

# Nutrient Limitations of Carbon Uptake: From Leaves to Landscapes in a California Rangeland Ecosystem

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## Abstract

Nutrient controls of ecosystem pattern and process have been widely studied at the Jasper Ridge Biological Preserve, a well-studied California rangeland ecosystem. Here we review these studies, from leaf to landscape scales, with the intention of developing a deeper understanding of carbon (C)–nutrient interactions in such an ecosystem. At the leaf scale, several studies conducted on diverse plant species have revealed a strong positive relationship between leaf nitrogen (N) concentrations and maximal rates of photosynthesis. This relationship, which has subsequently been observed globally, can be explained by the nutritional requirements of photosynthetic machinery. Consistent with this local physiological constraint, N availability has been shown to limit carbon uptake of California rangeland ecosystems. In some cases phosphorus (P; and N plus P) limits productivity, too—particularly in serpentine soils, pointing to the importance of parent material in regulating CO<sub>2</sub> uptake at landscape scales. Nutrient dynamics are also affected by herbivory, which seems to accelerate N and P cycles over the short term (years), but may lead to nutrient limitation of plant production over the longer term (decades). Simulated global change experiments at Jasper Ridge have also provided insight into C–nutrient interactions in grasslands. In particular, several field-based experiments have shown that CO<sub>2</sub> doubling does not necessarily simulate productivity of California grasslands; rather, the strength and sign of net primary productivity (NPP) responses to CO<sub>2</sub> doubling varies across years and conditions. Although simulated N deposition stimulates NPP, N plus CO<sub>2</sub> combinations do not necessarily increase productivity beyond N treatments singly. Poorly understood feedbacks between plants, microbes, and P availability may underlie variation in the response of California grasslands to increasing atmospheric CO<sub>2</sub> concentrations. We conclude that interactions between C, N, and P appear especially vital in shaping plant productivity patterns in California rangelands and the capacity of this ecosystem to store additional C in the future.

## Resumen

Los controles ejercidos por los nutrientes sobre los patrones y procesos del ecosistema han sido ampliamente estudiados en la Reserva Biológica de Jasper Ridge, un ecosistema de pastizales naturales de California que ha sido bien estudiado. Aquí hacemos una revisión de dichos trabajos desde la hoja de una planta hasta la escala de paisaje, con la intención de desarrollar una comprensión más profunda de las interacciones Carbono (C)-nutrientes de dicho ecosistema. A la escala de una hoja varios trabajos realizados en varias especies vegetales han revelado una fuerte correlación positiva entre la concentración de nitrógeno (N) y las tasas máximas de fotosíntesis. Esta relación, que subsecuentemente ha sido observada a nivel global, puede ser explicada por las necesidades nutritivas de la maquinaria fotosintética. En consonancia con esta restricción fisiológica local, se ha comprobado que la disponibilidad de N limita la captura de carbono de los ecosistemas de pastizales naturales de California. En algunos casos el fósforo (P) (y N más P) también limita la productividad – particularmente en suelos de serpentina, subrayando la importancia del material originario en la regulación de la captura de carbono a escalas de paisaje. La dinámica de nutrientes también es afectada por la herbivoría, que aparentemente acelera los ciclos de N y P en el corto plazo (años), pero podría resultar en una limitación de nutrientes para la producción vegetal en el más largo plazo (décadas). Experimentos realizados en Jasper Ridge simulando cambio global también han proporcionado una comprensión más profunda de las interacciones C-nutrientes en pastizales. En particular, varios experimentos de campo han demostrado que la duplicación de la concentración actual de CO<sub>2</sub> de la atmósfera no necesariamente estimula la producción de los pastizales de California; más bien, la intensidad y el sentido de las respuestas en PPN a la duplicación de la concentración de CO<sub>2</sub> varía con los años y las condiciones ambientales. Mientras que la deposición simulada de N estimula la PPN, la combinación de N más CO<sub>2</sub> no necesariamente incrementa la producción más allá de la adición de N solamente. Los procesos de retroalimentación pobremente comprendidos que vinculan a las plantas, los microbios, y la disponibilidad de P podrían ser responsables de la variación en la respuesta de los pastizales de California a incrementos en la concentración de CO<sub>2</sub> atmosférico. Concluimos que las interacciones entre C, N y P aparentan ser particularmente vitales en la conformación de los patrones de productividad de los pastizales naturales de California y la capacidad de este ecosistema de almacenar C adicional en el futuro.

