

Immobilizing nitrogen to control plant invasion

Laura G. Perry · Dana M. Blumenthal ·
Thomas A. Monaco · Mark W. Paschke ·
Edward F. Redente

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Abstract Increased soil N availability may often facilitate plant invasions. Therefore, lowering N availability might reduce these invasions and favor desired species. Here, we review the potential efficacy of several commonly proposed management approaches for lowering N availability to control invasion, including soil C addition, burning, grazing, topsoil removal, and biomass removal, as well as a less frequently proposed management approach for lowering N availability, establishment of plant species adapted to low N availability. We conclude that many of these approaches may be promising for lowering N availability by stimulating N immobilization, even though most are generally ineffective for removing N from ecosystems (excepting topsoil removal). C addition and topsoil removal

are the most reliable approaches for lowering N availability, and often favor desired species over invasive species, but are too expensive or destructive, respectively, for most management applications. Less intensive approaches, such as establishing low-N plant species, burning, grazing and biomass removal, are less expensive than C addition and may lower N availability if they favor plant species that are adapted to low N availability, produce high C:N tissue, and thus stimulate N immobilization. Regardless of the method used, lowering N availability sufficiently to reduce invasion will be difficult, particularly in sites with high atmospheric N deposition or agricultural runoff. Therefore, where feasible, the disturbances that result in high N availability should be limited in order to reduce invasions by nitrophilic weeds.

Keywords Carbon addition · Ecological restoration · Fire · Grazing · Plant–soil feedbacks

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L. G. Perry
Department of Biology, Colorado State University,
Fort Collins, CO, USA

D. M. Blumenthal
Rangeland Resources Research Unit, USDA-ARS,
Fort Collins, CO, USA

T. A. Monaco
Forage and Range Research Laboratory, USDA-ARS,
Logan, UT, USA

M. W. Paschke · E. F. Redente
Department of Forest, Rangeland, and Watershed Stewardship,
Colorado State University, Fort Collins, CO, USA

L. G. Perry (&)
Fort Collins Science Center, 2150 Centre Avenue,
Bldg C, Fort Collins, CO 80525, USA
e-mail: Laura.Perry@colostate.edu

Introduction

Increased N availability results from a variety of natural or anthropogenic disturbances. N fertilizer in agricultural runoff increases the N supply to downstream ecosystems (Carpenter et al. 1998). Volatile forms of N (i.e., NO_x and NH_x) from fossil fuel combustion and agricultural volatilization increase wet and dry atmospheric N deposition, thus increasing N supplies globally (Galloway et al. 1995; Schlesinger 2009). On a local scale, soil disturbances increase available N by removing resident vegetation, reducing N uptake or altering N cycling (Davis et al. 2000; Norton et al. 2007). Finally, invasions by exotic plants sometimes increase N availability through symbiotic N_2 fixation or rapid N cycling (Corbin and D'Antonio 2004b).

Increased N availability may often facilitate plant invasions, both because it increases the supply of unused resources for invaders (Davis et al. 2000) and because resident species may be less competitive under conditions with high resource availability than many invasive species (Shea and Chesson 2002). In particular, increases in N availability may favor invasions by fast-growing, “weedy” species adapted to high resource availability at the expense of resident species adapted to low resource availability, including many desired, late-successional native species (Vitousek and Walker 1987; Tilman 1990; Bazzaz 1996). Species adapted to high resource availability tend to have higher relative growth rates than other species under high-nutrient conditions (Chapin 1980) but also tend to have high nutrient requirements, rapid tissue turnover, and high nutrient loss rates that limit their ability to compete with species adapted to low resource availability under low-nutrient conditions (Chapin 1980; Shipley and Keddy 1988; McLendon and Redente 1994). Thus, under high-nutrient conditions species adapted to high resource availability tend to dominate plant communities and suppress species adapted to low resource availability, while under low-nutrient conditions species adapted to low resource availability often dominate plant communities and suppress species adapted to high resource availability (Carson and Barrett 1988; McLendon and Redente 1992; Inouye and Tilman 1995; Kalmbacher and Martin 1996; Paschke et al. 2000). Although some invasive, exotic species are adapted to low resource availability (e.g., Funk and Vitousek 2007) and some desired, native species are adapted to high resource availability (e.g., Stromberg et al. 2007), invasive exotic species tend to be better adapted to high resource availability than most desired, native species, have high-resource traits compared to native species (Leishman et al. 2007; Pysek and Richardson 2007) and are more successful in high-resource environments than native species (Daehler 2003). Therefore, increases in resource availability might be expected to facilitate many exotic plant invasions, as well as invasions by weedy, native species adapted to high resource availability.

