97**, 641–645.
- Tilman, D. (1982) *Resource Competition and Community Structure*. Princeton, NJ: Princeton University Press.
- Tilman, D. (1985) The resource-ratio hypothesis of plant succession. *American Naturalist*, **125**, 827–852.
- Turlings, T. C. J., Tumlinson, J. H. and Lewis, W. J. (1990) Exploitation of herbivore-induced plant odors by host-seeking parasitic wasps. *Science*, **250**, 1251–1253.
- Valladares, F., Gianoli, E. and Gómez, J. M. (2007) Ecological limits to plant phenotypic plasticity. *New Phytologist*, **176**, 749–763.
- Valladares, F., Sanchez, D. and Zavala, M. (2006) Quantitative estimation of phenotypic plasticity: bridging the gap between the evolutionary concept and its ecological applications. *Ecology*, **94**, 1103–1116.
- Van Valen, L. (1965) Morphological variation and width of ecological niche. *American Naturalist*, **99**, 377–390.
- Vandermeer, J. (1980) Indirect mutualism: variations on a theme by Stephen Levine. *American Naturalist*, **116**, 441–448.
- Vila, M. and Weiner, J. (2004) Are invasive plant species better competitors than native plant species? Evidence from pair-wise experiments. *Oikos*, **105**, 229–238.
- Wang, P., Stieglitz, T., Zhou, D. W. and Cahill Jr, J. F. (2010) Are competitive effect and response two sides of the same coin, or fundamentally different? *Functional Ecology*, **24**, 196–207.
- Weber, E. and D'Antonio, C. (1999) Phenotypic plasticity in hybridizing *Carpobrotus* spp. (Aizoaceae) from coastal California and its role in plant invasion. *Botany*, **77**, 1411–1418.
- Weir, T. L., Bais, H. P., Stull, V. J. *et al.* (2006) Oxalate contributes to the resistance of *Gaillardia grandiflora* and *Lupinus sericeus* to a phytotoxin produced by *Centaurea maculosa*. *Planta*, **223**, 785–795.

- Whitlock, M. C. (1996) The red queen beats the jack-of-all-trades: the limitations on the evolution of phenotypic plasticity and niche breadth. *American Naturalist*, **148**, S65–S77.
- Williamson, G. (1990) Allelopathy, Koch's postulates, and the neck riddle. In J. B. Grace and D. Tilman, eds., *Perspectives in Plant Competition*. San Diego, CA: Academic Press, pp. 143–162.
- Wilson, S. D. and Keddy, P. A. (1986) Measuring diffuse competition along an environmental gradient: results from a shoreline plant community. *American Naturalist*, **127**, 862–869.
- Woodburn, T. and Sheppard, A. (1996) The demography of *Carduus nutans* as a native and an alien weed. *Plant Protection Quarterly*, **11**, 236–238.