



7 The Effects of Plant–Soil Feedbacks on Invasive Plants: Mechanisms and Potential Management Options

Valerie T. Eviner¹ and Christine V. Hawkes²

¹ *Department of Plant Sciences, University of California, USA*

² *Section of Integrative Biology, The University of Texas, USA*

Introduction

There are countless examples of management projects that have attempted to decrease or eradicate invasive species at a site, only to have them rapidly recolonize within a few years. While this is often attributed to reinvasion through propagules remaining at the site, or high propagule pressure from the surrounding landscape (Leung *et al.*, 2004; Lockwood *et al.*, 2005), this also may be due to invasive species changing site conditions to favor conspecifics over native species. Many studies have documented that invasive plants can impact numerous soil properties and processes (Leffler and Ryel, Chapter 4, this volume; Ehrenfeld, 2010), and that invader impacts on soil can influence competitive dynamics between plant species, often favoring the invaders (Callaway and Aschehoug, 2000; Reinhardt and Callaway, 2006; Batten *et al.*, 2008; Kulmatiski *et al.*, 2008; reviewed in Eviner *et al.*, 2010). Some of the effects of invasive species on soils can persist after the invader has been removed, making the system more susceptible to reinvasion (reviewed in Eviner and Hawkes, 2008; Kulmatiski and Beard, 2011). In these cases, restoration efforts must be focused not only on removing invasive species, but also counteracting their effects on soil characteristics and processes (Heneghan *et*

al., 2008; Harris, 2009; Eviner *et al.*, 2010). In this chapter, we explore the mechanisms driving plant–soil feedbacks in invaded systems, and potential management tools to alter these feedbacks to be more beneficial to natives over invasive species.

The role of plant–soil feedbacks in shaping plant communities and plant invasions

Plant–soil feedbacks occur when a shift in plant community composition changes soil conditions, and these altered soil conditions further alter the plant community. Positive feedbacks occur when a given plant species alters the soil in a way that promotes its own persistence and growth (either directly by enhancing its own growth and that of conspecifics, or indirectly via greater inhibition of the growth of other species compared to conspecifics). Conversely, a plant species can alter a soil to its own detriment, or in a way that promotes other species more than itself, resulting in a negative feedback. Recent research has shown that plant–soil feedbacks can play an important role in shaping succession, species coexistence, species dominance, range expansion, and the success of invasive species (reviewed in Bardgett *et al.*, 2005;

Kardol *et al.*, 2006; Manning *et al.*, 2008; van der Putten *et al.*, 2009).

Plant–soil feedbacks are of particular relevance in understanding and managing species invasions, because positive feedbacks are more common in invaded communities, while negative feedbacks are more prevalent in native communities (Klironomos, 2002; Kulmatiski and Kardol, 2008; Kulmatiski *et al.*, 2008; van der Putten *et al.*, 2009). Of particular concern are cases of ‘invasional meltdown’ (Simberloff and Von Holle, 1999), when one invasive species changes the soil to enhance not only itself, but also the invasion of other non-native species. For example the invasion of *Bromus tectorum* enhances invasion of *Taeniatherum caput-medusae*, and invasion of *Taeniatherum* increases invasion of exotic forbs (reviewed in Eviner *et al.*, 2010). Similarly, the invasive *Bromus inermis* alters the soil microbial community to enhance the growth of the invader *Euphorbia esula* (Jordan *et al.*, 2008).

While, on average, invasive species are more likely than native species to create positive (or less negative) feedbacks, there are many exceptions to this general trend. Many plant–soil feedbacks are highly species-specific, so that a given invasive species may negatively impact a subset of native species, but not all of them, and different invaders are likely to impact different native species (Casper and Castelli, 2007; Manning *et al.*, 2008). In contrast to the general trends, some invasive species create soil conditions that generate negative feedbacks to conspecifics, while some native species create positive soil feedbacks to conspecifics and negative feedbacks to invaders (Kulmatiski *et al.*, 2004; van der Putten *et al.*, 2007). For example, in a shrub-steppe ecosystem in Washington State, USA, the native perennial grass, *Pseudoroegneria spicata*, alters soil in a way that decreases its own growth, but has even stronger negative effects on the invasive species *Centaurea diffusa*, reducing invader cover from 18% to 5% (Kulmatiski *et al.*, 2004). Promoting the specific native species that decrease the abundance of invasive plants can be a promising first step in restoration of native plant communities.

Invader plant–soil feedbacks enhance resilience of invaded state

Invasive species that generate positive feedbacks are of particular concern for conservation and restoration, because they often create a barrier to the reintroduction of native species. Regardless of what factors precipitated the initial success of an invader, established invasive species can alter the soil and create a ‘novel ecosystem,’ an alternative stable state that is difficult, if not impossible to revert back to the native state (Suding *et al.*, 2004; Seastedt *et al.*, 2008; Farrer and Goldberg, 2009; Hobbs *et al.*, 2009; Hardegree *et al.*, Chapter 6, this volume).

The degree of persistence versus reversibility of invader impacts on soils and associated ecosystem processes is a critical component of restoration potential. Some of the changes caused by invasive species may be rapidly reversible upon removal of the invader and do not require additional management. For example, decreased soil water availability caused by high plant transpiration rates should reverse quickly once the invasive plant species is removed. In contrast, alterations to soil properties such as soil structure, water infiltration, water holding capacity, carbon storage, and nitrogen cycling rates may persist for months to decades, even with active management (van der Putten *et al.*, 2009). In these cases, reinvasion is likely to take place before soil conditions can be restored, particularly if the altered state favors the invasive plant species relative to native species. For example, extensive erosion as a result of invasion of *Centaurea maculosa* (Lacey *et al.*, 1989) can take decades to centuries to reverse via soil formation processes and the gradual buildup of organic matter by the restored plant community. Such cases highlight the importance of disrupting invader–soil feedbacks early in the invasion process.