Among resources, N may be particularly likely to facilitate invasion because N tends to be a limiting resource in plant communities, including grasslands, wetlands, forests and tundra (LeBauer and Treseder 2008). Accordingly, increases in N availability often increase weedy or invasive species dominance, decrease native, late-successional species growth, and reduce diversity (e.g., Kalmbacher and Martin 1996; Young et al. 1997; Paschke et al. 2000; Seabloom et al. 2003; Suding et al. 2005). Increases in N do not facilitate all invasions, however (e.g., Brandon et al. 2004; Thomsen et al. 2006); effects of increased N on invasion depend on the nature of the invader, resident community, and ecosystem of interest.

In cases where high N availability facilitates plant invasion, controlling invasive species and restoring late-successional, native plant communities may require lowering N availability. Simply removing invasive species, chemically or mechanically, may provide temporary control, but is unlikely to limit reinvasion while N availability remains high. Disturbance associated with chemical or mechanical control may even increase N availability, facilitating reinvasion (e.g., Blumenthal et al. 2006). Addressing the causes of invasion, such as high N availability, rather than simply removing established invasive species, is more likely to reduce reinvasion and provide long-term control.

Here, we use a literature review to examine the potential efficacy of several commonly proposed management approaches for lowering N availability to control invasion, including soil C addition, burning, grazing, topsoil removal, and biomass removal (Marrs 1993; Suding et al. 2004a), as well as a less commonly proposed management approach for lowering N availability, establishment of plant species adapted to low N availability. We focus on papers that consider effects of the management approaches on N, rather than conducting comprehensive reviews of each approach. Thus, we do not evaluate the efficacy of the management approaches for controlling invasion temporarily by removing existing populations or for addressing other causes of plant invasion besides high N availability. We find that methods aimed at lowering N availability by stimulating N immobilization (i.e., C addition and establishment of plant species adapted to low N availability) have strong potential for invasive species control. Topsoil removal also lowers N substantially, but involves intense disturbance. Other approaches aimed at lowering N availability by removing N from ecosystems (i.e., burning, grazing, and biomass removal) most often do not lower total N meaningfully, but do lower N availability when they favor plant species that in turn stimulate N immobilization.

Soil C addition

To examine the effects of lowering N availability, most studies to date have used soil C addition to increase N immobilization. Labile C sources (e.g., sugar, sawdust, or wood chips), incorporated or leached into the soil, lower N availability through a sequence of effects on soil N processes. Briefly, the added C serves as a substrate for heterotrophic soil microbes and thus increases soil microbial biomass and activity (e.g., Zink and Allen 1998; Baer et al. 2003). Greater microbial biomass leads to greater microbial N uptake, thus increasing microbial N immobilization and lowering soil N availability (e.g., Baer et al. 2003; Averett et al. 2004). Soil microbes with adequate C are better competitors for N than vascular plants (Marion et al. 1982), so

the microbes are able to take up N that otherwise would be available to plants. In addition, in anaerobic soils C addition can increase activity of denitrifying bacteria and thus increase N loss via denitrification (e.g., Ullah and Faulkner 2006). C addition might not lower N availability if soil microbes are not C limited or if insufficient amounts of C are added for the particular environmental conditions. Also, labile C sometimes increases N availability, such as when plant rhizodeposition increases N mineralization (i.e., priming; Jones et al. 2004) or when low inorganic N stimulates biological N₂ fixation. However, most C addition studies that have measured N have observed significantly lower inorganic N with C addition (e.g., McLendon and Redente 1992; Schmidt et al. 1997; Young et al. 1997; Zink and Allen 1998; Michelsen et al. 1999; Morghan and Seastedt 1999; Paschke et al. 2000; Cione et al. 2002; Baer et al. 2003; Blumenthal et al. 2003; Monaco et al. 2003; Averett et al. 2004; Perry et al. 2004; Suding et al. 2004b; Huddleston and Young 2005; Prober et al. 2005; Vinton and Goergen 2006; Bleier and Jackson 2007; Eschen et al. 2007; Iannone et al. 2008; Blumenthal 2009; Rowe et al. 2009). Further, factorial experiments with C and N addition treatments have indicated that negative effects of C addition on plant growth are due to lower N availability (Schmidt et al. 1997; Michelsen et al. 1999; Blumenthal et al. 2003; Perry et al. 2004), although other mechanisms are possible, including immobilization of other nutrients, altered microbial community composition (Klein et al. 1996), or release of phytotoxic compounds during decomposition or fermentation (Ishii and Kadoya 1993).

