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Shifting rangeland mineral resource limitations : ecological responses to atmospheric Nitrogen deposition

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Key points : Deposition of fixed nitrogen (N) from the atmosphere into natural and managed systems is increasing worldwide, primarily as a result of fossil fuel combustion and agricultural fertilization practices. While historically most rangelands have been subjected to relatively low N deposition rates, N deposition is projected to increase in rangelands. This unintentional wide-scale fertilization has the potential to dramatically shift mineral resource limitations in rangeland ecosystems. In contrast to forested ecosystem response to N deposition, one of the most evident rangeland responses to N deposition is a shift in community composition, with declines in biodiversity and potentially shifts in the dominant functional groups. Evidence to date suggests that many other ecological processes, such as interactions with insect herbivores and carbon (C) and N cycling may in turn be affected by this shift in species composition. Increasing predictive capability of rangeland responses to N deposition is crucial for developing appropriate management strategies.

Key words : nitrogen deposition, biodiversity, nutrient limitations, global change

Introduction

Deposition of anthropogenically-fixed nitrogen from the atmosphere onto plant and soil surfaces is profoundly changing N availability and ecological stoichiometry in ecosystems worldwide. Since N is typically a major limiting resource in temperate terrestrial systems, this change in nutrient availability may have major consequences for plants and soils in both natural and managed rangelands. Historically N deposition research has focused on forests and, to a lesser extent, mesic grasslands in Europe and North America due to the high rates and long-term, chronic deposition in these areas. However, rates of deposition are currently increasing and the areas of impact expanding, with estimates of large increases in deposition over the next 100 years in rangeland areas including Asia, Africa, and South America (Lamarque et al., 2005). Understanding, and potentially mitigating, N deposition influences on rangelands requires development of predictive models of N enrichment on rangeland plant, community, and ecosystem properties and processes.

Anthropogenic activities have more than doubled the annual inputs of fixed N into the biosphere, and these inputs are expected to continue to increase in the coming decades (Vitousek et al., 1997; Lamarque et al., 2005). Some of this fixed N becomes volatilized from agricultural activities (primarily as NH_3) or emitted as a result of fossil fuel combustion (primarily as NO_x), and is later deposited from the atmosphere onto terrestrial systems (Lovett, 1994). Deposited N can then become incorporated into the biota through root or microbial uptake of N deposited into the soil surface and via foliar uptake of gaseous and particulate N compounds (Lovett, 1994). This deposited N may affect ecosystem properties, including fundamentally shifting the absolute and relative availability of nutrients (Vitousek et al., 1997).

Aber et al. (1998) developed a conceptual model overviewing the major influences of N deposition temperate forests. In this model, ecosystems at stage 0 are N limited, but chronic N deposition shifts systems to become progressively less N limited. By stage 3 systems are N saturated. Following N saturation, net primary production (NPP) and N mineralization decline, and N leaching losses are high. Aber et al. (1998) further suggest that land use history determines the initial degree of N limitation at the site, and that the forest stand type (deciduous or evergreen) dictates the rate at which sites progress through the stages and become N saturated. Predicting, and potentially mitigating, rangeland responses to N deposition requires a conceptual model similar to that developed by Aber et al. for forested systems. Considerable uncertainty remains in how rangeland response to N deposition will differ from the forest ecosystem responses described by the Aber et al. model. Here I present an overview on some of the potential effects of N deposition on rangeland plants, communities, and ecosystems, with particular emphasis on key ways in which rangeland responses may differ from forested ecosystems.