While invader-induced feedbacks may create a stable invaded state in an invader’s new range, these feedbacks do not always operate in the invader’s home range. For example, the negative effects of *C. diffusa* on its neighbors are much stronger in its

invaded range than its home range (Callaway and Aschehoug, 2000). In their home ranges, the invasive species are usually subject to the same negative plant–soil feedbacks common to native plants in general (Reinhart *et al.*, 2003; reviewed in Reinhart and Callaway, 2006). The existence of controls over invaders in their home ranges (e.g. through soil feedbacks, natural enemies, competitive effects, or of the evolution of neighbor resistance to allelochemicals), suggests that there may be long-term potential to control invaders in their new ranges through approaches such as bio-control agents or selection for native plant species that are resistant to the invader effects. Both of these will likely happen over the long term, even without active management. With increasing time since invasion, invaders tend to lose their initial advantage due to escape from negative interactions in the new range (Hawkes, 2007), and the invaders' impacts on the native community decrease (Strayer *et al.*, 2006; reviewed in Diez *et al.*, 2010). Alternatively, the invasive species may evolve to have increased competitive ability, which can strengthen both its negative impacts on native species and positive feedbacks to conspecifics. For example, an invader that benefits from its own litter buildup may evolve to have more recalcitrant litter, strengthening the positive feedback (Eppinga *et al.*, 2011). Because few studies have documented long-term impacts of invasive species on communities and ecosystems (reviewed in Strayer *et al.*, 2006), we are still unable to predict whether long-term presence of a specific invader will control versus enhance invasion through changes in the strength and direction of feedbacks.

Mechanisms of Feedbacks, and Potential Management Tools

Plant–soil feedbacks can be mediated through many mechanisms, including plant-induced changes to soil structure, chemistry, and biota (Ehrenfeld *et al.*, 2005; reviewed in Casper *et al.*, 2008), as well as the litter layer (Farrer and Goldberg, 2009). A number of

these mechanisms can be important in any given invasion, and little is known about their relative importance or the extent to which they strengthen or counteract one another to create overall positive versus negative feedbacks. While some mechanisms have similar management approaches for counteracting their associated feedbacks (Table 7.1), effective management will require knowledge of how feedbacks are generated by a given invader. Identifying the mechanisms driving feedbacks for an invasive species is often not straightforward, and even when they can be identified, management of these feedbacks is still largely in the experimental stage. This chapter highlights promising approaches to managing plant–soil feedbacks, but we recognize that continued research on management strategies is required, both across invasive species and sites, to improve these management tools and our ability to predict which approaches will be most effective for a given invader.

Litter

Plant litter dynamics are an important driver of plant community structure and ecosystem processes (reviewed in Ehrenfeld *et al.*, 2005). In general, increased litter accumulation often decreases plant diversity in herbaceous communities (Grime, 1979; Foster and Gross, 1998). Litter alters surface and soil microclimate, directly inhibiting the establishment of select species (Facelli and Pickett, 1991) or enhancing key plant herbivores or pathogens (Lenz *et al.*, 2003; reviewed in Flory and Clay, 2010). These physical effects of litter are often initially more important than associated nutrient feedbacks, which can take longer to develop (Amatangelo *et al.*, 2008). While invasive plant species can aggressively compete for resource uptake, in some cases, the litter, rather than the live plant, is directly responsible for the invader's impacts on the plant community and soil conditions (Farrer and Goldberg, 2009; Holdredge and Bertness, 2011). There are many examples where litter accumulation drives both

Table 7.1. Mechanisms that drive plant–soil feedbacks and potential management tools.

| Mechanism driving feedbacks | Potential management tools | Potential limitations |
|-----------------------------|--|--|
| Litter | Litter removal through mowing, burning, grazing/trampling | Timing is critical – may enhance or control invasion Not always possible at all sites or across broad scales |
| Allelochemicals | Activated charcoal | Also can impact nutrient availability, or inhibit the activity of other compounds |
| | Removal of invaders + time | Reinvasion can reintroduce the allelochemicals quickly |
| | Plant non-sensitive 'transition' species | Limited information available on which species may not be sensitive, and which can transition to the ultimate desired community |
| Soil microbial community | Activated charcoal | Also can impact nutrient availability, or inhibit the activity of microbes |
| | Plant 'transition' species which can tolerate invader soil or promote pathogens of invader | Interactions of plants and microbes are highly species-specific, so there is limited information on which species are impacted by, or resistant to given changes in the microbial community, and limited information on which species can transition to the ultimate desired community |
| | Soil inoculation | Local sources that specifically enhance native growth are usually not readily available, not always effective in establishing desired microbes |
| Nitrogen | Removal of N – burning, mowing, grazing | Disturbance may also enhance invaders and decrease natives in the short term |
| | Carbon additions to sequester soil N | Mixed effectiveness in sequestering soil N; have been shown to enhance, as well as inhibit invasion by some species |
| | Topsoil removal | Can disrupt native microbial community and seed bank |
| | Plant native species that take up high quantities of N | Often invaders are more aggressive than natives in taking up N, but has been effective in conjunction with burning and carbon additions |
| Salinity | Promote leaching of salts out of the upper layers of soil; method depends on soil, but can include increased water additions or promotion of soil drainage through increasing soil pores (through roots or soil organisms) | Can take a long time to reverse salinization, irrigation water may also add salts |
| | Plant salt-tolerant natives | Will not necessarily reverse salinity, or aid in reestablishment of natives that were on the site before it became saline |
| | Remove topsoil | Also removes nutrients, soil microbes, and seeds |

