

## Invited Review

# Creating Invasion Resistant Soils via Nitrogen Management

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Invasion by annual grasses, such as cheatgrass, into the western U.S. sagebrush-steppe is a major concern of ecologists and resource managers. Maintaining or improving ecosystem health depends on our ability to protect or re-establish functioning, desired plant communities. In frequently disturbed ecosystems, nutrient status and the relative ability of species to acquire nutrients are important drivers of invasion, retrogression, and succession. Thus, these processes can potentially be modified to direct plant community dynamics toward a desired plant community. The overall objective of this review paper is to provide the ecological background of invasion by exotic plants and propose a concept to facilitate the use of soil nitrogen (N) management to achieve desired plant communities that resist invasion. Based on the literature, we propose a model that predicts the outcome of community dynamics based on N availability. The model predicts that at low N levels, native mid- and late-seral species are able to successfully out-compete early-seral and invasive annual species up to some optimal level. However, at some increased level of N, early-seral species and invasive annual grasses are able to grow and reproduce more successfully than native mid- and late-seral species. At the high end of N availability to plants, the community is most susceptible to invasion and ultimately, increased fire frequency. Soil N level can be managed by altering microbial communities, grazing, mowing, and using cover crops and bridge species during restoration. In these cases, management may be more sustainable since the underlying cause of invasion and succession is modified in the management process.

**Nomenclature:** Cheatgrass, *Bromus tectorum* L. BROTE.

**Key words:** Invasive plant species, competition, growth rate, succession, plant available nitrogen.

Invasive plant species negatively affect agricultural and wild lands throughout North America by displacing native species, altering ecological processes, reducing wildlife habitat, degrading ecosystems, and decreasing productivity (DiTomaso et al. 2006; Masters and Sheley 2001). Invasive plants occupy over 100 million ha and are considered the second most important threat to biodiversity after habitat destruction (National Invasive Species Council 2001; Pimm and Gilpin 1989; Randall 1996; Whittenberg and Cock 2001). Westbrooks (1998) estimated the cost of invasive plant species to be \$13 billion per yr in the United States alone in 1994. In spite of major programs implementing integrated pest strategies, the amount of land overrun by invasive plants is rapidly increasing and the negative impacts associated with invasion are escalating

(Randall 1996; Westbrooks 1998).

Traditional methods for controlling invasive plant species on rangelands have largely relied on treating invasive plants, which are a symptom of some altered ecological process, rather than modifying the ecological processes that facilitate their invasion and disrupt natural successional dynamics (Hobbs and Humphries 1995; Sheley and Krueger-Mangold 2003; Sheley et al. 2006). Although a completely developed and unified model for managing invasive plants via nutrient management has not been developed, the potential to make significant progress by building on our knowledge of nutrient management relative to invasive plants is enormous.

In native plant communities, nutrient availability to plants tends to decrease as secondary succession proceeds in arid and semi-arid systems (McLendon and Redente 1992). Invasion by exotic plant species often follows changes in soil processes, particularly N and carbon (C) cycling (Ehrenfeld and Scott 2001) and can alter nutrient availability to plants (Jobbagy and Jackson 2001). In

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North America, many late-seral species have relatively slow growth rates, but are intensely competitive for nutrients in limited supply (Arredondo et al. 1998; Daehler 2003; Harpole 2006). This implies that they tend to dominate under low nutrient conditions. Increased nutrient availability can favor the invasion and success of invasive plant species in ecosystems where resource availability is typically low (Ehrenfeld 2003; Huenneke et al. 1990; Norton et al. 2007; Sperry et al. 2006). After water, N is often considered the next most limiting resource in arid and semi-arid ecosystems (Daehler 2003; James et al. 2005; Schaeffer and Evans 2005; Smith et al. 2000). Furthermore, competition for N by plants is thought to be generally greater than for other macronutrients (Krueger-Mangold et al. 2006). Therefore, the ability of a native species to lower critical soil resources to the point where they are unavailable to invasive species gives the native species a competitive advantage (Herron et al. 2001; Tilman 1988). Thus, it may be possible to prevent and/or manage invasive plant species by managing soil N availability to plants.