Plant mineral nutrition

At the individual level, Aber et al. (1998) suggest that N deposition leads to increases in foliar N concentration; subsequent increases in processes such as photosynthetic rates and growth are expected until negative effects of declining Ca:Al and Mg:N ratios dominate. Studies mesic rangeland plant responses to simulated and natural N deposition typically indicate strong responses to N for the first stages of N deposition, with generally positive responses to N additions in terms of leaf or shoot N, photosynthesis, and growth (e.g., Power et al., 1995; Kirkham, 2001; Throop, 2005). However, with the exception of the extremely long-running Park Grass experiment (Crawley et al., 2005), the short-term nature of most rangeland N fertilization studies makes results relevant only to the early stages of the Aber et al. model, while systems are still N limited. Long-term, chronic N addition experiments are needed to understand shifts in plant mineral nutritional trajectories following system N saturation.

How might these patterns differ for drier rangelands in which water, rather than N, limits plant growth? Studies to date suggest that dry rangeland plant responses to N are highly species-specific, with some species showing positive or neutral response to N additions, and others showing co-limitation by water and N (e.g., Lajtha and Whitford, 1989; Drenovsky and Richards, 2004; James et al., 2005). Across a precipitation gradient, there was conflicting evidence for shifts from N to water limitation with decreasing precipitation, with responses dependent upon the indices considered (Hooper and Johnson, 1999). The authors conclude that co-limitation affects plants at ecophysiological, community, and ecosystem levels, and that these influences are in turn affected by biogeochemical feedbacks in resource availability. Thus, a mechanistic understanding of individual plant-level responses to N deposition across varying precipitation regimes may require broader scale assessments of how N deposition-induced changes in larger scale (e.g., community and ecosystem) processes in turn affect mineral resource availability.

Community composition

In contrast to the ecosystem-focused Aber et al. model, some of the strongest impacts of N deposition in rangelands appear to be shifts in the composition of plant communities and interactions among organisms. Nitrogen deposition has been identified as the third main threat to biodiversity worldwide (behind changes in land use and climate); and grasslands, savannas, and Mediterranean systems may be among the most susceptible to N deposition as these systems are often limited, at least in part, by N (Sala et al., 2000). An analysis of functional group responses to N deposition across biomes suggests that rare species, perennials, N fixers, and native species may be most susceptible to local extinction following N enrichment (Suding et al., 2005). In rangelands, empirical evidence for decreased plant diversity in response to N deposition is particularly clear for European mesic grasslands and heathlands. A strong negative correlation between deposition load and species richness and cover has been documented in Great Britain (Stevens et al., 2006), and it has been estimated that a cumulative load of 714 kg N ha⁻¹ would cause species richness to decline by 25% (Stevens et al., 2004). Substantial declines in diversity may occur quite rapidly (within three years) with high rates of N additions, but would likely occur only after 10 or more years of chronic, low-level additions characteristic of N deposition (Dise and Stevens, 2005). Proposed driving mechanisms for species losses include shifts in plant competitive abilities with altered resource availability, with N deposition in California grasslands causing competitive exclusion of native forbs by invasive non-native grasses (Weiss, 1999) and losses of forb diversity (Zavaleta et al., 2003). In contrast, coastal sage scrub subject to N deposition transitions from dominance of shrubs to dominance of grasses (Egerton-Warburton et al., 2001; Wood et al., 2006). In Minnesota, species richness declined rapidly with N fertilization, and led to a shift from C₄ warm-season grasses (with typically high N use efficiencies) to C₃ cool-season grasses (with typically low N use efficiencies) (Wedin and Tilman, 1996). Though there are many system-specific differences in particular groups that are lost, there is a clear common pattern of declining rangeland diversity with N inputs. This is in strong contrast to forested ecosystem responses where shifts in dominant canopy species are not commonly reported. However, given the lifespan of trees, changes in community composition of forested ecosystems would be expected to occur over much longer temporal periods. Given strong controls of community composition on many ecological processes, deposition-induced changes in plant community diversity will likely be a key variable for understanding and predicting rangeland responses to N deposition.