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## INTRODUCTION

Mineral nutrients influence the diversity, dynamics, and interactions among plants, animals, and microbes in myriad fundamental ways—with important implications for ecosystem responses to global environmental changes, such as increasing atmospheric CO<sub>2</sub>, climate change, and rising levels of nitrogen (N) deposition (Field et al. 1992). Conceptual and numerical models have for decades highlighted the importance of nutrients in controlling basic ecosystem processes and carbon (C) cycles (Walker and Syers 1976; McGill and Cole 1981; Parton et al. 1988); more recently, nutrient cycles have been applied in the examination of global environmental change, revealing the potential for nutrients to limit CO<sub>2</sub> uptake in the terrestrial biosphere (Xiao et al. 1997; Hungate et al. 2003; Luo et al. 2004; Reich et al. 2006; Wang et al. 2007; Sokolov et al. 2008). Nevertheless, the multiple scales and kinds of interactions associated with organisms and element cycles complicate our ability to fully comprehend ecosystem responses to global change (Luo et al. 2004). The principal aim of this study is to examine nutrient pattern and process from leaf to landscape scales in a well-studied system, as a means toward developing a deeper understanding of the effect of nutrients on C storage and cycling in California rangeland ecosystems.

Scale is fundamental to many different aspects of ecology (Levin 1992), and nutrient cycling is no exception. At the leaf scale, for example, N correlates positively with rates of photosynthesis, explained by the importance of N in CO<sub>2</sub> uptake enzymes (Field and Mooney 1986; Wright et al. 2005). Over time, the uptake of C by plants can dilute N resources in foliage (Field 1983), coupled with N resorption (Aerts 1996), leading to litter with a high C:N ratio and poor nutritional quality, which in turn feeds back to lower rates of N mineralization (Vitousek 2004). Herbivory can dramatically affect such nutrient cycling as well, leading to positive and negative effects on nutrient availability depending largely on time scale (i.e., years vs. decades; Pineiro et al. 2006). Finally, at landscape to regional scales, other factors—geological parent material, time, dominant vegetation communities, and local climates (Jenny 1980)—determine the nature and extent of nutrient limitations on productivity, with N, phosphorus (P), or other resources limiting processes at ecosystem levels (Vitousek and Howarth 1991; Elser et al. 2007). Knowledge of controls on nutrients across scales can help inform management and understanding of C uptake and storage in floristically and geologically diverse landscapes, a common feature of many rangelands (Williams et al. 1968).

Here, we review over 30 yr of nutrient cycling and limitation studies of the Jasper Ridge Biological Preserve (JRBP), a well-studied California rangeland ecosystem. California rangelands fall largely in a Mediterranean-type climate, consisting of grasses, forbs, shrubs (chaparral), and oak woodlands (Keeler-Wolf 2007), with soils that are derived from sedimentary, meta-sedimentary, and volcanic rocks (O'Geen et al. 2007). The vegetation communities observed within the boundaries of

the JRBP encompass these general features, including chaparral, grasslands (including serpentine; Kruckeberg 1984), and oak woodlands, which are common to the Sierra foothills and the Coast Range (Keeler-Wolf 2007). These communities have been studied extensively for decades in the JRBP, allowing for synthesis of C–nutrient interactions across different scales in such an ecosystem.

Our synthesis is focused on the role of nutrients in limiting CO<sub>2</sub> uptake and productivity across scales, N vs. P limitation of ecosystem functions, and ecosystem responses to simulated global changes: elevated CO<sub>2</sub>, N deposition, warming, and increased rainfall. First, we explore the functional role of nutrients within individual leaves and canopies, a fundamental aspect of C–nutrient interactions in vegetation. Next, we move to the scale of plant–soil–microbe subsystems to examine the cycling and implication of nutrients within California rangelands. Still further, we move to the scale of entire ecosystems and landscapes, where nutrient limitation is seen as the product of life history evolution, ecological interactions, and biogeochemical processes. Finally, we review global change experiments conducted on JRBP grasslands, again moving across various scales of biological organization.

## METHODS

### Study Site: The Jasper Ridge Biological Preserve

The JRBP, located in the foothills of the Santa Cruz Mountains on the San Francisco Peninsula, is a 480-ha facility operated as Stanford University's biological preserve since 1975. Over more than 100 yr, Jasper Ridge has been used for ecological research, including important work on organisms, populations, communities, and ecosystems. Jasper Ridge is in a zone of active faulting, virtually atop the San Andreas Fault. As a consequence, its underlying geology is complex, with most soils derived from greenstone or serpentine rocks (McNaughton 1968). The climate is Mediterranean, with cool wet winters and very dry summers. Daily mean temperature ranges from 9°C during January to 22°C in July; mean annual precipitation was 582 mm from 1980 to 2000 (Joel et al. 2001). The plant communities vary significantly at the JRBP, including a mosaic of sandstone and serpentine grasslands, chaparral, broadleaf evergreen gallery forests (mainly *Quercus* spp.), and coniferous stands composed mainly of coast redwoods (*Sequoia sempervirens*; McNaughton 1968). Typical of rangelands in California's Mediterranean climate (Keeler-Wolf 2007), the dominant grasses at the JRBP include various naturalized species of *Avena* spp. and *Bromus* spp. (McNaughton 1968). In addition, there are native forbs and perennial grasses in serpentine soils (derived from ultramafic rock with high magnesium:calcium [Ca] ratios, low Ca, and high concentrations of metals), similar to those species that are distributed across most of California (Kruckeberg 1984). Herbivory has played—and continues to play—an important role in maintaining the structure and function of communities at the JRBP (Hobbs and Mooney 1995; Peters et al. 2006). Managed grazing ceased in the early