The literature on managing nutrient availability with respect to invasive plants is only partially developed, and much of the data were developed in the sagebrush-steppe plant communities (Bradley and Mustard 2006; D'Antonio and Vitousek 1992; Kyser et al. 2007; Young and Allen 1997). Invasive annual grass establishment and dominance of plant communities is one of the most significant and destructive plant invasions in North America. Invasive annual grasses that are a major concern in the sagebrush-steppe ecosystem include downy brome (cheatgrass, *Bromus tectorum* L.), medusahead [*Taeniatherum caput-medusae* (L.) Nevski], North Africa grass [*Ventenata dubia* (Leers) Coss. in Dur.], ripgut brome (*Bromus diandrus* Roth), Japanese brome (*Bromus japonicus* Thunb. ex Murr.), and rattlesnake brome (*Bromus briziformis* Fisch. & C. A. Mey.). For example, *B. tectorum* has infested over 22 million ha in the 17 western states (Belnap et al. 2005; Duncan et al. 2004) with an estimated cost of controlling *B. tectorum*-fueled fires at about \$20 million/yr (Knapp 1996). The introduction of *B. tectorum* has increased the fire frequencies in this system from 30 to 110 yr to 3 to 5 yr, especially in lower elevations (Chambers et al. 2007). The increase in fire frequency has caused major changes in species richness, vegetation composition, structure, ecosystem processes, and wildlife habitat (Knapp 1996; Pyke et al. 2003).

The search for effective methods for managing invasive plants, especially annual grasses, has been highly elusive. The need for management strategies that address the underlying ecosystem processes that facilitate invasion and drive succession is substantial and unmet. Past and recent discoveries about nutrient cycling, invasion, and succession suggest that insights about nutrient management may

provide ecologically-based integrated strategies that address some of the underlying causes of invasion and plant community dynamics.

Our overall goal is to provide the ecological background and propose soil N management strategies that may be used to establish desired plant communities that resist invasion. The objectives of this manuscript are to (1) provide a comprehensive ecological description of the factors influencing plant available N (PAN) as it relates to invasive plant management, (2) propose a predictive conceptual model based on current scientific understanding of how PAN influences invasion and succession, and (3) discuss potential management methods for altering N availability to direct plant communities on a trajectory toward those that are desired. Although much of this paper focuses on the sagebrush-steppe ecosystem, we suspect that many of the concepts, models, and management strategies apply to a broader spectrum of ecosystems that are being invaded by many nonindigenous plants.

### Factors Influencing Plant Available Nitrogen

**The Nitrogen Cycle.** Resource availability is the foundation to several theories and models of succession (Krueger-Mangold et al. 2006; Pickett et al. 1987; Sheley and Krueger-Mangold 2003; Tilman 1988) because of its influence on the relative growth rate and competition among plant species within a community (Grime and Hunt 1975). Both factors are dependent upon the quantity of plant available nutrients in the soil relative to the ability of the plants to acquire those nutrients. Because N is often the nutrient limiting net primary productivity, understanding ecosystem processes and their responses to disturbance and invasion requires a mechanistic knowledge of the soil N cycle (Jones et al. 2004).

The key to the N cycle with respect to PAN is the biological turnover of soil organic matter (SOM) through mineralization and immobilization (Figure 1a) (Stevenson and Cole 1999; Wedin and Tilman 1990). Most N is incorporated in SOM, and SOM decomposition primarily determines N mineralization (Knops et al. 2002). The initial N concentration, C-to-N ratio, soluble carbohydrates, amino acids, polyphenols, and lignin content are the main chemical factors determining the rate of decomposition and N release from residues (Handayanto et al. 1995; Jones et al. 2004). The amino forms of soil organic N are the main substrate for the production of inorganic N ions (i.e.,  $\text{NO}_3^-$ ,  $\text{NH}_4^+$ ), which represent the pool of readily mineralizable N in soils.  $\text{NH}_4^+$  ions may be converted to  $\text{NO}_3^-$  by autotrophic bacteria through the process of nitrification. Conversion of organic N to available mineral forms ( $\text{NH}_4^+$  and  $\text{NO}_3^-$ ) is mediated by microbial transformations and is influenced by factors that affect microbial activity (e.g., temperature, moisture, pH, etc.)

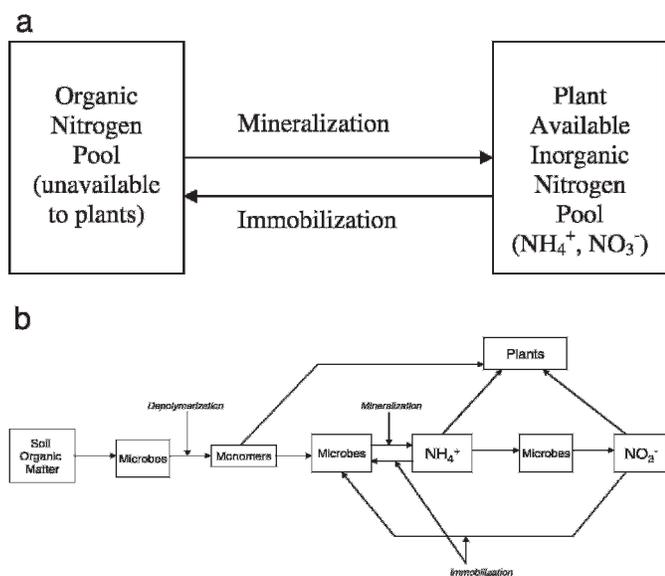


Figure 1. (a) Conceptual drawing of nitrogen mineralization vs. immobilization. (b) Conceptual nitrogen cycling model, NH<sub>4</sub><sup>+</sup> is the ammonium pool, NO<sub>3</sub><sup>-</sup> is the nitrate pool. This figure is adapted from Schimel and Bennet (2004).

