ROLE OF GRASSLANDS AS MODIFIERS OF GLOBAL CLIMATE CHANGE

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ABSTRACT
Grasslands may modify global climate change through impacts on carbon, nitrogen, and methane cycling. Carbon acquisition by C_3 species will increase in future atmospheres with elevated CO_2 due to reduced oxygen competition for the active site on Rubisco, thereby increasing primary production. Photosynthetic capacity of C_4 species will not be increased directly. Both C_3 and C_4 species will have reduced stomatal conductance which, particularly in water-stressed environments, will increase water use efficiency and further increase primary production**.** Higher C/N ratios of plant tissues will likely reduce decompositon of plant residues which will likely increase soil carbon stores. Carbon sequestration by grassland ecosystems will slow the rise in atmospheric CO_2 and lower the future peak concentration. Initial evidence from long-term, ecosystem-level elevated CO_2 experiments indicate increased carbon in all fractions of soil organic matter. Effects of elevated CO_2 on methane and nitrous oxide, also greenhouse gases, may increase their atmospheric concentrations and increase their effects on global warming. Grazing rate has the potential to affect carbon acquisition and storage more than atmospheric CO_2 concentration. Carbon acquisition in heavily grazed grasslands is extremely low, and root growth is reduced more than topgrowth which would reduce carbon storage.

KEYWORDS
grasslands, elevated CO_2, global climate change, greenhouse effect, methane, nitrous oxide

INTRODUCTION
The uncertainty associated with the effects of increasing levels of greenhouse gases in our atmosphere has centered on two areas: the impact of the increased levels on the climate and the direct effects on plants and ecosystems. The prediction of increased levels of CO_2 in the atmosphere is not of recent vintage. Weart (1997) has traced the history of the discovery of the risk of greenhouse gases on global warming, indicating that the first alarm was sounded in 1896 by Svante Arrhenius. That warning received little attention until recently, when the rate of increase of CO_2 in the atmosphere grew to 0.4% annually. Since CO_2 is the major greenhouse gas in our atmosphere, a major effort in determining the effects of elevated atmospheric CO_2 has occurred over the past 15 or so years. Grassland impact on the rate of CO_2 increase in our atmosphere revolves around the direct effects of elevated CO_2, and the impact of changing temperature and precipitation on ecosystem productivity and carbon storage in soils. Of late, the focus of research on the direct effects of elevated CO_2 has shifted from physiologic or single plant investigations to the ecosystem scale or greater, primarily to determine the potential for carbon sequestration by natural and managed ecosystems. If there is substantial long-term carbon storage in wood or in soil organic matter, the rise in atmospheric CO_2 may slow and lower the peak atmospheric CO_2 concentration estimates based on anthropogenic emissions. The role that forages and grasslands play in carbon storage may be significant in mitigating the effects of elevated CO_2 on climate change. The impact of elevated CO_2 on other greenhouse gas fluxes, though of lesser impact than that of CO_2, also may affect their potential to change climate. Though not direct mitigation, the reduced water and nitrogen requirements under elevated CO_2 may allow for forage plant communities to sustain current production levels in the face of reduced available water for plant growth. The primary greenhouse gas fluxes that forage plant communities can potentially alter are CO_2, methane (CH_4), and nitrous oxide (N_2O).

CARBON DIOXIDE
Responses to elevated CO_2 by forage plant communities can influence climate change through interactions among the effects on carbon acquisition, water use efficiency, nitrogen use efficiency, ecosystem respiration, microbial activity, litter quality, and change in plant community composition. The ultimate influence is centered around the potential for soils in forage plant communities to sequester carbon. The impact of elevated CO_2 on the carbon acquisition by the ecosystem is the based on the complex ecophysiological responses that ultimately lead to increased carbon sequestration or loss. Primary production in natural grassland ecosystems is most often limited by CO_2 concentration (primarily C_3-dominated systems), water, and nitrogen (Field et al., 1992). The impact of elevated CO_2 depends to a great extent on the photosynthetic pathway of the plant species in the grassland systems.

