

Evolutionary Trajectories in Plant and Soil Microbial Communities

CENTAUREA INVASIONS AND THE GEOGRAPHIC MOSAIC OF COEVOLUTION

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In this chapter, we review empirical evidence for stronger allelopathic effects of exotic European invaders on North American natives than on other European species. We argue that this evidence provides critical insights into the importance of coevolutionary relationships within plant communities. We discuss how the disruption of these and other biochemical coevolutionary relationships may lead to the success of some exotic species and the decline of the natives they encounter. Understanding this coevolution within the context of John Thompson's geographic mosaic theory may provide crucial insight into biological invasions, which in turn may provide deeper insight into the geographic mosaic theory of coevolution. We also review evidence for the evolution of native plant species in response to the allelopathic effects of invaders and for mechanisms by which native species might tolerate the effects of invaders. We look at how the disruption of evolutionary trajectories in plant–soil microbe interactions may also drive invasions. Such comparisons of interactions between native and non-native species are powerful tools for understanding the role of rhizosphere biochemistry as a driver of evolutionary trajectories in plant communities, and more generally, for understanding the geographic context of coevolution.

Introduction

Coevolution is one of the major processes organizing the earth's biodiversity.

JOHN THOMPSON

One of the most important challenges in evolutionary ecology is to understand how coevolution shapes and organizes natural communities across broad geographic landscapes (Thompson 1994, 1997, 1999). Thompson argued that explicit examination of genetically differentiated populations, and of geographic variation in their interactions, is crucial for developing a framework for coevolutionary theory. This geographic population structure exists for most interspecific interactions and must be part of any theory on the organization of the earth's biodiversity. Here, we link the geographic mosaic concept to biological invasions. Invasions are inherently biogeographic processes (Hierro et al. 2005), and they provide the most spectacular examples on earth of community patterns and dynamics that arise from rapid changes in geographic population structure. Furthermore, patterns and process in invaded communities can be dramatically different from those in the original communities. Here, we argue that the geographic mosaic theory of coevolution provides theory for understanding biological invasions, and that biological invasions provide insight into the geographic mosaic theory of coevolution.

Species can undergo rapid evolutionary changes under natural conditions (Thompson 1998) and when they are introduced to new parts of the world by humans (Rice and Emery 2003; Phillips and Shine 2005; Rice and Sax, this volume). These changes provide invaluable insight into the nature of adaptation and how it may affect coexistence among species and the formation of communities. Most plant species that are introduced into new ecosystems by humans appear to act more or less like the native species they join, but some transmogrify—they become far more abundant and competitively dominant than they are in their native regions. Unusually good luck for a newcomer is generally correlated with unusually bad luck for natives, manifested in lower local diversity and large changes in community composition (see D'Antonio and Vitousek 1992; Mack et al. 2000). Species-rich communities can be replaced by virtual monocultures (Braithwaite et al. 1989; Malecki et al. 1993; Meyer and Florence 1996; Bruce et al. 1997; Ridenour and Callaway 2001; Siemann and Rogers 2001). These dramatic changes in abundance and dominance indicate unusually strong ecological processes, which may initiate strong evolutionary responses. By drastically reducing the population sizes of native plants, invasive plants have the potential to be a powerful selective force.

Despite the explosion of interest in the evolution of invaders (Blossey and Nötzold 1995; Gaskin and Schaal 2002; Hänfling and Kollman 2002; Lee 2002), the evolution of native plants and microbes in response to invasive plants has largely been ignored, probably because the paradigms for invasive success are firmly embedded in resource or trophic interactions (Elton 1958; Maron and Vilà 2001; Keane and Crawley 2002). Furthermore, much plant community the-

ory is rooted in Gleason's (1926) individualistic theory, in which a plant community is "scarcely even a vegetational unit, but merely a coincidence" (see Lortie et al. 2004). This individualistic paradigm (reflected in current neutral theory and lottery models) does not provide a clear context in which invasive plants can drive adaptation in other plants. If the organization of plant communities is determined by the adaptation of members to a particular abiotic environment and competition for the same nutrient, light, and water resources, what mechanisms can transform an inferior competitor into an overwhelming dominant, and how do native plants adapt to the mechanisms of their new dominant neighbors?

Prevailing "individualistic" plant community theory does not have a place for coevolution among plants and may not provide an adequate paradigm for understanding exotic plant invasion. In this chapter, we explore recent evidence for novel allelopathic interactions among plants and novel biochemical interactions among plants and soil microbes (see Callaway and Ridenour 2004), focusing on *Centaurea* invasions as case examples.

We propose that shared evolutionary trajectories in different regions may mediate coexistence in the original communities of invaders where the species have been exposed to one another for a long time, while simultaneously facilitating competitive exclusion by those invaders in their new communities. We propose that when humans introduce some plant species to new regions, they may force together different biochemically driven coevolutionary trajectories from different continents and disrupt coevolved interactions. We have organized this chapter into two sections, one focusing on biochemically mediated plant interactions, allelopathy, and how these might drive the evolution of native species, and another focusing on interactions among plants and soil microbes. Both sections are organized to consider one fundamental question: Do regional coevolutionary trajectories in plant and soil microbial communities lead to the coexistence of species and community stability?

Allelopathic Interactions among Invasive and Native Plants

Some successful plant invasions appear to be based, at least in part, on biochemistry. Plants release up to 50% of their total photosynthate as organic exudates from their roots (Flores et al. 1999; Nardi et al. 2000). These exudates play mutualistic or defensive roles as a plant communicates with its environment and ultimately develops a suite of positive and negative responses to abiotic and biotic conditions in the rhizosphere (Bais et al. 2001; Walker et al. 2003; Bais et al. 2004). The role of root exudates, or chemical interactions in general among plants (allelopathy), has a murky history; ever since a highly touted early study was discredited by field experiments, other studies of allelopathy have been viewed with more skepticism than studies of resource-based interactions (see Callaway 2002). The skepticism is probably unwarranted, and the criteria for proof of allelopathy seem to far exceed criteria for other phenomena

(Williamson 1990). In this section, we briefly discuss evidence for allelopathy in exotic invasions in general, then focus on the details of the allelopathic effects of two knapweeds, *Centaurea maculosa* and *C. diffusa*. We use the term “allelopathy” to refer to the negative effect of one plant on another through the release of chemical compounds into the environment (*sensu* Muller 1966) and consider allelopathy just one of many forms of non-resource interaction among plants (Callaway 2002).