C addition studies on desired and invasive species have had mixed results, suggesting that C addition will often, but not always, favor desired species over invasive species. In the most successful cases, C addition reduces invasive species growth and concurrently increases desired species growth, apparently because of reduced competition from the invasive species (Young et al. 1997; Zink and Allen 1998; Schultz 2001; Blumenthal et al. 2003; Perry et al. 2004; Prober et al. 2005; Eschen et al. 2007). In other cases, C addition favors desired species by reducing invasive species growth while either not affecting desired species growth (Horn and Redente 1998; Young et al. 1998; Alpert and Maron 2000; Paschke et al. 2000; Averett et al. 2004; Iannone et al. 2008; Kardol et al. 2008; Rowe et al. 2009) or reducing desired species growth less than invasive species growth (Eschen et al. 2006; Bleier and Jackson 2007; Blumenthal 2009). On the other hand, in some cases, C addition reduces desired species growth as much or more than invasive species growth (Morghan and Seastedt 1999; Haubensak 2001; Monaco et al. 2003; Monaco et al. 2004; Suding et al. 2004b; Gendron and Wilson 2007; Seastedt and Suding 2007). Further, in some cases, C addition does not reduce growth of invasive species or desired species

(Cione et al. 2002; Roem et al. 2002; Corbin and D'Antonio 2004a; Huddleston and Young 2005; Vinton and Goergen 2006; Mangold and Sheley 2008).

Effects of C addition on invasive and desired species depend on methods of C application, target species, and environmental conditions. With regard to methods, higher rates of C addition are more likely to influence soil N, invasive species growth, and desired species growth (Blumenthal et al. 2003). General prescriptions for C addition rates are difficult to make, however, because the amount of C necessary to stimulate N immobilization depends on environmental conditions, especially of the soil (Cabrera et al. 2005). With regard to target species, several studies have suggested that C addition may be particularly likely to control invasive annuals and favor perennials (McLendon and Redente 1992; Young et al. 1997; Zink and Allen 1998; Paschke et al. 2000; Blumenthal et al. 2003; Prober et al. 2005; Eschen et al. 2006; Rowe et al. 2009), as might be expected given that annuals often dominate early successional, high-N habitats (Bazzaz 1996) and often benefit more from increased N than perennials (e.g., Milchunas and Lauenroth 1995). Other studies have suggested that C addition may inhibit grasses more than forbs or shrubs (Alpert and Maron 2000; Averett et al. 2004; Eschen et al. 2006; Eschen et al. 2007). C addition might be expected to consistently favor species adapted to low N availability over those adapted to high N availability, regardless of life history or growth form. The one explicit test of this hypothesis, however, suggested that life history and growth form were better predictors of C addition effects than were Ellenberg N values (an index of N adaptation; Eschen et al. 2006).

Although C addition is often effective for reducing invasion in experimental settings, its usefulness for management is less clear. A major problem with applying C addition for management is monetary expense. Applying sucrose at just 1 kg m⁻² to 1 ha requires 10,000 kg of sugar, which costs a considerable amount to purchase, transport, and apply. Wood products such as sawdust are cheaper to purchase but still expensive to transport, and incorporating them into the soil involves expensive equipment, disturbs resident desired vegetation, and is physically impossible in many landscapes. Therefore, C addition is most likely to be feasible in areas where there is a local source of labile C, such as burned or cleared forests with wood available for chipping or agricultural landscapes that produce C-rich byproducts [e.g., sugar beet pulp (Kumar et al. 2009) or rice hulls (Rogers et al. 2001)]. C addition also may be appropriate for restoration of small and highly valued areas, such as remnant tallgrass prairie patches or small wetlands, or for testing on a small scale whether lowering N availability is an effective weed control method for larger sites. In most cases, however, less expensive approaches will be needed for lowering N availability.

Another potential problem with C addition is that its effects on N immobilization are temporary. Over time, the N immobilized in microbial biomass will be released again, as added C is lost via microbial respiration and soil C:N ratios decline, perhaps more rapidly with labile C sources such as sucrose (e.g., Morghan and Seastedt 1999), but also eventually (and sometimes rapidly) with more recalcitrant C sources such as sawdust or wood chips (e.g., Zink and Allen 1998; Cione et al. 2002; Monaco et al. 2003; Huddleston and Young 2005; Bleier and Jackson 2007; Eschen et al. 2007; Iannone et al. 2008). Sawdust effects on N availability can last for as little as 2 months (Iannone et al. 2008) to more than 3 years (Baer et al. 2003). Immobilized N also may be released when environmental stressors such as microbial grazers, freeze–thaw cycles, or hot, dry spells reduce microbial biomass (Vangestel et al. 1992; Jones et al. 2004). C sources could be added repeatedly to maintain low N availability, but even the benefits of several years of C addition can disappear when C additions cease (Prober and Lunt 2009), and adding C indefinitely is unlikely to be economically feasible. Indeed, any management approach that requires labor and money will be difficult to apply for very long. Therefore, the best methods for lowering N availability will be those that generate plant–soil feedbacks that maintain low N availability.

