The influence of rising atmospheric CO_2 on grassland ecosystems

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ABSTRACT

Increasing atmospheric CO_2 concentrations and climatic change will have significant effects on the ecology of grasslands. This paper evaluates results from four CO_2 enrichment studies in contrasting grasslands. A Swiss study investigates the effects of elevated CO_2 (600 µL L^{-1} CO_2) on perennial ryegrass (*Lolium perenne* L.) and white clover (*Trifolium repens* L), a New Zealand study examines how elevated CO_2 (475 µL L^{-1} CO_2) affects a botanically diverse pasture, and studies in the Kansas tallgrass prairie and the Colorado shortgrass steppe investigate the effects of an approximate doubling of CO_2 in native grasslands. Productivity in all four grasslands was enhanced at elevated CO_2, with the largest relative increases occurring in dry years on the shortgrass steppe (71%) and on the tallgrass prairie (36%). Nitrogen additions, whether from fertilizer or legumes, enhanced the capability of these grasslands to respond to CO_2, and legumes were among the most competitive plant types in the Swiss and New Zealand grasslands under elevated CO_2. No evidence was found to support the notion that C_3 grasses were more competitive under elevated CO_2 compared to C_4 grasses. The results suggest that CO_2 enrichment and global warming will have important impacts on grasslands.

KEYWORDS: Carbon dioxide, climate change, clover, global change, perennial ryegrass, shortgrass steppe, tallgrass prairie

INTRODUCTION

Atmospheric CO_2 concentrations have risen from about 280 µL L^{-1} in pre-industrial times to 358 µL L^{-1} in 1995, and are projected to double over present CO_2 concentration by the end of this century (Mearns, 2000). A massive research effort has been undertaken to determine the direct (e.g. photosynthesis, growth) and indirect (climatic change responses) effects of elevated CO_2 and other trace gasses on agricultural and natural ecosystems. Although there is still uncertainty concerning the degree of climatic change that may result from increases in atmospheric trace gasses, a consensus is emerging that significant global warming will occur along with altered precipitation patterns and increased storm intensity.

Our interest is with grasslands, which can be broken down roughly into two categories: pastures that have been improved or created from forest clearing and other human activities for the expressed purpose of raising and feeding domestic livestock, and native grasslands that have evolved due to a particular regime of precipitation and temperature (Lauenroth, 1979). Both grassland types are important sources of food, and in many locations are the only viable and sustainable agriculture practice. Indeed, much of the land that has been converted to arable crops is not sustainable, and would be better managed by converting back to grassland.

Most of the global change research conducted on terrestrial ecosystems has focused on the direct CO_2 responses rather than on the more indirect climatic consequences, like warming. This focus on CO_2 has occurred because 1) the history and projections of atmospheric CO_2 concentrations are better documented and understood than the resultant climate change scenarios, and 2) considerable information already is available on temperature and precipitation responses of terrestrial ecosystems, whereas long-term field studies of CO_2 enrichment were rare until recently.

The responses of grasses to CO_2 were recently reviewed by Wand *et al.* (1999). They report strong growth enhancements of both C_3 and C_4 grasses from elevated CO_2, although greater responses of C_3 grasses. The greater sensitivity of C_3 species has been attributed to their photosynthetic metabolism, which is un-saturated at present atmospheric CO_2 concentrations. While photosynthesis in C_4 plants can respond directly to increases in CO_2 above present atmospheric concentrations (e.g. LeCain and Morgan, 1998), the response is considerably more limited compared to that of C_3 species. Ghannoum *et al.* (2000) suggest that in addition to increasing leaf intercellular CO_2, elevated CO_2 stimulates growth of C_4 grasses from improved water relations and increased leaf temperature. The water relations benefit of elevated CO_2 applies to C_3 species as well, since stomates of most plants close with rising CO_2, resulting in water conservation and enhanced water use efficiency. Production increases resulting from growth at elevated CO_2 are often accompanied by decreases in plant N concentration, and there is some evidence that N may limit plant response to rising CO_2 (Ghannoum and Conroy, 1998; Poorter *et al.* 1996). Similarly, there is some indication that plants capable of fixing their own N may have a greater capability to respond to rising levels of atmospheric CO_2 (Poorter, 1993). In addition to predicted productivity increases under elevated CO_2, species composition of plant communities are likely to change, although the exact nature of these changes are difficult to predict (Polley *et al.* 2000).

