Species Performance: the Relationship Between Nutrient Availability, Life History Traits, and Stress

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INTRODUCTION

Differences in species performance (i.e. how a species captures and utilizes resources to maintain and increase population size), influences the rate and direction of plant community change (Sheley *et al*., 2006). Species performance is determined by a number of interacting factors. This includes resource supply rates, physiological traits that determine how a species affects and responds to the environment, life history traits that determine patterns of birth, mortality and growth of individuals in a population, as well as abiotic and biotic stressors such as herbivory or drought. Researchers and land managers long have recognized that our ability to predict and manage the spread of invasive species directly depends on our understanding of the processes that differentially impacts the performance of invasive and native plants. In nutrient poor systems across the globe, increases in nutrient availability increases the susceptible of ecosystems to invasion (Mack *et al*., 2000). This general and widespread response indicates that increases in nutrient availability are likely favoring the performance of invasive species over native species.

Having recognized this, restoration practitioners have long considered soil nutrient management to be a fundamental component to restoring invasive plant infested systems. However, the role soil nutrient availability plays in our ability to restore invasive plant dominated systems is not as straightforward as it initially appears. The objectives of this chapter are to: 1) Examine current paradigms and assumptions about how nutrient availability influences the relative performance of invasive and native plants. 2) Develop the argument that the influence of nutrient availability on species performance is mediated by life history traits and stressors such as drought and herbivory. 3) Describe how these principles that determine species performance in different nutrient environments can be used to develop more effective invasive plant management strategies.

CURRENT PARADIGMS OF NUTRIENT AVAILABILITY AND INVASION

Background

Theoretical and empirical work has established a positive relationship between resource availability and habitat invasibility. For example, in nutrient-poor systems dominated by slow-growing species, invasions have commonly been attributed to increased soil nitrogen (N) availability following disturbance (McLendon and Redente, 1991; Kolb *et al*., 2002; Brooks, 2003). Due to their faster growth rates and ability to rapidly take up N, fast-growing invasive species are thought to be more competitive than slow-growing native species in high N soils (Norton *et al*., 2007; Mazzola *et al*., 2008; MacKown *et al*., 2009; Perry *et al*., 2010). In contrast, slow-growing native species, with their greater investment in belowground structures and ability to recycle and store N (Chapin, 1980; Fargione and Tilman, 2002), are thought to be favored

under low N conditions. These observations have lead to the logical assumption that managing soils for low nutrient availability will facilitate restoration of invasive plant dominated systems.

Based on the positive relationship between nutrient availability and habitat invisibility, land managers and researchers have been applying a range of techniques to lower soil N prior to native plant restoration, including the use of cover crops, carbon amendments, and topsoil removal (Perry *et al*., 2010). Following decades of manipulations, however, the effect of soil-N management on the relative performance of native and invasive species has been mixed. For example, work in some grassland systems has shown that reductions in soil N availability may reduce the growth of invasive species and facilitate the establishment of native species (Morgan, 1994; Blumenthal *et al*., 2003). Likewise, reduction in soil N availability to invasive annual grass-dominated coastal prairie and old-fields in North America and pasture in Australia lowered soil-N availability and facilitated re-establishment of perennial grasses (Alpert *et al*., 2000; Paschke *et al*., 2000; Prober *et al*., 2005). While these studies did not identify how decreasing soil N facilitated establishment of native species, these results have been largely attributed to an overall lower N requirement of native plants or to changes in competitive relationships among species as N availability declined.

A number of other studies, however, have not observed the expected effect of lowering soil N on invasive and native species performance. For example, lowering soil N in invasive plant dominated coastal and interior grasslands, as well as sagebrush steppe communities in North America, did not facilitate reestablishment of perennial grasses (Morghan and Seastedt, 1999; Corbin and D'Antonio, 2004; Huddleston and Young, 2005; Mazzola *et al*., 2008). The discrepancies between these studies and the current paradigm of soil-N effects on invasive and native plant performance have been explained a number of ways including lack of long-term effects of treatments on soil N, the type of treatments used to reduce soil N, and environmental conditions such as drought (Blumenthal, 2009; Brunson *et al*., 2010; Perry *et al*., 2010). While some variation among studies could be due to these factors, the large discrepancies in overall conclusions reached in these research efforts suggests the current conceptual framework for understanding the role nutrient management plays in our ability to restore invasive plant dominated systems is incomplete.