Establishment of low-N plant species

Fortunately, short-term management approaches such as C addition may have lasting effects on N availability and weed invasion if they facilitate establishment of desired, native species adapted to low N availability. For example, Prober et al. (2005) used C addition and burning to encourage establishment of a native tussock grass, *Themeda triandra*, in disturbed Australian grassy woodlands that had been invaded by exotic annuals. Once established, *T. triandra* itself lowered N availability by 30–60% relative to the resident vegetation (Prober et al. 2005; Prober and Lunt 2009), reduced exotic, annual forb cover, and increased native, perennial forb germination and survival and native grass cover (Smallbone et al. 2007; Prober and Lunt 2009), suggesting that over time *T. triandra* might restore both ecosystem function and native community composition. When C addition ceased after 3 years of regular additions, soil N availability and exotic species abundance remained low where *T. triandra* was seeded, but reverted to the undesired, starting conditions where *T. triandra* had not been seeded (Prober and Lunt 2009). Similarly, Iannone et al. (2008) used C addition to encourage establishment of native sedge meadow species in competition with an invasive grass, *Phalaris arundinacea*, in a restored Midwest US wetland. Once established, the sedge meadow community

reduced N availability by 69% and reduced *P. arundinacea* biomass by 78%.

Many species adapted to low N availability (hereafter “low-N species”) create and maintain low inorganic N concentrations. Firstly, low-N species often produce relatively recalcitrant, high C:N litter that slows N cycling and increases N immobilization (Vitousek and Walker 1987; Wedin and Tilman 1990; Hobbie 1992; Aerts and Chapin 2000; Fig. 1, Low-N system). In addition, low-N species may have lower minimum N requirements that allow them to continue to grow, capture available N, and thus reduce N availability under lower N conditions than weedy species (Tilman and Wedin 1991; Seabloom et al. 2003). For example, in Midwest US tallgrass prairie successions, early successional species adapted to high N availability (hereafter “high-N species”) are gradually displaced by later-successional, low-N species that have lower minimum N requirements, greater allocation to roots and higher C:N tissue and therefore maintain lower N availability (Tilman 1990). Once they are established, late-successional tallgrass prairie species reduce weed invasion more than early and mid-successional species do, in part via lower soil N availability (Blumenthal et al. 2005). Similarly, in coastal California grasslands with adequate summer moisture, native perennial grasses lower soil N availability more than exotic annual grasses and may displace exotic annuals given sufficient propagule pressure (Seabloom et al. 2003; Corbin et al. 2007). In Dutch heathlands, native shrubs maintain lower soil N mineralization rates than invasive grasses (van Vuuren et al. 1992; Berendse 1998) and suppress the grasses in the absence of nutrient pollution (Aerts et al. 1990). Thus, for plant communities in which the desired, native species are low-N species that compete well for limited N and generate plant–soil feedbacks that lower N availability, establishment of low-N species may be a promising approach for maintaining low N availability and controlling high-N weeds.

In those ecosystems where the desired, native species do stimulate N immobilization, simply waiting for native low-N species to establish may sometimes be sufficient to achieve low N availability and displace high-N weeds. However, natural successional processes sometimes take decades or centuries, which may be too long for invasive weed control. Further, when high-N, invasive species are abundant, they often generate feedbacks that increase N availability (Ehrenfeld 2003; Liao et al. 2008), because they produce low C:N litter that increases decomposition and N mineralization rates (Vitousek and Walker 1987; Hobbie 1992; Vinton and Burke 1995; Berendse 1998; Allison and Vitousek 2004; Fig. 1, High-N system). Therefore, short-term, intensive management to remove invasive species, introduce native species, or remove environmental stressors that inhibit succession often may be necessary to