(Stevenson and Cole 1999). The processes of continuous transfer of mineral N into biomass and of immobilized N into inorganic decay products underlie the building up or dying away of the heterotrophic and autotrophic biomass. This determines the size or pool of available N in soils for plants.

However, within the last decade, there is growing evidence that some of the nitrogen absorbed by many plants is organic in nature (Chapman et al. 2005; Clark et al. 2005; Harrison et al. 2007; Lipson and Näsholm 2001; Weigelt et al. 2005). Schimel and Bennet (2004) summarized a conceptual model that considers depolymerization of N-containing polymers rather than ammonium (NH<sub>4</sub><sup>+</sup>) production as the controlling mechanism in terrestrial N cycling (Figure 1b) and Cookson et al. (2006) expanded on this model to include both auto- and heterotrophic nitrification. Jones et al. (2004) also speculated that upstream elements of the N cycle such as the conversion of protein and peptides to amino acids or the rate of microbial biomass turnover by micro-fauna with subsequent excretion of NH<sub>4</sub><sup>+</sup> may be the primary factor limiting N mineralization. Nitrogen containing compounds are cleaved by extracellular enzymes to release low molecular weight monomers (e.g., amino acids) that may be used by either plants or microorganisms. A survey of the literature by Jones et al. (2005) reveals that dissolved organic N (DON) constitutes a major soluble N pool in most soils and that plant roots have the potential to access some of these pools through various transporter systems for low molecular weight amino acids.

**Nitrogen Demand by Microbes and Plants.** There is a demand for N by both soil microbes and plants in the soil beneath a plant community. The demands for inorganic N by plants and microbes have been well studied (Balser and Firestone 2005; Cookson et al. 2006; Hawkes et al. 2005; Herman et al. 2003). Nitrogen uptake by microbes is generally greater than uptake by plants (Jackson et al. 1988), and any change in the mineralization-immobilization balance will affect PAN (Holland and Detling 1990). Harrison et al. (2007) found that soil microbes competed intensely with plants and showed no preferences for N forms (organic and inorganic) in the short-term (50-h incubation). However, after 33 days, plants became more effective competitors for added N. Microbial activity can vary greatly due to the temporal (hours to days) variation in the supply of C and other nutrients from roots to soil, via root death and turnover, and through exudation of easily degraded compounds (Bardgett et al. 2005). As NH<sub>4</sub><sup>+</sup> declines and soil microbes switch to NO<sub>3</sub><sup>-</sup>, the energetic cost of reducing NO<sub>3</sub><sup>-</sup> prior to assimilation may further increase microbial requirements, which can magnify C limitations (Chen and Stark 2000). Jackson et al. (1988) investigated short-term partitioning of NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup> between plants and microbes in an annual grassland community. The microbes took up five and two times more NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup> than plants, respectively. This may be due to the large surface area of the microbes compared to that of plant roots that are capable of nutrient uptake. However, grasses appear to compete with microbes more intensely for NO<sub>3</sub><sup>-</sup> than for NH<sub>4</sub><sup>+</sup> (Jackson et al. 1988), possibly because NO<sub>3</sub><sup>-</sup> diffuses readily through the soil (Clarke and Barley 1968).

Mechanisms of NH<sub>4</sub><sup>+</sup> and NO<sub>3</sub><sup>-</sup> assimilation differ considerably within plants. Primary NO<sub>3</sub><sup>-</sup> assimilation can occur in both the root and leaf. NO<sub>3</sub><sup>-</sup> is readily mobile from the roots to shoots, especially with increasing NO<sub>3</sub><sup>-</sup> availability, and can be stored in vacuoles without deleterious effects (Clarke and Barley 1968; Evans et al. 1996). NO<sub>3</sub><sup>-</sup> has to be reduced to NH<sub>3</sub> then immediately incorporated into organic compounds before it can be incorporated into organic structures, which requires a significant amount of energy. NH<sub>4</sub><sup>+</sup> and its equilibrium partner NH<sub>3</sub> are toxic to plants and are immediately converted to amino acids, amides, and related compounds in root cells before they are transported to the shoots (Marschner 1986). Grass species with high growth rates can take up significantly more inorganic N than their slower growing counterparts (Weigelt et al. 2005). Harrison et al. (2007) found no evidence for species-specific preferences for N; however, all species tested showed a significant preference for inorganic N over organic N forms and for simple over more complex amino acids. Kinetic parameters of amino acid uptake vary for different plant species (Lipson and Näsholm 2001). Harrison et al. (2007)

