

PHENOTYPIC PLASTICITY AND INTERACTIONS AMONG PLANTS

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Abstract. We know a great deal about the plastic responses of plant phenotypes to the abiotic and biotic environment, but very little about the consequences of phenotypic plasticity for plant communities. In other words, we know that plant traits can vary widely for a given genotype, but we know little about the importance of trait-mediated interactions (TMI) among plants. Here, we discuss three major factors that affect the expression of phenotypic plasticity: variation in the abiotic environment, variation in the presence or identity of neighbors, and variation in herbivory. We consider how plastic responses to these factors might affect interactions among plants. Plastic responses to the abiotic environment have important consequences for conditionality in competitive effects, to the point of causing shifts from competitive to facilitative interactions. Because plants show a high degree of plasticity in response to neighbors, and even to the specific identity of neighbors, phenotypic plasticity may allow species to adjust to the composition of their communities, promoting coexistence and community diversity. Likewise, plastic responses to consumers may have various and counterintuitive consequences: induction of plant resistance, compensatory growth, and increased resource uptake may affect interactions among plants in ways that cannot be predicted simply by considering biomass lost to consumers. What little we know about TMI among plants suggests that they should not be ignored in plant community theory. Although work to date on the community consequences of phenotypic plasticity has been hampered by experimental constraints, new approaches such as manipulating phenotypes by using signals instead of actual environmental conditions and the use of transgenic plants should allow us to rapidly expand our understanding of the community consequences of plant plasticity.

Key words: *allelopathy; chemical defense; clonal morphology; competition; facilitation; herbivory; induced resistance; phenotypic plasticity; plant interactions; roots.*

INTRODUCTION

Phenotypic plasticity is the property of a given genotype to produce different physiological or morphological phenotypes in response to different environmental conditions (Bradshaw 1965, 1973, Schlichting 1986, Sultan 1987, Schlichting and Pigliucci 1998, Pigliucci 2001). A given plant genotype can experience different environmental conditions as a result of variation in the abiotic environment, variation in the presence or identity of neighbors, or variation in consumer pressure. Variation in trait expression induced by these or other environmental factors might then affect interactions among plants. Although the evolutionary aspects of phenotypic plasticity in plants have been extensively examined, the ecological ramifications are less well understood.

As a rule, plants are highly plastic (Sultan 1987, 2000). Individuals within a species may vary by orders of magnitude in size, growth rates, allocation to different organs, reproduction, and chemical constituency.

Manuscript received 25 September 2001; revised 16 April 2002; accepted 19 April 2002; final version received 6 June 2002. Corresponding Editor: F. R. Adler. For reprints of this Special Feature, see footnote 1, p. 1081.

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Plants display plastic responses to a wide variety of ecological conditions including variation in the abiotic environment, disturbance, herbivory, parasitism, mutualistic relationships, and the presence, absence, or identity of neighbors. Plastic responses may be permanent once induced, relatively fixed for a given growing season, or may be dynamic on a scale of hours, as in the case of light effects on photosynthetic chemistry or herbivore effects on defense chemistry (Baldwin 1999, Pearcy 1999). Although the cues that trigger phenotypic differences are environmental, the ability to respond to cues is genetically based and can evolve under natural selection (Bradshaw 1973, Via 1994). Genetic variation in phenotypic plasticity (known as a significant $G \times E$ interaction) is an indicator of the potential for response to selection and the maintenance of plasticity in a population (Via and Lande 1985, Van Tienderen 1991). Plasticity is favorable if the environment is variable, if environmental cues are reliable such that individuals can express the appropriate phenotype in each environment, and if there are costs to inappropriate, specialized phenotypes. Specialization is favored over plasticity when these conditions are not met, and is also favored by a variety of inherent costs to plasticity (Van Tienderen 1991, Dorn et al. 2000, Re-

lyea 2002; but see Sultan 1995). Because individual genotypes have the potential for adaptive divergence, plasticity in plants probably broadens ecological ranges and reduces the impact of selection (Mazer and Schick 1991, Sultan 1995).

Although phenotypic plasticity may not always be adaptive, the adaptive benefits of plastic traits as “buffers against spatial or temporal variability in habitat conditions” and “means of optimizing the acquisition and use of resources” (Grime et al. 1986, Robinson and Rorison 1988) have been widely documented and reviewed (Bradshaw 1965, Schlichting 1986, Sultan 1987, 1995, Stearns 1989, Debat and David 2001). In contrast to our understanding of the evolutionary ecology of phenotypic plasticity, which is well established and rapidly advancing, we know little about the consequences of plasticity for ecological interactions in plant communities. For example, phenotypic plasticity may alter the sign and magnitude of interactions among plants, but the role of such trait-mediated interactions (TMI) has been largely overlooked in plant community ecology. Thus, an explicit research focus on TMI could revolutionize some aspects of plant ecology.