Reconsideration of the Nutrient Availability-Invasibility Paradigm
The development of the current nutrient management paradigm is largely centered on the assumptions that traits such as fast-growth make invasive species better "adapted" to high nutrient environments than native species while slow-growth makes native species better "adapted" to low nutrient environments than invasive species. However, over the last decade or so, there have been major advances in understanding the plant physiological and morphological traits underpinning the different ecological strategies displayed by native and invasive species as well as the ecological trade-offs associated with these traits (Weiher and Keddy, 1999; Diaz *et al*., 2004; Wright *et al*., 2004). These insights are instrumental for determining how our ability to predict nutrient availability effects on species performance can be improved.

For example, current plant trait frameworks suggests plant ecological strategies may be more clearly differentiated based on how a species balances the trade-off between resource acquisition and resource conservation, rather than growth potential (Weiher and Keddy1999; Diaz *et al*.,

2004; Wright *et al*., 2004). Under this framework, some species maximize resource conservation by making mechanical and chemical investments in tissue that increase tissue lifespan and decrease tissue loss due to herbivory or environmental stress (Lambers and Poorter, 1992; Westoby *et al*., 2002; Wright *et al*., 2004). While these investments decrease relative growth rate (RGR), these traits increase mean nutrient residence time, allowing a greater duration of return on nutrients captured and greater nutrient conservation (Berendse and Aerts, 1987). Over the long-term, these traits are expected to be advantageous in low nutrient soils (Berendse, 1994, Aerts, 1999). On the other hand, some species make thin, short-lived tissue. While this decreases tissue life span and increases tissue susceptibility to herbivory or environmental stress, it allows these species to construct more absorptive root and leaf surface area per unit of biomass allocated to tissue, resulting in more rapid resource capture (Lambers and Poorter, 1992). These traits are expected to provide an advantage in nutrient-rich soils where resource capture is favored over resource conservation.

This research suggesting tissue construction strategy (thin, short-lived vs. thick, long-lived) influences the balance between resource acquisition and resource conservation and, consequently, differentiates the ecological strategies of plants, and has major implications for predicting how we expect soil N management to impact restoration efforts. Specifically, because certain invasive species invest little in tissue protection and defense, over the short-term they may achieve greater growth rates than native species even in low nutrient soils (Burns, 2004; Garcia-Serrano *et al*., 2005; James, 2008). In addition, the advantages native species have in low nutrient soil, including greater nutrient mean residence time and greater protection form environmental stress or herbivory, are only going to be manifested through time and when environmental stress or herbivory pressure is high. Therefore, in a restoration scenario where both native and invasive species are recruiting from the seed bank, invasive species may maintain an initial growth advantage even in low nutrient soils. If this initial growth advantage allows invasive species to interfere with the growth a survival of native species, then native species will have little opportunity to capitalize on traits that ultimately will provide them an advantage in nutrient-poor soils. Given this potential and the variable results seen in soil N manipulation studies, it may be helpful to examine a quantitative synthesis of the literature and determine if the balance of evidence supports the current paradigm or suggests a need to further refine a predictive framework for the role soil nutrient management plays in restoring invaded systems.

Evaluation of the Nutrient Availability-Invasibility Paradigm
A recent study used meta-analysis to evaluate the degree to which soil N management differentially impacts growth and competitive ability of invasive annual and native perennial grasses (James *et al.,* 2011). Meta-analysis is a useful tool to quantitatively synthesize results of independent studies (Gurevitch and Hedges, 1993). In the experiments analyzed in this meta-analysis, all species were started from seed and thus provides useful insight into how soil conditions may impact initial growth and competitive interactions and set the stage for long-term plant community changes in a restoration setting where both native and invasive species are starting as seed. Here three hypotheses were tested: 1) Decreasing soil N availability has a greater negative effect on biomass and tiller production of annual compared to perennial grass seedlings. 2) However, seedlings of fast-growing species, including invasive annual grasses, maintain a higher RGR than seedlings of slow-growing species in low N environments, allowing

invasive annual grasses to construct more biomass and tillers than perennials in the short-term. 3) As a result, lowering soil N availability will not alter the competitive advantage annual that grass seedlings have over perennial grass seedlings.