demonstrated that coexisting plant species of temperate grasslands can take up simultaneously various forms of inorganic and amino acids of varying complexity. This suggests that co-occurring species of grasslands are highly versatile in their ability to capture different resource types. In low productivity grasslands, slow growing species may be able to persist due to the dominance of organic N as soluble N in those soils.

**Disturbance.** Major disturbances such as rangeland fire can initiate, retard, or accelerate plant succession (Connell and Slatyer 1977; Sheley and Krueger-Mangold 2003). However, in sagebrush-steppe ecosystems, native shrubs such as sagebrush (*Artemisia*) cannot sprout following fires that destroy the canopy (Radosevich et al. 1997). In contrast, some seeds of invasive annual grasses are still viable following most fires and retain the ability to germinate and establish during the next growing season. Because  $\text{NH}_4^+$  is a direct product of biomass burning (Knicker 2007), significant increases in plant available  $\text{NH}_4^+$  and  $\text{NO}_3^-$  can occur following a fire (Davies et al. 2007). Provided there is an adequate seed source present, this can provide the needed N flux for invasive annual grass seedling establishment. Fire can increase the rate of N mineralization (Hobbs and Schimel 1984; Knicker 2007) whereby immediately after a fire, there can be an accumulation of mineralized  $\text{NH}_4^+$ , which is then converted to  $\text{NO}_3^-$  by nitrifying bacteria (Anderson et al. 2004; Covington et al. 1991; DiTomaso et al. 2006). Fire can increase the availability of  $\text{NO}_3^-$  and  $\text{NH}_4^+$  in both canopy and interspace areas for several months following a fire (Kaye and Hart 1998; Kutiel and Naveh 1987; Rapp 1990; Singh 1994), but be heterogeneously distributed (Blank et al. 1994). Burned soils under shrubs can contain significantly less  $\text{NO}_3^-$  immediately after the wildfire (possibly due to volatilization), but increase significantly after one year (Blank et al. 1994). In contrast, Evans et al. (2001) show a decrease in N following a fire because of volatilization. In areas where SOM is the single largest pool of ecosystem N, high fire intensity or the amount of SOM consumed by fire can result in significant losses in total N (Mack et al. 2001). However, depending on the timing and intensity, rangeland fire does have the ability to create N pulses immediately after the disturbance whereby site availability and resource availability are enhanced.

Drought is another type of disturbance that can dramatically influence N availability. When annuals die in desert communities they release a large pulse of nutrients, especially N (Parker et al. 1984). Although hot, dry conditions retard the accumulation of organic N in the soil (Schlesinger et al. 1990), dry periods in many arid and semi-arid ecosystems can ultimately cause an accumulation of mineral soil N (Austin et al. 2004; Shaeffer and

Evans 2005). Part of the explanation is that plants reduce N uptake during dry periods, but microbes maintain some mineralization activity. Wet and dry cycles can result in higher net N and C mineralization when compared to continuously moist soils, possibly resulting from the inability of microbes to adjust osmotically to the sudden flush of moisture (Austin et al. 2004). In contrast, soil microbes still have some growth even at fairly low water potentials and nitrification can continue even after plants have reached their wilting points (1,500 kPa—average plant wilting point). Davidson et al. (1990) suggested that  $\text{NH}_4^+$  oxidizing bacteria may have mechanisms for tolerating severe desiccation. Thus, as with fire, the period immediately following a drought may be decisive for keeping invasive plant species from spreading (Svejcar 2003).

**Plant Species Composition.** Invasion by annual grasses may significantly alter PAN through changes in the microbial community (Belnap and Phillips 2001; Kuske et al. 2002), mineralization (Wedin and Tilman 1990), micro-climate (Mack and D'Antonio 2003), and redistribution of nutrients (Jobbagy and Jackson 2001, 2004). On arid rangelands, native plant communities are often characterized by a large amount of bare ground (40 to 60%) and significant space between individual plants. In contrast, monotypic stands of invasive annual grasses are much more uniformly distributed. Invasive annual grasses can greatly increase plant litter (Belnap and Phillips 2001; Bovey et al. 1961). Many exotic plants tend to produce litter that decays more rapidly than co-occurring native species (Ehrenfeld 2003). However, invasive annual grass shoots and roots typically have a higher C:N ratio than co-occurring natives (Evans et al. 2001; Monaco et al. 2003; Norton et al. 2004), allowing them to accumulate over time and suppress desirable plants (Bovey et al. 1961).