Biogeographic differences in allelopathic effects among plants: Case studies with Centaurea

Unlike locally based theories of coevolution, the hypothesis of geographic mosaics of coevolution predicts the routine occurrence of transient mismatches of traits, or “maladaptations,” that lead to breakdowns in coevolved coexistence (Thompson 1999); perhaps these occasional mismatches drive the crashes in community composition and diversity that occur when monocultures of invaders develop. Whether long-lasting adaptations develop to promote coexistence or become maladaptive is thought to depend on three components: the existence of selection mosaics (which exist, by definition, when species are introduced around the world), coevolutionary hot spots (which *may* exist if the right combinations of species are introduced to one another), and trait remixing among populations (which will exist as exotics and natives encounter either novel environments or neighbors with novel traits). All of these components may be relevant to the biogeography of invasions.

The replacement of diverse native communities with monospecific stands of an invading species is a clue that unusually powerful mechanisms may be at work (see Hierro and Callaway 2003). In a search for such mechanisms, many studies have suggested that allelopathy may contribute to the ability of particular exotic species to become dominants in invaded plant communities. This possibility has been explored for some of the best-known plant invaders in the world, including *Eltrygia repens* (ex. *Agropyron*: Korhammer and Haslinger 1994), *Bromus tectorum* (Rice 1964), *Cirsium arvense* (Stachon and Zimdahl 1980), *Cyperus rotundus* (Quayyum et al. 2000; Agarwal et al. 2002), *Euphorbia esula* (Steenhagen and Zimdahl 1979), *Parthenium hysterophorus* (Pandey 1994), *Setaria faberii* (Bell and Koeppel 1972), and *Sorghum halepense* (Elmore 1985). As a more detailed example, *Zoysia*-dominated seminatural grasslands of Japan have been heavily invaded by *Anthoxanthum odoratum* (Yamamoto 1995), and coumarin, a compound released from this invader, inhibits the development of native *Zoysia japonica* seedlings. As another example, Czarnota et al. (2001) found that the chemical sorgoleone constituted about 85% of the total root exudates from the invasive *Sorghum halepense* (johnsongrass) and suppressed other species by docking into the QB-binding site of the photosystem II complex; soil impregnated with sorgoleone suppressed a number of different plant species.

The evidence for allelopathic effects of *Centaurea maculosa* (spotted knapweed) and *C. diffusa* (diffuse knapweed), two of North America’s worst inva-

TABLE 13.1 Summary of evidence for the effects of phytotoxic and antimicrobial root exudates from *Centaurea* species

Exudate	Produced by	Autotoxicity	Effect on plants in invaded range	Effect on plants in native range	Effect on microbes
(±)-Catechin	<i>C. maculosa</i>	None	Strong	Weak	Strong
8-Hydroxyquinoline	<i>C. diffusa</i>	None	Strong	Moderate	Strong

ders, is strong and integrates ecological, physiological, biochemical signal transduction, and genomic approaches (Callaway and Aschehoug 2000; Bais et al. 2002, 2003; Fitter 2003; Baldwin 2003; Vivanco et al. 2004). Although these congeners are closely related, the allelopathic chemicals produced and the results they mediate differ between these two species (Table 13.1). *C. maculosa* produces (±)-catechin, which has been clearly demonstrated to have both phytotoxic and antimicrobial properties (Box 13.1). In contrast, *C. diffusa* produces 8-hydroxyquinoline, a compound with well-known abilities as a metal chelator, fungicide, and antiseptic (Vivanco et al. 2004; Merck Index 1996). In laboratory experiments, a suite of plant species showed 100% mortality after the addition of root exudates from *C. diffusa* and after application of 8-hydroxyquinoline. Further, like those of its congener *C. maculosa*, whose roots are unaffected by the allelopathic chemical it produces, the root exudates of *C. diffusa* are not autotoxic. In North America, 8-hydroxyquinoline is abundant in soil extracts from *C. diffusa*-invaded fields, but has not been found in the rhizosphere of any other plant species. In fact, 8-hydroxyquinoline had not been previously described as a natural product (Vivanco et al. 2004). Application of concentrations of 8-hydroxyquinoline much lower than those found in the field to natural soils reduces the growth of North American species (Vivanco et al. 2004).

If biochemical interactions are involved in the transmogrification of species from mild members of their native communities into competitive dominants in new communities, then it might be expected that the allelopathic effects of these species would be much weaker at home than in the communities they invade. Evidence for this is rapidly accumulating.

The root exudates from *C. maculosa* and *C. diffusa*, and the specific biochemicals in those exudates, have very different effects on plant species from communities where they are native than on plant species in communities that the weeds have invaded (Callaway and Aschehoug 2000; Bais et al. 2003; Vivanco et al. 2004). Strong biogeographic differences in the effects of allelochemicals circumstantially suggest that plants, as well as the microbes that mediate plant interactions (see below), that have coexisted for long periods have coevolved to tolerate one another's biochemistry. Furthermore, much stronger biochemical interactions in invaded systems suggest that in some cases exotic species may bring biochemicals to new communities rendered vulnerable by their naïveté—the “novel weapons” hypothesis (Rabotnov 1982; Call-

BOX 13.1 *Summary of the Evidence for Allelopathic Effects of Centaurea maculosa*

Centaurea maculosa roots produce an enantiomeric compound (a compound composed of two mirror-image entities), (±)-catechin, with clearly documented phytotoxic properties belonging only to the (–)-form of the chemical and antimicrobial properties belonging only to the (+)-form of the chemical. (±)-Catechin is present in natural soils at concentrations above that which affects other plants, and its presence is associated only with *C. maculosa* plants.