invasive plant species' impacts and feedbacks, including: *Typha × glauca* invasion into wetlands with associated increases in nitrogen availability and decreases in light and native species diversity and abundance (Farrer and Goldberg, 2009); *Taeniatherum caput-medusae* invasion into western US rangelands where its recalcitrant litter inhibits the germination of other species, leading to monotypic stands (Young *et al.*, 1971); and *Microstegium vimineum* invasion of northeastern US forests where the physical litter barrier inhibits native tree seedling establishment and reduces seedling survival through enhanced vole activity (Flory and Clay, 2010). Litter buildup can also promote fires, further leading to ecosystem alterations that may benefit invasive over native species (reviewed in Davies and Svejcar, 2008). Plant litter inputs are also one of the main mechanisms driving species' impacts on soil chemistry, structure, and biology (reviewed in Eviner and Chapin, 2003a).

Litter accumulation does not always benefit invasive plants. In some cases, the accumulation of litter from invasive plants may also benefit native species. In California, USA, coastal sage scrub, accumulation of invasive grass litter benefits a suite of invasive grasses, but also enhances growth of native shrubs by enhancing soil moisture availability (Wolkovich *et al.*, 2009). In other cases, native species may negatively affect invasive plant species through native litter accumulation. The invasive *M. vimineum*, for example, which benefits from its own litter, has lower seedling survivorship in patches where the litter of native species builds up (Schramm and Ehrenfeld, 2010). Litter can play a key role in shaping the community, but the relative feedbacks to invasive and native species may need to be considered in litter management strategies.

Management

Grazing, mowing, and burning are effective for litter removal and often increase native species in invaded stands (Sheley *et al.*, 2007; reviewed in Holdredge and Bertness, 2011). The seasonality of litter removal has

strong impacts on which species benefit, because timing of these disturbances can also greatly impact seed production (Pollak and Kan, 1996; DiTomaso *et al.*, 2006; Holdredge and Bertness, 2011).

Allelochemicals

A number of studies have suggested that some invasive species decrease the performance of native plant species through the release of allelochemicals: organic compounds that are either directly phytotoxic, or inhibit the activity of microbes that are symbiotic with plants (Wardle *et al.*, 1998; Ridenour and Callaway, 2001; reviewed in Bais *et al.*, 2006). For example, *Alliaria petiolata* can decrease the growth of native plant species by releasing compounds that decrease arbuscular mycorrhizal fungi (Stinson *et al.*, 2006). Similarly, *Carduus nutans* releases compounds that inhibit nodulation and nitrogen fixation in legumes, which is likely the cause for this invasive plant species decreasing the growth of a neighboring legume species (Wardle *et al.*, 1993, 1994). Other invaders that negatively impact native communities by releasing allelochemicals include: *C. maculosa* and *C. diffusa* (Callaway and Aschehoug, 2000; Callaway and Vivanco, 2007; Thorpe *et al.*, 2009), *Fallopia × bohemica* (Murrell *et al.*, 2011), and *Acroptilon repens* (Stermitz *et al.*, 2003).

Management

The most direct way to manage allelochemicals is to add compounds that can sequester these allelochemicals, thus inhibiting their impact on soil microbes and native plants. Activated carbon, also known as activated charcoal, is highly absorptive due to its high density of micropores and sequestration of compounds through ionic bonding or adsorption (reviewed in Kulmatiski, 2011), which has resulted in its common use for chemical purification and pollutant removal from water and air. Additions of activated carbon have been effective in decreasing the negative impact of

invasive species on native species in a number of systems (Callaway and Aschehoug, 2000; Ridenour and Callaway, 2001; Kulmatiski and Beard, 2006; Callaway and Vivanco, 2007; Lau *et al.*, 2008; Thorpe *et al.*, 2009; Kulmatiski, 2011). For example, the native grass *Festuca idahoensis*, when grown with the invasive *C. maculosa*, grew 85% larger with activated carbon than without (Ridenour and Callaway, 2001). It is important to note that activated carbon additions on their own are often not sufficient to decrease the abundance of invasive plants – clearing of invasive plants along with native seed planting is frequently required. In ex-arable fields in Washington State, USA, that were dominated by invasive plants for decades, the combination of clearing of invasive vegetation, a single application of activated carbon, and native seed additions shifted dominance from invasive to native plants, and this was maintained even after 6 years (Kulmatiski, 2011).

Allelochemicals can be highly species-specific in their impacts, which likely accounts for the fact that additions of activated carbon vary in their effectiveness in controlling invasive species, and may promote some, but not all native species (Lau *et al.*, 2008; reviewed in Kulmatiski, 2011). Activated carbon additions also can increase the prevalence of some invasive species (Kulmatiski and Beard, 2006; Lau *et al.*, 2008). Beyond the species-specific nature of activated carbon impacts, its use is far from straightforward because it not only sequesters allelochemicals, but also alters nutrient availability, rates of nutrient cycling, and the soil microbial community (Lau *et al.*, 2008; Kulmatiski, 2011).