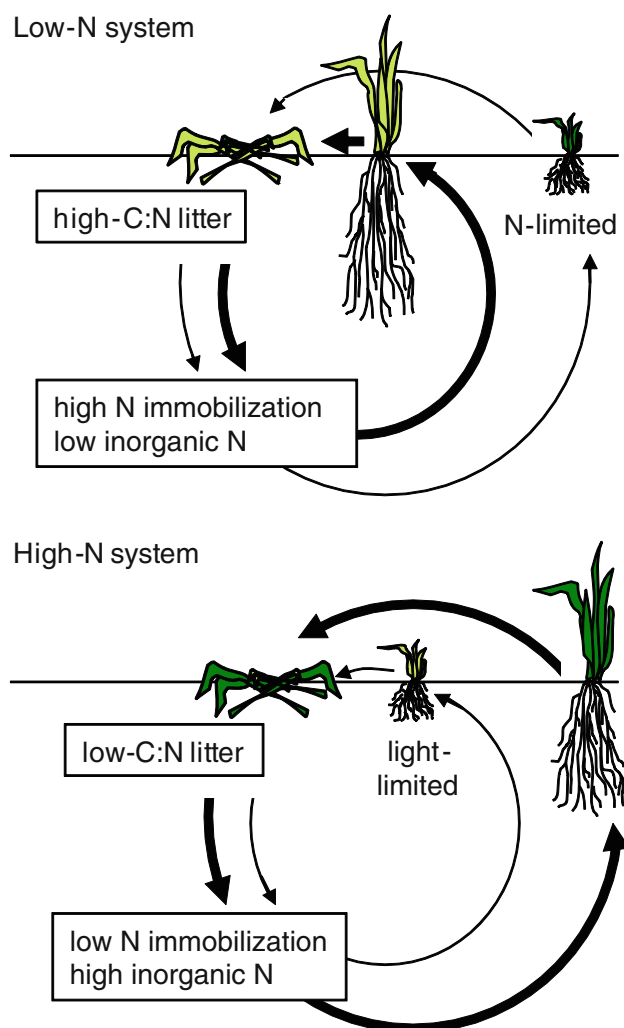


Fig. 1 Plant–soil feedbacks in relatively undisturbed, N-limited ecosystems with low available N (*Low-N system*) and ecosystems with high available N due to atmospheric N deposition, agricultural runoff, soil or vegetation disturbance, or biological N fixation (*High-N system*). Plants with lighter-colored leaves (*left*) represent low-N species (i.e., species adapted to low N availability), and plants with darker-colored leaves (*right*) represent high-N species (i.e., species adapted to high N availability). Low-N species are characterized by slow growth rates, high C:N litter, and low minimum N requirements compared to high-N species. *Thick lines* indicate the dominant production and decomposition components of the N cycle in each system. In low-N systems, dominant, low-N species increase N immobilization by producing relatively recalcitrant, high C:N litter, which decomposes slowly, limiting N mineralization. Because low-N species are better competitors for limited N, greater N immobilization increases their competitive advantage over high-N species. In high-N systems, dominant, high-N species decrease N immobilization by producing relatively labile, low C:N litter, which decomposes readily, increasing N mineralization. Because high-N species are better competitors under high-N, light-limited conditions, increased N mineralization increases their competitive advantage over low-N species

encourage establishment of native, low-N species that can then maintain low N availability (Suding et al. 2004a). In addition, management sometimes may be required to main-

tain established populations of low-N species. For example, under high-N conditions, burning or biomass removal may be necessary to remove excessive litter and thus prevent mortality of the native, low-N grass *T. triandra* in Australian grassy woodlands (Prober et al. 2009).

An important question is: how much N can be immobilized by established low-N species? High N deposition rates allow high-N species to displace established, low-N species in some ecosystems (Bobbink et al. 1998), suggesting that the presence of low-N species may not always be sufficient to maintain low N availability. When high rates of N deposition or agricultural runoff continue to increase N availability indefinitely, low-N species may not be able to continue to immobilize enough N. Further, even when N inputs are low, there is likely an upper limit to the amount of N that low-N species can immobilize over acceptable time-scales for invasive weed control. While N immobilization by low-N species can lead to very low soil N availability despite high total N in late-successional tallgrass prairie and conifer forest (Risser and Parton 1982; DeLuca et al. 2002), such intense N immobilization develops over centuries. Over shorter time-scales, low-N species may immobilize only smaller quantities of N (DeLuca et al. 2002; McLauchlan et al. 2006). Therefore, low-N species may be able to immobilize sufficient N to inhibit invasion only when N availability is below certain thresholds (Prober et al. 2009). Establishment of low-N species may be most effective for lowering N availability and controlling high-N weeds when high N availability is due to local soil disturbances rather than to increased N inputs, or when high N inputs can be reduced (e.g., by reducing N in local agricultural runoff).