Interactions among plants vary along a continuum from strongly competitive to strongly facilitative. The nature of the interaction between two species of plants is not always fixed, but may be conditional depending on environmental conditions. In other words, a species may be competitively superior to a particular neighbor under one set of conditions, but not under another. Similarly, a species may have positive effects on neighbors (facilitation) in some conditions and negative effects (competition) in other conditions (Bertness and Callaway 1994, Callaway 1995). A wide range of environmental circumstances including the particular suites and amounts of available resources, various environmental stresses, the composition of surrounding communities, herbivory, and physical disturbance may shift the balance of competition among species (Wilson and Keddy 1986, Louda et al. 1990, Miller 1994, Levine et al. 1998, Callaway and Pennings 2000). All of these conditions also have important effects on phenotypic plasticity (Sultan and Bazzaz 1993a, b, c, Emery et al. 1994, Donohue et al. 2000a, b, 2001, Weinig 2000a, b, c, Weinig and Delph 2000). Although many studies have considered the direct consequences of variation in environmental factors on competition, relatively few have considered the impact of effects mediated through phenotypic plasticity. In general, high phenotypic plasticity has been thought to confer superior invasive and competitive abilities (Bloom et al. 1985, Poorter and Lambers 1986, Aerts et al. 1991, Grime et al. 1991, Aerts 1999, Sultan 2000, 2001), but few studies have explicitly tested this hypothesis.

Here we explore three major factors that affect the expression of phenotypic plasticity: variation in the abiotic environment, variation in the presence or identity of neighbors, and variation in herbivory. Under-

standing the relationship between phenotypic plasticity and plant interactions has been limited by experimental constraints. First, it is difficult to separate the effects of plasticity from the confounding effects of the treatments used to create plasticity. Second, it is difficult to assess the performance of all phenotypes in all environments because plasticity prevents the expression of inappropriate phenotypes in each environment (Schmitt 1993, Schmitt et al. 1999). Because of these experimental constraints, we know far more about the plastic *responses* of plants to the environment than we do about the *consequences* of plasticity for interspecific interactions. Although we have strong reason to suspect that TMI are important in plant communities, in only a few cases has this been explicitly demonstrated.

Phenotypic plasticity in response to the abiotic environment

Many studies have shown that plant species may produce a broad range of phenotypes in response to variation in the abiotic environment (Silvertown and Gordon 1989, Sultan 1993a, b, c, Pigliucci 2001). In one of the few experiments explicitly designed to examine the effects of plastic responses to abiotic factors on competition, Poorter and Lambers (1986) measured the outcome of competition, in environments that differed in resource fluctuations, between two inbred lines of *Plantago major*. One line was highly plastic in morphology and physiology and the other was restricted in plasticity. They found that, with increasing frequency of fluctuations in nutrient level, the highly plastic line outcompeted the less plastic line. This study supports the hypothesis that plastic individuals are superior competitors in temporally variable environments. Although Poorter and Lambers (1986) did not attribute differences in competitive ability to specific traits, other studies have examined the relationship between plasticity of specific traits and plant interactions. In particular, root systems are highly plastic and are fundamentally related to plant interactions. In this section, we focus on how variation in abiotic conditions may affect root systems and, thus, interactions among plants.

The proportional allocation of biomass to roots vs. shoots is fundamental to interactions among plants (Fitter 1994, Robinson 1994, Reynolds and D'Antonio 1996, Colasanti and Hunt 1997, Aerts and Chapin 1999). Among species, plants allocate proportionally more biomass to roots in nutrient-poor and water-poor environments and more biomass to shoots in light-limited environments (Chapin 1980, Ericsson 1995, Aerts 1999). This response is thought to maximize growth rate (Ågren and Ingestad 1987) and competitive ability (Crick and Grime 1987, Tilman 1988, Grime et al. 1997). In fertile, productive environments, the ability to allocate soil resources to leaf production is characteristic of highly competitive species (Grime 1979, Ryser and Notz 1996). In general, species that invest

more in roots are thought to competitively dominate habitats with low productivity, and those that invest more in shoots are thought to competitively dominate habitats with high productivity (Tilman 1988).

Despite the importance of root : shoot ratios to a plant's performance, plasticity in root : shoot ratios may provide a relatively poor predictor of competitive ability. Reynolds and D'Antonio (1996) found no consistent relationship between experimentally induced differences in root mass ratio (root mass divided by total plant mass) and competitive ability. Of eight relevant studies, three found that the least plastic species was the most competitive (Zangerl and Bazzaz 1983, Aerts et al. 1991, Dakheel et al. 1993), one found that the most plastic species was the best competitor (McGraw and Chapin 1989), and four found no relationship between plasticity in root mass ratio and competitive ability (Gurevitch et al. 1990, Wilson 1991, Cheplick 1995, Figiel et al. 1995). It may be that differences in the mass of roots and shoots are less important than finer details in root and shoot morphology and physiology (Aerts et al. 1991).

Root systems can show considerable plasticity in absorptive capacity, total surface area, mass to surface area ratios, rooting density, the timing of growth and placement, and architecture (Biswell 1935, Muller 1946, Drew and Saker 1975, Jackson and Caldwell 1989, Callaway 1990, Kolb et al. 1990, Pregitzer et al. 1993, Fitter 1994, Jackson et al. 1990). Caldwell and Richards (1986) surmised that high rooting density and root thickness would be advantageous for competitive potential, but little is known about the effect of such plasticity on plant interactions. Using data-based models, Jackson and Caldwell (1996) estimated that plasticity in root proliferation and nutrient uptake rates in resource-rich patches increased nitrogen and phosphorus acquisition from 28% to 70%. Confirming the hypothesis that plastic responses to resource availability should provide a competitive advantage, empirical studies in the system used to develop Jackson and Caldwell's model indicated that belowground plasticity in root morphology and root : shoot ratios of *Pseudoroegneria spicata* improved its ability to withstand competition from the more vigorous, but less plastic *Agropyron desertorum* (Huber-Sannwald et al. 1996).