Allelochemicals generally are short-lived in the soil (hours to days) (Blair *et al.*, 2005; Reigosa *et al.*, 2006), suggesting that activated carbon may be most useful to minimize the effects of invaders currently at a site, or early in restoration, when it can sequester allelochemicals from newly invading individuals. To ameliorate potential longer term legacies of allelochemicals deposited through plant litter (Reigosa *et al.*, 2006), best practices should include

removing all invasive plant material from a site.

Because the effects of allelochemicals are species-specific, another potential restoration approach is to plant native species that are not susceptible to these compounds (Perry *et al.*, 2005; Alford *et al.*, 2009). Plant species are being tested for innate resistance to the allelochemicals of the invasive *C. maculosa*. The establishment of these resistant species can prevent *Centaurea* from reinvading and may eventually facilitate the establishment of native species that are susceptible to these allelochemicals (Callaway and Aschehoug, 2000; Callaway and Vivanco, 2007; Thorpe *et al.*, 2009).

The allelopathic effects of invasive species on native species may decrease with time, as native species adapt to these inputs (Callaway *et al.*, 2005). Allelochemicals can have stronger impacts on heterospecific neighbors in their invaded ranges, compared to their home ranges (Bais *et al.*, 2003; Callaway *et al.*, 2008; Thorpe *et al.*, 2009), suggesting that there has been ongoing selection for resistance in the home range. Over time in the new range, the inhibitory effects of allelochemicals may decrease as native species similarly evolve resistance to invasive species (Callaway *et al.*, 2005; reviewed in Strayer *et al.*, 2006). Breeding of resistant native plant genotypes may be a potential management approach. With time since invasion, the impacts of allelochemicals on the soil microbial community can also vary. Comparisons of sites that had been invaded by *A. petiolata* for 20–50 years, demonstrated that resistance of the microbial community to allelochemicals increased over time. In the longest invaded sites, *Alliaria* populations decreased allelochemical inputs, further decreasing overall impacts of the invasion on the microbial community (Lankau, 2011). These cases suggest that invasions that are facilitated by allelochemical inputs may be controlled over the course of 4 to 5 decades through the strong selection imposed by allelochemicals on the native plant and microbial communities. However, this selection may be at the cost of decreased diversity (e.g. Lankau, 2011).

Soil microbial community

The soil microbial community frequently mediates soil feedbacks associated with invasive plant species, but their specific effects can be difficult to predict. For example, the soil microbial community is altered by invasion of *Aegilops triuncialis* into an herbaceous serpentine community, leading to decreased growth and flowering time of one native forb, *Lasthenia californica*, but not other native species (Batten *et al.*, 2008). Similarly, in the Great Plains, the soil microbial community is altered by the invasion of *Agropyron cristatum*, *B. inermis*, and *Eu. esula*; each invader benefits from the changes it induces, but only a subset of native species are affected by the altered soil community of each invasive plant species (Jordan *et al.*, 2008). The lack of apparent generality, and thus unpredictability, of invasive species effects on soil microbial communities may be partly due to our poor understanding of the specific microbial taxa and mechanisms responsible for the observed feedbacks.

Our understanding of the mechanisms underlying soil microbial community feedbacks is most developed for pathogens and symbionts. Some invasive plant species are successful because they have escaped soil pathogens common in their native range, and this release from pathogens makes them more competitive against native species, which commonly experience negative feedbacks with the soil pathogen community (reviewed in Reinhardt and Callaway, 2006). However, invasive plants can exacerbate this feedback, because their leachates enhance the pathogens of native species (Mangla *et al.*, 2008). In other cases, invasive plants may be successful because the benefit obtained from local mycorrhizal mutualists is greater than the negative effects of pathogens in the new range (Klironomos, 2002).

Invasive plant species are usually colonized by local mycorrhizal fungi and can have direct effects on the composition and abundance of the mycorrhizal community that can feed back to the plant community (Hawkes *et al.*, 2006; Stinson *et al.*, 2006;

Callaway *et al.*, 2008; Wolfe *et al.*, 2008). As with the general soil microbial community, the strength and direction of feedbacks from mycorrhizal fungi are context-dependent, based on factors such as the identities of the invader and fungi, the ecosystem, and the identities and life stages of neighboring native plant species (reviewed in van der Heijden and Horton, 2009). For example, in California grasslands, USA, the invasive forb *Carduus pycnocephalus* grows best in soils without arbuscular mycorrhizal (AM) fungi and its growth decreases AM fungal densities in soil, resulting in reduced colonization of native roots and decreased growth of the native forb *Gnaphalium californicum* (Vogelsang *et al.*, 2004; Vogelsang and Bever, 2009). Other invaders, such as *C. maculosa*, appear to tap into existing native mycorrhizal networks, essentially parasitizing resources, which results in substantial growth benefits (Marler *et al.*, 1999; Callaway *et al.*, 2003; Carey *et al.*, 2004). Invasive plants can also alter the composition of AM fungi mycorrhizae that colonize native plant roots. Invasion of annual grasses in California, USA (Hawkes *et al.*, 2006; Hausmann and Hawkes, 2009), as well as *C. maculosa* in Montana, USA (Mummey *et al.*, 2005), can shift the AM fungal community infecting native plant roots to substantially overlap with that of the exotic plants. While the mechanisms driving invasive plant effects on mycorrhizal communities are often unknown, in some cases, invasive plants that are less reliant on mycorrhizal fungi may release inhibitory compounds that can broadly reduce the abundance of mycorrhizal fungi in soil (Stinson *et al.*, 2006; Callaway *et al.*, 2008; Wolfe *et al.*, 2008). In other cases, invasive plants can associate with a subset of the mycorrhizal community, such as fungal generalists (Moora *et al.*, 2011) or those fungi most beneficial to the invader (Zhang *et al.*, 2010), which may promote the selected fungal taxa over others. In these cases, the network of mycorrhizal fungi supported by invasive plants may create a priority effect (reviewed in Hausmann and Hawkes, 2010).