Burning

In some areas, repeated prescribed burning may be a relatively affordable tool for both lowering N availability and encouraging low-N species that can then maintain low N availability by increasing N immobilization. Although fires can cause an initial flush in inorganic N and N mineralization (Wan et al. 2001), repeated fires also can lower soil N availability, at least in many grasslands (Ojima et al. 1994; Blair 1997; Turner et al. 1997; Fynn et al. 2003; Dijkstra et al. 2006). Fires lower N availability in part by volatilizing plant tissue N and thus reducing the total soil-N pool. In addition, repeated fires can favor low-N plant species that produce large quantities of high C:N root or leaf litter and thus slow N cycling and increase N immobilization (Ojima et al. 1994; Dijkstra et al. 2006; Fig. 1, Low-N system). For example, in established tallgrass prairie, fires remove leaf litter and thus reduce shade, favoring species that are stronger competitors for N, rather than light, and that have

greater root production, N use efficiency, and tissue C:N; as a result, fires reduce N mineralization (Blair 1997). Both N volatilization and altered plant community composition may contribute to effects of fire on N availability, but changes in plant community composition appear to be more important than lower total N for explaining effects of fire on N cycling in at least some ecosystems (Dijkstra et al. 2006). In disturbed or N-enriched areas dominated by weedy species, repeated fires might have similar effects, shifting predominantly light-limited communities to N-limited communities and thus encouraging dominance of strong competitors for N that in turn can maintain low N mineralization rates. A number of studies have found that burning can favor native, desired species over invasive exotic species, sometimes simply by reducing invasive species seed production or recruitment (DiTomaso et al. 2006), but also sometimes by reducing exotic species growth (e.g., Stacy et al. 2005; Brudvig et al. 2007), which could be linked to effects on soil N.

Fire does not, however, lower N availability or favor native over exotic species in all plant communities. For example, in ponderosa pine forest, fire increases N mineralization by removing recalcitrant leaf litter on the soil surface that slows N cycling in the absence of fire (DeLuca and Sala 2006). Similarly, in Hawaiian submontane woodlands, fire increases N mineralization by favoring exotic grasses with labile litter that releases N rapidly rather than native trees with more recalcitrant litter (Mack et al. 2001). Further, in Great Basin grasslands, fire promotes invasion by *Bromus tectorum* (Knapp 1996), which initially reduces N mineralization (Evans et al. 2001) but eventually increases N availability, particularly in subsurface soil (Sperry et al. 2006). Fire also may promote some N₂-fixing species, such as the shrub *Ceanothus cordulatus* in Sierra Nevada forests (Oakley et al. 2003), which then increase soil N. Thus, fire may be effective for lowering N availability and controlling high-N weeds, but only when the desired species are both fire-adapted and generate plant-soil feedbacks that maintain low N availability in response to fire.

Grazing

Livestock grazing has been suggested as a method for removing N from ecosystems (Marrs 1993), and can also alter N cycling (Pastor et al. 2006). Grazers influence N availability in part by redistributing plant tissue N, either concentrating it where they defecate or urinate or removing it via movement to off-site locations, urea volatilization, and eructation of gases (Marrs 1993; Augustine 2003). However, the few studies that have examined effects of cattle or sheep harvests on N budgets suggest that they remove

relatively little N compared to other N inputs and outputs (Lauenroth and Milchunas 1991; Marrs 1993). Instead, grazing, like fire, may influence N availability by encouraging low-N species that slow N cycling and increase N immobilization (Fig. 1, Low-N system). Unfortunately, grazing is more likely to achieve this in sites that are already relatively N limited than in highly N-enriched ecosystems where lowering N availability might be most useful for invasion control (Augustine and McNaughton 1998; Bardgett and Wardle 2003). In less productive, nutrient-limited ecosystems, such as the Minnesota sandplain and Texas tallgrass prairie, selective grazing or browsing on more palatable species favors less palatable species (Brown and Stuth 1993; Anderson and Briske 1995; Ritchie et al. 1998; Sirotnak and Huntly 2000), which often have higher C:N tissue (e.g., Pérez-Harguindeguy et al. 2003) and slower decomposition and N mineralization rates (Grime et al. 1996; Cornelissen et al. 1999; Bardgett and Wardle 2003; Pastor et al. 2006). Slower N mineralization in turn favors less palatable species and other species with high tissue C:N ratios, further slowing N mineralization (Hobbie 1992; Wardle et al. 2004).