Typically, *genotypic* variation in root architecture is thought to reduce niche overlap and, therefore, competition among species (Parrish and Bazzaz 1976, Cody 1986). However, plastic responses to abiotic conditions could also increase competitive interactions if the result is a high overlap of rooting zones (Silvertown and Gordon 1989). In a review of root form and depth distribution, Richards (1986) observed that the development of deep taproots vs. wide-spreading lateral roots of phreatophytic plants (species that typically utilize deep ground water) was dependent on environmental conditions such as the depth to the water table. Such root architectural plasticity could either increase or decrease

competition depending on whether or not the target plant adopted a morphology that caused rooting zones to overlap with neighbors.

Studies of *Quercus douglasii* (blue oak) provide a good example of how root plasticity can mediate competition with neighbors (Fig. 1). *Quercus douglasii* dominates a wide range of habitats in California, USA, including the mesic fringes of grasslands in the Central Valley, transitional vegetation near the Great Basin, the Sierra Nevada foothills, and throughout the coastal Santa Lucia Mountains. Based on predawn water stress and stable isotope analyses, individuals of *Q. douglasii* vary at the scale of meters with regard to utilization of the water table (Lewis and Burghy 1964, Griffin 1973, Callaway et al. 1991). Callaway et al. (1991) measured predawn water potentials and fine roots in the upper 50 cm of soil of 24 *Q. douglasii* individuals and found evidence for two basic architectural patterns. Some trees had high water potentials (-1.5 to -3.0 MPa at the end of the dry season) and a low biomass of fine roots in the shallow soil beneath their canopies, whereas other trees had low water potentials (-3.5 to -4.5 MPa) and approximately five times greater fine root biomass near the surface (Fig. 1). These data suggest that some trees do not access the water table (very low water potentials) and develop a dense root system near the surface, whereas other trees access the water table and do not invest as much in root biomass near the surface. These architectural differences were not definitively produced by phenotypic plasticity (i.e., Callaway did not manipulate root morphologies in genetically identical oak trees); however, neither examination of leaf and acorn characteristics nor isozyme analysis suggested genetic differences between the two groups of trees (Callaway 1990). Furthermore, controlled experiments with seedlings demonstrated a high degree of plasticity in lateral root development (Callaway 1990). When the taproots of *Q. douglasii* seedlings were grown into dry substrate 30 cm below moist topsoil, lateral root biomass in topsoil increased by 80% and lateral root number by $>50\%$ over the five-month experimental period compared to seedlings with access to damp, deeper soils, which invested most of their root biomass into deep taproots. Thus, it is likely that the differences in root architecture among adult trees reflect a similar plastic response that is cued by the accessibility of the water table to the root system, and are not due to genetic differences among trees.

Variation in root architecture has substantial consequences for the plant communities associated with *Q. douglasii*. In the field, the biomass of the herbaceous understory beneath trees with shallow root systems was $\sim 50\%$ lower than the biomass in surrounding open grassland, indicating a strong competitive effect of shallow tree roots. In contrast, the biomass of plants under trees that had accessed the water table was approximately two times greater than the biomass in open grassland (four times greater than under shallow-rooted

