
CLIMATE CHANGE AND AGRICULTURE PAPER

Application of a conceptual framework to interpret variability in rangeland responses to atmospheric CO₂ enrichment

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SUMMARY

Plant productivity and other ecosystem processes vary widely in their responses to experimental increases in atmospheric carbon dioxide (CO₂) concentration. A conceptual framework first suggested by Chapin *et al.* (1996) was adapted to address the question of why CO₂ effects on primary productivity vary so greatly among rangelands and among years for a given ecosystem. The ‘interactive controls’ framework is based on the premise that the influence of elevated CO₂ on productivity is governed by a set of internal variables that interact dynamically with ecosystem processes. These interactive controls, which include regional climate, soil resource supply, major functional groups of organisms and disturbance regimes, both regulate CO₂ effects on ecosystems and respond to CO₂ effects. Changes in interactive controls resulting from CO₂ enrichment may feed back to dampen or amplify ecosystem responses to CO₂. Most feedbacks from interactive controls will be negative and dampen CO₂ effects on ecosystems. Negative feedbacks promote homeostasis in ecosystem processes and reduce the response of plant productivity to CO₂. Positive feedbacks on CO₂ responses are fewer, but can sustain or even increase benefits of CO₂ enrichment for productivity. Positive feedbacks on CO₂ responses occur most frequently through changes in plant species and functional group composition. Understanding positive and negative feedbacks on CO₂ responses could be one key to predicting consequences of CO₂ enrichment for rangeland productivity and other processes.

INTRODUCTION

Atmospheric carbon dioxide (CO₂) concentration has increased by >35% since Industrialization, to the current level of 385 ppmv (Keeling *et al.* 2009) and may reach twice the Pre-Industrial concentration by the middle of the 21st century (IPCC 2007). CO₂ enrichment directly affects just two physiological processes of plants, photosynthesis and stomatal conductance to water vapour, but may increase plant

productivity and influence many other ecosystem processes via these effects. For reasons that are not fully understood, CO₂ responses vary widely among ecosystems. For example, increasing CO₂ to 680–720 ppmv increased the productivity of shortgrass steppe by 95% during a dry year (Morgan *et al.* 2004b), but had no effect on or even reduced biomass of annual grassland when productivity was high (Shaw *et al.* 2002; Dukes *et al.* 2005).

Following a brief review of the influence of CO₂ on plant physiology, the question of why CO₂ impacts on productivity and other processes vary among ecosystems will be explored. A conceptual framework

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is applied to interpret this variability. The focus will be on rangeland ecosystems, defined as natural or semi-natural herbaceous formations composed mostly of grasses (Polley 1997), but the framework described may be applied to any ecosystem. Rangelands and other grazing lands together form the largest and most diverse land resource on Earth and support livestock industries worldwide (Follett & Reed 2010). In the USA alone, grazing lands support more than 60 million cattle and 8 million sheep (National Agricultural Statistics Service of USDA 2006).

Leaf and plant responses to CO₂

Net photosynthesis of C₃ plants usually increases almost linearly from sub-ambient CO₂ to the current CO₂ concentration when measured at high light intensity (Percy & Ehleringer 1984). Typically, C₃ photosynthesis continues to increase, albeit at a lesser rate, at greater-than-present CO₂ levels. At full illumination, net photosynthesis tends to be greater in C₄ than C₃ leaves at sub-ambient CO₂, but C₄ photosynthesis approaches saturation at the current CO₂ concentration.

An increase in CO₂ usually reduces stomatal conductance to water vapour, especially among herbaceous species (Field *et al.* 1995; Wand *et al.* 1999). Conductance declines by a similar proportion in C₃ and C₄ plants (Wand *et al.* 1999). Transpiration per unit of leaf area may decline as a result, although feedbacks at the canopy and higher scales typically lessen the anti-transpiration effect of reduced conductance (McNaughton & Jarvis 1991). When transpiration rates do decline, effects may include slower rates of soil water depletion by plants, improved plant water relations, and greater biomass production on rangelands and other water-limited ecosystems (Fredeen *et al.* 1997; Owensby *et al.* 1997; Niklaus *et al.* 1998; Morgan *et al.* 2001, 2004b; Grünzweig & Körner 2001; Polley *et al.* 2002a).

There is often a strong correlation between physiological sensitivity and growth response to CO₂ when plant densities are low and resources such as light and nitrogen (N) are plentiful. That correlation weakens when plant densities are high or conditions are less than optimal for growth. Thus, stand-level responses to CO₂ often depend as much on exogenous factors as on physiological sensitivity to CO₂. As a consequence, CO₂ effects on productivity have been found to vary widely among grasslands and other rangelands. The effects of experimentally increasing CO₂ concentration range from no change or even a decrease in aboveground biomass of annual grassland when productivity is high (Shaw *et al.* 2002; Dukes *et al.* 2005) to a 95% increase in aboveground biomass during a dry year on shortgrass steppe (Morgan *et al.* 2001, 2004a). Why is sensitivity to CO₂ so variable among ecosystems and years on a given ecosystem?

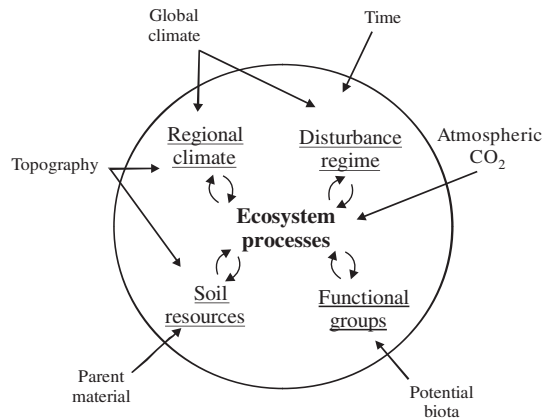


Fig. 1. Conceptual relationships between state factors (listed outside the circle; i.e. Parent Material and Potential Biota), interactive controls (underlined; i.e. Soil Resources and Functional Groups) and ecosystem processes. State factors are static over ecological time scales and constrain interactive controls. Interactive controls both regulate and respond to ecosystem processes. Like state factors, atmospheric CO₂ concentration is determined by factors that are largely external to and independent of ecosystem processes at the local scale. Unlike state factors, atmospheric CO₂ concentration is not static. Rather, the continuing increase in CO₂ concentration represents a chronic and cumulative change in the availability of an essential resource for plants (Smith *et al.* 2009). The figure is adapted from Chapin *et al.* (1996).