Evans et al. (2001) conclude that litter amount increased in invaded sites and lignin : N and C : N ratios were significantly higher in *B. tectorum* litter compared to *Hilaria* spp. and *Stipa* spp. These authors suggest that “the change in the quantity and quality of litter is the likely mechanism responsible for the changes observed with *B. tectorum* invasions, causing relatively greater N immobilization and decreasing plant available N” (Evans et al. 2001, pp. 1306–1307). Norton et al. (2004) found higher  $\text{NO}_3^-$ -N concentrations under *B. tectorum*, which appears to support the scenario of more rapid, shallow SOM turnover. Thus, different feedback systems may be established.

Clark et al. (2005) describe three different mechanisms that may drive positive and negative feedbacks. These are (1) differences in plant litter quality, through differences in conversion rate between different forms of plant accessible N; (2) differences in plant litter quality, through differences

in the fraction of N recycled in reasonable ecological timescales; and (3) differences in inter- and intraspecific competition for resources other than N. However, with respect to *B. tectorum*, conflicting feedback mechanisms have been suggested. For example, *B. tectorum* either establishes a positive feedback system within a plant community (e.g., decrease N availability or mineralization and alter species composition) (Evans et al. 2001; Rimer and Evans 2006) or establishes no feedback system (e.g., no apparent change in N availability between native and invaded sites) (Svejcar and Sheley 2001). Sperry et al. (2006) suggested *B. tectorum* is accessing subsurface N, while the native grasses appear to use more surface N produced by  $N_2$ -fixing processes from biological soil crust. *B. tectorum*-dominated grasslands generate a positive feedback loop by acquiring and assimilating subsurface N ( $NO_3^-$ ) and depositing it at the surface as litter, where decomposition and leaching return that N to subsurface layers that are again available for *B. tectorum* uptake. Booth et al. (2003) show that  $NH_4^+$  concentrations did not differ between vegetation types, but  $NO_3^-$  concentrations in *B. tectorum* soils were up to 10 times higher than those in *Artemisia*-dominated soils in the late summer and fall. Furthermore, results from a study by Harrison et al. (2003) indicate that  $NO_3^-$  availability was greater in *B. tectorum*-dominated soils compared to native soils, but soil  $NH_4^+$  availability was similar, suggesting that *B. tectorum* soils may accumulate  $NO_3^-$  formed during out-of-phase mineralization in late spring. The conditions where these studies were conducted (cool deserts vs. arid grasslands) or differences in water availability may explain the conflicting results (Evans et al. 2001; Ehrenfeld 2003).

Ample supply of N is a key factor in the ability of invasive annuals to achieve and maintain dominance on recently disturbed sites on semi-arid ecosystems (McLendon and Redente 1991). There are two basic ways that resource availability can increase (Davis et al. 2000). Either the use of resources by the resident vegetation declines, or resource supply increases at a faster rate than the resident vegetation can sequester those resources. In an annual grassland, all N acquired by plants must come from their surrounding environment since they cannot store N from one season to the next. Our understanding of the dynamics of N cycling in arid and semi-arid ecosystems suggests that management of PAN offers strong possibilities with respect to ecologically-based invasive plant management and restoration.

### A Predictive Conceptual Model of Invasion and Succession based on PAN

Ecologically-based invasive plant management requires the ability to predict community dynamics in natural and manipulated systems (Sheley and Krueger-Mangold 2003).

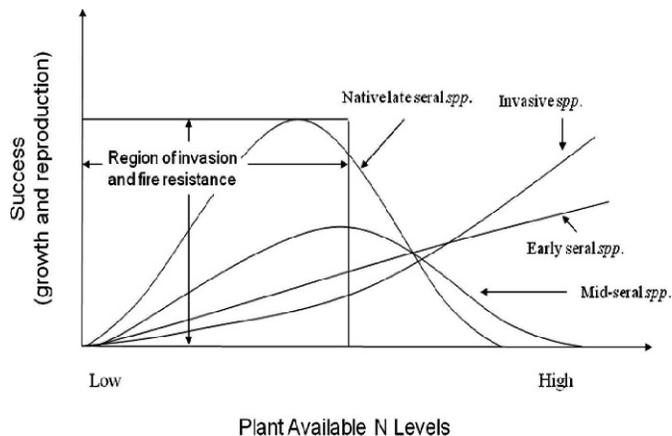


Figure 2. A conceptual model showing the competitive success among differing seral plant species as a function of plant available nitrogen as influenced by an invasive plant species.