Co-invasion by plants and their mycorrhizal fungi may also facilitate plant invasion

success through positive feedbacks, such as with *Pinus* species and ectomycorrhizal fungi in New Zealand (Dickie *et al.*, 2010). Where ectomycorrhizal associates are spatially limited, the spread of exotic *Pinus* species can also be limited (Nuñez *et al.*, 2009). More than 200 species of ectomycorrhizal fungi have been introduced to new ranges worldwide; these fungi are largely associated with plantation forestry (Vellinga *et al.*, 2009) and thus the spread of the ectomycorrhizal fungi and their plant hosts may be linked in many cases.

Management

As described above, when invader-induced feedbacks are strong enough to prevent the original native species from persisting long enough to alter soil conditions, a multi-stage successional approach can be employed by initially planting species that are more tolerant of the invaded soil conditions. This is feasible because most plant–microbial interactions are species-specific. Once the initial plantings ameliorate the invaded soil legacies, the target native community can be reestablished as seeds or transplants (Jordan *et al.*, 2008). This plant-induced change to the microbial community may take time. While changes in plant species can impact some components of the microbial community within weeks to months, the microbes mediating plant–soil feedbacks can persist unchanged for at least a growing season (Kulmatiski and Beard, 2011).

A more aggressive approach would be to plant native species that culture soil pathogens that decrease the growth of invasive species (Knevel *et al.*, 2004). Finding and promoting such native species could be a key tool for disrupting invasive species' positive feedbacks within the soil community. Even without intervention, the strength of negative feedbacks on invasive species increases with time since establishment, suggesting that over the long term, the soil microbial community may decrease the dominance of invasive species (Diez *et al.*, 2010).

Another management option is to interfere with the plant inputs that shape

the microbial community. Litter removal, or inputs of activated carbon to deactivate key plant metabolites have been effective in managing invasive species, but may also promote some invaders (reviewed in Kulmatiski, 2011). As described above, activated carbon can inhibit the impacts of allelochemicals on the microbial community. For example, in a case where a tropical invasive plant increases generalist soil pathogens, addition of activated carbon decreases pathogen spore numbers and increases native plant growth (Mangla *et al.*, 2008).

Few studies have assessed the impacts of disturbance regimes on invader–soil feedbacks. In Portuguese coastal dunes, fire decreased AM fungal colonization in all species, and rhizobial colonization in native, but not invasive legumes. Overall, fire enhanced invasive species performance by changing invader–soil biota feedbacks from neutral to positive, and native species feedbacks from negative to neutral (Carvalho *et al.*, 2010). The impacts of disturbance regimes on plant–soil feedbacks may be important to consider, because it may result in disturbance events that were meant to control invaders having the unintended consequence of strengthening of invader–soil feedbacks. While this example demonstrates that disturbance further strengthens invader feedbacks, disturbance may be effective in disrupting invader–soil feedbacks in other cases.

A number of studies have investigated the potential to inoculate soils with desirable microbial communities (reviewed in Vessey, 2003; Schwartz *et al.*, 2006). On highly degraded soils with a depauperate soil community, inoculation with microbes, particularly mycorrhizal fungi, can enhance plant establishment unless soil conditions are too stressful (Kardol *et al.*, 2009). Where sites dominated by invasive plants have an intact soil community, inoculation can be more complicated because the inoculated microbial community may be inhibited by the microbes already present (Kardol, *et al.*, 2009; Mummey *et al.*, 2009). However, in other cases, inoculation into intact communities can be effective. In the tallgrass

prairie of the Central Plains, USA, for example, inoculation with AM fungi increased the cover of native grasses over weedy plants (Smith, M.R. *et al.*, 1998).

The effectiveness of microbial inoculation in controlling invasive plants is also complicated by the ecological specificity of interactions between plants and their microbial communities. Inoculation can increase or decrease plant growth, depending on the identity of inoculated microbes, the plant species, and the environmental conditions (reviewed in Harris, 2009; Mummey *et al.*, 2009), which supports the use of local microbes for inoculation efforts. The source of inocula can have a strong impact on restoration success. Most commercial inocula contain generalist AM fungi that may not support the native plant community and may decrease soil mycorrhizal diversity (reviewed in Harris, 2009). While generating native inoculum can be challenging, it can be critical for effective results. For example, on degraded shrublands in Spain, the biomass of plants was twice as high when inoculated with a mixture of indigenous AM fungi compared to inoculation with an exotic AM fungus (Requena *et al.*, 2001). Pre-inoculation of native seedlings with desirable AM fungi may further help to minimize the AM fungal taxa associated with exotic species (Mummey *et al.*, 2009).