The purpose of this report is to compare the results of four long-term field studies of CO_2 enrichment conducted in four contrasting grasslands, a Swiss pasture, a New Zealand grazed pasture, Kansas tallgrass prairie, and Colorado shortgrass steppe. Possible interactions of temperature with CO_2 will be only briefly addressed since the focus of these studies has been primarily on CO_2 responses. The contributors of this report are all participants in the Global Change and Terrestrial Ecosystems project, a Core Project of the International Geosphere-Biosphere Programme. The following hypotheses of predicted grassland response to elevated CO_2 will be examined by evaluating the results of each particular study as well as comparing results across studies.

1. Elevated CO_2 will enhance production of grasslands.
2. Grassland responses (relative and absolute) to elevated CO_2 will be limited by soil N, and will be greatest with additional N inputs (fertilizer & legumes).
3. As water becomes more limiting, the relative response of grasslands to CO_2 will become enhanced due to improved water use efficiency.
4. C_3 species will be more competitive than C_4 species under elevated CO_2.
5. Legumes will be among the most competitive groups under elevated CO_2.
6. Forage quality will decline as production increases under elevated CO_2.

FIELD CO_2 ENRICHMENT EXPERIMENTS

Swiss Pasture FACE Experiment. The Swiss FACE experiment (Free Air Carbon Dioxide Enrichment) started in May 1993 and will continue until the end of 2002. Its objectives are to measure the long-term effects of elevated atmospheric CO_2 (600 µL L^{-1} CO_2) on different processes that affect growth, dry matter partitioning, symbiotic nitrogen fixation, competitive ability and carbon sequestration into the soil.

FACE is a technology for fumigating plant communities with CO_2 (Lewin *et al.* 1994). It involves mixing CO_2 with air and then releasing this CO_2 enriched air from a system of pipes on the upwind side of a circular target area. A feedback system uses wind speed, wind direction and the CO_2 concentration at the center of the circle to adjust the point of release and the amount of CO_2 delivered.

Perennial ryegrass (*Lolium perenne* L.) and white clover (*Trifolium repens* L.) were grown as monocultures and as a bi-species mixture. These two species are representative of intensively managed semi-natural grassland in humid temperate climate. They are the backbone of productive grassland with high quality forage.

The FACE experiment is located at Eschikon (8°42'E, 47°27'N), 20 km northeast of Zurich, at an altitude of 550 m above sea level. Monthly average daily mean temperature was 12.3°C and the sum of precipitation was 853 mm during the growing season. The soil was classified as a fertile, eutric cambisol with pH between 6.5 and 7.6. The soil consists of approximately 28% clay, 33% silt, and 36% sand and was designated as a clay loam (US classification). Soil organic matter varied between 2.9% and 5.1%. Available phosphorus and potassium content were considered sufficient for high productivity (Lüscher *et al.* 1998). The effect of elevated CO_2 was combined with two N fertilization treatments (140 and 560 kg N $ha^{-1}y^{-1}$) and two cutting frequencies (four to eight cuttings per year). The sampling area in each plot was fertilized with ^{15}N-enriched NH_4NO_3 at the beginning of the growing season and three days after each cutting. The experiment consisted of three replicates (see also Hebeisen *et al.* 1997, Daepp *et al.* 2000).