Greenhouse experiments have demonstrated the inhibitory effects of *C. maculosa* roots on the roots and overall growth of a native American grass; activated carbon added as a purification agent ameliorated these inhibitory effects (Ridenour and Callaway 2001). The concentration of (–)-catechin appears to be about twice as high in soils occupied by *C. maculosa* in North America as in similar habitats in Europe. Experiments show inhibition of the growth and germination of native species in field soils at natural concentrations of (–)-catechin. This allelochemical shows cell-specific targeting of meristematic and elonga-

tion-zone cells in the roots of target plants, as evidenced by cytoplasmic condensation followed by a cascade of cell death proceeding backward up through the root stele, induction of reactive oxygen species (ROS)-related signaling that leads to rhizotoxicity in susceptible plants, a ROS-triggered Ca^{2+} signaling cascade leading to cellular pH decrease, and allelochemical-induced genome-wide changes in gene expression patterns. Injection of (±)-catechin into soil in the field strongly suppresses native species, and the degree of suppression is dose-dependent (R. M. Callaway, unpublished data). (–)-Catechin has no effect on *C. maculosa*, apparently due to the presence of a barrier/avoidance mechanism located in the root membrane that precludes the reentrance of (–)-catechin once secreted from the root of this species. The lack of autotoxicity is an answer to one of the strongest criticisms of allelopathy theory (Williamson 1990). Finally, the germination and growth of European grasses are more resistant to (–)-catechin than those of their North American counterparts.

away and Aschehoug 2000; Mallik and Pellissier 2000; Callaway and Hierro, in press; Callaway and Ridenour 2004).

In one of the earliest examples of biogeographic differences in allelochemical effects, Callaway and Aschehoug (2000) compared the inhibitory effects of *C. diffusa* on three bunchgrass species that coexist with *C. diffusa* in Eurasia with its effects on three bunchgrass species from invaded communities in North America. Each of the three grass species from North America was paired with a congener (or closely related species) from Eurasia of a similar morphology and size. *Centaurea diffusa* had much stronger negative effects on the North American species than on the Eurasian species. Correspondingly, none of the North American species had a significant competitive effect on the biomass of *C. diffusa*, but Eurasian bunchgrasses significantly reduced *C. diffusa* biomass.

The addition of activated carbon (a potent adsorbent of allelopathic compounds: Mahall and Callaway 1992) to soils had strikingly different effects on these interactions between *C. diffusa* and the grass species from the different regions. In the presence of *C. diffusa*, the overall effect of carbon on the growth of North American species was positive: activated carbon reduced the competitive strength of *C. diffusa*. In contrast, the biomass of all the Eurasian grass species growing with *C. diffusa* was reduced dramatically in the presence of activated carbon. Correspondingly, activated carbon put *C. diffusa* at a disadvantage against the North American grasses (*Centaurea* growth decreased), but conferred an advantage to *C. diffusa* when with the Eurasian grasses (*Centaurea* growth increased). Activated carbon has a high affinity for organic compounds, such as potentially allelopathic chemicals, and a weak affinity for inorganic electrolytes, such as those in nutrient solution, and has previously been shown to reduce the negative effects of root exudates from *C. maculosa* and other species (Schreiner and Reed 1907; Cheremisinoff and Ellerbusch 1978; Mahall and Callaway 1992; Ridenour and Callaway 2001). Furthermore, the strong effects of the place of origin on the competitive ability of grass species against *C. diffusa*, and the contrasting effects of activated carbon, suggest that *C. diffusa* produces allelopathic chemicals that long-term and familiar Eurasian neighbors have adapted to, but that this adaptation and tolerance has not developed in *C. diffusa*'s new North American neighbors.

Vivanco et al. (2004) further explored these biogeographic differences in the resistance or susceptibility of plant communities to *C. diffusa* by building microcosms in which North American and Eurasian plant communities were established in both North American and Eurasian soils. In full support of the previous experiments, the regional source of the plant community was by far the most important factor in resistance to interference by *C. diffusa*: Eurasian plant communities were much more resistant to invasion. Finally, North American plant species were found to be more susceptible to identical concentrations of 8-hydroxyquinoline than Eurasian species, forging a crucial link between the general effects of *C. diffusa* and the suspicious biochemical it exudes (Vivanco et al. 2004).

Mallik and Pellissier (2000) conducted experiments comparing the effects of leaves, leaf extracts, and humus from *Vaccinium myrtillus*, a widespread understory shrub in coniferous forests of Eurasia with strong allelopathic effects, on an exotic North American neighbor, *Picea mariana*, and on a native neighbor, *Picea abies*. They found that *V. myrtillus* generally had stronger biochemical effects on the exotic *P. mariana* than on the native *P. abies*. Their results also suggest that species without a common evolutionary history have stronger allelopathic interactions.

Using a biogeographic approach similar to that of Callaway and Aschehoug, Prati and Bossdorf (2004) tested the allelopathic effects of *Alliaria petiolata* (garlic mustard), an aggressive invader of the understory of forests in North America, on the germination of two congeneric species that co-occur with *Alliaria* in the field: the North American *Geum laciniatum* and the European *G. urbanum*.

They also investigated whether the allelopathic potential of *A. petiolata* varied between native European and exotic North American populations of the weed. In support of the “novel weapons” hypothesis, they found that invasive North American populations of *A. petiolata* significantly reduced the germination of “*Alliaria*-naïve” North American *G. laciniatum* seeds, but had no effect on “*Alliaria*-experienced” European *G. urbanum* seeds. European collections of *A. petiolata*, on the other hand, significantly reduced seed germination in both North American *G. laciniatum* and European *G. urbanum* in similar proportions, a result that only partially supports the “novel weapons” hypothesis. The contrasting inhibitory effects of *A. petiolata* populations from Europe and from North America on European *G. urbanum* suggest that North American *A. petiolata* has lost competitive ability against a former neighbor.