More specifically, what regulates the sensitivity of productivity and other ecosystem processes to CO₂? Do the constraints on ecosystem processes that are evident in short-term (years to decades) experiments operate indefinitely with little change? Or, do changes associated with CO₂ enrichment feed back to affect ecosystem sensitivity to CO₂? If so, long-term responses of ecosystems to CO₂ may not match short-term dynamics.

The interactive controls framework for assessing variability in CO₂ responses

Chapin *et al.* (1996) noted that ecosystem processes are regulated by both internal and external factors (Fig. 1). External factors or 'state factors', as the descriptors imply, are external to and independent of ecosystem processes. External factors include parent material, global climate, topography, potential biota and time (Jenny 1941), and may be regarded as static over an ecological timescale of decades. Chapin *et al.* (1996) suggested that ecosystems also are regulated by internal factors that are dynamic over ecological timescales. These dynamic, internal regulators of ecosystems were termed 'interactive controls' and include regional climate, soil resource supply, major

functional groups of organisms (where functional groups are defined as organisms that have similar effects on ecosystem processes) and disturbance regime. Unlike state factors, interactive controls both *regulate* and *respond* to ecosystem processes. Interactive controls are constrained by state factors, but interact dynamically with ecosystem processes.

Atmospheric CO₂ concentration has changed through geological time (Jouzel *et al.* 1993; Petit *et al.* 1999), cycling between 180 and 300 ppmv during the past 650 000 years (Jansen *et al.* 2007). However, atmospheric CO₂ has remained virtually constant for all but the most recent 200 of the last 12 000–15 000 years. For much of the recent past then, atmospheric CO₂ concentration may be regarded as static. Photosynthesis and respiration by terrestrial and other ecosystems influence the global growth rate of atmospheric CO₂ concentration (Heimann & Reichstein 2008), but at local and regional scales, ecosystem processes have little influence on long-term values of atmospheric CO₂. At these spatial scales, CO₂ concentration may be regarded as external to and independent of ecosystem processes. In contrast to state factors, however, CO₂ concentration is no longer static over ecologically relevant timescales. Atmospheric CO₂ concentration has increased by >35% since Industrialization, exceeding 300 ppmv for the first time in more than 650 000 years during the middle of the 20th century (Jansen *et al.* 2007), and is currently increasing at the rate of almost 2 ppmv per year (Canadell *et al.* 2007). Rising CO₂ represents a chronic and cumulative change in the availability of an essential resource for plants (Smith *et al.* 2009).

Ecosystem responses to CO₂ enrichment are ultimately constrained by state factors. For example, the response of plant productivity to CO₂ enrichment depends on pool sizes and cycling rates of essential elements such as phosphorus (Smith *et al.* 2009), which in turn depend on characteristics of the parent material from which soil was derived. Within limits imposed by state factors, however, proximal responses of ecosystems to CO₂ will be governed by dynamic relationships between ecosystem processes and interactive controls. Interactive controls *regulate* CO₂ effects on ecosystems, but the magnitude and nature of this regulation depends partly on how interactive controls *respond* to or are affected by CO₂. Ecosystem responses to CO₂ will be dampened if changes caused by CO₂ enrichment intensify negative effects or reduce positive effects of interactive controls on CO₂ responses. Conversely, ecosystem responses to CO₂ will be amplified if changes at elevated CO₂ reduce negative effects or amplify positive feedbacks of interactive controls on CO₂ responses.

Global change experiments, including those with CO₂ treatments, are usually designed to determine how treatment effects on primary productivity and

other processes depend on soil resource levels, climatic variables and plant species composition. That is, most experiments are designed to determine how interactive controls *regulate* ecosystem responses to CO₂ and other treatments. Less frequently addressed is the critical question of how interactive controls *respond* to CO₂ and whether changes in controls caused by CO₂ exert a positive or negative feedback on the rate and magnitude of ecosystem responses to atmospheric change. As an ecosystem's response to CO₂ increases, so does the perceived sensitivity of that ecosystem to CO₂.

Considered in the sections that follow are ways in which (1) regional climate, soil resources, disturbance regime and functional groups of organisms may regulate ecosystem responses to CO₂ and (2) feedbacks resulting from the response of controls to CO₂ may affect ecosystem sensitivity to CO₂ enrichment. It is important to recognize that the amount by which a given interactive control responds to CO₂ and regulates ecosystem sensitivity to CO₂ will depend on changes in other interactive controls. Human intervention in ecosystems is pervasive, with effects that often operate independently of changes in CO₂. The present paper focuses on dynamic interactions between CO₂ levels and interactive controls, but it is recognized that anthropogenic changes in controlling factors can substantially alter ecosystem processes and their responses to CO₂ concentration.

REGULATION OF CO₂ RESPONSE

Regional climate

Rangeland productivity is governed largely by the effects of the spatial and temporal distribution of precipitation on soil water availability and the climatic effects on evaporative demand (Campbell *et al.* 1997; Morgan 2005; Fay *et al.* 2008; Heisler-White *et al.* 2009). Most rangelands, but especially those on which productivity is strongly water-limited, should be sensitive to the positive effects of CO₂ enrichment on soil water content and plant water relations. Unless stomatal closure is compensated by atmospheric or other feedbacks, such as an increase in leaf area, CO₂ enrichment should slow canopy-level water loss (Polley *et al.* 2008) and the rate or extent of soil water depletion (Owensby *et al.* 1997; Polley *et al.* 2002a; Nelson *et al.* 2004) and increase leaf and plant water use efficiency (Polley *et al.* 2002a; Fay *et al.* 2009). Indeed, variability in water availability may be the single most important factor mediating the biomass response of rangeland vegetation to CO₂ (Morgan *et al.* 2004b).