Photosynthetic pathway. Responses of plants with C_3 and C_4 photosynthetic pathways to elevated CO_2 have been summarized by numerous authors (Kimball, 1983; Bazzaz, 1990; Newton, 1991; Woodward et al., 1991; Drake, 1992). Plants with the C_3 photosynthetic pathway generally respond to elevated CO_2 with increased net photosynthesis as a result of reduced oxygenase activity of ribulose-1,5-bisphosphate carboxylase (Rubisco) (Pearcy and Bjorkman, 1983). In contrast, C_4 species initially capture carbon in the leaf mesophyll with phosphenolpyruvate carboxylase (PEPc) (Edwards and Walker, 1983) and are not subject to measurable photorespiration. In the absence of other limiting resources, a greater primary production response exists under elevated CO_2 for C_3 than for C_4 species. Knapp et al. (1993), reported that for the C_4 grass, *Andropogon gerardii*, photosynthetic capacity was greater under elevated CO_2 than ambient when frequent water stress occurred. Apparently, the more frequent water stress under ambient CO_2 reduced the photosynthetic capacity of *A. gerardii*, but maintained it under elevated CO_2. In a wet year, no differences in photosynthetic capacity were detected when ambient and elevated CO_2 grown plants were compared. Although the photosynthetic capacity of C_4 species may not be directly enhanced under elevated CO_2, they concluded that water-stress related reductions in photosynthetic capacity are less likely to occur under elevated CO_2 compared to ambient CO_2 for C_4 grasses. Ultimately, that will lead to higher photosynthetic rates at elevated vs. ambient CO_2.

Increased carbon acquisition through greater photosynthetic rates under elevated CO_2 bodes well for mitigation of climate effects on grassland ecosystems provided other resources do not limit productivity. If increased photosynthesis can be sustained with a reduced water supply, then the opportunity exists for mitigation of the impact of climate change on grassland ecosystem productivity. There is also the opportunity to increase carbon storage in the ecosystem.

Water use efficiency. Water stress in grasslands is frequent, particularly for those dominated by C_4 species (Doliner and Jolliffe, 1979). Increased atmospheric CO_2 reduces water loss through reductions in stomatal conductance (g_s) (van Bavel, 1974). If carbon assimilation increases under elevated CO_2, reduced g_s provides increased water use efficiency (WUE) (Eamus, 1991; Newton, 1991;

Koch and Mooney, 1996). Stomatal conductance under elevated CO_2 is typically reduced by 30-40% for both C_3 and C_4 plants (Eamus and Jarvis, 1989; Woodward et al., 1991). Therefore, the reduced transpirational loss of water under elevated CO_2 has the potential to alleviate water stress while maintaining optimal carbon fixation. Owensby et al. (1993a), Ham et al. (1995), and Bremer et al. (1996) concluded that in a Kansas tallgrass prairie ecosystem fumigated with twice ambient CO_2, evapotranspiration was significantly reduced compared to that in an ambient CO_2 environment. Newton (1991) indicated that leaf area of a plant canopy usually increases with exposure to elevated CO_2, and total canopy water use may be the same for plant communities under elevated and ambient CO_2 levels. However, in the C_4-dominated tallgrass prairie, where increased ecosystem-level production is tied to reduced transpiration, water use is less than under ambient CO_2 even with an increased plant canopy. For plant communities dominated by C_3 species, total water use may not decline due to increased photosynthesis and resultant greater leaf area (Nijs et al., 1988). Also, improved water relations could be realized through decreased stomatal density as atmospheric CO_2 increases due to the reduced requirement for gas exchange if the vapor pressure deficit is not substantially increased. Knapp et al. (1994) measured stomatal density of *A. gerardii* in ambient and elevated CO_2 environments and found that for *A. gerardii*, stomatal density was significantly higher for plants under ambient CO_2 than for those with elevated CO_2. Improved water relations could also result from increased root exploration as well (Curtis et al., 1990; Owensby et al., 1993a).

Hammerlynck et al. (1997) exposed undisturbed tallgrass prairie to ambient and elevated (twice ambient) levels of atmospheric CO_2 and experimental dry periods. Seasonal and diurnal midday leaf water potential (ψ_{leaf}), net photosynthesis (A_{net}), and stomata conductance (g_s) responses of three tallgrass prairie growth forms, a C_4 grass, *A. gerardii*, a broad-leaved woody C_3 shrub, *Symphoricarpos orbiculatus*, and a C_3 perennial forb, *Salvia pitcheri*, were assessed. ψ_{leaf} in *A. gerardii* and *S. orbiculatus* was higher under elevated CO_2, regardless of soil moisture, while ψ_{leaf} in *S. pitcheri* responded only to drought. Elevated CO_2 always stimulated A_{net} in the C_3 species, while A_{net} of *A. gerardii* increased only under dry conditions. However, A_{net} under elevated CO_2 in the C_3 species declined with drought, but not in the C_4 grass. Under wet conditions, g_s was reduced in elevated CO_2 for all species. During dry periods, g_s at elevated CO_2 was sometimes higher than in ambient CO_2. Their results support claims that elevated CO_2 will stimulate tallgrass prairie productivity during dry periods, and possibly reduce temporal and spatial variability in productivity in these grasslands. In water-stressed grasslands, it appears that the C_4 grasses may have a competitive advantage over C_3 species under elevated CO_2 due to improved water relations.