In contrast, in more productive, fertile ecosystems, such as the Serengeti, more palatable species may be able to support herbivory without being displaced by less palatable species (Augustine and McNaughton 1998; Pastor et al. 2006). Thus, herbivory does not necessarily affect community composition in the same way in fertile ecosystems as in infertile ecosystems. Further, grazing in fertile ecosystems sometimes increases N mineralization rates and soil inorganic N pools (McNaughton et al. 1997; Frank and Groffman 1998; Johnson and Matchett 2001), perhaps because productive ecosystems can support large herbivore populations that ingest a large proportion of net productivity and convert it to more labile forms (i.e., urine and feces), leaving less N immobilized in plant tissue and litter (Bardgett and Wardle 2003). Increased inorganic N in turn favors species with rapid growth rates and low C:N tissue, which maintain high N mineralization rates and herbivore populations (Hobbie 1992; Wardle et al. 2004; Fig. 1, High-N system).

The exact environmental conditions that determine whether grazing reduces or increases N mineralization are uncertain. Current working hypotheses suggest that grazing may be more likely to favor low-N species and increase N immobilization in ecosystems where N, rather than water or light, is the primary limiting resource (Ritchie et al. 1998) or where tissue N of the desired, low-N species is <1.5% (Pastor et al. 2006). Thus, in ecosystems that are already N limited grazing may be a useful tool for maintaining low N mineralization rates and low N availability, but in highly N-enriched ecosystems grazing may be more likely to increase N mineralization than to reduce it. Also, as with

fire, for grazing to be a useful tool for maintaining low N availability in relatively unproductive ecosystems, the desired plant species must be both grazing-adapted and capable of generating plant–soil feedbacks that maintain low N availability. Other potential effects of grazing, such as soil and vegetation disturbance, selective herbivory on desired species over less palatable invasive species, and altered seed dispersal, also must be considered before using grazing for soil N management (van der Wal et al. 2003; Mouissie et al. 2005; Lunt et al. 2007).

Topsoil removal

Topsoil removal is the fastest and most effective method for removing N, because typically most of the total N pool is held in the uppermost layers of soil (Hardtle et al. 2006). The material sometimes can be sold to defray the costs of removal (Marrs 1993). Many experiments have demonstrated that topsoil removal favors species associated with nutrient-poor environments over those from nutrient-rich environments (e.g., Choi and Pavlovic 1998; Tallowin and Smith 2001; Allison and Ausden 2004; Buisson et al. 2008). Inverting the soil to bury topsoil beneath nutrient-poor subsoil has similar effects (e.g., McLendon and Redente 1990). Few studies, however, have identified the mechanisms behind effects of topsoil removal on plant community composition. Some studies have suggested that effects of topsoil removal were due to lower P or K availability (Tallowin and Smith 2001; Allison and Ausden 2004), but effects of topsoil removal may have been due to lower N availability in other studies. Because topsoil removal constitutes such a large disturbance, it is appropriate only when desired communities are adapted to sod removal, such as some European heathlands, or when little of the resident community is desired, such as during restoration of highly invaded or disturbed areas. Even then, topsoil removal can inhibit desired species substantially (Kardol et al. 2008). Topsoil removal has numerous other effects besides lower N availability, including removal of seed banks (Bakker et al. 2005) and soil flora and fauna (Vergeer et al. 2006), and altered soil structure and chemistry (van den Berg et al. 2003), which must be considered when deciding whether to use this approach.

Biomass removal

Plant biomass removal, via cropping or haying, is less effective for removing N than topsoil removal, because plant aboveground biomass typically contains a much smaller portion of the total N pool than does topsoil (Hardtle et al. 2006). Biomass removal may be preferable

in many cases, however, to avoid undesired effects of topsoil removal. In restoration of highly disturbed areas, planting and harvesting arable crops before beginning the restoration could remove considerable quantities of N (Marrs 1993; Marrs et al. 1998). Many arable crops have high productivity, high N requirements, high tissue N concentrations, and high allocation to aboveground tissue, which make them good candidates for rapid N removal (Chapin 1980). The few tests of this approach, however, have found that while cropping removed considerable quantities of N, it resulted in small to no reductions in plant-available, inorganic N (Marrs et al. 1998; McCrea et al. 2001). Effects of cropping on restoration success and weed abundance have rarely been examined (but see Jones 1993).