1960s (McNaughton 1968); since then, small rodents (rabbits, gophers), black-tailed deer, and gastropods have taken over as the dominant herbivores (Hobbs and Mooney 1995; Peters et al. 2006). For more information about the plant communities and herbivory at the JRBP, we point the reader to McNaughton (1968) and Hobbs and Mooney (1995).

## RESULTS AND DISCUSSION

### Field Studies of Carbon–Nutrient Interactions at the JRBP

By field studies we mean those that have taken place across the different ecological communities, separate from those studies examining grassland ecosystem responses to multiple global changes (see Jasper Ridge Global Change Experiments, below). The field studies at the JRBP involve aspects of the nutrition of individual leaves, plants, and intact ecosystems, including those underlain by sandstone vs. serpentine substrates.

**Nutrients and Leaves: The N Economy of Vegetation for C Uptake.** N is an integral component of ribulose-1,5-bisphosphate carboxylase oxygenase (RUBISCO), the enzyme involved in plant CO<sub>2</sub> uptake, and it is essential to plant–leaf functioning and photosynthesis: RUBISCO consists of ~17% N on average (Sternner and Elser 2002). Consequently, N allocation to leaves is a major determinant of atmospheric CO<sub>2</sub> uptake by vegetation (Wright et al. 2004, 2005). In their study of *Lepechinia californica*, for example, a shrub that occurs either along the margins of or within California's chaparral, Field and Mooney (1983) examined relationships between leaf N, leaf age, photosynthetic capacity, and stomatal conductance. For all leaf ages, they observed decreasing net photosynthesis per unit of leaf mass as the season progressed. Combining data for all leaves at light saturation, photosynthetic capacity was significantly correlated with leaf N, consistent with the notion that as *Lepechinia californica* leaves age, N is removed and reallocated to younger leaves, such that this removal does not affect intrinsic resource use efficiencies. Part of this effect is a result of a seasonal decrease in leaf N concentrations, concurrent with increasing leaf specific mass, implying a dilution of N resources with new biomass (Field et al. 1983; Reich et al. 1999). Overall, these results fit with economic paradigms of plant functioning, whereby plants invest resources so as to maximize benefits (Bloom et al. 1985).

To test this interaction between N and photosynthesis more broadly, Field et al. (1983) examined intrinsic water and N use efficiencies in five evergreen sclerophyll shrubs and trees that are common to California's rangeland environments. Photosynthetic capacity decreased with increasing leaf age across species, and all species showed a strong linear relationship between photosynthetic capacity and leaf N content (Fig. 1). This relationship is a key piece of evidence supporting the generality of the role of N in controlling photosynthesis (Wright et al. 2004, 2005). Moreover, across all functional growth forms, neither nutrient nor water use efficiencies changed with leaf age, consistent with results from Field and Mooney (1983), above.

Together, these studies point to the physiological basis for N controls of photosynthesis across diverse kinds of woody rangeland vegetation, with similar relationships observed for

vegetation in other biomes and at the global scale (Field and Mooney 1986; Wright et al. 2004, 2005). Nonetheless, one cannot necessarily assume that this physiological control of N scales to C uptake and storage in entire ecosystems; examining this notion requires information at higher levels of ecological organization, such as entire nutrient cycles.