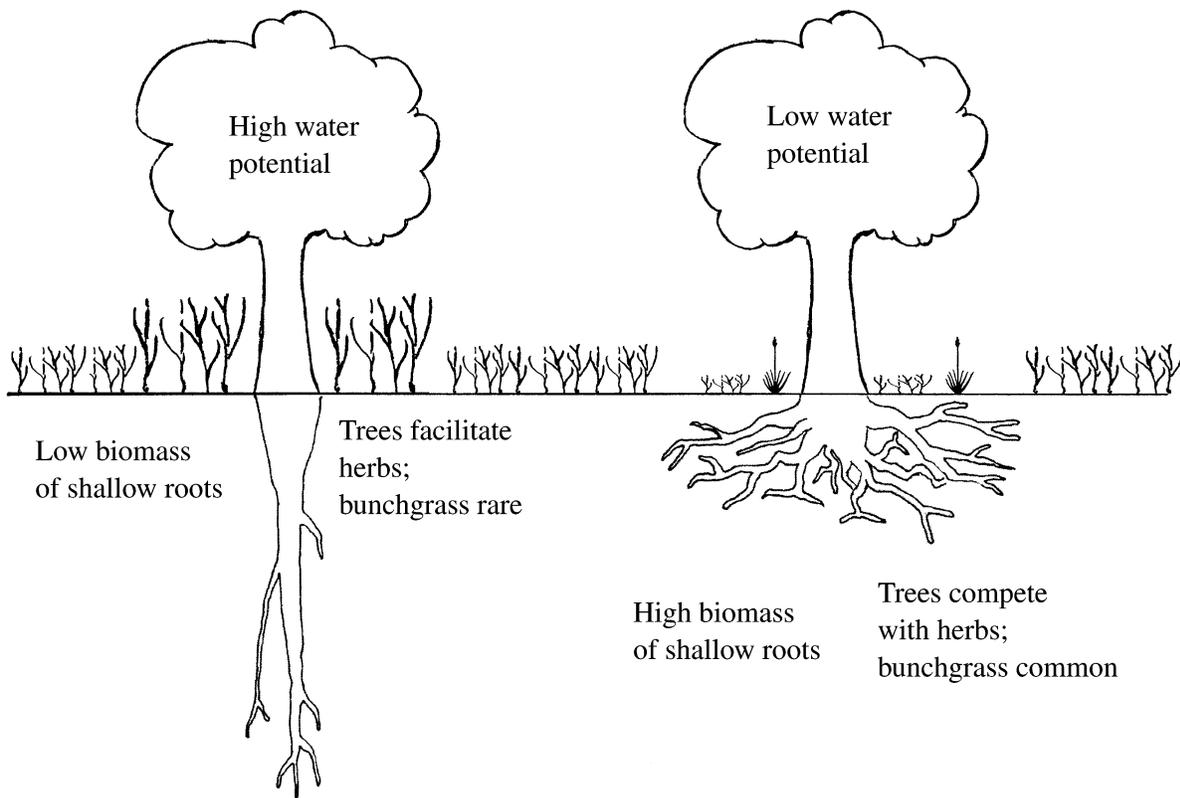


FIG. 1. Interactions between oaks and understory herbs vary depending on plastic responses of oaks to water. Oaks that are able to access the water table have high water potentials, few shallow roots, and facilitate understory herbs by adding litter and nutrients leached from foliage by rain. Oaks that cannot access the water table have low water potentials, many shallow roots, and compete with understory herbs. The native bunchgrass *Stipa pulchra* is much more common under shallow-rooted oaks than under deep-rooted oaks.

trees), indicating a facilitative effect. This facilitative effect was due to nutrients added through litter fall and precipitation filtering through the tree canopies. Experiments confirmed that only shallow-rooted trees competed with understory grasses. When tree roots were experimentally excluded under shallow-rooted trees, the biomass of grasses almost doubled, but root exclusions under deep-rooted trees had no effect on grasses. In addition to affecting productivity, the plasticity of *Q. douglasii* root systems also affected the species composition of the understory community (Callaway et al. 1991). In savannas, the native bunchgrass *Stipa pulchra* constituted <0.5% of the biomass beneath deep-rooted trees. In contrast, the biomass of *S. pulchra* under shallow-rooted trees was 3.9% of the total herbaceous understory.

Theory predicts that plasticity in behavior, defined broadly to include plastic morphologies of plants (Silvertown and Gordon 1989) can transmit heterogeneity from the environment to the population or community (Chesson and Rosenzweig 1991). These studies on *Q. douglasii* provide one of the few documented examples of this phenomenon for plants; however, similar effects are likely to occur whenever variation in access to re-

sources strongly modifies the architecture of root systems.

Root systems also affect some types of facilitative interactions by redistributing water laterally and vertically throughout the soil profile. In 1929, Magistad and Breazeale hypothesized that deep-rooted plants that maintained some living roots near the surface might extract water far below the surface, but lose a portion of this water into dry soils at the surface. Since then, the passive redistribution of soil water along gradients of water potential through root systems (hydraulic lift) has been shown for many species, including *Q. douglasii* (Ishikawa and Bledsoe 2000), in a wide variety of conditions (Caldwell et al. 1998). Hydraulic lift may benefit individual plants by allowing them to cache water in shallow soils during the night and increase their total daily transpiration rates the following day (Caldwell and Richards 1989). Facilitation of neighboring individuals may occur when cached water at the surface becomes available to other plants (Caldwell 1990, Dawson 1993). A form of hydraulic lift, or "water transfer" has also been described at a far smaller scale (centimeters) in the soil (Corak et al. 1987), raising the possibility of much broader impacts of root

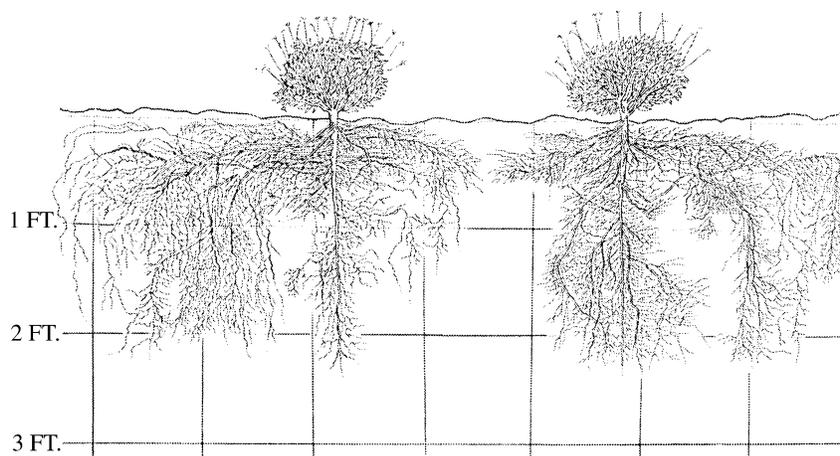


FIG. 2. Root architecture of excavated *Paarthenium argentatum* (guayule) plants (Muller 1946). At the time of excavation, the plants were 17 months old and lacked other nearby neighbors. Note the reduced spread of root toward the conspecific neighbor. (Units: 1 foot [ft] \approx 30.5 cm.)

plasticity on water movement in soils. Although we are not aware of any studies that have clearly linked plasticity in root system architecture to differing effects on neighbors via hydraulic lift, this would be a fruitful area for future research.