In contrast to mesic systems, N deposition into dry rangelands may have fewer consequences for community composition if plants are limited by soil moisture rather than N. However, relatively little is known about mineral nutrient-induced shifts in species composition in arid and semi-arid rangelands. In the northern Chihuahuan Desert, fertilization studies suggest that N deposition may cause increased grass cover and decreased legume abundance, as well as lead to a shift in the dominant grass species (Baez et al., 2007). In the same desert, N treatments shifted species composition, leading to a loss of C₄ summer annuals (Gutierrez and Whitford, 1987). Species diversity in dry rangelands may be maintained in part by resource pulses (Chesson et al., 2004), suggesting that temporal relationships between precipitation and N deposition patterns could also affect community patterns. Additional N fertilization studies in dry rangeland systems are needed to develop an understanding and generalize about how, if at all, N deposition and precipitation patterns interact to affect plant communities.

In addition to driving changes in plant community composition due to alteration of mineral resource availability, evidence to date suggests that N deposition may affect relationships between plants and secondary stresses such as insect herbivory. These shifts may in turn influence community and ecosystem processes (Throop and Lerdau, 2004). In mesic grasslands, simulated N deposition affects the survival or performance of insect herbivores (e.g., Power et al., 1998; Throop, 2005); these changes may affect herbivore populations (e.g., Haddad et al., 2000) and may ultimately affect plant community composition (Power et al., 1998; Carroll et al., 2003). In the case of the dominant heathland shrub *Calluna vulgaris* in Britain, N deposition-induced increases in susceptibility to secondary stresses such as insect herbivory and winter frost injury appears to be a factor in community change from shrubland to grassland (Power et al., 1998; Carroll et al., 2003). Similarly, simulated N deposition increased the fungal pathogen load for C₄ grasses in a Minnesota grassland, apparently as a result of increased foliar N concentration (Mitchell et al., 2003). Conversely, N deposition-induced shifts in plant communities may also affect herbivore and pathogen diversity. In Sweden, declines in butterfly species richness appear to be due, at least in part, to changes in plant community composition driven by N deposition. Butterfly species most likely to be lost are those reliant on nutrient-poor conditions, with greatest local extinctions occurring for those species in areas with greatest encroachment of woody plants into grasslands (Ockinger et al., 2006). Similarly, checkerspot butterfly populations in California have declined in areas where N

deposition facilitates invasion by non-native grasses and competitive exclusion of butterfly host plants . This cascade of events is prevented with moderate grazing as cattle graze preferentially on grasses (Weiss , 1999) .

Ecosystem processes

Aber et al . (1998) focus their model on the ecosystem level , positing that net primary production (NPP) increases with initial N deposition , but begins to decline as the system becomes N saturated (stage 2) . Simulated N deposition typically increases NPP in mesic rangelands (Dukes et al . , 2005 ; Bassin et al . , 2007 ; Chung et al . , 2007) , but it is unclear whether sustained N deposition will eventually cause declines in NPP similar to those exhibited by forests . These declines occur as a result of deposition-induced losses of base cations , mobilization of aluminum , and subsequent nutrient imbalances and aluminum toxicity (Aber et al . , 1998) . Initial increases in NPP in response to N deposition may not occur in drier rangelands where water and N co-limit production , although eventual declines in NPP could still occur if nutrient imbalances or aluminum toxicity occur . However , the response of NPP to N deposition in rangelands may be much more complex than in forested systems if deposition-induced shifts in community composition substantially affect NPP . Studies with manipulated plant community diversity patterns have found that simulated N deposition leads to greater stimulation of NPP in high diversity communities than low diversity communities (Reich et al . , 2001 ; Chung et al . , 2007) . Thus , there may be complex interactions between diversity and NPP whereby N deposition initially causes increases in NPP , but that these increases are offset by declines in plant diversity and by a subsequent dampening of the positive influence of N on NPP .