To test these hypotheses, 70 comparisons were extracted from 25 studies and effect size was calculated as the natural log response ratio (ln RR) where $\ln RR = \ln \frac{T_z}{T_b} = \ln T_z - \ln T_b$, and T_z and T_b are means of the response variable for two different treatment groups (Hedges *et al*. 1999). The parameter ln RR estimates the proportional difference between treatment groups. An ln RR of zero indicates the response variables do not vary between groups, and a positive or negative ln RR indicates the response variable is larger for the T_z or T_b group, respectively.

Figures 8.1-3 show the results of this quantitative synthesis. Figure 8.1 shows the effect of soil-N availability on the difference in (A) biomass, (B) number if tillers and (C) relative growth rate (RGR) of invasive annual grasses and native perennial grasses growing in low and high N environments. Confidence intervals on biomass differences (annual – perennial) for high and low N do not overlap (Figure 8.1A). This supports the first hypothesis that reducing soil N decreased annual grass biomass by a greater proportion than perennial grass biomass. The confidence interval on the RGR difference (fast growing species – slow growing species) is greater than 0 for low N (Figure 8.1C). Therefore, fast growing invasive annual grasses maintained higher RGR under low and high N compared to slow-growing perennial grasses. As a result of this higher RGR, invasive annual grasses produced more biomass and tillers than perennial grasses when N availability was low (Figure 8.1A, B). This supports the second hypothesis that seedlings of fast-growing species, including invasive annual grasses, maintain a higher RGR than seedlings of slow-growing species in low N environments, allowing invasive annual grasses to construct more biomass and tillers than perennials in the short-term.

Figure 8.1. Most likely parameter values (dots) and 95% confidence intervals (bars) on log response ratios (ln RR) where A) ln RR = ln(perennial grams per plant) – ln(annual grams per plant), B) lnRR = ln(perennial tillers per plant) – ln(annual tillers per plant), and C) ln RR = ln(RGR of fast growing species) – ln(RGR of slow growing species).

Consistent with the greater growth rate, biomass and tiller production by invasive annuals compared to native perennials in low N soil, and in support of the third hypothesis, lowering soil-N availability did not alter the competitive advantage of invasive annual grass seedlings have over native perennial grass seedlings. While all point estimates of competition parameters were negative, indicating plants competed under low and high N, confidence intervals for low and high N overlapped substantially (Figure 8.2), suggesting N availability had little effect on competition intensity. Moreover, the competition studies showed that annual grass neighbors had a stronger competitive effect on both annual and perennial targets compared to perennial neighbors and that the competitive effects of annual neighbors on perennials did not decrease with lower N availability (Figure 8.2). In addition, perennial targets competing with annual grass neighbors did not incur a net cost in biomass production in high-N environments (Figure 8.3). Point estimates and confidence intervals describing the difference in perennial plant biomass when perennial plants were grown with annual neighbors under high N compared to when perennial plants were grown with annual grass neighbors under low N were positive or overlapped zero in the different types of competition designs used. This indicates perennials

produced either more biomass when grown with annual grass competitors under high N compared to when grown with annual grass competitors under low N or that there was no detectable difference in biomass produced under high and low N.

Figure 8.2. Most likely parameter values (dots) and 95% confidence intervals (bars) on log response ratios (ln RR) from addition series studies included in the meta-analysis. More negative values indicate more competitive effects of neighbors on target plant biomass.

Figure 8.3. Most likely parameter values (dots) and 95% confidence intervals (bars) on log response ratios (ln RR). The ln RR describes effects of nitrogen availability on biomass production of perennial grasses growing with invasive annual grass neighbors. Specifically, ln RR = ln(biomass of perennial plants grown with annual grasses under high N) – ln(biomass of perennial plants grown with annual grasses under low N). Separate estimates are provided for the three types of competition designs analyze din the meta-analysis (addition series, replacement series, and simple addition).