Although we have focused primarily on plasticity of roots, abiotic factors also induce plastic responses by shoots and leaves (e.g., Cipollini 1997, 1999). We are unaware of studies that have addressed how these responses affect interactions among plants, but effects are likely and further research in this area is warranted.

Phenotypic plasticity in response to neighboring plants

Neighboring plants cause dramatic phenotypic responses in many plant species. For example, Rice et al. (1993) grew *Quercus douglasii* seedlings in three different plant communities. Morphological traits differed and water use efficiencies were higher for seedlings grown with annuals than for those grown with perennials. Soil water depletion was more rapid in annual plant communities, suggesting that plasticity in water use efficiency may have been adaptive, enhancing the competitive ability of oak seedlings. Clonal plants provide many examples of plastic responses to neighbors (Hutchings and Slade 1988, Hutchings and DeKroon 1994). Turkington (1991; also see Turkington 1983) found that the morphology of *Trifolium repens* responded plastically to the presence of different grass species. Moreover, the plastic response of *T. repens* clones to different grass species in the greenhouse depended on which species the clone had previously been associated with in the field. Furthermore, *T. repens* responded differently to the presence of root systems of three different grass species (Turkington 1990). Because grass shoots were removed in this study, the plastic responses of *T. repens* were not likely to have been caused through effects on aboveground resources.

The presence and identity of neighboring plants can also induce plastic responses in root allocation and architecture. Root plasticity in response to neighbors is striking in natural communities (Fig. 2; see Muller 1946, Nye and Tinker 1977, D'Antonio and Mahall 1991, Brisson and Reynolds 1994, Mou et al. 1995) and agricultural settings (Schenk et al. 1999). Experimental analyses indicate that neighbors may affect the phenotypic expression of root systems in two fundamentally different ways: either through direct effects on soil resources, or independently of soil resources. In the first case, the roots of neighbors alter below-ground resource availability and therefore affect neighbors in much the same way as variation in abiotic resources (Crick and Grime 1987, Robinson and Rorison 1988). Clearly, many plant species can concentrate their roots in small patches of high resources and reduce proliferation in resource-poor patches (Wiersum 1958, Drew and Saker 1975, Jackson and Caldwell 1989, Caldwell et al. 1991). Because different species differ in resource uptake abilities, neighbor identity can have large effects on responses to resource patches. For example, Jackson and Caldwell (1996) found that the proliferation of roots of *Artemisia tridentata* in resource-rich patches was much greater when the patch was shared with *Pseudoroegneria spicata* than when shared with *Agropyron desertorum*. Similarly, in the field, D'Antonio and Mahall (1991) found that two chaparral shrub species had markedly lower root lengths and occupied less soil volume when they were interacting with a superior competitor for water, *Carpobrotus edulis*.

The assumption that root plasticity caused by neighboring plants operates through this first mechanism has important consequences for the theoretical relationship between plasticity and competitive ability and for theory on processes that organize plant communities. If root plasticity caused by neighboring plants is primar-

ily determined by resource limitations, then superior competitors ought to be more plastic than poor competitors because plasticity allows for the rapid projection of resource-capturing roots into nutrient-rich soil patches (Fitter and Hay 1981, Crick and Grime 1987). Taking this perspective a step farther, plasticity—and therefore competitive ability—should be more important in more productive communities where high rates of resource exploitation create localized zones of depletion (Crick and Grime 1987).

As previously described, there is a substantial body of literature that supports the role of resources in neighbor interactions and root phenotypic plasticity (see also Bookman and Mack 1982, Fitter 1986, Gordon et al. 1989, Nobel 1997). However, there is also evidence that many plant species affect the root morphology of their neighbors independently of effects on soil resources (Lund 1947, Dicke and Sabelis 1988, Miller and Gow 1989, Mahall and Callaway 1992, 1996, Stenz and Weisenseel 1993, Krannitz and Caldwell 1995, Schenk et al. 1999). In 1907, Schreiner and Reed found that roots of *Lolium perenne* would grow away from the roots of other conspecific individuals. However, when they added “carbon black” to the substrate, roots intermingled. More recently, activated carbon, which adsorbs charged organic molecules and is probably similar to the carbon black of Schreiner and Reed, has been shown to ameliorate the negative effects of *Larrea tridentata* roots on the root elongation of conspecifics and of *Ambrosia dumosa* roots (Mahall and Callaway 1991, 1992; see also Brisson and Reynolds 1994). Similar ameliorating effects of activated carbon have been documented for *Centaurea maculosa* root systems on the root elongation of *Festuca idahoensis* (Ridenour and Callaway 2001). These results suggest that chemicals exuded from the roots of one species can alter root growth, distribution; and architecture of other species (Schenk et al. 1999). Presumably, by reducing overlap of root systems, these root avoidance mechanisms reduce competition.

A recent experiment by Gersani et al. (2001) provides a contrasting example of the potential consequences of neighbor-induced plasticity of root growth. Gersani and colleagues compared the growth and reproduction of *Glycine max* (soybean) plants with sole possession of the rooting zone to those of plants sharing the rooting zone with a conspecific. They found that sharing individuals produced 85% more root mass than non-sharing plants. Virtually all other work on root plasticity has demonstrated inhibitory effects resulting in avoidance and spatial segregation of root systems. In contrast, *G. max* plants appeared to proliferate roots aggressively to contest resources when they were forced to share the rooting zone with another plant. The increase in root growth in response to neighbors contradicts theoretical models of nutrient foraging that emphasize reduced root growth in response to low nu-

trient levels, which would be expected where roots are dense.