Without predictive capabilities, the decision to manage using a particular strategy is based on previous experience, intuition, or is arbitrary. Any complete cost/benefit analysis and risk assessment of management must be based on models that provide an understanding of the plant community composition after implementing the practice. Predictive capability requires a mechanistic understanding of those factors that direct plant successional dynamics (Pickett et al. 1987; Sheley et al. 1996; Sheley et al. 2006). It is possible that understanding the role of PAN provides an ecological basis for making predictions about community composition in disturbed and managed systems.

Invasion and plant community dynamics are a function of many processes, but resource supply and the relative ability of species to acquire those resources may provide a basis for predicting successional dynamics (Krueger-Mangold et al. 2006; Tilman 1988). Our conceptual model describes the success (growth and reproduction) among coexisting successional groups and invasive species as a function of increasing PAN levels during plant competition and succession based on each groups competitive ability and growth rates (Figure 2). A major principle of this model is that in native, semi-arid ecosystems low in PAN, plant competition is the key process controlling dynamics (Fowler 1986). In this case, late-seral native species have been shown to be more competitive than invasive weeds (Herron et al. 2001; McLendon and Redente 1992). Low PAN may increase the intensity and importance of interference as plants compete more intensely for essential resources, thus creating competition-driven plant assemblages (McLendon and Redente 1992). Competitive species, such as late-seral native plants, that can persist under the lowest resource conditions may eventually dominate (Tilman 1988).

The second principle central to our model is the reciprocal tenet. In systems high in PAN, the species with

the most rapid growth rate may dominate because they can establish quickly, rapidly increase in size, and gain more access to resources than slower growing species (Berendse and Elberse 1990). In addition, these species create positive feedback mechanisms between size and resource uptake, resulting in exponential growth (Radosevich et al. 2007). Grime and Hunt (1975) describe  $R_{max}$  as the maximum potential relative growth rate. A species with a low  $R_{max}$  could be adapted to low PAN environments by making small demands on resources and is less likely to exhaust them. On the other hand, species with a high  $R_{max}$ , such as many invasive plant species, are favored in high PAN environments by rapid use of the soil resources. In growth-rate-driven plant assemblages (high PAN), the most successful species gains its dominance by preempting resources from other species, sometimes termed resource exploitation (Grace 2003) or asymmetric competition (Connell 2003).

The conceptual model predicts that at low PAN levels, native mid- and late-seral species are able to successfully out-compete early-seral and invasive species up to a critical level of PAN. Ultimately, lower PAN levels increase resistance to invasion, thereby creating invasion resistant soils. Conversely, beyond the critical level of PAN, early-seral and invasive plant species are able to successfully grow and reproduce more efficiently than native mid- and late-seral species because they can capitalize on their high growth rates and usurp the majority of the PAN. Furthermore, we predict that invasive plant species will out-compete native early-seral species in high nutrient environments because of their higher growth rate, which allows them to preempt soil resources. Our model predicts that ecosystems high in PAN are most susceptible to invasion and those low in PAN are most resistant to invasion in North America.

One of the more profound criticisms of restoration ecology is the need for process- and mechanistic-based principles and models that land managers can use to make decisions (Werner 1999). This model uses our knowledge of PAN to predict successional dynamics based on the traits of species that determine their ability to acquire PAN in low vs. high environments. This model implies that in order to successfully restore native plant communities, PAN should be reduced to some critical level where the principle driving process is competition and native species acquire PAN at higher quantities than invasive species. We believe that this mechanistic- and process-based model offers potential for planning, implementing, and predicting the outcome of restoration and invasive plant management.

### Managing Soil Nitrogen

**Soil Amendments.** Previous studies suggest that carbon soil amendments may increase microbial activity, and thus,

N immobilization (Figure 1b) (Blumenthal et al. 2003; McLendon and Redente 1992; Prober et al. 2005; Witwicki 2005). However, the effectiveness of carbon amendments appears to depend on the form of carbon applied, the rate and frequency of application, initial soil fertility, and particular species. Paschke et al. (2000) found that a reduction in N availability from the addition of sucrose resulted in decreases in the relative biomass of annual plant species (grasses and forbs) and increases in perennial species in old-field succession. Zink and Allen (1998) had some success immobilizing N (mainly  $\text{NO}_3^-$ ) by adding organic amendments (pine bark vs. oat straw) to increase microbial activity, especially fungal biomass. The authors showed improved native plant growth and reduced weed competition in bark-amended plots compared to control plots. Reeve Morghan and Seastedt (1999) had similar results with carbon additions, but they also noticed that this reduction did not last long once the carbon additions were stopped, and therefore recommended that soil amendments be added at regular intervals. In addition, there was no significant increase in native species densities or decrease in invasive densities; only plant growth was affected.