Positive effects of CO₂ enrichment on productivity generally increase as precipitation and water availability decline, especially when water is saved at elevated CO₂ while plants are active. In general,

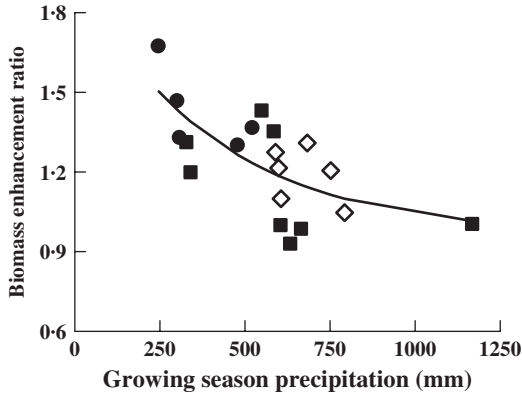


Fig. 2. The ratio of aboveground plant biomass at elevated compared to ambient CO_2 (biomass enhancement ratio) in Kansas tallgrass prairie (closed square), Colorado shortgrass steppe (closed circle) and Swiss calcareous grasslands (open diamond) as a function of yearly precipitation. The fitted line has an R^2 of 0.48, $P=0.005$. The figure is adapted from Morgan *et al.* (2004b).

then, the CO_2 stimulation of biomass should be proportionally greater or more consistent on semi-arid than mesic ecosystems and, for a given ecosystem, during dry than wet years (Morgan *et al.* 2004b). For example, CO_2 enrichment increased biomass production proportionally more on semi-arid shortgrass steppe (Morgan *et al.* 2004a) than on mesic tallgrass prairie (Owensby *et al.* 1997) and calcareous grassland in Switzerland (Niklaus & Körner 2004) and, for each ecosystem, during relatively dry than wetter years. Morgan *et al.* (2004b) found that the ratio of aboveground biomass production at elevated CO_2 to production at ambient CO_2 (biomass enhancement ratio) increased across these three grasslands as growing season precipitation declined from *c.* 750 mm to 250 mm (Fig. 2).

Positive effects of CO_2 enrichment on productivity do not consistently extend to arid ecosystems, however. CO_2 enrichment increased plant biomass in the Mojave Desert in the western USA only during a wet year, when the total precipitation was 2.4 times the long-term average for the site (Smith *et al.* 2000). These findings imply that a minimum level of precipitation or soil water availability exists below which CO_2 has little influence on productivity (Morgan *et al.* 2004b; Nowak *et al.* 2004). CO_2 effects are negligible during most years in arid environments partly because a significant fraction of water loss is not under plant control. Much of precipitation probably is lost to evaporation rather than transpiration in arid and semi-arid ecosystems because evaporative demand of the atmosphere is high, plant cover is sparse, vegetation often must recover from extended periods

of drought in order to appropriate water for growth, and most precipitation events are small (e.g. Sala & Lauenroth 1982; Wythers *et al.* 1999).

Soil resources

Low N availability frequently limits plant productivity on rangeland ecosystems (e.g. Seastedt *et al.* 1991) and may reduce or even eliminate any benefit of CO_2 enrichment for plant growth (Owensby *et al.* 1994; Reich *et al.* 2006). Productivity is probably limited more often by N than by insufficiencies in other elements, but limits on the availability of any essential element of plants could constrain CO_2 effects on productivity.

Soil water content is a critical determinant of plant productivity, both because of its direct effect on plant water status and activity and its indirect effect in stimulating decomposition, mineralization, nutrient cycling and mass flow of elements to roots (Burke *et al.* 1997; Dijkstra *et al.* 2008). The water-relations benefit of CO_2 to plant growth may result in part from an increase in N mineralization rates in wetter soils (Morgan *et al.* 2004b; Dijkstra *et al.* 2008).

Disturbance regime

Many rangeland ecosystems are sustained in their current states by disturbances, the two most influential of which are grazing and fire. Disturbances, like other interactive controls, regulate CO_2 responses both directly and indirectly, the latter by affecting other controlling factors. Grazing and fire directly modify plant growth and physiology by removing plant tissues. Grazers can also serve as a vector for seed dispersal in faecal deposits (Kramp *et al.* 1998; Brown & Archer 1999), with the potential for profound changes in plant community structure. Many of the other effects of these disturbances on ecosystem processes are indirect, mediated through changes in soil resource levels or the biota.

Grazers strongly influence plant productivity on rangelands, but our understanding of how defoliation regulates productivity in response to changes in CO_2 levels is limited. It might be expected that defoliation would enhance the effects of changes in CO_2 levels on plant growth and speed plant recovery from defoliation by stimulating photosynthesis, at least in C_3 species. Recent results confirm this expectation (D. J. Augustine, personal communication). Defoliated plants of *Pascopyrum smithii* recovered more rapidly when grown at elevated levels of CO_2 than at ambient levels. Photosynthesis rates were doubled in defoliated compared to non-defoliated plants grown at 780 ppmv CO_2 , but not in the plants grown at 400 ppmv CO_2 . Similarly, increasing CO_2 to 235 ppmv above ambient levels enhanced the production of vegetation growing in monoliths extracted

from semi-natural grassland in Wales when plants were defoliated six times per year (Harmens *et al.* 2004). CO₂ treatment had no effect on production of plants defoliated just twice per year. In contrast, results from other studies do not support the view that defoliation magnifies CO₂ effects on plant growth. For example, re-growth following defoliation was no greater at elevated than at ambient levels of CO₂ for a C₃ forb (Fajer *et al.* 1991) or a C₄ grass (Wilsey *et al.* 1994). Plants of three grass species from each of three grassland ecosystems showed similar responses to CO₂ when clipped and not clipped (Wilsey *et al.* 1997), as did vegetation on shortgrass steppe (Milchunas *et al.* 2005) and a New Zealand pasture subjected to sheep grazing (Newton *et al.* 2006). Herbivory may even reduce plant sensitivity to CO₂. Clipping reduced aboveground biomass of *Arabidopsis thaliana* more at elevated than at ambient CO₂, for instance (Lau & Tiffin 2009).