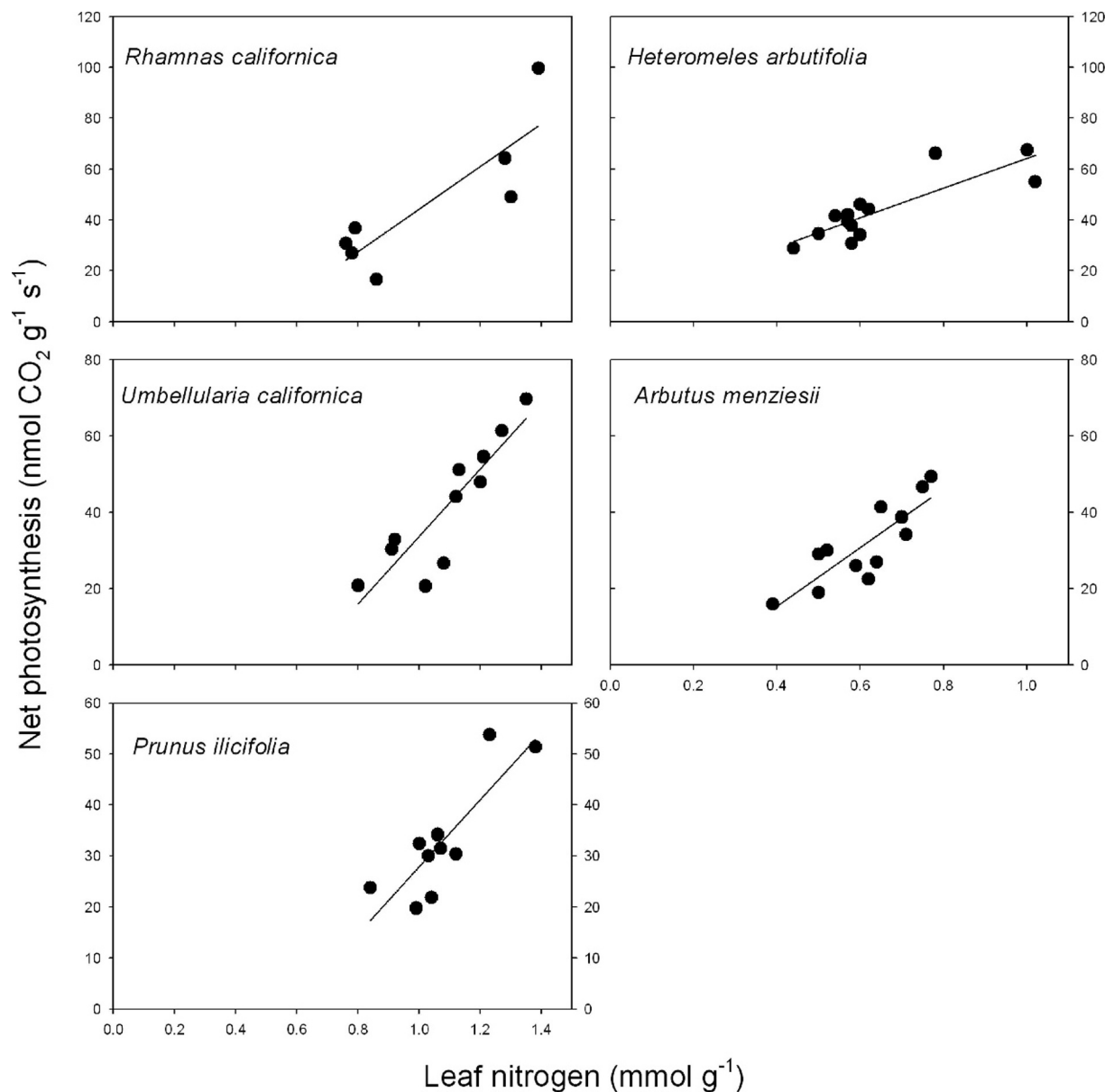
### Nutrient Controls on C Uptake in Oaks: Influence of Herbivory.

Nutrient cycles integrate complex interactions between plants, microbes, and soils, thus displaying system-level feedbacks (Schlesinger 1997). In particular, as leaves senesce and drop to the soil, microbes begin breaking down the complex organic compounds synthesized by plants, extracting mineral nutrients that eventually enter the soil, where they are once again available for plant uptake (Vitousek 2004). Although this classical view is applicable to nearly all terrestrial ecosystems, herbivory can markedly alter these interactions, mainly by converting recalcitrant plant materials into organic forms that decompose and mineralize nutrients rapidly (Frank et al. 2000; Lovett et al. 2002). In a California oak woodland, for example, populations of *Quercus agrifolia* and *Quercus lobata* display substantially higher N and P cycling rates in response to defoliation by the oak moth, *Phryganidia* sp. (Hollinger 1986). As the leaves are consumed, dominant vectors of nutrient loss from oak canopies switch from leaves to frass (i.e., fecal matter), the latter of which is more rapidly decomposed than leaf litter in the soil. *Phryganidia* sp. thereby causes large increases in N and P cycling rates, so that productivity and reproductive output of oaks remain unchanged in response to defoliation; *Quercus agrifolia* and *Quercus lobata* rapidly develop new sets of leaves. These impacts of insectivorous herbivory on nutrient cycles and plant dynamics are similar to those observed for grazing effects on herbaceous rangeland communities (Seastedt 1985).