Nitrogen

While many nutrients are critical in regulating plant growth, interactions between invasive plants and nitrogen (N) are particularly important because N is the most commonly limiting nutrient to plant growth in temperate terrestrial ecosystems, and as such, has strong impacts on plant species composition and diversity (Eviner and Chapin, 2003b; reviewed in Clark *et al.*, 2007; Suding *et al.*, 2008). On average, invasive compared to native plant species, enhance N availability through increases in decomposition and N mineralization rates (Ehrenfeld, 2003; Corbin and D'antonio, 2004; Liao *et al.*, 2008), although some

invasive species decrease N availability, such as the invasion of *Ae. triuncialis* into grasslands of California, USA (Drenovsky and Batten, 2007), *Bromus tectorum* into western US shrublands (Bradley *et al.*, 2006), and *A. cristatum* into the northern Central Plains of the USA (Christian and Wilson, 1999). Whereas shifts in the soil microbial community tend to have species-specific impacts on plant growth, enhanced N availability often will increase the performance of most plants when grown alone in an invaded soil (Casper *et al.*, 2008). However, in mixed communities, increased soil N can shift plant community composition through selection for species that are more competitive (Clark *et al.*, 2007; Suding *et al.*, 2008). Of particular concern is that invader-induced increases in soil N availability will feed back to enhance invasion, because soils with high N availability are more susceptible to plant invasion (reviewed in Heneghan *et al.*, 2008; Suding *et al.*, 2008).

While the amount of soil N can be a key regulator of plant species composition, invasive species may also change the timing and location of N availability. For example, leaching from *Bromus tectorum* litter redistributes soil nitrate deep in the soil profile, where native grasses cannot access it, thus increasing N availability to *Bromus*. This enhances *Bromus* growth at the expense of the native grasses (Sperry *et al.*, 2006). *Bromus* also alters the timing of soil-N availability, with high soil-N availability occurring after the senescence of *Bromus* (Adair and Burke, 2010). Similarly, invasion of exotic grasses into Hawaiian woodlands greatly alters the seasonality of soil-N availability. Grass invasion shifts most net-N mineralization from the dry season to the wet season due to grass impacts on soil organic matter enhancing wet-season N cycling, and grass impacts on microclimate decreasing dry-season N cycling rates (Mack and D'Antonio, 2003). Invasive plants also can alter the form of N available. For example, in California grasslands, USA, invasive grasses increase the soil nitrifier population, and thus nitrification rates (Hawkes *et al.*, 2005). Conversely, the

invasion of *Andropogon garanus* into Australian grasslands inhibits nitrification (Rossiter-Rachor *et al.*, 2009). While there are not clear examples of native versus invasive species performance being impacted by the form of N, the relative amount of N available as ammonium versus nitrate has been shown to alter competition between species (reviewed in Marschner, 1986; Crabtree and Bazzaz, 1993).

Management

Soil nitrogen can be removed by repeated disturbances, including burning, grazing, or mowing and removal of vegetation, and this decrease in N can cause a shift from dominance by competitive, weedy species, to a more diverse plant community (reviewed in Marrs, 1993; Walker *et al.*, 2004; Perry *et al.*, 2010). In many cases, these techniques are also used to directly decrease the prevalence of invaders (e.g. by removing invasive plants before they set seed), and while the timing of disturbance may have minimal impacts on N removal, it will be critical in influencing which plant species reestablish (Pollak and Kan, 1996; DiTomaso *et al.*, 2006; Holdredge and Bertness, 2011). In the long term, repeated disturbances can reduce N availability, but in the short term, N availability can be enhanced immediately after disturbance, and in some cases, this increase in N can be sustained during the next few disturbance cycles (reviewed in Perry *et al.*, 2010), making the system vulnerable to reinvasion if invasive species propagules are present.

In extremely high fertility sites, such as those that have been fertilized for years, it can take decades to adequately restore target N cycles and the plant community through grazing, burning, or mowing (reviewed in Walker *et al.*, 2004). In these extreme cases, topsoil removal (also known as sod-cutting) can rapidly remove accumulated nutrients and organic matter, as well as soil microbes and many invasive plant propagules in the seed bank (reviewed in Marrs, 1993; Walker *et al.*, 2004). Topsoil removal is the most effective method of quickly and reliably removing N (Perry *et al.*, 2010), but it also

removes the native seed bank and microbial community, which will need to be restored. While effective, topsoil removal can only be used in smaller restoration projects, and is limited to sites accessible to heavy machinery.

Additions of biologically available carbon, such as sawdust or sugar (as opposed to the more inert activated carbon), can fuel growth of soil microbes, thus sequestering N in microbial biomass. This approach has been effective in reducing a number of invasions, and seems to be particularly effective in inhibiting grasses (rather than forbs or shrubs), and in shifting dominance from invasive annual to native perennial species (reviewed in Perry *et al.*, 2010). However, its effectiveness in reducing soil-N availability and controlling invasive species is variable, and often short-lived. In some cases, adding carbon can actually enhance N availability and/or invasive species (Blumenthal *et al.*, 2003; Krueger-Mangold *et al.*, 2006; Corbin *et al.*, 2007; Eviner and Hawkes, 2008; reviewed in Alpert, 2010; Eviner *et al.*, 2010; Perry *et al.*, 2010; Kulmatiski *et al.*, 2011). The amount and type of carbon needed to sequester N can vary by species and site (Blumenthal *et al.*, 2003; Prober *et al.*, 2005). In some cases, the amount of carbon needed may be prohibitive due to expense and logistics, suggesting that it may be a tool appropriate to small, high-intensity restoration sites, but may not be feasible across large areas (Perry *et al.*, 2010). Even when it is effective in sequestering N, much of this N is re-released within a few months to a few years, so this technique is most often effective in conjunction with quickly restoring native plant species (reviewed in Perry *et al.*, 2010).