Alpert and Maron (2000) tested the effect of adding sawdust to high N patches left by dead yellow bush lupin (*Lupinus arboreus* Sims) shrubs in two grassland areas that had contrasting levels of existing invasion. After 2 yr, the total biomass of non-native plants was about 40% lower in plots with added sawdust. In contrast, the total biomass of natives showed no significant difference between plots with and without sawdust. Possible explanations for these results as suggested by the authors may be that greater reductions in non-native biomass is required to release natives from competition with non-natives, or that more time is needed for dispersal of natives into patches. These results were specific to grasses as opposed to forbs. The authors suggest that sawdust addition is most likely to be a useful countermeasure against invasion when the major invasive species are grasses.

Although the cost and short-term effect of sucrose make it impractical (Witwicki 2005), waste carbon such as sawdust may be a viable alternative. Carbon amendments may be an effective strategy on smaller-scale landscapes where cost is more affordable. It should be noted, however, that with increases in C availability along with the associated increased immobilization of N in microbial biomass and thus, lower N loss, total ecosystem N has the potential to increase over the long term (Schaeffer et al. 2003). In addition, there is a potential for N fluxes and pulses to occur as a result of microbial population die-off.

**Reseeding with Cover Crops and Bridge Species.** There is little debate about the difficulty of reseeding native species directly into areas dominated by invasive annual

grasses (Cox and Anderson 2004). However, few studies have investigated the possibilities of using high nutrient uptake cover crops or early- and mid-seral bridge species to facilitate the establishment of native late-seral species during rangeland restoration. Cover crops such as winter rye have been successful in reducing  $\text{NO}_3^-$  loads and concentrations of drainage water (Feyerseisen et al. 2006; Kaspar et al. 2007), lowering residual soil  $\text{NO}_3^-$  (Kessavalou and Walters 1999), and suppressing weeds (Brainard and Bellinder 2004). Herron et al. (2001) were able to reduce soil  $\text{NO}_3^-$ -N from 0.40 mg/kg to 0.11 mg/kg using annual rye. In addition, annual rye shifted the competitive advantage from spotted knapweed to blue-bunch wheatgrass in their competition study. Thus, N can be sequestered during the seedling establishment phase of restoration with the ultimate goal of setting the successional trajectory toward desired late-seral native species. Further research of this type is warranted.

**Burning.** Prescribed burns have the potential to exacerbate the establishment and growth of exotic winter annuals such as *B. tectorum* and *T. caput-medusae*, which germinate after fires and are able to quickly take up available N in the fall and grow roots during the winter (Stubbs and Pyke 2005). The root system of *B. tectorum* utilizes soil resources that otherwise would have been used by the native plants after a fire (Melgoza and Nowak 1991). *B. tectorum* and *T. caput-medusae* fires tend to have soil heating of short duration and cause  $\text{NO}_3^-$  to increase (Blank et al. 1996). In addition, soil  $\text{NH}_4^+$  levels can increase considerably because the charred organic debris is subject to rapid mineralization by increasing ammonifying heterotrophic bacteria (Blank et al. 1996). There has been some success controlling invasive annual grasses over the short term, mainly with repeated treatments (DiTomaso et al. 2006). However, these treatments are mainly addressing the symptoms of invasion and not the underlying cause. Provided that the management goal is to drive the successional trajectory toward a native late-seral plant community over the long-term, using fire as a management tool is not recommended in invasive annual grass-dominated systems.

**Grazing.** Most of the literature reviewed suggests that heavy grazing ultimately increases PAN, which implies that light to moderate grazing is better with respect to weed invasion. Klipple and Bement (1961) define heavy grazing as the degree of herbage utilization that does not permit desirable forage species to maintain themselves. After a 4 yr grazing intensity study conducted by Baron et al. (2001), soil  $\text{NO}_3^-$ -N concentrations for heavy grazed treatments were 1.7 to 2.4 times greater than lightly grazed treatments (0 to 60-cm soil depth). There was no significant difference between light and moderate grazing treatments for  $\text{NO}_3^-$ -N or  $\text{NH}_4^+$ -N. Heavy grazing can decrease primary

productivity, decrease plant N uptake and ultimately create greater soil mineral N levels (Seagle et al. 1992). Frequent and repeated grazing can lead to higher decomposition rates, decreased carbon inputs from roots resulting in decreased N immobilization, increased net N mineralization, and increased PAN (Holland and Detling 1990; Risser and Parton 1982). Nitrogen availability to plants may also be promoted by altering the form in which inorganic N exists (Coughenour 1991; Frank and Evans 1997; Zheng et al. 2002). Grazers tend to harvest nutrients over large areas and concentrate them into smaller areas (e.g., watering areas). The waste from grazers is more readily mineralized than plant tissues and are easily incorporated directly into the soil (McNaughton 1985). In one sense this may induce a positive feedback on herbivore grazing (Day and Detling 1990), but may also provide initial safe sites of invasion by weedy annual grasses.