Overall, it is clear that *Phryganidia* sp., which follows a ~5-yr outbreak cycle in California oak woodlands (Hollinger 1986), does not necessarily harm the overall nutrition of *Quercus agrifolia* and *Quercus lobata*; these oaks appear to have adapted to herbivory-induced changes in nutrient cycling. This finding seems to fit with the role of insectivorous herbivores in accelerating nutrient cycles observed for a wide array of ecosystems (Lovett et al. 2002); though negative effects on N availability have been observed in oaks elsewhere (Kay et al. 2008). The effect of insect defoliation in opening N cycles in California oaks seems consistent with the effects of larger grazers in general (Seastedt 1985; Seagle et al. 1992; Verchot et al. 2002), which may allow for instantaneous increases in rates of CO<sub>2</sub> uptake. However, over the long term (decades), herbivore-driven changes in nutrient recycling can have negative impacts, because nutrients can be lost from systems while cycles are accelerated (Pineiro et al. 2006); the balance between nutrient inputs and losses ultimately determines the capacity of ecosystems to store C.

### Nutrient Limitation on C Uptake of Serpentine Ecosystems.

Nutrient limitation theory postulates that the productivity of most ecosystems most of the time is limited by one (or more) mineral nutrients in the soil (Vitousek and Howarth 1991). The nature, magnitude, and pattern of nutrient limitation can vary widely among ecosystems, depending principally on five state-factors: parent material, topography, climate, biota, and time



**Figure 1.** Relationship between net photosynthesis and nitrogen content of leaves of various shrub and tree species at the Jasper Ridge Biological Preserve. Data originally published in Field et al. (1983).

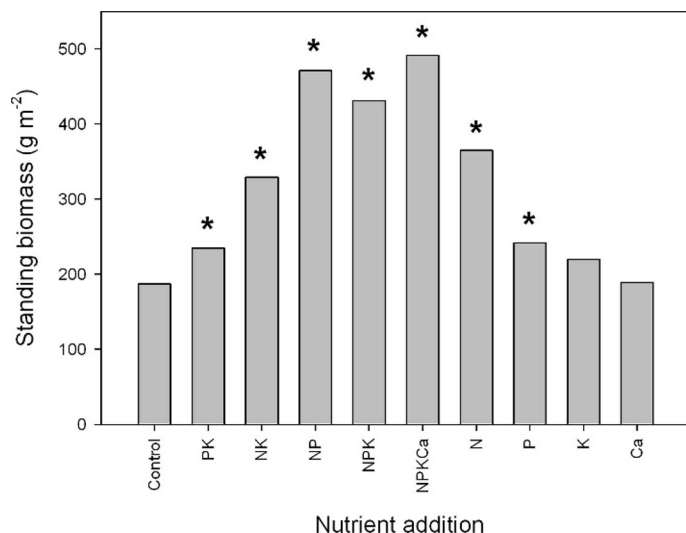
(Jenny 1980). Nutrient fertilizations conducted at the JRBP—which have almost exclusively been conducted in the serpentine (but see global change experiments below)—have revealed mixed results, with limitation by N and P alone in some cases, and N and P together in others.

Turitzin (1982), for example, observed both isolated and additive effects of N and P fertilization on the productivity of two common nonnative annual grasses in the field; N increased biomass by 94%, P by 28%, N plus P by 149% in serpentine soils dominated by *Bromus mollis* and *Vulpia microstachys* (Fig. 2). In pot experiments carried out on these two grasses, N and P fertilizations resulted in synergistic effects on plant biomass. In contrast, Turitzin (1982) observed little stimulation of plant growth with added Ca, potassium, and sulfur in both field plots and pot studies. Such an interaction between N and P, and the lack of real effect of Ca alone, is consistent with fertilization experiments conducted in serpentine soils in

Tuscany, Italy (Chiarucci et al. 1999). The lack of a Ca effect is somewhat surprising given that Ca availability is low in serpentine soils (Turitzin 1982; Kruckeberg 1984).

In contrast, Koide et al. (1988) reported that N, not P, was the principal nutrient limiting the productivity of forb-dominated serpentine communities in California serpentine grassland. In this study, the communities were composed largely of two nonleguminous native forbs (accounting for ~77% of total biomass): *Plantago erecta* Morris and *Lasthenia californica* DC. ex Lindley. The difference between Turitzin's (1982) results and those of Koide et al. (1988) may reflect intrinsic differences in nutritional requirements between grasses and forbs, or could be due to heterogeneities in nutrient availabilities within serpentine soil. Also, these authors speculated that species adaptations to nutrient-poor sites may be the most important factor in precluding their responses to added nutrients. For instance, plants adapted to low-nutrient





**Figure 2.** Nutrient limitation of serpentine grassland communities. Data originally published in Turitzin (1982). Results are for fertilized trials in the field. Fertilizations were conducted twice over the course of 1 yr of study. Asterisks indicate  $P < 0.05$  relative to control plots.

sites may be physiologically or evolutionarily constrained from responding to certain nutrients (Chapin 1980).