The current soil N management framework rests on the assumption that because increasing N availability facilitates invasion, decreasing N availability should facilitate restoration of systems dominated by invasive plants (McLendon and Redente, 1992; Alpert *et al*., 2000; Blumenthal *et al*., 2003). The meta-analysis described here rejects this assumption for invasive annual grasses. In addition, because many invasive plant species display traits that favor resource acquisition over resource conservation compared to their native counterparts (Grotkopp *et al*., 2002; James and Drenovsky, 2007; Leishman *et al*., 2007), these findings likely apply to other invasion scenarios. This means it is very likely that when invasive and native species are establishing from seed, soil nutrient management alone will not directly facilitate establishment of native species. While this conclusion is supported by an array of studies showing soil-N management failed to facilitate restoration of invasive plant dominated systems (e.g. Corbin and D'Antonio, 2004; Huddleston and Young, 2005; Mazzola *et al*., 2008), this conclusion is at odds with studies that have demonstrated that soil-N management facilitates restoration of systems infested by a range of invasive plants (e.g. Alpert *et al*., 2000; Paschke *et al*., 2000; Prober *et al*., 2005). An important question then is how can we use these results and current understanding of plant life history trade-offs to reconcile these discrepancies and improve our ability to predict how nutrient availability impacts species performance?

INFLUENCE OF NUTRIENT MANAGEMENT ON SPECIES PERFORMANCE: THE ROLE OF LIFE HISTORY, DROUGHT, AND HERBIVORY

Advances in understanding traits underlying variation in plant ecological strategies have been made. These advancements can improve our ability to understand and predict how soil nutrient management may influence restoration outcomes. Potential growth rate long has been a key trait used to characterize different plant ecological strategies (e.g. Grime, 1977; Goldberg and Landa, 1991; Loehle, 2000). When grown under optimum conditions, species that dominate nutrient-rich sites typically have a higher RGR than species that dominate nutrient-poor sites (Lambers and Poorter, 1992). While a high RGR allows rapid growth and resource capture, the ecological advantage a low RGR provides is less clear. Early interpretations focused on advantages directly due to low RGR, such as the potential for low RGR species to function closer to their

physiological optimum in infertile soils compared to high RGR species (Grime and Hunt, 1975; Chapin, 1980). The current consensus, however, argues that traits associated with low RGR, not RGR itself, have been the target of selection in nutrient-poor systems (Lambers *et al*., 1998; Aerts, 1999). Specific leaf area (SLA) is the principle trait influencing RGR variation among species (Lambers and Poorter, 1992). Morphological and chemical adjustments that increase leaf tissue toughness and protection from abiotic stress or herbivores decrease SLA and consequently, RGR (Poorter *et al*., 2009). While a low SLA indirectly reduces growth and resource capture rates, it increases the ability to conserve resources because low SLA species tend to have longer leaf lifespan than high SLA species (Westoby *et al*., 2002). A high SLA, on the other hand, allows quicker return on nutrients and dry matter invested in leaves, resulting in rapid resource capture but poor resource conservation due to shorter leaf lifespan. Variation in SLA among species, therefore, represents a key axis describing different plant ecological strategies that range between rapid resource capture and effective resource conservation (Diaz *et al*., 2004; Wright *et al*., 2004; Leishman *et al*., 2007).

While we would expect resource conservation strategies to become increasingly important as soil nutrient availability declines, favoring low SLA species, the meta-analysis demonstrated that fast-growing, high SLA species, including invasive annual grasses, maintained greater growth rates in low-N soils than slow-growing species. These differences in initial RGR were reflected in the greater biomass and tiller production by invasive species in low-N soils compared to native species. High-SLA species also may produce thinner and less dense root tissue compared to low-SLA species, resulting in a lower specific root length (SRL) (Elberse and Berendse, 1993). Construction costs per unit tissue dry weight are similar among species (Poorter and Bergkotte, 1992). As a result the thinner or less dense root and leaf tissue generally produced by invasive compared to native species allows invasive species to maintain a greater rate of return on biomass allocated to leaves and roots and ultimately grow faster than native species. At the seedling stage, this difference in tissue production cost allows invasive species to preempt more belowground resources than native species in nutrient-poor soils (James, 2008). Therefore, because of these differences in tissue construction strategies, at the seedling stage, slow-growing native species have no direct advantage in terms of initial growth in nutrient-poor soils compared to invasive species. If restoration outcomes are largely determined during the seedling establishment phase, then soil nutrient management alone likely will not influence restoration outcomes.