However, grazing has been shown to reduce the abundance of competitive dominants and increase species richness despite enriching N in the ecosystem (Collins et al. 1998; Wilson et al. 1995). Lavado et al. (1995) provides evidence that not-grazed sites can have higher mineral N compared to moderately grazed sites, possibly reflecting higher biological activity. Neff et al. (2005) found that never-grazed sites had two to five times higher concentrations of N in the top 10 cm of soil compared to historically grazed sites in southeast Utah. Steffens et al. (2008) also found lower total N in grazed areas compared to ungrazed areas and attribute this to the combined effect of animal trampling, reduced above- and belowground organic matter input, and root growth as a result of grazing. In addition, the amount of litter, standing dead tissue, and total N in litter and standing dead tissue can increase in non-grazed areas (Berg et al. 1997; Schuman et al. 1999). Light to moderate grazing removes old plant litter undergoing senescence. Thus, in pastures or allotments that are grazed, the timing, intensity, and frequency of grazing should be chosen to be as beneficial as possible with respect to invasive plant management (Harrison et al. 2003). Heavy grazing should be avoided, especially if there is high potential (seed source) for the site to be invaded by annual grasses. Light to moderate grazing may help to reduce mineral N content in the soil as well as increase species richness. In addition, the class of livestock should be chosen to suit the particular invasive species in question.

**Mowing.** Intuitively, mowing may also be an effective method for removing N within an ecosystem. As invasive plant species develop through the growing season, PAN is being immobilized within their biomass. If the biomass could be removed before seed set while the plants are at peak standing crop and taken off the site, total soil N levels could possibly be reduced. The reduction of litter build up

could be more evenly distributed throughout the landscape compared to grazing (Moog et al. 2002). In addition, the reduction of biomass may also help to increase biodiversity within the plant community (Oomes 1990). Maron and Jefferies (2001) found that after 5 yr of mowing and biomass removal, the overall characteristics of the soil N pool changed little compared to the not-mowed control plots. However, the timing of mowing may have been late into the growing season when the plants were not actively growing. Mowing earlier in the growing season may produce different results. We believe that mowing and biomass removal to reduce soil N warrants further research. Initially, areas that could be mowed are power line right-of-ways, some roadsides, ditch-banks, abandoned croplands, or vacant lots (Radosevich et al. 1997). Areas such as these are prime sources of propagules that can spread into adjacent rangelands (Svejcar 2003).

### Creating Invasion Resistant Soils

A mechanistic understanding of the N cycle is critical to the development of ecologically-based invasive plant management strategies. Microbial activity is one component of the N cycle that appears amenable to manipulation and hence, to immobilizing or reducing total soil nitrogen levels. Disturbances such as fire and drought can have a strong impact on decomposition of litter and microbial activity depending on its timing, frequency, and intensity. This in turn influences N fluxes and pools, and is when ecosystems are most susceptible to invasion if the seed source is available.

Our conceptual model of PAN and its influence on the success of native vs. invasive plant species offers a potential foundation in which invasive plant management and restoration projects can be based. Research has yet to determine precise levels of PAN; however, our testable hypothesis is that at low levels of N, late-seral native plants are able to out-compete early-seral and invasive plants effectively because of their slow growth-rate characteristics. Based on our conceptual model, resource managers and restoration ecologists are more likely to be successful with respect to invasive plant management and restoration because it is based on ecological principles.

Because net mineralization/immobilization of soil N can determine the quantity of PAN within a plant community, managing soil N may be an important aspect of ecologically-based invasive plant management. There are several methods that offer potential for managing soil N and thus, invasive plants. Ecologically-based invasive plant management strategies may include soil carbon amendments, reseeding with cover crops, grazing, and mowing. Provided that the long-term goal is to set the successional trajectory toward a native late-seral plant community, burning is not recommended as a management tool for invasive annual grass species.

Invasive weed management is likely to become more mechanistically oriented in the future. Understanding the drivers and causes of invasive weed invasion will increase opportunities for successful management. If we can identify the causes of weed invasion, our chances of identifying fixes increase dramatically. We believe that soil nutrient availability is one of the drivers of weed invasion and a factor that we must understand more completely if we are to develop successful long-term, ecologically-based invasive plant management strategies.

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