In sum, both N and P (either separately or in combination) appear to limit the productivity of California serpentine grasslands; the effect of N makes sense based on its widely known biochemical role in photosynthesis (see above), which may be related to P via stoichiometric requirements of autotrophs (Sterner and Elser 2002). Such conutrient limitation of net primary productivity (NPP) fits with widespread N and P limitation of grasslands from around the globe (Elser et al. 2007). The extent to which one or the other limits productivity appears to be a function of the substrate (sandstone vs. serpentine), plant functional type (forbs vs. grasses), and whether the plant species are native or invasive (Koide et al. 1988; Huenneke et al. 1990). Regardless, it appears that both N and P can and do limit the CO<sub>2</sub> uptake capacity of California grasslands, implying that resource managers should consider effects of both of these nutrients.

### Jasper Ridge Global Change Experiments

An extensive body of work has involved the effects of simulated global changes on the ecology and biogeochemistry of sandstone and serpentine grasslands at the JRBP. Here, we examine these global change experiments across organizational scales, beginning with individual plants and ending with ecosystems, and also address implications for rangelands in general.

**Effects of Plant Nutrient Acquisition and Tissue Chemistry Responses on C Uptake.** The capacity of plants to adjust to CO<sub>2</sub>-induced changes in the availability, distribution, and forms of mineral nutrients is an important determinant of ecosystem responses to global change. Jackson and Reynolds (1996) examined the effect of elevated CO<sub>2</sub> on plant root uptake of nutrients across six common species (including forbs and grasses) in California grassland. They reasoned that, under elevated CO<sub>2</sub>, plants would increase investments in acquiring

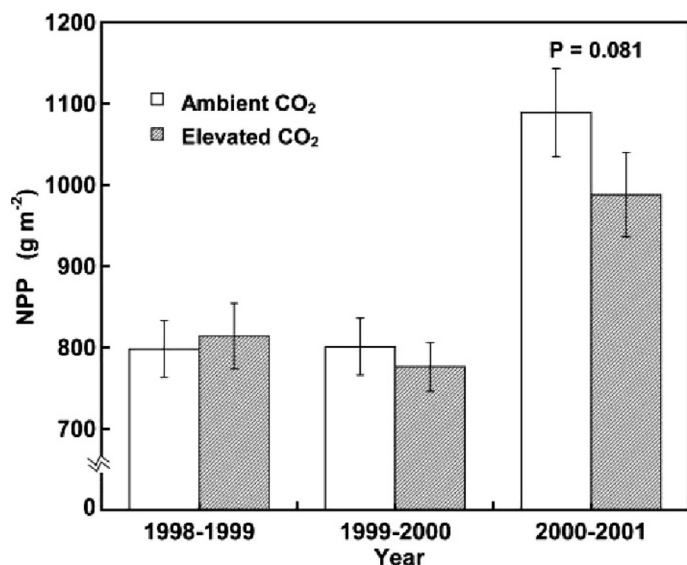
soil N, regardless of N forms (i.e., nitrate or ammonium); however, their study did not support this hypothesis. Rather, these authors observed little change in ammonium uptake in response to CO<sub>2</sub> enrichment and nitrate uptake rates decreased despite no consistent changes in soil nitrate availability. Jackson and Reynolds (1996) speculated that the decrease in nitrate uptake may have been because of the life histories of the plants studied; grasslands commonly have substantial ammonium-N pools and thus plants may largely meet their N demands through ammonium acquisition. A recent analysis of N uptake preference in native and exotic California grasses offers support for life history effects (Aanderud and Bledsoe 2009); preference of N forms varied among species in this study, depending principally on species dominance patterns. Moreover, the lack of changes in C allocation to roots to acquire additional N under elevated CO<sub>2</sub> at Jasper Ridge (Shaw et al. 2002; Dukes et al. 2005) may or may not be close to the optimal pattern for maximizing growth (Luo et al. 1994).

Chu et al. (1996) examined the effects of nutrient fertilizations and elevated CO<sub>2</sub> on plant leaf chemistry and quality in *Avena fatua* (sandstone grass) and *Plantago erecta* (serpentine forb) planted in microcosms. The response of the species' tissue chemistry and quality to CO<sub>2</sub> enrichment depended critically on mineral nutrient conditions. For example, N, C, and lignin pools (g·m<sup>-2</sup>) increased substantially in the shoots and roots of both species with added N, P, and potassium, whereas elevated CO<sub>2</sub> had much less of an effect on tissue chemistry and quality.