Although there are many examples of plastic growth responses of plants in response to neighbors, the consequences of this plasticity have been addressed in only a few cases. Perhaps the best examples are those of plasticity in stem elongation, clonal architecture, and photosynthetic chemistry. High densities of neighbors often have dramatic effects on the aboveground plasticity of biomass allocation, leaf morphology, and stem elongation. Phytochrome-mediated stem elongation in response to the red : far red ratio is a well-documented example of density-dependent plasticity (Dudley and Schmitt 1995, 1996). Chlorophyll absorbs light in the red region of the spectrum and therefore low red : far red indicates the presence of neighbors and triggers stem elongation in many species of plants. As part of the “shade avoidance response,” stem elongation enhances fitness by increasing light interception under competitive conditions. Because stem elongation occurs in response to the red : far red ratio rather than to the amount of photosynthetically available radiation, it is possible to induce stem elongation without altering light availability, thereby decoupling the cue from the resource (Schmitt et al. 1999). Dudley and Schmitt (1995, 1996) tested the adaptive value of plasticity in stem elongation by using this technique and transplanting manipulated phenotypes of the same genotype of *Impatiens capensis* into different competitive environments. They found that elongated phenotypes were more fit at a high density of conspecific neighbors than non-elongated phenotypes, but that non-elongated phenotypes were more fit at low neighbor densities. Moreover, Schmitt et al. (1995) found that transgenic tobacco plants in which elongation responses to shade had been disabled had decreased fitness when grown in competition with wild-type plants with intact elongation responses. They also found that constitutively elongated *Brassica ein* plants had lower fitness, relative to a non-elongated wild type, at low densities than in competition with the elongated wild type at high density. Their findings that phytochrome-mediated elongation is advantageous when competing in dense stands indicates that phenotypic plasticity can increase a species' tolerance to competition. Harley and Bertness (1996) induced elongated and non-elongated morphologies of four species of marsh plants by growing plants in different density treatments. Plants grown at high density developed slender, elongated stems that approached or exceeded their theoretical maximum heights based on mechanical considerations. Elongated plants depended on neighbors for physical support and often suffered stem failure if neighbors were removed, indicating that elongated plants interacted positively with neighbors in a way that non-elongated plants did not. These studies indicate that phenotypic plasticity in stem elongation can change the nature of interactions

among individual plants and improve performance in a competitive context.

Similarly, studies on *Abutilon theophrasti* showed differential patterns of plasticity in response to neighbors. In soybean fields, competition is initially low for *Abutilon* and intensifies later in the season. Populations of *Abutilon* from soybean fields demonstrated selection for increased elongation at later nodes when they could overtop surrounding soybeans. In contrast, late elongation was selected against in cornfield *Abutilon* populations because no individuals were able to overtop the corn (Weinig 2000a). The onset of competition varied with the species of competitor, and the fitness benefits of elongation therefore also depended on the timing of the plastic response. These population differences suggest that there is adaptive response to different competitive environments and that different life history stages can have different levels of phenotypic plasticity (Weinig 2000a, b, Weinig and Delph 2000).

Finally, an excellent example of the adaptive value of plasticity in clonal architecture comes from studies of the clonal plant *Ranunculus reptans* (Van Kleunen and Fischer 2001). Genotypes of *Ranunculus* varied in their plastic responses (changes in stolon length and growth angle) to the presence of a competitor: those from habitats containing competitors were more plastic than those from habitats where *Ranunculus* grew alone. When grown in experimental habitats with and without competitors (*Agrostis stolonifera*), the more plastic genotypes had a higher fitness, averaged over both habitats, than the less plastic genotypes. Whether the more plastic genotypes also had greater competitive effects on *Agrostis* was not tested.

These studies generally indicate that plastic responses to competitors reduce competition, in concordance with theoretical predictions that increasingly flexible "behavior," defined broadly to include morphological plasticity (Silvertown and Gordon 1989) increases the probability of coexistence of species (Chesson and Rosenzweig 1991). Similarly, forest models that allow plastic development of individual canopies in response to neighbors predict that plasticity promotes overall stand productivity by reducing competition (Sorrensen-Cothern et al. 1993).

The photosynthetic chemistry of plants can be as plastic as leaf and stem morphology (Pearcy 1999); however, little is known about how plasticity in photosynthesis correlates with competitive ability. In general, fast-growing species adapted to high light conditions (which are often superior competitors) are more plastic in their maximum photosynthetic capacity than slow-growing, shade-tolerant species (Strauss-Debenedetti and Bazzaz 1996). Species with plastic photosynthetic responses should be able to persist in a wide variety of environments. This plasticity in photosynthetic chemistry and leaf morphology appears to allow the seedlings of some species to benefit from "nurse plants" in harsh environments. For example, in some

Californian woodlands *Quercus agrifolia* seedlings are more common under shrubs than in the open grassland, and experiments indicate that seedling survival is higher under shrubs than in the open (Callaway and D'Antonio 1991). The effects of the shade from shrubs appear to be somewhat conditional, as shrubs and *Q. agrifolia* seedlings are highly associated in south-facing savanna communities, but much less so in north-facing woodland communities (Callaway and Davis 1999).