If invaders are indeed transformed from inferiors to dominants because they bring novel biochemicals to naïve native communities—and the jury is certainly still out—then the species that co-occur naturally with them may have adapted to the biochemicals they release. If species in an invader’s place of origin can adapt to the biochemicals released by that invader, then the invader’s new neighbors should be able to do so as well. We pursue this possibility in the following section.

Invaders and the evolution of native plants

Plants evolve rapidly in response to man-made chemical herbicides (Powles and Holtum 1994), and may evolve as rapidly to the natural allelopathic herbicides produced by invaders. The evolution of resistance to invaders by the species they encounter in their new communities would have profound consequences for ecological and evolutionary theory as well as for conservation. Such evolutionary processes would suggest that naturally intact biological communities may be, to some degree, functionally organized units (Goodnight 1990; Wilson 1997), rather than simple mixtures of species with similar adaptations to a particular abiotic environment. If natives can evolve resistance to invaders, then invaded communities may recover some aspects of their natural structure and function, and invaders and natives may eventually coexist.

As clearly presented in the geographic mosaic theory of coevolution (Thompson 1999), it is by no means necessary to view adaptive responses to allelochemicals as indicative of selective processes occurring over whole regions. Allelochemicals may drive selection in plants occurring in a particular local area, exerting strong selective pressures much like those exerted by anthropogenic herbicides.

In an experiment with five native grass species, Callaway et al. (in press) found that *C. maculosa* harmed “naïve” grass clones (individuals that had not experienced *C. maculosa* as neighbors) more than “experienced” clones (individuals that had survived *C. maculosa* invasion), suggesting the possible development of resistance to the inhibitory effect of *C. maculosa* by natives. When activated carbon was added to the sand to adsorb organic exudates, the

growth of all the experienced clones of native species combined improved significantly. Analyzed separately, activated carbon significantly increased the growth of the experienced clones of only one species, *Stipa occidentalis*. In contrast, activated carbon improved the growth of the naïve clones of all native species analyzed together by 105%, and of three species when analyzed separately. *Stipa occidentalis*, *Festuca idahoensis*, and *Koeleria cristata* all showed much stronger resistance to *C. maculosa* when they had previously experienced *C. maculosa* invasion. *Centaurea*-tolerant individuals may have simply survived invasion; however, even if *Centaurea* has simply driven large shifts in genotype frequencies in surviving populations, this would be the first step toward evolution.

When in competition with *C. maculosa*, *Festuca* and *Stipa* grown from the seeds of naïve maternal plants were smaller than those grown from the seeds of experienced maternal plants, and activated carbon eliminated these differences (Callaway et al., in press). Plants grown from seeds of experienced and naïve maternal plants of *Festuca* and *Stipa* did not differ in size when grown with activated carbon in the soil, suggesting that allelopathy may have been a selective mechanism.

In another experiment (which used the allelochemical directly, instead of using the plant that produces it), the germination of seeds from both experienced and naïve native species was highly suppressed by a low concentration of (\pm)-catechin. However, the germination of seeds from some populations of native grasses demonstrated selection for tolerance to the allelochemical, as they did for the *C. maculosa* plants that produce the chemical. When exposed to (\pm)-catechin, 16% of *Stipa* seeds from experienced maternal plants germinated, whereas no seeds from naïve maternal plants germinated in (\pm)-catechin. Populations of *Pseudoroegneria spicata* tested in this experiment differed substantially in their responses to (\pm)-catechin. Germination of seeds from one population was almost completely suppressed by (\pm)-catechin; however, in another population, 6% of seeds from experienced maternal plants germinated, in comparison to none of the seeds from naïve maternal plants.

The enantiomer (\pm)-catechin elicits the production of reactive oxygen indicators (ROI) in root cells, and this production of ROI is related to the phytotoxic effects of the chemical (Bais et al. 2003). ROI production precedes cell death by 5 to 10 minutes. Seedlings grown from *Centaurea*-experienced *P. spicata* plants showed qualitatively different ROI production than those grown from seeds from *Centaurea*-naïve *P. spicata* (R. M. Callaway, unpublished data). Tolerance to (\pm)-catechin corresponded with much slower ROI reactions after exposure to the allelochemical.

To our knowledge, this research on the resistance of native species to *C. maculosa* and their tolerance to its root exudates is the only work that has been conducted on potential selection for resistance to invasive plants in native plants. However, other researchers have observed variation in interactions among species from different populations, suggesting that coexistence may result in ecotypic selection. For example, Martin and Harding (1981) found that when

seeds of co-occurring individuals of *Erodium cicutarium* and *Erodium obtusifolium* were planted together, the total seed output and reproductive rates of the two species were higher than when seeds of individuals from distant communities were grown together. Evans et al. (1985) found that ecotypes of *Lolium perenne* and *Trifolium repens* that had been collected from fields in Switzerland, Italy, France, and England grew larger when paired with a “familiar” genotype of the other species—the genotype that co-occurred naturally in the same field. Joy and Laitinen (1980) found a similar response in experiments with *Phleum pratense* and *Trifolium pratense*. Turkington and Mehrhoff (1990) transplanted *Trifolium repens* and *Lolium perenne* into three fields in British Columbia, Canada, that varied in age since clearing: 0 years, 8 years, and 46 years. They found that *T. repens* genets from older fields transplanted into 46-year-old pastures grew much larger, either in competition or when competitors had been cleared away, suggesting that selection was occurring over time. In another experiment, Turkington and Harper (1979) collected ramets of *T. repens* from different sites dominated by one of four different grass species for competition experiments. When ramets were transplanted in all possible combinations with the four grasses, each clover “type” grew best with the grass species from the site where it had originally been sampled, suggesting the occurrence of microevolutionary changes in *T. repens* in response to different constraints imposed by different neighbors.