Mounting concerns over rising concentrations of atmospheric carbon dioxide , along with the possibility of economic incentives for carbon (C) sequestration , underscore the importance of understanding the extent to which N deposition influences system C sequestration capacity . If N deposition affects NPP , these changes could translate into altered C storage , although N deposition has less potential to strongly affect C sequestration in rangelands than forested systems because of minimal capacity in rangelands for C storage in woody tissue (Townsend et al . , 1996) . Once again , empirical evidence suggests that N deposition-induced changes in community composition may be an important driver of rangeland C sequestration response to N deposition . Soil organic C storage increased in a Minnesota grassland under simulated N deposition , but only under diversity treatments where the plant species present exhibited elevated foliar lignin concentration in response to N deposition (Dijkstra et al . , 2004) . Nitrogen deposition could potentially lead to large changes in rangeland C sequestration if deposition leads to increased woody plant biomass . However , although positive correlations between N deposition rates and woody plant expansion have been reported (Kochy and Wilson , 2001 , 2005) , conclusive drivers of woody plant expansion in rangelands remain elusive (Archer et al . , 1995) .

Ecosystem processes mediated by microbial activity may be strongly affected by N deposition , with Aber et al . (1998) proposing that N mineralization mirrors NPP with declines following N saturation , while nitrification and N leaching increase following N saturation . Indeed , simulated N deposition can increase N mineralization rates in rangelands (Morecroft et al . , 1994 ; West et al . , 2006) . However , as with foliar N and NPP , it is not clear whether chronic N deposition-induced shifts in mineral resource availability will cause eventual declines in N mineralization in rangelands . Also in congruence with the Aber et al . model , simulated N deposition caused increased nitrification and leaching in a dry coastal dune grassland (ten Harkel et al . , 1998) and increased nitrification in a Mediterranean grassland (Barnard et al . , 2006) . These patterns may be the result of altered resource availability to microbes driving changes in metabolic activities and biomass , although evidence to date suggests that simulated N deposition in rangelands can also strongly affect microbial community composition and function (Bradley et al . , 2006 ; Chung et al . , 2007) . However , changes in these microbially-mediated processes may also be indirectly affected by changes in plant species richness , with the positive response of microbial biomass to N additions positively related to species richness in a Minnesota grassland (Chung et al . , 2007) . Leaching of N from a Minnesota grassland was also enhanced with N additions , but once again these were affected by plant species richness , with greater losses from monoculture plots as compared to high diversity plots (Dijkstra et al . , 2007) . Predicting rangeland ecosystem responses to N deposition will thus require understanding not only how N enrichment directly affects microbially-mediated processes , but also the nature of N deposition impacts on plant community composition , and how these changes in turn indirectly mediated ecosystem-level processes .

Conclusions

Projected increases in the deposition of anthropogenically-fixed N into rangelands will drastically shift mineral resource availability in these systems . The majority of N deposition research to date on the impacts of atmospheric N deposition has taken place in forested ecosystems . As such , much uncertainty remains regarding rangeland response to chronic , low-level N additions . This is particularly true in drier rangelands where water is typically a major limiting or co-limiting resource . Developing predictive models for rangeland response to N deposition will require long-term experimental work spanning from the physiological to the ecosystem level . One clearly apparent contrast from the conceptual model developed by Aber et al . (1998) for N deposition influences in forested ecosystems is that decreases in plant community diversity are a major consequence of N deposition in rangelands . Thus , N deposition in rangelands may have both direct consequences from altered mineral resource availability , as well as indirect consequences mediated by shifts in plant community composition . The sustainability , forage quality and quantity , and aesthetic value of rangelands may all be affected by N deposition . Indeed , a recent economic

analysis suggested that the net financial benefits for decreasing N deposition loads may be particularly high in grassland ecosystems (Wamelink et al., 2007). These benefits can only be clearly calculated, however, with a comprehensive understanding of rangeland responses to N deposition. Rangeland researchers must face the challenge of developing predictive models of N deposition impacts on rangeland plant, community, and ecosystem properties and processes. Characterizing these responses and making generalizations across sites that differ in dominant vegetation and precipitation regime is crucial for understanding, and potentially mitigating, the negative consequences of N deposition on rangelands.

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