In less degraded areas, where the disturbances associated with cropping or topsoil removal would be undesirable, repeated mowing or haying of resident vegetation and removal of the biomass also can remove N (Marrs 1993; Mitchell et al. 2000). Although biomass removal has been expected to reduce total N, effects of mowing and haying (followed by biomass removal) on total N have tended to be small or undetectable (Halassy and Török 1997; Maron and Jeffries 2001; Tix et al. 2006). Also, reductions in inorganic N and N cycling have been observed only rarely (Halassy and Török 1997; Maron and Jeffries 2001; Tix et al. 2006), and effects on productivity are inconsistent even within studies (Berendse et al. 1992; Oomes et al. 1996). Nevertheless, mowing could reduce N availability if it favors plant species with high C:N tissue that slow N cycling (Fig. 1, Low-N system). In particular, effects of mowing on community composition and N availability might be similar to effects of burning, because both mowing and burning remove aboveground biomass and increase light (Tix et al. 2006). Mowing in N-enriched grasslands sometimes favors perennials over annuals (Maron and Jeffries 2001; but see Seabloom et al. 2003; Bonanomi et al. 2006) and species associated with nutrient-poor sites over those associated with nutrient-rich sites (Bobbink and Willems 1991; Bakker et al. 2002; Halassy and Török 2004), suggesting that over time mowing could increase litter C:N concentrations and thus slow N cycling. However, such indirect effects of mowing on N cycling have not been demonstrated.

Conclusion

Numerous C addition studies published over the past two decades suggest that lowering soil N availability may reduce or prevent many plant invasions. Lowering N availability may reduce invasion by simply reducing invasive species growth, by increasing the competitive ability of desired species, or by interrupting feedbacks between invasive species and soil N availability (Fig. 1, High-N system).

Among methods for lowering N, most have only small effects on total N, suggesting that lowering total N for invasive species control will be difficult without intensive disturbances such as topsoil removal. Lowering N availability by increasing N immobilization, instead of removing N from ecosystems, appears more promising. Establishment of low-N species, C addition, burning, grazing, and plant biomass removal, while seemingly disparate management approaches, all may be most effective for lowering N availability in the long-term when they favor low-N species that have high C:N litter and high N uptake efficiency and thus generate plant–soil feedbacks that increase N immobilization (Fig. 1, Low-N system).

The degree to which increasing N immobilization will control invasion is likely to depend on environmental conditions. In particular, desired, native species are most likely to lower N availability and control invasion in ecosystems that were historically N limited. Most of the research to date on lowering N availability for invasion control, and much of the research on effects of plant community composition on N cycling, has been conducted in grasslands and grassy woodlands. Therefore, our conclusions are most likely to be robust for these biomes. However, established, low-N species also can lower N availability, and lowering N availability also can reduce invasion, in wetlands (Perry et al. 2004; Iannone et al. 2008) and shrublands (Young et al. 1997; Berendse 1998; Zink and Allen 1998; Paschke et al. 2000; Schultz 2001; Rowe et al. 2009). There is less evidence to suggest that lowering N availability will reduce invasion in forests. Although N can be a limiting resource in forests (LeBauer and Treseder 2008), and low-N tree species, once established, can immobilize large amounts of N (DeLuca et al. 2002), lowering N availability did not reduce invasion in the one C addition study conducted in a forest (Cassidy et al. 2004). In addition, the management approaches that might favor low-N, native species may vary among biomes. For example, the effects of burning, grazing and mowing have been most studied in grasslands and grassy woodlands, and seem most likely to benefit low-N, native species in these biomes, whereas other management approaches might be required to encourage low-N species in wetlands or shrublands.

Using low-N plant species to stimulate N immobilization and control plant invasion will require research to understand both where this strategy is likely to be effective and how to implement it effectively in these areas. Research is needed to quantify how much N different low-N species can immobilize, in order to identify circumstances where N immobilization by low-N species might counterbalance current N availability and future N inputs. For example, N immobilization may be most effective for invasion control when current N inputs are low, such as when high N availability is the result of previous disturbances or plant–soil

feedbacks mediated by high-N invaders. However, N immobilization also might be effective for invasion control when high N availability results from atmospheric N deposition or agricultural runoff, which make up an increasing proportion of the global N budget (Schlesinger 2009), if the low-N species in a given ecosystem are able to immobilize sufficient N to counterbalance local rates of N pollution (Holland et al. 2005). Research also is needed to improve predictions of which invasive species are likely to be inhibited by N immobilization. Perhaps most importantly, we will need to identify the circumstances under which management practices such as seed addition, C addition, burning, grazing or biomass removal will favor desired, low-N species over invasive, high-N species. To the degree that short-term management can be used to increase desired, low-N species, it may lead to long-term increases in N immobilization and community resistance to invasion.

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