Plasticity in response to herbivory

Herbivory triggers plastic responses in morphology, reproduction, and tissue chemistry in many plant species. Herbivory almost always places a plant at a competitive disadvantage (Strong et al. 1984, Louda et al. 1990, Crawley 1992) because of the carbon and resource costs of losing biomass. In contrast to the effects of biomass loss, little is known about how herbivore-induced plasticity affects plant interactions. What is known about the responses stimulated by herbivory (the induction of plant resistance, compensatory growth, and increased resource uptake) suggests that plasticity affects interactions among plants in ways that cannot always be predicted on the basis of simple biomass losses alone.

Some of the best documented plastic responses of plants are the induction of morphological and chemical traits that confer resistance to herbivores and pathogens (Harvell 1990, Myers and Bazely 1991, Baldwin 1999). The negative effects of induced resistance on herbivores and pathogens have been well documented and reviewed (Karban and Myers 1989, Karban and Baldwin 1997, Agrawal et al. 1999, Baldwin 1999), and we will not discuss effects on consumers further except to point out that the dynamic consequences of induced resistance on communities of multiple consumers will depend, in part, on whether induced resistance is specific to particular consumers or general (Karban and Baldwin 1997, Bolker et al. 2003).

Here, we will focus on the effects of induced resistance on interactions among plants, i.e., trait-mediated indirect interactions (TMII; Werner and Peacor 2003) between herbivores and nonconsumed plants in the community. To explain why resistance is plastic (inducible) and not constitutive (always present at high levels), most theories postulate that growth or reproductive costs exist, but that they can be minimized by deploying resistance mechanisms only when they are needed (Karban and Myers 1989, Harvell 1990, Zangerl and Bazzaz 1992; but see Adler and Karban 1994). Attempts to document the fitness costs of resistance in plants have had mixed success (Simms and Rausher 1987, Baldwin et al. 1990, Simms 1992, Karban 1993, Adler and Karban 1994, Sagers and Coley 1995, Mauricio 1997, Mauricio and Rausher 1997, Zangerl et al. 1997, Agrawal 1998, Baldwin 1998, Siemens and Mitchell-Olds 1998, Heil et al. 2000, Redman et al.

2001, Koricheva 2002). However, costs of resistance are clear in at least some cases, and in theory should reduce the ability of a plant to compete with its neighbors (Herms and Mattson 1992). Karban (1993) examined the costs of induced resistance in a desert shrub in combination with factorial manipulations of neighbors, but costs of induced resistance were not detectable in this system and so did not interact with neighbor treatments. In contrast, recent studies with wild tobacco found that induced plants had less of a competitive effect on neighbors than did uninduced plants, and that induced plants had larger costs of induced resistance in the presence than in the absence of competitors (Van Dam and Baldwin 1998, Baldwin and Hamilton 2000). This suggests that induced resistance can reduce both the effect and response components (Goldberg 1990) of competitive ability. Agrawal (2000) also found that costs of induced resistance in an annual herb were higher, and competitive effects on neighbors were reduced, when induced plants were grown at high vs. low densities. In contrast, Cipollini (2002) found no effect of competition on costs of induced defenses in *Arabidopsis*, probably because plants experiencing competition did not increase their defenses to the same degree as did control plants.

Siemens et al. (2002) studied the costs of secondary metabolite production by *Brassica rapa* in the presence and absence of the generalist competitor *Lolium perenne*. They used artificial selection and herbivore-induction treatments to produce genetic and environmental variation in concentrations of the defense chemicals myrosinase and glucosinolate in different genetic lines of *B. rapa*. In contrast to theoretical predictions, the costs of defense that occurred in the absence of competitors did not occur in the presence of competitors. The breakdown products of the glucosinolate-myrosinase reaction appeared to also function as allelopathic agents (see also Bell and Muller 1973), which may have benefited *B. rapa* plants in competition, but not when alone, and may have reduced the costs of chemical production. In general, activated carbon treatments designed to neutralize allelopathic effects restored costs in competition treatments. Others have found evidence for dual antiherbivore/allelopathic roles in inducible plant metabolites (Lovett and Houlton 1995, Tang et al. 1995), and Callaway et al. (1999) found that exudation of some compounds from the roots of *Centaurea maculosa* increased after moderate leaf herbivory. *Centaurea maculosa* roots are allelopathic (Ridenour and Callaway 2001), and root herbivory increases the exudation of (–)-catechin, a phytotoxic chemical (R. M. Callaway and J. Vivanco, unpublished data). If secondary compounds that provide resistance to herbivory commonly have dual roles as allelopathic agents, then induced resistance to herbivores might routinely increase negative allelopathic interactions with neighbors. If so, this could partially

offset any reduced competitive ability caused by the costs of production of the secondary compounds.

The growth rates of some plant species are plastic in response to herbivory. Herbivory often increases growth rates and, in some cases, may even stimulate “overcompensation,” i.e., larger final biomass or enhanced reproduction, although this latter concept is highly controversial (Paige and Whitham 1987, Müller-Schärer 1991, Trumble et al. 1993, Frank et al. 2002). Agrawal (2000) found that induced *Lepidium virginicum* plants overcompensated in biomass even though they also induced defenses. Similarly, the invasive weed, *Centaurea maculosa*, demonstrates a remarkable indifference to herbivory and defoliation (Müller-Schärer 1991, Callaway et al. 1999). Although the mechanisms for compensatory growth in *C. maculosa* are not fully understood, fine-root growth of this plant increases with herbivory (Steinger and Müller-Schärer 1992). Although it is reasonable to hypothesize that the phenomenon of plastic compensatory growth increases resource uptake and therefore competitive impacts on neighbors, to our knowledge no studies have investigated this possibility.