In a multifactorial study, Henry et al. (2005a) found that litter chemistry was substantially influenced by multiple simulated global changes, including climate, N deposition, and CO<sub>2</sub>. Elevated CO<sub>2</sub> appears to increase lignin concentrations of grass and forb communities, but increased rainfall, increased temperature, and higher rates of N deposition may combine to attenuate this response (Henry et al. 2005a).

**Effects of Plant-Microbe Interactions, Nutrient Cycling, and Elevated CO<sub>2</sub> on C Uptake.** Plant-microbe interactions, operating over diverse space-time scales, control different aspects of ecosystem responses to global change. Hungate et al. (1996) examined how plant-microbe interactions affected competition for N among native vs. nonnative plant species in response to changes in nutrient and CO<sub>2</sub> levels. At low levels of soil nutrients, they found that microbial N pools were positively related to plant N pools; thus, they found no evidence for a tradeoff between the microbial N immobilization and plant N capture. At higher nutrient levels, however, this correlation was not observed, indicating a decoupling between plant and microbial N acquisition under N-rich conditions. Although elevated CO<sub>2</sub> had no discernable effect on plant-microbe-nutrient interactions, it did promote greater plant ammonium uptake in systems composed of nonnative as opposed to native species. Nonnative plants exhibited greater N accretion under elevated CO<sub>2</sub>, suggesting that rising CO<sub>2</sub> may encourage the invasion of native serpentine ecosystems as a consequence of plant-nutrient competition in the future.

Hu et al. (2005) observed significant increases in N acquisition by *Avena* spp. exposed to elevated CO<sub>2</sub>, corresponding to an 11% to 53% increase in total shoot biomass depending on sampling dates. In contrast, microbial N pools did not increase under CO<sub>2</sub> enrichment. The lack of increase in



**Figure 3.** Net primary productivity (NPP) response to elevated CO<sub>2</sub> over the course of 3 yr. Data originally published in Shaw et al. (2002). Open bars represent all treatment combinations (nitrogen addition, water addition, heat) at ambient CO<sub>2</sub>. Gray bars represent all treatment combinations at twice the ambient CO<sub>2</sub> concentrations. Explanation of statistics can be found in the original publication.

microbial N has been linked to suppressed decomposition rates at the JRBP, which could lead to increased C accumulation at ecosystem scales (Hu et al. 2001). Similarly, Hungate et al. (1997) showed that increases in gross N mineralization rates under elevated CO<sub>2</sub> were not accompanied by an increase in microbial N immobilization. Rather, microbial immobilization decreased, leading to increased N available for plant uptake in California grasses.

Franck et al. (1997) evaluated N cycling and decomposition feedbacks to elevated CO<sub>2</sub> in the native (serpentine) grass *Vulpia microstachys*, and the most common nonnative (sandstone) grasses, *Avena fatua*, *Bromus hordeaceus*, and *Lolium multiflorum*. With the exception of the native species, litter decomposition rates increased under elevated CO<sub>2</sub>, perhaps reflecting an increase in plant leaf carbohydrates supplying microbial decomposers with a new labile C source (Franck et al. 1997). The authors concluded that, overall, the effects of CO<sub>2</sub> on plant C:N ratios, N mineralization, and decomposition rates can be highly species-dependent. This conclusion was further supported by a meta-analysis showing that the C:N ratios of California grassland vegetation do not necessarily increase in response to CO<sub>2</sub> enrichment (Dukes and Hungate 2002).

In sum, the picture emerging from these studies is that plant-microbe responses to elevated CO<sub>2</sub> are diverse, but that site conditions and plant types provide some means for prediction. Henry et al. (2005b) showed that microbial enzymes in the soil respond to different treatments, thereby linking plant-microbe interactions, nutrient cycles, and decomposition in ecosystems. A combined approach—enzymes, processes, and patterns—may reveal insight into the complexity of ecosystem responses to global changes (Menge and Field 2007). For example, phosphatase activity in soil increases with N fertilization, indicating rapid movement toward P limitation with added N (Henry et al. 2005b; Menge and Field 2007). Drawing

inferences on how these feedbacks may regulate CO<sub>2</sub> uptake patterns requires nutrient fertilization experiments conducted at ecosystem scales, our next topic.

**Combined Effects of Multiple Global Changes in Determining C Uptake.** In a world of rapidly increasing atmospheric CO<sub>2</sub>, terrestrial ecosystems are predicted to become increasingly nutrient deficient (Hungate et al. 2003). Plants require mineral nutrients to assimilate CO<sub>2</sub>; as CO<sub>2</sub> stimulation of photosynthesis takes place over decades, however, the nutrient capital of ecosystems may accumulate in plant materials that are characterized by long turnover times and poor nutritional quality (Luo et al. 2004). This, in turn, can result in negative feedback—especially on N availability—as microbial mineralization slows, ultimately culminating in a phenomenon known as progressive N limitation (Luo et al. 2004; Wang et al. 2007). However, it remains an open question as to whether and how N limitation can affect ecosystem responses to CO<sub>2</sub> enrichment, especially in the context of multiple global changes.