Planting native species that decrease N availability through high N uptake has decreased the prevalence of some invaders. In rangelands of northwestern USA, planting *Secale cereale* or the native perennial grass *Elymus elymoides* decreased available soil N, shifting competitive dominance from the invasive *C. maculosa* to the native late-seral species *Pseudoroegneria spicata* (Herron *et al.*, 2001). Effective management often requires a combination of approaches; using

disturbance and/or carbon additions to temporarily decrease available N, in combination with fostering plants that can maintain low soil-N availability. For example, in Australian grasslands, the combination of burning, carbon additions, and seed additions of a native grass with high-N uptake (*Themeda triandra*) was required to effectively decrease weed cover and reduce soil nitrate to levels found on native-dominated sites (Prober and Lunt, 2009). Alternatively, if soil N can be adequately reduced by carbon additions or disturbance, low-N adapted plants can be introduced, and their low litter quality can feed back to maintain or further decrease low-N availability (reviewed in Perry *et al.*, 2010).

In instances where invasive plant species may inhibit nitrification through allelochemicals, activated carbon may be effective in binding these allelochemicals and increasing nitrification rates (reviewed in Lau *et al.*, 2008). In contrast, when invasive plant species enhance nitrification rates, commercial nitrification inhibitors can be used. These are commonly added to fertilized agricultural sites (Prasad and Power, 1995), and have been effective in decreasing some invasions, while enhancing native species (Young *et al.*, 1997, 1998).

Soil salinity

A few invaders have been shown to increase soil salinity, thus decreasing the performance of native competitors. Examples include *Tamarix* species (Smith, S.D. *et al.*, 1998; Ladenburger *et al.*, 2006), *Carpobrotus edulis* (Kloot, 1983), and *Halogeton glomeratus* (Harper *et al.*, 1996; Duda *et al.*, 2003). Conversely, invasion of brackish marshes by *Phragmites australis* decreases salinity (cited in Ehrenfeld *et al.*, 2005).

Management

Natural flooding and/or high rainfall can leach salts from soils in the short term, and can be used in conjunction with promoting native species tolerant of higher electrical

conductivity levels. However, in many cases, longer term decreases in salinity will require restoration of historic flood regimes and/or ground water-table levels (reviewed in Ladenburger *et al.*, 2006). Where invasive plants have redistributed salts to be concentrated at the soil surface, such as *Mesembryanthemum crystallinum* (Vivrette and Muller, 1977), topsoil removal may be required.

Disturbance as an important feedback pathway

While this chapter focuses on plant–soil feedbacks, invasive species can also greatly alter disturbance regimes to benefit themselves. For example, *B. tectorum* in the Great Basin, USA (Knick and Rotenberry, 1997), *T. caput-medusae* in the western USA (Davies and Svejcar, 2008), and invasive grasses in Hawaii, USA (D’Antonio and Vitousek, 1992), can increase fire frequency, thus enhancing their own growth at the expense of native species. *Brassica nigra* in California grasslands, USA, enhances herbivory of the native bunchgrass, *Nassella pulchra*, by small mammals, and this effect extends 30 m away from invaded patches (Orrock *et al.*, 2008).

Challenges in Understanding and Managing Feedbacks

It is clear that invasive plant species can alter the soil in a way that benefits their own performance, and in these cases, their effective eradication may require interference with invader–soil feedbacks. However, the study of feedbacks is still a relatively new field, and effective management requires a better predictive ability of feedback mechanisms and their relative importance, specificity, context-dependence, and spatial and temporal patterns (reviewed in Ehrenfeld *et al.*, 2005). Key challenges to understanding and managing feedbacks are discussed below.

1. Relative importance of different feedback mechanisms. Clearly, many mechanisms can

drive plant–soil feedbacks, and these mechanisms vary in both how specific their impacts are for various native species and which management approaches will likely be effective. Although some broad management techniques are similar in method (e.g. planting transitional species that can tolerate invasive species' soil legacies), the selection of native species will depend on the underlying mechanisms. Individual invasive species may have multiple mechanisms driving soil feedbacks that must be considered when attempting to ameliorate invasive soil legacies. For example, *B. tectorum* alters the amount and distribution of available soil N (Sperry *et al.*, 2006), as well as disturbance regimes (D'Antonio and Vitousek, 1992), and microbial communities (Belnap and Phillips, 2001; Hawkes *et al.*, 2006). The relative importance of different feedback mechanisms likely varies with the specific invasive species, native species, and site conditions. Where multiple mechanisms are at play, selection of restoration approaches will require knowing if one key feedback mechanism can be targeted, or if management of each feedback pathway is required.

2. Specificity of feedback mechanisms. As reviewed in this chapter, many feedbacks depend on the identities of the invasive and native species. Soil feedbacks from one invader can impact a number of native species, while a second invader in the same ecosystem can have feedbacks that affect an entirely different set of native species. As we increase the number of well-developed case studies of invader feedbacks, we will improve our understanding of the types of native plants that are more sensitive to specific changes in the soil physical, chemical, and biotic environment.