Grazing may indirectly influence CO₂ effects on productivity by contributing to seed dispersal, seedling recruitment and, ultimately, vegetation change. Elevated CO₂ has been found to enhance seedling establishment on rangeland (Morgan *et al.* 2004a) and mesic pasture (Edwards *et al.* 2001), but evidence for an effect of grazers is limited because of the difficulty of incorporating large animals into manipulative CO₂ experiments. In a rare CO₂ experiment with animals, Newton *et al.* (2006) found that grazing by sheep enhanced aboveground production of two important *Trifolium* species in CO₂-enriched New Zealand pasture. Enhanced recruitment under grazing appears to have been an important factor in the CO₂ response of one of the species, *T. subterraneum*.

Fire indirectly affects CO₂ response via changes in soil resources and vegetation. Fires volatilize substantial quantities of N (Seastedt *et al.* 1991), hence frequent burning may constrain ecosystem responses to CO₂ by reinforcing N limitations on plant growth. Fire also can affect ecosystem processes by changing plant abundances or composition. Henry *et al.* (2006) found that summer wildfire removed the suppressive effect of elevated CO₂ on primary productivity of annual grassland by increasing production of forb species. Conversely, spring burning favours C₄ grasses at the expense of C₃ forbs on tallgrass prairie (Howe 1994), potentially diminishing biomass response to CO₂. By increasing plant growth, CO₂ enrichment may also lessen the time period during which woody seedlings or saplings are most susceptible to fire and enhance woody incursion into grasslands (Bond 2008), with potential consequences for future CO₂ response.

Functional groups

Results from several studies have shown that the response of productivity to CO₂ is regulated by the

number or identities of species or species groups present in plant assemblages (Leadley *et al.* 1999; Niklaus *et al.* 2001; Reich *et al.* 2004). Increasing the number of species or functional groups of species enhanced positive effects of CO₂ enrichment on aboveground and total biomass of herbaceous communities (Reich *et al.* 2004). Similarly, Niklaus *et al.* (2001) reported a positive correlation between the diversity of grassland communities and biomass enhancement at high CO₂. Biomass may respond more to CO₂ in diverse than in depauperate communities simply because diverse communities are more likely to contain responsive species (Niklaus *et al.* 2001). Alternatively, increasing diversity may increase CO₂ effects on biomass by maximizing plant capture of N, light and other resources that are required for greater production (Reich *et al.* 2004).

Summary – regulation of CO₂ response

Results from manipulative experiments demonstrate that three interactive controls, regional climate, soil resources and functional groups of plants, strongly regulate CO₂ effects on rangeland productivity. The effects of the disturbance regime on CO₂ responses are variable in direction and are often inconsequential. The benefits of CO₂ enrichment for productivity generally increase as precipitation (regional climate) declines and species diversity (functional groups) increases, and decline as N availability decreases (soil resources). Consequently, differences in regional climate, functional groups and soil resources among rangeland ecosystems and among years for a given ecosystem contribute to variability in CO₂ effects on productivity. However, we must ask whether these controls on the response of a given ecosystem operate indefinitely without variation, or whether changes in controls caused by alterations in levels of CO₂ might feed back to amplify or dampen ecosystem sensitivity to CO₂.

FEEDBACKS ON CO₂ RESPONSES FROM CHANGES IN INTERACTIVE CONTROLS

Regional climate

Elevated CO₂ can lead to changes in canopy-level and local climatic factors that reduce water savings from a decrease in stomata conductance and, hence, the benefits of CO₂ enrichment for water-limited ecosystems. One of these negative feedbacks involves stomatal effects on leaf temperature. Partial stomatal closure reduces the transpiration rate and latent heat flux, leading to a rise in leaf temperature (Idso *et al.* 1993; Kimball *et al.* 1995). The saturation vapour pressure of air increases as temperature rises, causing an increase in the leaf-to-air vapour pressure gradient.

This increase in the driving gradient for water loss tends to offset effects of reduced conductance on transpiration. Higher canopy temperatures and reduced transpiration contribute to a second negative feedback on plant regulation of transpiration. The vapour pressure deficit of air within and immediately above vegetation depends partly on transpiration. Slower transpiration tends to dry air in the canopy boundary layer, further increasing the vapour pressure gradient for transpiration. Bunce *et al.* (1997) simulated these and other processes that regulate transpiration with a model calibrated using crop species. Simulations indicated that elevated CO₂ increased leaf temperature and the vapour pressure difference between leaves and air. This feedback, together with other feedbacks operative at regional scales, almost completely negated effects of a 20–60% decrease in canopy conductance on water loss. Negative feedbacks also have been shown to attenuate stomatal effects on rangeland transpiration. Elevated CO₂ often reduces leaf conductance to 20–50% of that measured at ambient CO₂, but rarely reduces evapotranspiration on grasslands by greater than 20% (Morgan *et al.* 2004b). Elevated CO₂ also may reduce the tolerance of photosynthesis to acute heat stress, especially among C₄ species and plants grown at supra-optimal temperatures (Hamilton *et al.* 2008).