Average photosynthetic rates of the youngest fully expanded leaves of *L. perenne* increased by 30 to 80% under elevated CO_2 as compared to ambient CO_2 (Rogers *et al.* 1998, Isopp 2000). Enhanced C assimilation led to different responses of dry matter (DM) production of *L. perenne* and *T. repens*. In the beginning of the experiment there was a fundamental interspecific difference in the yield response to CO_2, irrespective of nitrogen fertilization. Annual yield of *T. repens* in monoculture, averaged over all management treatments, increased by 25% when grown at elevated CO_2. The CO_2 response of T. repens was independent of cutting frequency and nitrogen fertilization. In contrast, the annual DM yield of *L. perenne* in the high N treatment (Table 1A) was more than twice as high as in the low N treatment (Table 1B). At high N, the relative effect of elevated CO_2 on the annual DM yield increased significantly over the six years and reached a relative increase of 25% under elevated CO_2 in 1998. At low N, however, the relative effect of elevated CO_2 on DM yield did not increase with time and remained weak (-11 to + 9%) over all six years. The consequence of these interspecific differences between *T. repens* and *L. perenne* in the CO_2 response was a higher proportion of *T. repens* in the mixed swards at elevated CO_2. This was evident in all the combinations of defoliation and nitrogen treatments.

However, the proportion of these species was more strongly affected by N fertilization and cutting frequency than by elevated CO_2.

L. perenne monoculture in the low N treatment exhibited marked nitrogen deficiency symptoms like increased root growth (Hebeisen *et al.* 1997) and a highly significant reduction in herbage nitrogen concentration. *L. perenne* growing in association with *T. repens* and *T. repens* growing in monoculture or mixture showed no nitrogen deficiency symptoms (Hartwig *et al.* 1999); nitrogen yield correlated well with biomass production.

In the high N treatment the contribution of fertilizer N to plant growth increased strongly over the years, indicating important net N input into the ecosystem. In parallel, the response of N yield to elevated CO_2 increased, and the negative effect of CO_2 on specific leaf area disappeared, indicating that sinks for photosynthate no longer limited the response to elevated CO_2. In the high N treatment, the ecosystem seems to adapt to the new environmental conditions within a few years. However, in the low N input system the availability of mineral N strongly limited growth in both CO_2 treatments.

An evaluation of the N-sources revealed that all nitrogen that was additionally assimilated in *T. repens* under elevated CO_2, both in mixture and monoculture, derived from symbiotic N_2 fixation. No additional nitrogen was derived from the soil mineral nitrogen pool. Total symbiotic N_2 fixation increased by 66% in the grass legume mixture under elevated CO_2 (Zanetti *et al.* 1997, Lüscher *et al.* 2000)

The Swiss FACE grassland experiment demonstrates that CO_2 - induced changes in floristic composition, in dry matter allocation and composition, in symbiotic N_2 fixation, and in soil processes leads to multiple changes in a grassland ecosystem. Thus, knowledge of CO_2 responses at the community level based on long-term field experiments is a prerequisite to understand, predict or model the response of grasslands to elevated CO_2.

New Zealand Pasture Grazed FACE Experiment. The New Zealand Face experiment is situated on a botanically diverse pasture that has been under permanent grass since at least 1940. Prior to the start of the experiment a botanical survey found 26 vascular plant species including annual and perennial C_3 grasses (e.g. *Anthoxanthum odoratum* L., *Lolium perenne* L., *Agrostis capillaries* L., *Poa annua* L.), C_4 grasses (*Paspalum dilatatum* Poir., *Cynodon dactylon* L.), annual and perennial forbs (e.g. *Hypochaeris radicata*, *Leontodon saxatilis*, *Cerastium glomeratum*) and annual and perennial legumes (e.g. *Trifolium repens* L., *T. subterraneum*, *T. glomeratum*). The management is typical of an extensive New Zealand system; nitrogen is provided by the legumes and the fertilizer regime (phosphate and potassium) is applied to encourage these species; grazing continues all year. The site is on the west coast of the North Island of New Zealand (40°14'S, 175°16'E) with a mean annual rainfall of 875 mm evenly distributed throughout the year. Long term (30 year average) values for maximum and minimum temperatures (°C) are: spring 16.6, 8.2; summer 21.3, 12.2; autumn 18.2, 9.1; winter 13.0, 4.2. The soil type is a black sand and soil moisture deficits are a frequent occurrence during the summer period. Total N is of the order of 4.0 g kg soil^{-1} and total C 50 g kg soil^{-1}.