3. Context-dependence of feedbacks. Many studies have shown that the impacts of plant species on soils vary with environmental conditions and the amount of time an invader has been present (reviewed in Ehrenfeld *et al.*, 2005; Strayer *et al.*, 2006; Eviner and Hawkes, 2008). For example, in North America, *B. tectorum* can increase rates of N cycling in cool deserts, and decrease N-cycling rates in warmer arid

grasslands (reviewed in Ehrenfeld *et al.*, 2005; Ehrenfeld, 2010). Similarly, the strength and magnitude of feedbacks are likely to vary across space and time, and depending on which species are interacting (reviewed in Bardgett *et al.*, 2005; Eviner *et al.*, 2010). While some species consistently generate negative soil feedbacks to conspecific species across sites, the direction and magnitude of feedbacks can differ by site for other species (Casper *et al.*, 2008). In a particularly interesting example from an annual-herb-dominated community in the UK, eight plant species significantly differed in their effects on soil properties, which then fed back to impact the relative growth of these species. N enrichment did not impact the effects of these species on soil properties, but the interaction of N enrichment with plant effects on soils greatly altered plant growth responses to species-specific changes to soils (Manning *et al.*, 2008).

Time is a particularly important driver of context-dependence of plant–soil feedbacks. Vulnerability to pathogens differs with life stage for a given plant species, and in the extent to which mycorrhizal fungi can be negative or beneficial (reviewed in Bardgett *et al.*, 2005; Casper and Castelli, 2007; van der Heijden and Horton, 2009). The length of time an invader has been at a site has large impacts on the extent to which it changes the soil (reviewed in Strayer *et al.*, 2006), and can thus alter feedbacks (reviewed in Bardgett *et al.*, 2005). For example, *B. tectorum* has its strongest positive feedback in its third generation on a given soil (Blank, 2010). Changes over time may be due to the accumulation of impacts (e.g. accumulation of soil organic matter) or shifts in the relative strengths of positive versus negative feedback pathways (e.g. soil symbionts versus pathogens), as occurs during succession (Kardol *et al.*, 2007).

Another key time-related concern is the persistence of invader effects on soils, even after invasive plant species have been removed from a site. When an invader has been at a site for decades to centuries, its impacts on soil microbes, organic matter,

and nutrients can persist long after the invader has been removed (reviewed in Eviner and Hawkes, 2008; Eviner *et al.*, 2010). Even when an invader has been at a site for a short duration, its impacts on soil may persist long enough to interfere with native plant restoration (Grman and Suding, 2010).

4. Relative importance of feedbacks versus other drivers of invasion. There are many potential mechanisms driving invasions (Theoharides and Dukes, 2007), and a number of these may be operating simultaneously. It is critical to compare the relative importance of soil feedbacks to other mechanisms such as competition (Casper and Castelli, 2007), propagule pressure (Eppstein and Molofsky, 2007), and release from aboveground natural enemies such as herbivores and pathogens (Mitchell and Power, 2003; Agrawal *et al.*, 2005). For some invasive species, factors such as competition and climate are more important than soil-feedback effects (e.g. Yelenik and Levine, 2011). In other cases, invasive plant species dominance may be maintained by the combination of asymmetric competition generated through early germination and the negative feedbacks to native plants generated by soil legacies (Grman and Suding 2010). More work will be required to understand the role of soil feedbacks relative to other mechanisms in invasive species success.

5. How prevalent does an invader need to be to induce feedbacks? It is often assumed that the impacts of a plant species on the soil are proportional to its biomass in the community (Grime, 1998; Parker *et al.*, 1999), but recent work has shown that some invasive species can have significant impacts on soils even when they are relatively rare. For example, in a river floodplain in New Zealand, non-native plants made up less than 3% of plant community biomass, but had significant impacts on soil carbon, microbial biomass, and microbial community structure (Peltzer *et al.*, 2009). Similarly, varying proportions of native and invasive plant litter demonstrated that the effects of litter of the invasive *Berberis*

thunbergii on the soil microbial community were not proportional to its relative abundance in the mixture (Elgersma and Ehrenfeld, 2011).

Summary

While there is still much to learn about the role of plant–soil feedbacks in exotic plant species invasions, they clearly do play an integral role in some systems, and must be addressed to restore resilient native communities. Despite the considerable variation in the effects of invasive species across space and time within a specific area, current tools for altering plant–soil feedbacks show considerable promise and will be improved with more case studies and collaborations between land managers and researchers. While few ‘rules of thumb’ for management are available from this emerging field, some general principles do apply:

- As with other mechanisms of invasion (e.g. high propagule availability), the most efficient management approach will be to quickly eradicate new infestations of invasive species, before they are able to alter soil conditions to benefit themselves.
- Testing potential approaches to manage plant–soil feedbacks (Table 7.1) without knowing the mechanism driving the feedback can be risky. The species-specific nature of most of these feedback mechanisms indicates that many of these management techniques have a chance to promote, rather than control invasive species. In cases where the mechanisms are not known, trials should be small-scale and well monitored, before they are applied to broader areas of invasion.
- The mechanisms driving plant–soil feedbacks, and the strength and direction of these feedbacks can change greatly over time since invasion, as well as site-to-site. Thus, even when management has successfully disrupted invader–soil feedbacks at one site, preliminary trials under different conditions (or at sites

with a very different length of time since invasion) should be undertaken.

- Restoration of sites that have been invaded for decades are likely to have strong soil legacies that may not be quickly reversed. In these cases, screening for native species which can tolerate the invader-cultured soil may be the best first stage of restoration, when little is known about the mechanisms driving the invader–soil feedbacks.

More concrete management recommendations will undoubtedly emerge in this rapidly developing field. Setting up field trials with control areas as comparisons, and follow-up monitoring of these trials, will increase the rate at which such ‘rules of thumb’ are available.

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