Over the course of 3 yr of CO<sub>2</sub> enrichment, Shaw et al. (2002) found no consistent stimulation of the NPP in a California grassland. In fact, the NPP of CO<sub>2</sub>-treated plots fell below that of ambient ones in the third year of study (Fig. 3). Although N fertilization stimulated NPP relative to controls—demonstrating N limitation—it did not reverse the pattern of NPP among ambient and elevated CO<sub>2</sub> treatments (Shaw et al. 2002). The authors concluded that other resources, particularly P, may be acting as a “shadow constraint” on NPP responses to elevated CO<sub>2</sub>, whereby P becomes limiting only when other factors increase NPP to a level that is potentially above the limit set by P availability, causing systems to move into the shadow of P limitation. It seems that ecosystems can enter the shadow of P limitation in response to increased CO<sub>2</sub> and N deposition (Menge and Field 2007).

In their examination of longer-term responses, Dukes et al. (2005) observed similarly strong effects of N fertilization on grassland productivity, coupled with a general lack of temporal coherence in NPP responses to elevated CO<sub>2</sub>. Other global change simulations (i.e., warming and increased precipitation) did not increase NPP unless in the presence of added N (Dukes et al. 2005), implying little evidence for water limitation of these grassland ecosystems. Moreover, shoot and root production patterns behaved somewhat independently across years; N additions increased shoot production regardless of the year, whereas root production showed no consistent response to N additions. This lack of C investment into root biomass may help explain the lack of CO<sub>2</sub> stimulation of NPP; increased root proliferation would be needed for plants to exploit soils for P.

In sum, it is clear that progressive N limitation does not appear to be responsible for the lack of NPP responses to elevated CO<sub>2</sub> in this California grassland. This stands in contrast to multifactor studies conducted on temperate grasslands at Cedar Creek in Minnesota, where N appears to progressively limit plant production under elevated CO<sub>2</sub> (Reich et al. 2006). In a temperate perennial grassland in Australia, progressive N limitation was also observed with CO<sub>2</sub> enrichment in microcosms; however, experimental warming of 2°C sufficiently offset this effect (Hovenden et al. 2008), pointing to the importance of multifactor global change experiments in making informed predictions about C-nutrient

interactions. It may be that P (or N plus P) becomes more limiting under elevated CO<sub>2</sub> in California grasslands; however, the mechanisms by which ecosystems may transition between N and P limitation remain poorly understood. Additional work on the ecosystem scale budgets of N and P would help shed light on the ultimate controls of nutrients on C cycling in California grasslands in response to multiple global changes.

## IMPLICATIONS

The major point of this paper is that although ecosystems may store additional C in response to elevated CO<sub>2</sub>, nutrients such as N and P appear to constrain this capacity substantially. This is observed across different scales and among different types of vegetation in California rangeland habitats. Top-down herbivore effects can also alter such interactions between C, N, and P, especially in California oak woodlands, where insectivorous herbivores convert foliage into readily decomposable frass, temporarily stimulating rates of N cycling (Hollinger 1986). The long-term consequences of such interactions are less clear, however: herbivores can stimulate rates of N cycling in the short term, though lead to high N losses and declines in NPP over long time scales (Pineiro et al. 2006). Overall, our results highlight the need for managers to consider both N and P cycles in understanding constraints to C uptake and storage in California rangelands.

Regarding global change, our synthesis points to diverse modes of grassland responses to elevated CO<sub>2</sub>, with the details sensitive to soil and plant characteristics. Particularly striking is that, despite expectations of global C models (Hungate et al. 2003), CO<sub>2</sub> does not necessarily stimulate terrestrial plant productivity of grasslands (Shaw et al. 2002; Reich et al. 2006). These results should be approached with a healthy level of caution when extrapolating to the future—the time frame of CO<sub>2</sub> rise is much slower than for experiments and open-top chambers and edge effects may impose artifacts as well. Nevertheless, that nutrients will limit plant responses to elevated CO<sub>2</sub> in California grasslands is very likely, though these interactions may be complex in detail. The nutrient that limits plant growth will vary depending on various ecosystem state controls such as geology, climate, time, topography, herbivory, and biological composition—and especially the presence of plant functional groups such as N-fixing legumes (Houlton et al. 2008). We believe that future studies in rangelands should build toward a more synthetic theory of C–climate–nutrient interactions that explicitly consider interactions between C, N, and P cycles across various vegetation types, soils, and conditions.

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