Taken together the increased photosynthesis and reduced transpiration under elevated CO_2 could sustain high productivity under elevated CO_2, but only if other resources did not limit productivity. Normally, nitrogen is in short supply in grassland ecosystems. If elevated CO_2 reduces nitrogen required for optimal photosynthesis, then the improved water relations and photosynthetic efficiency should be realized.

Nitrogen use efficiency. Similar to the impact of elevated CO_2 on water use, the nitrogen requirement of plants to sustain high productivity appears to be reduced. Initially the speculation was that increased biomass production under elevated CO_2 could not be supported as a greater proportion of the nitrogen was tied up in the increased productivity with a slower turnover time due to the increased C/N ratio of the tissues. Higher C:N ratios of plant litter reduce mineralization rates of nutrient resources (Mellilo, 1982; Berendse et al., 1987; Agren et al., 1991). There are both short- and long-term implications regarding nutrient limitation and response to elevated CO_2. The short-term response reflects the inherent low N availability of most natural ecosystems which affects the ability of the ecosystem to increase productivity with increased atmospheric carbon dioxide availability. The long-term response relates to reduced N availability results from slower decomposition of litter because of reduced litter quality. Because essentially all nutrients are cycled within the ecosystem and nutrient supplies in natural systems are relatively constant, increased productivity indicates an increased nutrient-use efficiency (Curtis et al., 1989; Owensby et al., 1993a). Even though nitrogen requirement is apparently reduced under elevated CO_2, Owensby et al. (1993b) reported that the response of biomass production to elevated CO_2 on N-fertilized plots in tallgrass prairie was much greater than in the unfertilized plots and concluded that the response to elevated CO_2 was suppressed by N limitation. Since a primary resource limitation in grasslands is nitrogen availability, the reduction in requirement (improved nitrogen use efficiency) will likely allow grasslands to maintain a greater productivity for a long period of time, thereby increasing carbon acquisition and potential carbon sequestration. Rice et al. (1994) reported that under CO_2 enrichment, soil microbial activity was consistently greater, but was regulated by soil moisture levels. There was a significant increase in microbial respiration in elevated CO_2 plots compared to ambient when the plots were nitrogen fertilized, which may indicate a N limitation to decomposition.

Carbon Storage in Soils. The consequence of increased biomass production and reduced decomposition in a high CO_2 environment may be increased carbon storage. Numerous modeling studies have predicted that consequence (Hunt et al., 1991; Ojima et al., 1993; Smith and Shugart, 1993). Owensby et al. (1993a) and Morgan et al. (1994) both showed that under elevated CO_2 root growth was significantly increased. They also reported that the C/N ratio of that material was increased, indicating the potential for greater soil carbon under elevated CO_2. Large open-top chambers (Ham et al., 1993) and free atmosphere carbon enrichment systems (FACE) (Hendry, 1992) offer an opportunity for destructive sampling with adequate sample size to determine temporal changes in soil carbon. Prior et al. (1994) working with cotton in a FACE system in Arizona reported that there was an increased carbon accumulation in soil measured indirectly using the ^{13}C tracer technique. Rice et al. (1994) reported that there was an increased soil carbon on nitrogen-fertilized tallgrass prairie under twice-ambient CO_2 compared to ambient in large open-top chambers after three years, but no difference could be detected in unfertilized plots. Recent sampling of the unfertilized area, following eight years of treatment, showed that there was an increased soil carbon in labile and long-term storage forms as well (Jastrow and Miller, 1997, unpublished). Rice et al. (1997, unpublished) working on the same plots have shown that there was a greater CO_2 evolution from soils from elevated CO_2 plots compared to those from ambient CO_2 during long-term incubation.