Restoration outcomes, however, also are influenced by longer-term processes, not just processes associated with the seedling establishment phase. Internal plant nutrient recycling, for example, contributes significantly to the long-term performance of natives in low nutrient soils (Killingbeck and Whitford, 1996). Plants have two primary sources of nutrients: soil nutrient pools and nutrients retained within the plant. The reliance on these two different nutrient sources depends on a variety of factors, including internal plant nutrient recycling, soil nutrient availability, and life history. During tissue senescence, biomolecules are broken down and the mineral nutrients are translocated to storage tissues, such as stems and roots. Internal nutrient recycling buffers plants against variation in soil nutrient availability (Aerts and Chapin, 2000), impacts plant fitness (May and Killingbeck, 1992), and may be less costly than acquiring and assimilating soil nutrients (Wright and Westoby, 2003). Although the amount of nutrients resorbed (i.e. realized resorption) may vary annually, the maximum amount of nutrients that can

be resorbed physiologically (i.e. potential resorption) is considered an evolved "target value" (Killingbeck, 2004). As such, potential resorption is greater in plants from low-nutrient habitats compared to plants that dominate nutrient-rich systems (Killingbeck, 2004). If native species resorb more nutrients from dying tissue in nutrient-poor soils than invasive species, then over time natives will accumulate larger nutrient pools, which should place them at a competitive advantage.

In addition to nutrient recycling, native plants also conserve nutrients by investing heavily in structural support for leaf and root tissue. While these investments decrease SLA and SRL and lower rates of growth and resource capture, they increase tissue life span. As a consequence, these traits result in longer mean nutrient residences time and a lower relative nutrient requirement for native compared to invasive species (Berendse and Aerts, 1987; Berendse *et al*., 2007). Similar to nutrient recycling traits, because these traits deflect some biomass away from growth functions (e.g. creation of leaf or root surface areas for photosynthesis and nutrient uptake) toward nutrient conservation functions, these traits place native seedlings at an initial disadvantage in nutrient-poor soils. Modeling and empirical work, however, demonstrate that over time, these traits allow slow-growing species to accumulate more biomass and have faster population growth rates than fast-growing species in nutrient-poor soils (Berendse *et al*., 1992; Berendse, 1994; Ryser, 1996).

The outcome of competition at the seedling stage, however, is not solely based on resource capture differences, and other abiotic and biotic factors likely will be important in influencing the outcome of competition between invasive and native species in nutrient-poor soils. In addition to increasing tissue life span and nutrient residence time, the thicker, longer-lived leaf and root tissue constructed by native compared to invasive species can decrease tissue loss from drought. Structural investments in leaf and root cells and tissue xylem increase tissue density and are an opportunity cost in terms of investment of biomass in surface area for resource capture. These investments, however, allow plants to maintain physiological function as soils dry compared to plants that invest less in these structures. These differences in drought tolerance may heavily influence competition outcomes in environments with low and variable precipitation inputs (Goldberg and Novoplansky, 1997; Chesson *et al*., 2004). Likewise, mechanical investments in tissue, that decrease susceptibility to drought, also can decrease tissue palatability, making these plants less susceptible to attack by generalist invertebrate herbivores. For example, Buckland and Grime (2000) showed that in field microcosms, fast-growing species dominated low, moderate, and high fertility soils in the absence of a generalist invertebrate herbivore. When a generalist herbivore was added, the abundance of slow-growing species increased in low-fertility soils but not in high-fertility soils. Thus, population dynamics of invertebrate herbivores that target fast-growing species with less structural investment in tissue, may play an important role in determining outcomes of competition and assembly in nutrient-poor soils (Fraser and Grime, 1999; Olofsson, 2001; Burt-Smith *et al*., 2003)

DESIGNING ECOLOGICALLY BASED INVASIVE PLANT MANAGEMENT STRATEGIES BASED ON PRINCIPLES OF SPECIES PERFORMANCE IN LOW AND HIGH NUTRIENT ENVIRONMENTS