Any process that reduces the influence of plants on the amount of soil water that is returned to the atmosphere or the rate at which water is depleted from soil will limit the response of rangeland productivity to CO₂. These processes include those regulated by other interactive controls, such as soils and disturbance regimes. Drainage of water below the rooting zone of plants represents a negative feedback on biomass response to CO₂ that depends, in turn, on soil texture. Deep drainage almost doubled at elevated compared to pre-industrial CO₂ in model grassland assemblages of Israel during the wet part of the growing season (Grünzweig & Körner 2001). Similarly, CO₂ enrichment increased water storage at 0.75–1.05 m depth in semi-arid shortgrass steppe (Nelson *et al.* 2004). Disturbances also can reduce plant regulation of water loss by reducing the cover of plants relative to bare soil.

Soil resources

Most terrestrial N occurs in organic forms that are not readily available to plants, hence rangeland responses to CO₂ depend partly on how quickly N cycles between organic and inorganic N compounds and whether changes associated with CO₂ enrichment accelerate or slow N cycling. The Progressive N Limitation (PNL) hypothesis holds that changes associated with CO₂ enrichment will create or reinforce N limitations on production by reducing N recycling to inorganic forms (Luo *et al.* 2004).

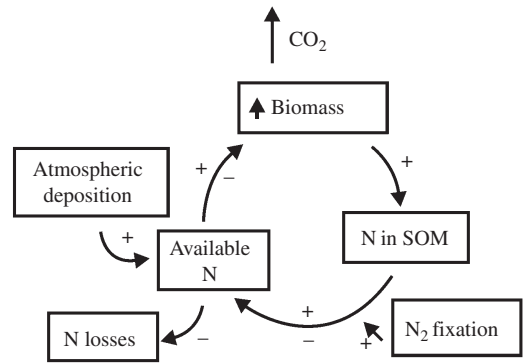


Fig. 3. Possible feedback effects of an increase in plant growth at elevated CO₂ on ecosystem N pools and N availability to plants. By increasing plant production, higher CO₂ increases N sequestration in plant biomass, litter pools and eventually SOM. CO₂ enrichment may increase or decrease the net rate at which N in SOM is mineralized to plant-available forms depending on whether microbial activity is 'primed' or inhibited by the extra C input to soil at elevated CO₂. Increasing CO₂ also may increase the pool of available and total N by stimulating N₂ fixation, reducing gaseous or liquid losses of N, or increasing retention of atmospheric N deposition.

According to the PNL hypothesis, CO₂ enrichment may lead to N limitation of productivity even in ecosystems in which N availability does not currently prevent a growth response to CO₂. The PNL hypothesis arises from the observation that organic matter, whether in plants or soil, contains N and other elements in rather fixed ratios to C. To the extent that CO₂ enrichment increases plant production and C accumulation in ecosystems, it also increases the sequestration of N and other elements in organic matter (Fig. 3). As more N is sequestered over time, the availability of mineral N to plants could decline and limit CO₂ effects on productivity. It is the progressive decrease in N availability to plants, rather than the initial amount of available N, that distinguishes the PNL hypothesis. Consistent with the PNL hypothesis, two differently configured ecosystem models, G'DAY and DAYCENT, predict that CO₂-stimulation of net ecosystem production on tallgrass prairie and shortgrass steppe will decline over a 100-year period because of a decline in soil N availability (Pepper *et al.* 2005).

Elevated CO₂ has been found to reduce soil N availability (Reich *et al.* 2006), but results from most experiments indicate that various processes operate at elevated CO₂ to reduce the strength of this negative feedback by either delaying the onset of N limitation or enhancing N accumulation in soil/plant systems. Nitrogen limitation may be delayed by maximizing the amount of C sequestered per unit of N, that is by

maximizing the C:N ratio of organic matter. Organic matter accumulation is increased, for example, by transferring N from soil organic pools with relatively low C:N ratios to plants with higher C:N ratios, as demonstrated recently on mesic grassland (Gill *et al.* 2002, 2006) and semi-arid shortgrass steppe (Pendall *et al.* 2003). On mesic grassland, microbes mineralized resident soil organic matter (SOM) to meet their nutritional needs at high CO₂. The N released by decomposition of SOM contributed to an increase in total N content of plant tissues (Gill *et al.* 2006) and sustained an increase in plant productivity at high CO₂ (Polley *et al.* 2003). In the absence of additional N required to stabilize organic C in soil pools, however, much of the extra organic C that was added to soil at elevated CO₂ was dissipated through rapidly cycling soil pools and did not accumulate (Gill *et al.* 2002). Decomposition rates of resident SOM more than doubled at elevated CO₂ on shortgrass steppe in Colorado (Pendall *et al.* 2003). The N released by more rapid decomposition of SOM reduced N limitations on growth and contributed to an increase in productivity at elevated CO₂ (Dijkstra *et al.* 2008).

Various other processes may increase N accumulation in soil/plant systems and contribute to a positive feedback on CO₂ responses. These processes include increased biological fixation of N, greater retention of atmospheric N deposition, reduced losses of N in gaseous or liquid forms, and more complete exploration of soil by expanded root systems (Luo *et al.* 2004; Fig. 3). Perhaps the most rapid and direct manner by which CO₂ enrichment could increase N accumulation on rangelands is by stimulating fixation of atmospheric N₂ by the legume-*Rhizobium* symbiosis. The absolute amount of plant-available N that can be derived from additional N₂ fixation at elevated CO₂ is large. For example, enrichment to 600 ppmv CO₂ was found to increase the annual N yield of mixed grass/legume swards by 9–13% (Zanetti *et al.* 1997). All additional N at elevated CO₂ was derived from enhanced N₂ fixation. Similarly, increasing CO₂ by 80–150% above the ambient concentration increased N₂ fixation by the woody legume *Acacia smallii* Isely (huisache) by a factor of 3–4 (Polley *et al.* 1997). Elevated CO₂ stimulated N₂ fixation by increasing both the mass of root modules per plant and fixation per unit of nodule mass. In the absence of large N input from legumes, the N concentration of leaves or aboveground tissues declined on shortgrass steppe, tallgrass prairie, and mesic grassland at elevated CO₂ and on tallgrass prairie with warming, but total N content of aboveground tissues increased as plant biomass increased on these ecosystems and on annual grasslands (Owensby *et al.* 1993; Hungate *et al.* 1997; King *et al.* 2004; Wan *et al.* 2005; Gill *et al.* 2006; Dijkstra *et al.* 2008). The implication is that plants accessed more, rather than less, N at elevated CO₂,

thereby delaying the onset of N limitation to productivity. Pepper *et al.* (2005) point out that a modest and gradual increase in soil N may be sufficient to overcome PNL in the long term.