METHANE

Since methane is a greenhouse gas, any significant change in CH_4 fluxes in the future could affect climate. Net methane flux from soils are a product of CH_4 production and oxidation. In most grassland ecosystems, oxidation is far greater than production, with production coming more from perennially wet ecosystems. The only research that has reported on CH_4 fluxes from a grassland ecosystem with elevated CO_2 is from the Swiss FACE Experiment (Ineson et al., 1997). They reported up to three times as much CH_4 oxidation under ambient CO_2 compared to elevated CO_2, which they attributed to the greater carbon input into the belowground portion of the ecosystem. Obviously, if that result is propagated across the many grassland ecosystems, methane concentrations in the atmosphere would be higher in the future high CO_2 world. Even though ruminants are considered a major source of methane, they only represent 3% of the total emissions. Van Soest (1994) concluded that manipulation of methane output in ruminants is likely to have little effect on net world methane output.

NITROUS OXIDE

Another greenhouse gas, N_2O, can be affected by grasslands in a future high CO_2 world.

Soils represent about 60% of the of N_2O source for the atmosphere (IPPC, 1994), largely a result of the nitrogen turnover rates in the soil (Mosier et al., 1996). Elevated CO_2 increases the labile carbon available for the soil microbial community and reduces water use, thereby extending the period of microbial activity. Ineson et al. (1997) reported that there was a 27% increase in N_2O output from the soil for a *Lolium perenne* sward under elevated CO_2 compared to ambient in the Swiss FACE experiment. They speculated that the increased carbon input to the soil likely increased microbial activity and stimulated denitrification. Even though there has been little research into the nitrogen transformations in grassland ecosystems exposed to elevated CO_2, the potential alteration of N_2O fluxes may significantly impact global climate in the future.

MANAGEMENT

Grasslands offer tremendous storage potential for soil carbon because of their relatively rapid root turnover rates (Dahlman and Kucera, 1965) as evidenced by the high soil organic matter in grassland soils. Obviously, the utilization rate by herbivores can dramatically alter the carbon flow to the root system. With high removal rates of leaf area, root growth is reduced significantly. Indeed, Crider (1955) showed that with 80% removal of leaf area, root growth stopped for up to six weeks. Even if the productivity of grasslands is enhanced in a high CO_2 environment, the impact on carbon storage of high utilization rates could negate any effects that grasslands might have on reducing atmospheric CO_2 through increased soil carbon. Glenn (1993) predicted that management of arid lands would have a greater impact on atmospheric CO_2 concentrations than the direct effects of elevated CO_2 on plant productivity. Ojima et al. (1993) presented two model scenarios that showed heavy grazing of grasslands would result in a significant reduction in carbon storage in grassland soils in a high CO_2 environment. The other important aspect of management relates to the prospect of plowing grasslands in the face of a greater need for grain production with an increasing world population. Cole et al. (1993) indicated that following plowing for crop production, there was a huge loss of carbon from the soil. The reverse is obviously true, in that planting of croplands to permanent grasslands will lead to a sequestration of significant amounts of carbon. Nitrogen fertilization leads to increased losses of the greenhouse gas, N_2O (Cole et al.,1993; Ineson et al., 1997). Ultimately, management may be the most important aspect of the ability of grasslands to modify global climate change through its impact on greenhouse gas fluxes.

CONCLUSIONS

Grasslands may modify global climate change through the following:

- Due to reduced oxygen competition for the active site on Rubisco, photosynthetic capacity for C_3 plants will increase under elevated CO_2 with an increased primary production.

- Reduced stomatal conductance under elevated CO_2 will increase water use efficiency and further increase primary production for both C_3 and C_4 plants.

- With a fixed N supply, the C/N ratio of plant tissues will increase under elevated CO_2, and decomposition will likely slow, resulting in an increase in soil carbon.

- The increased sequestration of carbon under elevated CO_2 has the potential to slow the rate of increase of atmospheric CO_2 and lower the future peak concentration.

- The effects of elevated CO_2 on other greenhouse gases such as CH_4 and N_2O may actually increase their effects on global warming.

- Management, particularly degree of use (heavy grazing), has the potential to negate any positive impacts of elevated CO_2 on global warming, or with improved management, more conservative use (moderate grazing), there may be a greater beneficial impact than that of direct CO_2 effects on the climate.

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