Although the empirical evidence is limited so far, the studies cited indicate that plants may be able to adapt to the presence of species-specific neighbors in ways that favor coexistence or higher productivity. So far in this chapter, we have considered the evidence that biochemical interactions drive this sort of adaptation. In other words, plants may eventually get used to the peculiar biochemistry of their neighbors, and when they do so, they may coexist. This does not mean that plants are necessarily evolving allelochemical production for competitive advantage per se. Such selection is possible, but it is just as likely that the release of particular chemicals evolves for other reasons (defense against herbivores or resource acquisition, for example) and some of these chemicals also happen to have strong effects on naïve neighbors. Biochemicals may not evolve to combat neighbors, but neighbors may have to evolve tolerance to those biochemicals anyway.

Centaurea maculosa and (\pm)-catechin may provide a good example of this “inadvertent” allelopathy. Catechins (and *C. diffusa*'s 8-hydroxyquinoline) function as metal chelators for Al, Fe, and Ca and thereby increase the solubility of inorganic soil phosphorus. This form of P acquisition efficiency may play an important role in plant community dynamics in P-limited environments. Hydroxyl-substituted polyphenols also have the potential to increase P solubility via chelation of metals (Stevenson and Cole 1999). The high affinity of catechin for metals increases P solubility by lowering the concentration of metals available for the precipitation of insoluble metal phosphates (A. S. Thorpe et al., unpublished data). It is possible that (\pm)-catechin has evolved primarily to enhance P acquisition in *C. maculosa*'s native habitat, and that (–)-catechin,

the highly toxic and rare enantiomer, has strong allelopathic effects on North American species as a by-product.

Interactions between Plants and Soil Microbes

Microbial communities in the soil can have strong effects on plant populations (Burdon 1993; Packer and Clay 2000; van der Putten et al. 2001; Reinhart et al. 2003). The inhibitory and facilitative effects of soil microbes on plants, and the reciprocal effects of plants on soil microbes, create contrasting dynamic feedback interactions between plants and the microbial communities that develop around their roots (Bever et al. 1997; Bever 2002). Positive feedbacks occur when plant species accumulate microbes near their roots that have beneficial effects on the plants that cultivate them, such as mycorrhizal fungi and nitrogen fixers, and are thought to lead to a loss of local microbial community diversity (Bever et al. 1997; Bever 2002). Negative feedbacks occur when plant species accumulate pathogenic microbes in their rhizospheres, creating conditions that are increasingly hostile to the plants that cultivate these pathogens (van der Putten et al. 1993; Bever 1994; Klironomos 2002). Such plant-soil feedbacks have been hypothesized to be a strong selective force on both plants and microbes (van der Putten 1997). Plant-soil microbe interactions are often mediated by biochemical processes, and much as we have argued for allelopathic interactions, geographic evolutionary trajectories may also be driven by interactions among plants and soil microbes. Combining plant and microbial species without shared evolutionary trajectories may result in the unusually strong competitive interactions that appear to be characteristic of many invasions.

It is well established that different microbial communities are associated with different plant species (Bever 1994; Westover et al. 1997; Grayston and Campbell 1998; Priha et al. 1999, 2001; Grayston et al. 2001; Klironomos 2002), probably due in part to species-specific rhizosphere biochemistry. So it should be no surprise if exotic invaders also have species-specific effects on soil microbes. We are beginning to learn how invaders (and their associated soil microbiota) may produce soil conditions that differ fundamentally from those that occur in native communities and how these changes may provide a means by which invaders transmogrify into ecosystem-altering dominants.

Understanding invasive plant-microbe interactions in the context of geographic mosaic theory is complicated because microbes affect interactions among plants in more complex ways than the allelopathic interactions described above. Microbes can act as pathogens, shifting the balance of competition in favor of a less infected plant species. They can also act as mutualists, shifting the balance of competition in favor of a plant species more highly colonized by mutualistic microbes. Microbes run the nitrogen cycle and affect the availability of other nutrients through decomposition, shifting the balance of competition in ways that are hard to predict. Despite this mechanistic complexity, in this section, we continue to pursue the fundamental question

addressed in this chapter: Do regional coevolutionary trajectories within plant and soil microbe communities lead to the coexistence of species and community stability?

Introduced microbial pathogens

In this chapter, we are primarily interested in what invasive plants might teach us about regional evolutionary relationships among plants and soil microbes. However, there is strong evidence for the importance of shared evolutionary trajectories for coexistence between other types of microbes and plants—as evidenced by the devastating effects of exotic microbial pathogens on plant species that are related to, but do not share a coevolutionary trajectory with, the natural hosts of the pathogens.

Some fungal species that are merely parasitic in their native range are virulently pathogenic when introduced to new ranges. *Cronartium ribicola*, the white pine blister rust fungus, is native to Asia and has been introduced into Europe and North America. Infected trees in Europe show minimal signs of infection, perhaps because of coevolutionary interactions with the fungus on the fringes of where strong coevolutionary interactions occur (Thompson 1999). However, in North America, far removed from its Eurasian coevolutionary trajectories, *Cronartium* has devastating effects on a number of *Pinus* species in the subgenus *Strobus*. Eurasian and North American evolutionary trajectories are similar enough for *Cronartium* to complete its complex life cycle, which requires *Ribes* and *Pinus* species as alternate hosts, but dissimilar (or maladaptive, in Thompson's terms) enough to allow far greater disruption of community processes than occurs in native local communities. *Cryphonectria parasitica* (syn. *Endothia*), a relatively benign parasite of *Castanea* species (chestnut) in Eurasia, was introduced into North America at the turn of the twentieth century. Within decades, a North American species, *Castanea dentata*, was transformed from a widespread ecologically dominant canopy tree to a relictually distributed understory shrub persisting solely through clonal growth. In an ironic twist, the fact that other plant species did not disappear with the near-eradication of *C. dentata* has been a primary argument *against* the occurrence of interdependent processes among members of a plant community (Woods and Shanks 1959; McCormick and Platt 1980; Johnson and Mayeux 1992). A similar but more complex case occurred when the Dutch elm fungal parasite *Ophiostoma ulmi* (syn. *Ceratocystis*) was introduced into North America. As in the other examples, a North American species, *Ulmus americana*, was harder hit than *Ulmus* species in Eurasia, where the fungus originated. However, the fungus is spread in North America by two species of bark beetles, one European and the other North American. Because of the particular feeding patterns of the latter species, the effects of the disease tend to be stronger. These disruptions of coevolved host-parasite relationships and their consequences provide evidence for the importance of a geographic context for understanding

coevolution. Below, we continue to explore this geographic context for plant–soil microbial interactions and exotic plant invasions.