Finally, if consumers alter the morphology of the plant, they may have large effects on species that use plants as habitat. For example, infection by dwarf mistletoe (*Arceuthobium* spp.) alters tree allocation patterns by inducing massive “brooms,” and consequently increases the density and diversity of forest insects and birds (Stevens and Hawksworth 1970, Scharpf 1975, Bennetts et al. 1996).

CONCLUSIONS

Plastic responses of plants to the abiotic environment, neighbors, and herbivory can result in genetically identical individuals that have very different phenotypes. We have argued that these phenotypic differences should have broad implications for how plants interact with their neighbors. We acknowledge, however, that this view is likely to be controversial, considering that many plant ecologists argue that even differences among species, let alone differences within species, are largely irrelevant to interactions (Goldberg and Werner 1983, Gaudet and Keddy 1988, Hubbell 2001). Present data cannot conclusively adjudicate between these different viewpoints: in contrast to work with animal communities, where a great deal is known about TMI, at least using short-term measures (Bolker et al. 2003, Dill et al. 2003, Werner and Peacor 2003), we know relatively little about the consequences of plasticity for interactions among plants. In large part, this inequality has arisen because of the experimental difficulties in assessing the impacts of phenotypic plasticity in plants. In particular, (1) it is difficult to separate the effects of plasticity from the confounding effects of the treatments used to create plasticity (Bolker et al. 2003), and (2) it is difficult to assess the consequences of plasticity in a natural setting because of the very

nature of plasticity: plants continue to change after they have been manipulated (Sultan 2000). Recent developments in experimental design and technology have begun to overcome these difficulties (Schmitt et al. 1999). One promising approach is to manipulate plant morphology using signals of environmental conditions rather than the actual environmental conditions, thus decoupling the plastic response from the environmental context. For example, red : far red light ratios can be used to induce "high-density" stem morphologies without actually subjecting plants to increased competition (Dudley and Schmitt 1995, 1996, Dorn et al. 2000). The presence of root exudates can be manipulated with activated charcoal without changing the density of competitors (Siemens et al. 2002). Similarly, stem elongation can be induced with gibberellic acid in the absence of competition (Cippollini and Schultz 1999), and plant resistance can be induced with jasmonic acid without actually damaging plants (Baldwin 1999). Another promising approach is the use of transgenic plants that lack the ability to induce plastic responses (Schmitt et al. 1995). Application of these and similar techniques in future research should allow us to make great strides toward understanding the consequences of phenotypic plasticity in natural communities. We suggest profitable research directions for each of our three major categories of plasticity. In each case, because plasticity should be most advantageous when environmental heterogeneity is high (Silvertown and Gordon 1989), TMI among plants should be most important among species experiencing a wide range of environmental conditions.

Plasticity induced by the abiotic environment.—Because variation in the abiotic environment may lead to variability in plant phenotype, the nature of plant interactions may vary across the landscape in concert with abiotic factors. As indicated by work on the rooting morphology of oaks, the effects can be as striking as reversing the sign of interactions from negative to positive. Many of these TMI probably have been overlooked because variation in belowground resources is not immediately apparent to ecologists. Collaborations between ecologists and earth scientists would be likely to uncover a pervasive suite of mechanisms whereby "hidden" abiotic variation resulted in TMI between plants and neighbors across superficially homogenous landscapes. Because groundwater availability can be highly heterogeneous and has large effects on root morphology, an obvious first step would be to better explore the link between hydrology and TMI.

Plasticity induced by neighbors.—It is well established that neighbors affect plant morphology. Various techniques that allow us to manipulate plant morphology without altering the biotic environment are now available, as we have described. We need a suite of studies using these techniques to determine the importance of neighbor-induced plasticity in mediating interactions among plants. We predict that these studies

will reveal that TMI are widespread and that they generally serve to reduce competitive interactions between plants. Because some of the plastic responses of plants to neighbors are apparently species specific, interaction coefficients among plants may change as a function not only of neighbor density, but also of neighbor identity, lending a new level of complexity to plant community theory.

Plasticity induced by consumers.—Plastic responses of plants to consumers are common and can involve both chemical and morphological responses. The consequences of induced resistance for interactions with consumers have been well documented and are reviewed elsewhere (Karban and Baldwin 1997, Agrawal et al. 1999). Theoretical considerations suggest that induced responses to consumers should reduce the competitive ability of induced plants, creating TMII between herbivores and nonconsumed plants in the community. Recent advances in understanding of plant wound signals now allow us to manipulate the plant phenotype in the absence of differences in tissue damage, as previously described. We need a suite of such studies to examine herbivore-induced TMI. Such studies also are likely to make major contributions to the debate over whether defenses against consumers have costs, because they can assess potential costs in a variety of environments.

ACKNOWLEDGMENTS

We thank Frederick Adler, Steve Franks, Jonathan Rothman, Giles Thelen, Heather Tone, and two anonymous reviewers for helpful comments on the manuscript and other assistance. We thank the Georgia Coastal Ecosystems LTER (OCE 99-82133, S. C. Pennings and C. L. Richards) and the Andrew W. Mellon foundation (R. M. Callaway) for financial support. This is contribution number 830 from the University of Georgia Marine Institute.

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