Disturbance regime

CO₂ enrichment may change the behaviour of grazers and possibly the intensity of grazing by altering forage quality (Polley *et al.* 2000), with potential feedback effects on plant responses to CO₂. Plant N concentration usually declines at elevated CO₂ (Owensby *et al.* 1993; Cotrufo *et al.* 1998; Morgan *et al.* 2004a), implying that CO₂ enrichment will reduce the crude protein content of forage. Conversely, elevated CO₂ may improve forage quality by increasing tissue concentrations of non-structural carbohydrates (Read *et al.* 1997). On shortgrass steppe, CO₂ enrichment reduced the crude protein concentration of autumn forage below critical maintenance levels for livestock in 3 out of 4 years and reduced the digestibility of forage by 14% in mid-season (Milchunas *et al.* 2005). Significantly, the grass most favoured by CO₂ enrichment also had the lowest crude protein concentration. In addition, the unpalatable shrub *Artemisia frigida* exhibited the largest biomass increase of all plant species, a 40-fold increase during 5 years at elevated CO₂ (Morgan *et al.* 2007). The magnitude and even sign of the feedback of changes in forage quality on CO₂ responses will probably depend on whether changes in forage quality result in an increase or decrease in grazing intensity.

Increased CO₂ could increase fire frequency or intensity (Sage 1996) and thereby reinforce the effects of fire on ecosystem processes by increasing plant production, fuel load, or fuel flammability. The flammability of plants should increase if, as often observed, CO₂ enrichment increases the accumulation of non-structural carbohydrates in plant tissues (Read *et al.* 1997). Conversely, rising CO₂ could reduce the intensity or frequency of fires by delaying soil water depletion during dry periods (Morgan *et al.* 2004b) and increasing the water content of fuel or the ratio of live to dead tissues in plant stands. This suppressive effect of CO₂ on fire will probably be most important for rangelands on which dry intervals are relatively brief (Sage 1996). A delay of days to weeks in canopy senescence would probably have little effect on fire in rangelands which regularly experience extended periods of drought. Plant growth appears to be particularly responsive to CO₂ among several fire-adapted annual grasses, including *Bromus tectorum* and *Avena barbata* (Smith *et al.* 1987; Jackson *et al.* 1994; Ziska *et al.* 2005), evidence that CO₂ enrichment can promote a positive feedback on productivity by enhancing flammability or fuel load. On the other hand, more frequent fires may dampen CO₂ effects on productivity by reducing N availability to plants

(Seastedt *et al.* 1991) or increasing the fraction of water that is lost to evaporation.

Functional groups

CO₂ enrichment has been shown to alter plant abundances, and thus the potential response of productivity to CO₂, in most experiments with multi-species communities (Körner *et al.* 1997; Niklaus *et al.* 2001; Polley *et al.* 2003; Morgan *et al.* 2007). It might be predicted that CO₂ enrichment would increase the size or abundance of legumes and favour potentially more responsive C₃ over C₄ species, but CO₂ effects vary among ecosystems. Legumes were more abundant at elevated than ambient CO₂ in New Zealand pasture and Mediterranean grasslands (Edwards *et al.* 2001; Joel *et al.* 2001), but as a group responded little to CO₂ in calcareous grassland (Leadley *et al.* 1999). Similarly, as predicted by differences in photosynthetic pathway (Polley 1997), elevated CO₂ enhanced productivity of C₃ over C₄ grasses in shortgrass steppe (Morgan *et al.* 2007), but did not benefit C₃ grasses on C₄-dominated tallgrass prairie (Owensby *et al.* 1999). Several factors likely contribute to inconsistencies in CO₂ effects on vegetation. First, the life stage of plants most affected by CO₂ differs among experiments. In relatively closed canopies of perennial species, species change probably results mostly from differences in the growth responses of established plants to CO₂. Over longer time periods or in other ecosystems, vegetation change results partly from differences in the responses of seed production (Edwards *et al.* 2001) or seedling recruitment and survivorship among species to CO₂ (Smith *et al.* 2000; Morgan *et al.* 2004a). Secondly, it is likely that CO₂ effects on vegetation differ among ecosystems because factors that limit seedling establishment and plant growth differ among ecosystems or among years for a given ecosystem (Belote *et al.* 2003). Species change in water-limited systems is often linked to CO₂ effects on soil water content (Morgan *et al.* 2004b). CO₂ enrichment changed species abundances in ecosystems as diverse as Swiss grassland and semi-arid shortgrass steppe by slowing soil water depletion and preferentially increasing seedling recruitment of certain species (Niklaus *et al.* 2001; Morgan *et al.* 2004a). In contrast, CO₂ had little effect on species abundances in C₄-dominated tallgrass prairie in Kansas, USA (Owensby *et al.* 1999), presumably because the growth of the shorter C₃ species was limited by low light or N availability, or C₃ plants were incapable of exploiting the mid- to late-season improvement in soil water that occurred at elevated CO₂.