Effects of invasive plants on soil microbes

We know a lot about how soil microbes affect the performance and abundance of plants (Burdon 1987; Bever 1994, 2002; Bever et al. 1997; van der Putten and Peters 1997), but we know less about how invasive plants alter soil microbial communities. Kourtev et al. (2002) found that effects on microbial communities associated with the invasion of Japanese barberry (*Berberis thunbergii*) and Japanese stilt grass (*Microstegium vimineum*) extended beyond the soil in direct contact with the roots of these invaders and into the bulk soil. They suggested that these effects could be long-lasting. In field experiments conducted in the invaded range of *C. maculosa*, Callaway et al. (2004b) found that suppressing soil fungi in the presence of different native competitors caused *C. maculosa* biomass to vary from a 10-fold decrease to a 1.9-fold increase depending on the identity of the competitor. In untreated soils, *C. maculosa* grew larger in the presence of *F. idahoensis* or *K. cristata* than when alone. When fungicide was applied, these positive effects of *F. idahoensis* and *K. cristata* on *C. maculosa* did not occur. These results suggest that soil microbes may play a role in successful invasions, but that role may not be manifested in simple direct effects.

A number of plant compounds may mediate interactions between plants and microbes. One of the mechanisms driving the interaction between *C. maculosa* and microbial communities may be biochemical: the exudation of (±)-catechin from the roots of *C. maculosa*. As previously stated (see Box 13.1), (+)-catechin displays strong antimicrobial properties for at least some groups of bacteria (Bais et al. 2002, 2003). Other invasive species produce chemicals with antimicrobial activity; however, the roles of these chemicals in the plants' invasive success are generally unknown (Ehrenfeld 2003). The allelochemical produced by *C. diffusa*, 8-hydroxyquinoline, also has strong antimicrobial properties. This chemical inhibits the activity of several important plant pathogens, including the bacteria *Xanthomonas campestris*, *Pseudomonas syringae*, *Agrobacterium radiobacter*, *Erwinia carotovora*, *E. amylovora* and the fungi *Aspergillus niger*, *Rhizoctonia solani*, *Phytophthora infestans*, and *Fusarium oxysporum* (Vivanco et al. 2004). The dry mass of leaves of *Melaleuca* spp., which has invaded large areas of the coastal southeastern United States, particularly the Everglades, can be composed of up to 7% monoterpenes (Boon and Johnstone 1997). These compounds inhibit microbial colonization and decomposition of leaf litter in both the native and invaded ranges of *Melaleuca* spp. It has also been suggested that allelopathic chemicals released by some invasive species may alter nitrogen fixation in neighboring plants (Wardle et al. 1994, 1995).

The effects of invasive plants on soil microbes set the context for exploring the role of plant-microbe interactions in invasive success and the development of evolutionary trajectories on a geographic matrix. Explicit biogeographic com-

parisons of the effects of soil microbes in original and invaded systems are crucial tests of the hypothesis that shared evolutionary trajectories among soil microbes and plants lead to the coexistence of species and community stability.

Biogeographic evidence for regional plant–soil microbe evolutionary trajectories

In a review of 473 plant species that have become naturalized in the United States, Mitchell and Power (2003) found that 84% fewer fungi and 24% fewer virus species infected the species in their invaded ranges than in their native ranges. Furthermore, they reported that species that experienced greater release from microbial pathogens were more invasive. Klironomos (2002) found that locally rare native species consistently exhibited negative feedback interactions with the soil microbial community (a relative decrease in growth on “home” soil in which conspecifics had previously been grown), whereas common non-native species consistently exhibited positive feedback interactions with the soil community. Klironomos’s results suggest that the biogeographic origin of a plant species is crucial to the direction of its interaction with soil microbes (although not clearly separated from the effects of locally low abundance), thus suggesting an important role for shared evolutionary histories. In Klironomos’s research, it appeared that plant species developed geographically tight coevolutionary relationships with pathogenic fungi, but loose (less host-specific) relationships with mutualistic fungi.

The highly contrasting soil feedback effects demonstrated by Klironomos (2002) set the stage for two recent studies in which a geographic context was explicit. In an explicitly biogeographic test of the Janzen-Connell hypothesis (Janzen 1970; Connell 1971) for local diversity, Reinhart et al. (2003) compared the effects of soil microbes on the growth of *Prunus serotina* in its native and in its invaded ranges. In the native North American range, the soil microbial community occurring near *P. serotina* strongly inhibited the establishment of neighboring conspecifics and reduced seedling performance in the greenhouse. In contrast, in the non-native European range, *P. serotina* readily became established in close proximity to conspecifics, and in greenhouse experiments the soil community enhanced the growth of seedlings. Previous research had demonstrated that soil-borne *Pythium* species (Oomycota) inhibit the survival, growth, and abundance of *P. serotina* in its home range in North America (Packer and Clay 2000, 2002). Although the genus *Pythium* is found around the world, genotypes are often host-specific (Deacon and Donaldson 1993; Mills and Bever 1998). These findings suggest that the loss of the coevolved relationship between fungal consumer and host plant in North America has facilitated the invasion of the host in Europe.