Theory, empirical work, and the results of the meta-analysis described here all support the notion that increases in nutrient availability favor invasive species performance over native species (Huenneke *et al*., 1990; Stohlgren *et al*., 1999; Davis *et al*., 2000). There also is evidence that invasive species, once established may accelerate nutrient cycles and maintain high levels of nutrient availability, ensuring resource conditions continue to favor dominance of invasive species (Liao *et al*., 2008). From these results, it is clear that invasive plant managers should carefully examine how management decisions and natural processes impact nutrient availability. Management decisions and natural processes that increase nutrient availability will favor the performance of invasive over native species. Therefore, maintaining low nutrient environments is a central goal of ecologically based invasive plant management programs.

However, the meta-analysis and our current understanding of traits underlying variation in plant ecological strategies suggest nutrient management alone will not be sufficient for facilitating establishment of native species in invasive plant dominated systems. By considering the meta-analysis and the trait-based frameworks of plant ecological strategies we can formulate some principles and predictions about how and when soil N management will positively influence restoration outcomes. Three principles emerge:

1. Managing environments for low nutrient availability will favor resource conservation over resource capture by plants, favoring desired species over invasive species
2. Initial establishment of desired species needs to be successfully managed to realize any benefit of nutrient management
3. When desired species are establishing from seed, a sufficient amount of stress that inhibits the performance of invasive species will need to be applied to realize any benefit of nutrient management

To understand how these principles can be incorporated into a practical invasive plant management program it may be useful to consider two contrasting restoration scenarios. In both scenarios there is a significant invasive plant seed bank, but in scenario one, most native plants must be seeded, while in scenario two, a significant number of native plants are still present at the site. If native species must be seeded, they cannot capitalize on key traits that provide them an advantage in low nutrient soils, such as the ability to recycle stored nutrients or their greater mean nutrient residence time. Managing soils for low nutrients will not provide a growth advantage to native compared to invasive species at the seedling stage. If herbivore pressure or abiotic stress is pronounced, the lower SLA and SRL of native seedlings may be advantageous due to greater investment in lignin or other compounds that tissue increase tissue toughness. On the other hand, if stresses like drought or herbivory do not occur, or cannot be applied in a manner that preferentially impacts invasives (e.g. livestock grazing at inappropriate times), the performance of invasive species will have to be controlled via other means (e.g. herbicide) for a long enough period to give native species an opportunity to establish and realize the benefits of their resource conservation traits. If this is achieved, managers should expect a long-term benefit to soil nutrient management. If, however, the initial performance of invasive species is not managed, managers should not expect to receive a benefit from nutrient management. For the second restoration scenario, in which there is a significant amount of native plants established or if factors such as dispersal heterogeneity or low annual grass propagule pools allow perennial grasses to survive the first growing season (e.g. DiVittorio *et al*., 2007), mangers should expect

soil nutrient management to have a direct positive impact on restoration efforts. Here, established plants have an opportunity to begin to capitalize on their resource conservation traits and do not have to compete with invasive species during the seedling stage. The greater size and greater nutrient conservation ability should rapidly place natives at a competitive advantage in low nutrient soils (e.g. Lulow, 2006; Abraham *et al*., 2009).

CONCLUSION

By considering our current understanding of traits underlying variation in plant ecological strategies, the meta-analysis presented here, and the two contrasting restoration scenarios outlined above, it is possible to improve prediction and management of native and invasive plant performance. In situations in which a remnant native plant community exists or there is sufficient time for seeded species to establish, management to reduce nutrient availability likely will have a direct positive effect on relative performance of native compared to invasive species, resulting in long-term positive changes in plant community dynamics. In the more common and complex situation in which both native and invasive species recruit from seed, soil nutrient management will not have a direct effect on restoration outcomes. Instead, management strategies or natural processes that reduce invasive species performance over the short-term and allow seeded species to establish will need to be applied before any soil nutrient management benefit is realized. If invasive plant propagule pools and performance can be successfully managed the first year, then low-nutrient soils should begin to place native species at a competitive advantage, and this advantage should increase through time.

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