If the plants that benefit most from CO₂ enrichment are dominant species or become important contributors to communities, species change should increase the positive effect of higher CO₂ on productivity (e.g. Stöcklin *et al.* 1998). The link between the change

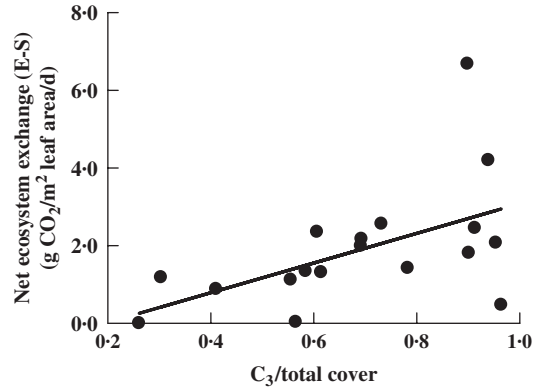


Fig. 4. The response of net ecosystem CO₂ exchange (NEE) of grassland to a 1–2-day change in CO₂ concentration of 175 ppmv. Mesic grassland was exposed for 3 years to a continuous gradient in CO₂ spanning sub-ambient to elevated concentrations in elongated chambers. Daytime NEE was measured continuously in each of 18 plots, 5 m long and 1 m wide, along the gradient. The amount by which NEE of each plot was greater at elevated than sub-ambient CO₂ following brief change in CO₂ (E-S) increased linearly as the ratio of C₃ plant cover to total cover increased. The graph is reproduced from Polley *et al.* (2007).

in relative abundance of a species and its growth response to CO₂ should be strongest in communities that establish following disturbances and when plants of all species are of similar size. On the other hand, species change that is caused by factors other than CO₂ may reduce CO₂ effects on productivity. Elevating CO₂ increased biomass of newly planted grassland communities by increasing the growth of ruderal species (Niklaus *et al.* 2001). The response of community biomass to CO₂ decreased over time, apparently because N availability declined following planting and favoured species that were more stress-tolerant but less CO₂-responsive than ruderals.

Unfortunately, there is little evidence from which to infer the impact of species feedbacks on productivity and other ecosystem processes. Biomass of C₃ species increased at the expense of C₄ grass biomass in mesic grassland, irrespective of CO₂ treatment (Mielnick *et al.* 2001; Polley *et al.* 2003). This shift towards C₃ plants, physiologically more responsive than C₄ plants (Anderson *et al.* 2001; Maherali *et al.* 2002), would be expected to increase plant growth response to CO₂ enrichment. Indeed, a temporary increase in CO₂ of 150–200 ppmv increased net ecosystem uptake of CO₂ more in C₃- than C₄-dominated vegetation (Fig. 4). The proportional increase in CO₂ uptake increased from 0 to 26% as the contribution of C₃ cover to total cover increased from 0.26 to 0.96 (Polley *et al.* 2007). Species interactions also proved an especially strong mediator of the response of annual grassland to

changes in the seasonality of precipitation (Suttle *et al.* 2007). Feedbacks resulting from species shifts reversed the initial responses of productivity and plant and food web diversity to precipitation change within a few years.

To the extent that species change reinforces CO₂ effects on productivity, the current composition or relative abundances of species may be considered to constrain CO₂ responses. There are at least two consequences of this constraint. First, the full response of ecosystem processes to CO₂ may not be evident in the short-term. Secondly, factors that reduce the species pool, limit the dispersal of propagules, or reduce plant establishment could limit CO₂ effects on productivity.

SYNTHESIS

Atmospheric CO₂ enrichment is a chronic and cumulative perturbation that could lead to a sustained increase in primary productivity and changes in other ecosystem processes, such as hydrology and element cycling (Smith *et al.* 2009), unless constrained by regional climatic factors, soil resource levels, disturbance regimes, or the functional groups of organisms present (Fig. 1). Three of these interactive controls, regional climate, soil resources and functional groups, have been shown to regulate proximal effects of CO₂ on rangeland productivity in fairly predictable fashion and thus to contribute to the variability in CO₂ responses that have been observed among ecosystems or years. Because these controls interact dynamically with ecosystem processes, the magnitude and nature of the effect of controls on ecosystems may change as CO₂ modifies ecosystem processes.

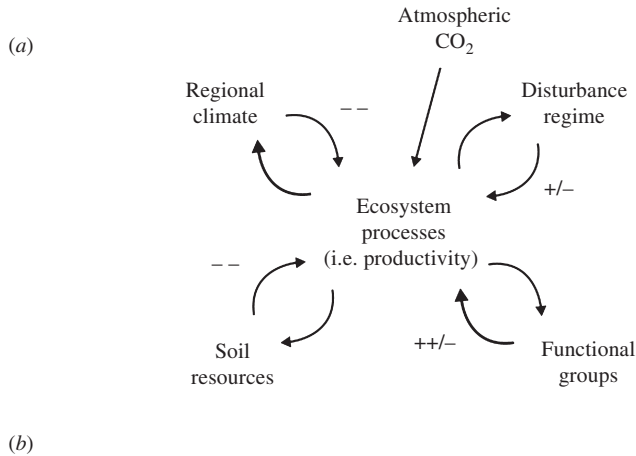
It would be expected that most feedbacks from CO₂-caused changes in interactive controls are negative and thus dampen rangeland responses to CO₂ (Fig. 5). Indeed, yields of even intensively managed crop species typically increase far less at elevated CO₂ than is theoretically possible because negative feedbacks constrain benefits of CO₂ enrichment for yield (Long *et al.* 2006). On most rangelands, plant growth is regulated by water availability. Productivity increases across broad geographic gradients on grasslands as annual precipitation increases (Sala *et al.* 1988). Rangeland productivity and net CO₂ exchange also vary with changes in precipitation (Knapp & Smith 2001; Heisler-White *et al.* 2009; Polley *et al.* 2010). To a first approximation then, rangeland responses to CO₂ will depend on the fraction of precipitation that plants transpire and the efficiency with which C is captured per unit of transpiration. Most feedbacks on CO₂ effects on water use and water use efficiency are negative because they reduce the ratio of transpiration to other losses of water or lessen the increase in water use efficiency expected as CO₂ rises. By reducing stomatal conductance, for example,

higher CO₂ increases leaf temperature and dries air within the canopy (local/regional climate), both of which tend to minimize changes in transpiration rates (Field *et al.* 1995; Bunce *et al.* 1997) and, ultimately, productivity. More frequent fires or other disturbances will negatively affect CO₂ responses if they increase the amount of water that is lost to evaporation, runoff, or deep drainage by reducing canopy leaf area.