Callaway et al. (2004a) found that sterilization of European soils caused a 166% increase in the total biomass of *C. maculosa*, compared with only a 24% increase when North American soils were sterilized. The stronger suppressive effects of European soil biota lend experimental support to the demonstrations of much

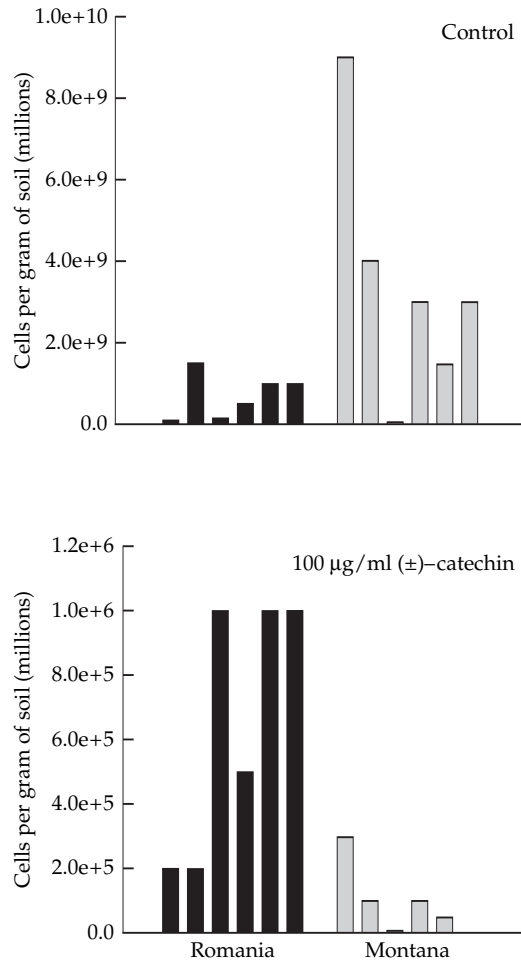
higher richness of fungal and viral infections on plant species in their home ranges than in invaded ranges (Mitchell and Power 2003) and indicate that *C. maculosa* in North America has escaped the controlling effects of soil biota.

Callaway et al. (2004a) further examined biogeographic differences in plant–soil microbe relationships in a feedback experiment. The microbial community in soil from a selected population in France was “trained,” or pre-conditioned (Bever et al. 1997; Bever 2002), by growing either *C. maculosa* or *Festuca ovina*, a perennial bunchgrass that is native to Eurasia, in the soil for several months. The microbial community in soil from a selected population in Montana was trained with *C. maculosa* or *F. idahoensis*, a bunchgrass similar to *F. ovina* but native to western North America. As would be predicted by Klironomos (2002), *C. maculosa* experienced negative feedback interactions with soil microbial communities from its native European region—*C. maculosa* plants grown alone in nonsterile French soil trained by conspecifics were significantly smaller than those grown in French soils trained by *F. ovina*. In contrast, *C. maculosa* experienced positive feedback interactions with soil microbial communities from its invaded range. *Centaurea maculosa* planted alone in Montana soils trained by conspecifics were significantly larger than those in Montana soils trained by *F. idahoensis*. Sterilization of the soils eliminated these feedbacks.

Considered together, the results of these feedback experiments suggest that *C. maculosa* is able to modify the microbial community in invaded soils to its advantage. In contrast, *C. maculosa* is inhibited by negative feedback in European soils, probably due to the accumulation of pathogens and, potentially, adaptation by inhibitory microbial populations to antimicrobial compounds produced by *C. maculosa* (Bais et al. 2003). If coevolutionary relationships between microbial pathogens and invasive plants exist, then negative feedbacks would be expected in the native range of the exotic species due to the accumulation of species-specific soil pathogens. In contrast, positive feedbacks should be observed in the invaded range, where the exotic species is largely free from species-specific soil pathogens (Klironomos 2002; Mitchell and Power 2003). If van der Putten (1997) is right about the potential for such feedbacks as a strong selective force, we should find many more examples of regionally specific plant–soil microbial relationships occurring on geographic mosaics.

In an experiment, not previously published, designed to explicitly test biochemically mediated evolutionary trajectories involving root exudates and soil microbes, we compared the effects of (\pm)-catechin on microbial communities extracted from soil in the rhizospheres of *C. maculosa* plants in six populations in Romania, thought to be close to the source of the invasive genotypes, and six populations in western Montana. In the controls, bacterial growth was uniformly high, but was far greater in isolates from Montana soils than in those from Romanian soils (Figure 13.1). This difference may possibly be due to the effects of transporting the soils across the Atlantic, although other explanations are possible, including potential trade-offs between (\pm)-catechin tolerance and absolute bacterial growth rates. Bacterial growth was reduced in both soil types by the catechin treatment, but bacterial growth in the isolates from Romanian

Figure 13.1 Growth of bacteria cultured from soil from the native range of *Centaurea maculosa* in Romania and its invaded range in Montana in control isolates and in isolates treated with (\pm)-catechin. Each bar represents an isolate from soil collected from the rhizosphere of one *C. maculosa* individual in one population. Note the large difference in scale between the treatments, such that the (\pm)-catechin treatment reduces the number of microbes by several orders of magnitude from control levels; note also that the degree of suppression by (\pm)-catechin is much greater for bacteria in soil from the invaded than from the native range. These results were garnered by taking 1 gram of soil from a randomly selected individual from each of six populations in each range, adding 9 ml of sterile phosphate buffered saline solution and 0.1% Tween 80, and vortexing to separate bacteria from soil particles. Isolates from each of these 12 solutions were plated onto R2A medium in two petri dishes containing 300 $\mu\text{g/ml}$ cycloheximide, added to inhibit fungal growth (total $n = 24$). For each pair of petri dishes, one was treated with an ethanol control and one was treated with 100 $\mu\text{g/ml}$ (\pm)-catechin/ethanol.



soils was over 7 times higher than in the isolates from Montana soils. Tentative identification of bacteria in the Romanian soils included *Micrococcus* sp., *Pseudomonas fluorescens*, *Staphylococcus* sp., and *Flavobacterium* sp. It would appear that microbial communities from the native range of *C. maculosa* have developed tolerance to (\pm)-catechin [probably the (+) enantiomer] due to a coevolutionary history. However, we do not know whether the particular microbial species in these (\pm)-catechin experiments are the same ones involved in the feedback experiments described earlier (Callaway et al. 2004a).

Invaders and the evolution of soil microbes

Plant-microbe interactions and relationships are often regulated by plant biochemistry (Bais et al. 2004), but we do not know of a parallel to the allelopathic

evidence we presented above for selection of resistance in native species in response to *C. maculosa* and the (\pm)-catechin it exudes (R. M. Callaway et al., unpublished data). Even though studies have not explicitly addressed the evolution of microbial communities in response to invasive species, it is reasonable to expect strong selection based on these interactions (van der Putten 1997). It has been suggested by van Breeman and Finzi (1998) that if the effect that a plant has on the soil alters the growth and survival of that plant, as in the feedback experiments we have described, then the soil can be considered part of the extended phenotype of the plant, and thus will be under selective pressure (see Thorpe and Callaway, in press, for a broader discussion of this idea). Microbes have short generation times and thus can respond to evolutionary pressures quickly, so they may respond relatively rapidly to pressures exerted by the invasion of exotic plants and the unique biochemicals they release. Although species-specific soil-borne pathogens are common (Agarwal and Sinclair 1997; Mills and Bever 1998; Blaney and Kotanen 2001), many soil-borne pathogens are generalists (Dix and Webster 1995). Thus, native pathogenic microbes may be able to adapt to a new invasive host relatively easily. As an example of this potential, *Sclerotinia sclerotiorum*, a generalist fungus native to North American intermountain prairies, causes very high mortality of *C. maculosa* when directly applied to the plant; however, this species does not disperse efficiently among *C. maculosa* individuals, even in dense populations of the weed (Jacobs et al. 1996; Ridenour and Callaway 2003). *Centaurea maculosa* certainly provides a large and untapped resource for consumers in North America, and perhaps selection will eventually result in an increased ability of local pathogens like *Sclerotinia* to utilize it—as suggested by the operation of the taxon cycle, in which invading species are expected to accumulate coevolved pathogens over time (Ricklefs, this volume).

We have emphasized the importance of escaping pathogens in invaded regions; however, not having a coevolutionary history with the organisms in a new region may also mean that the new species has no resistance to the pathogens that occur there. In other words, novel biochemical interactions may inhibit invasive success as well as promote it. Because most exotic introductions probably do not result in establishment, invasion, and suppression of the locals, this idea is very difficult to test. Nevertheless, future studies should consider this possibility, as it may present an important clue to a better understanding of the geographic mosaic of coevolution.

Conclusion

The idea that rhizosphere biochemistry can drive evolutionary trajectories in plant communities is derived completely from what we have learned from the study of invaders or comparisons of interactions between native and non-native species—the contrasts in biochemical (allelopathic) effects of *Centaurea maculosa* (Bais et al. 2003), *Centaurea diffusa* (Callaway and Aschehoug 2000;

Vivanco et al. 2004), *Alliaria petiolata* (Prati and Bossdorf 2004), and *Vaccinium myrtillus* (Mallik and Pellissier 2000) on neighbors in their native communities versus neighbors in their invaded communities. These biogeographic contrasts suggest that different evolutionary trajectories may occur in different plant communities, and in particular, in communities that are isolated from one another. When different evolutionary trajectories in communities are forced together, there may be the potential for exceptionally intense biochemical interactions.

Experiments demonstrating that invasive *Centaurea* species have stronger allelopathic effects on their new neighbors in North America than on their old neighbors in Eurasia suggest the possibility that coevolutionary relationships can develop among plant species over time. Furthermore, these results imply that biochemically based evolutionary trajectories are different in different parts of the world, and that mixing species from these different trajectories increases the potential for introduction of powerful novel weapons that are inordinately effective against naïve species. Ecologists must increase the number of studies of general allelopathic interactions that utilize persuasive experimental designs, integrate biochemical and ecological approaches, take explicit biogeographic perspectives, and link competitive biochemical processes to trophic interactions (see Siemans et al. 2002).

We must also reconcile the novel weapons hypothesis and the potential evolutionary responses of natives with other theory. For example, many invasive species appear to have undergone a “lag phase,” during which they spread very slowly or not at all (Kowarik 1995). If the novel weapons hypothesis is a valid explanation for some invasions, then it would seem that species with novel weapons would be highly successful from the beginning, and not undergo a lag phase. On the other hand, even exotics possessing novel weapons might be expected to experience lag phases, as these lags may occur for many reasons that are independent of the initial competitive advantage novel weapons may provide. Some potential reasons for these lags include the evolution of further increases in competitive ability after colonization has occurred (Holt et al., this volume), biological inertia exerted by the resident community on the invader (von Holle et al. 2003), and the dynamics of exponential population growth (whereby initial growth may appear to have a lag).

Another primary direction for future research would be to investigate adaptive evolution in specific microbial species in response to invasive plants. We also know very little about the effects of specific root exudates of invaders on microbial species, and to our knowledge, the experiment reported above on the comparative effects of (\pm)-catechin on Romanian and North American microbes is the only one of its kind. Exploring such biochemical processes will shed light on the geographic nature of plant–soil microbe coevolution and could allow integration of biochemical interactions among plants with those among plants and soil microbes. So far, biogeographic experiments on plant–soil microbe feedback (Reinhart et al. 2003; Callaway et al. 2004b) have not matched seeds from specific exotic plant populations with their co-occur-

ring soil microbes. Until local exotic plant populations and the soil microbial communities that occur with them are studied in comparative experiments, our understanding of escape from local pathogens will continue to be limited. We encourage experiments designed to link biochemical interactions among plants with those that occur among plants and microbes. For example, some forms of catechin are consumed by microbes (e.g., *Acinetobacter calcoaceticus* utilizes catechin as its only carbon source: Arunachalam et al. 2003), so abundant and novel root exudates such as (\pm)-catechin produced by invasive plants constitute a potential food source for the soil microbes in their new communities, but only after the microbes have adapted to eat those exudates. Exploring microbial consumption of such root exudates in soils from native and invaded communities will be important. Finally, understanding biochemically driven evolutionary processes among invasive plants and soil microbes may open the door to a greater understanding of the regulation of populations and coexistence among species in natural communities, as well as the collapse of such regulation and coexistence that is so common in many exotic invasions.

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