Positive feedbacks on CO₂ responses are fewer and may develop more slowly than some negative feedbacks, but can sustain or even increase initial changes (Fig. 5). The greater is the impact of CO₂ on interactive controls that provide positive feedback, the greater is the possibility that CO₂ effects on productivity will exceed bounds documented in manipulative experiments. The most common source of positive feedbacks on CO₂ responses appears to be through changes in plant species and functional group composition. For example, CO₂ enrichment may relieve the N limitation on biomass response by increasing the relative abundance of legumes among plant functional groups (Edwards *et al.* 2001; Joel *et al.* 2001).

Although positive feedbacks amplify CO₂ responses, CO₂ enrichment probably will not lead to large and continuous changes in ecosystem processes in extensively managed systems such as rangelands, for two reasons. First, positive feedbacks may not become fully expressed when they depend on factors in addition to CO₂. Vegetation change can enhance CO₂ effects on productivity, but is mediated by aspects of plant demography over which CO₂ has little or no influence. Second, atmospheric CO₂ is increasing rapidly compared to the rate at which positive feedbacks from some interactive controls develop. CO₂ may increase more rapidly than soil N accumulation in some ecosystems, for example. Constraints on positive feedbacks imply that rangeland responses to a given increase in CO₂ may currently be limited more by plant composition, soil N availability, or other controls than during the geological past when CO₂ concentration rose more slowly.

Positive feedbacks on CO₂ responses can be exploited more fully in intensively managed ecosystems. Indeed, a primary goal of agricultural management is to lessen constraints of soil resources, disturbances and undesired plants on crop productivity. Several adaptive measures may be taken to maximize plant responses to CO₂ enrichment and increase the resilience of production systems to variability in temperature and precipitation (Smith & Olesen 2010). The most easily implemented measure involves a change in the species or cultivar of crops that are grown. The magnitude and even direction of crop responses to CO₂ enrichment are species or cultivar-specific (Baker & Allen 1993; Ziska *et al.*



(b)

| CO ₂ effect | Feedback (inactive control) | Nature and temporal scale of feedback on productivity |
|--|--|---|
| Decrease in stomatal conductance | Drier air; increase in leaf temperature (Climate) | Negative (minutes to days) |
| Increase in productivity or flammability | Increase in fires and abundances of CO ₂ -responsive species (disturbance regime) | Positive (years to decades) |
| Increase in productivity or flammability | Increase in fires and decrease in plant-available N (disturbance regime) | Negative (years to decades) |
| Greater establishment or growth of legumes | Increased input of plant-available N (functional groups) | Positive (years to decades) |
| Increased C input and sequestration of N in organic matter | Decrease in N availability to plants (soil resources) | Negative (years to decades) |

Fig. 5. Hypothesized effects of CO₂-caused changes in interactive controls of ecosystem processes on the response of rangeland productivity to CO₂ enrichment. (a) Changes in regional and local climate, soil resources, disturbance regime and functional groups of organisms that result from CO₂ effects on ecosystem processes may feed back to either dampen (–) or amplify (+) the initial response of productivity and other processes to CO₂. Feedbacks resulting from CO₂-caused changes in climatic factors and soil resources levels or cycling are hypothesized to strongly dampen CO₂ effects on productivity, whereas changes in the composition or abundances of functional groups of plants may amplify CO₂ effects on rangelands. (b) Examples of how CO₂ effects on plant and ecosystem processes contribute to changes in interactive controls that feedback to affect the response of rangeland productivity to CO₂ enrichment.

1996). Other options for maximizing crop productivity at elevated CO₂ include the addition of diversity to crop rotations and of legumes to cereal-based systems.

Interactive controls have been discussed as if they depended on state factors and interactions with ecosystem processes alone. In reality, human activities are contributing to large and directional changes in all interactive controls of rangeland processes: regional climate (land use changes), soil resources (N fertilization and deposition), disturbance regime (fire control and overgrazing) and functional groups of organisms (species introductions and simplification of biotic communities). Some of these changes have amplified

impacts of higher CO₂. For example, plant growth appears to particularly responsive to CO₂ among annual grasses, such as *Bromus tectorum* (Smith *et al.* 1987; Ziska *et al.* 2005), that proliferated on rangelands in western North America because of livestock movement and overgrazing (Mack 1986). Others, such as simplification of plant communities, may be depressing CO₂ effects (Niklaus *et al.* 2001; Reich *et al.* 2004).

Higher CO₂ concentration, together with directional changes in interactive controls, also are reducing the strength of negative feedbacks that sustained rangeland structure and functioning in the past. For example, positive effects of CO₂ enrichment on

establishment and growth rates of woody plants (Polley *et al.* 2002b; Morgan *et al.* 2007), together with directional change in disturbance regimes on grass-dominated ecosystems (fire control and overgrazing), have contributed to tree encroachment on rangelands and to substantial changes in ecosystem structure and functioning (Bond 2008).

The 'interactive controls' approach discussed earlier provides a framework for determining why CO₂ effects on productivity vary among ecosystems and, importantly, how changes in interactive controls may

feed back to affect ecosystem sensitivity to CO₂. The approach is flexible enough to accommodate human influences, ecosystem processes other than productivity, and ecosystems in addition to rangelands. Using this approach, it is concluded that shifts in plant species composition will be required on most rangelands if CO₂ enrichment is to continue to increase productivity. Vegetation change and, ultimately, rangeland responses to CO₂ thus may depend on how quickly species that can best utilize CO₂ in a given area will reach and colonize appropriate sites.

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