The FACE system comprises 3 enriched and 3 control rings each of 12 m in diameter. The enriched rings have CO_2 added so that the concentration at 25 cm height above ground level is 475 µL L^{-1} during the photoperiod. The rings are periodically grazed by adult sheep when the herbage mass reaches 1800-2000 kg ha^{-1} and grazed down to a residual of 500-700 kg ha^{-1}. During periods of low growth rates (e.g. during summer soil moisture deficits) grazing is used to remove rank growth in accordance with good management practice. Two areas in each ring are protected from grazing and harvested by cutting. Enrichment of the pastures started in October 1997 and has been continuous since that time.

After 27 months of enrichment the cumulative total of herbage grown (herbage harvested to 2 cm above ground level) was significantly greater at elevated CO_2 (18%) with the bulk of this response occurring during the period of peak growth rates in spring (Fig 1A). The CO_2 effect was least marked during the autumn and winter. The most responsive groups of species were the forbs and legumes (Fig 1b); of these, the legumes were considerably more important in terms of dry matter produced. There was a wide diversity of C_3 grasses present, both annual and perennial, and no consistent pattern of response to CO_2; for example, *A. odoratum* responded positively to elevated CO_2 while *A. capillaris* responded negatively. The major C_4 species *Paspalum dilatatum* was stimulated by elevated CO_2. The mechanism for this has not been identified, but Ghannoum *et al.* (2000) list increased intercellular CO_2 partial pressure, changes in diurnal CO_2 fixation patterns, improvements in shoot water relations and increased leaf temperatures as possible ways in which C_4 species might respond to elevated CO_2. Note that while C_4 species in this system can play an important role during periods of summer moisture deficits, their contribution to total dry matter is small (less than 2%). The reason for the greater stimulation in spring and summer is not clear, but there is evidence to suggest that greater responses might be expected at higher temperatures and, given differences in seasonal growth patterns of plant species, that interactions are likely between this 'seasonal' effect and the CO_2 responsiveness of different species (Newton *et al.* 1994).

The mechanisms driving changes in species composition at elevated CO_2 are

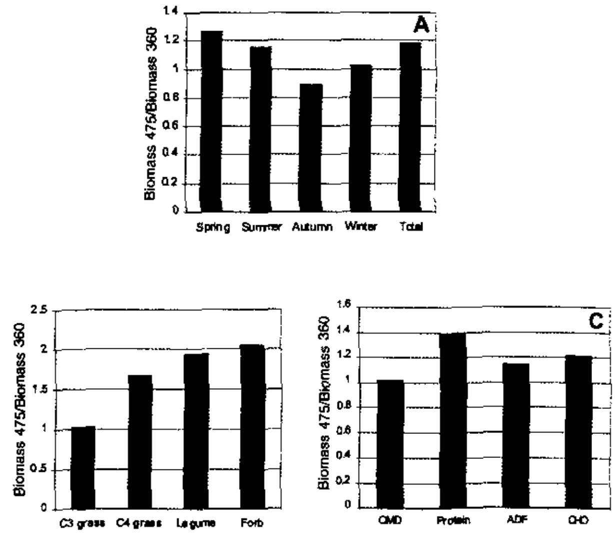

Figure 1 - Relative effects of elevated CO_2 (475 µL L^{-1}; the concentration expected in 30 years time compared to the current concentration of 360 mL L^{-1}) on a grazed pasture in New Zealand after 27 months of enrichment: A) seasonal and total dry matter measured from pre- and post- grazing cuts to 2 cm above ground level (there was a significant effect of CO_2 on total mass); B) species composition of the total dry matter presented as functional groups (there was a significant group*CO_2 interaction; C) nutrient content of herbage (measured as g m^{-2}); OMD=digestible organic matter (not significantly different); protein, ADF=acid digestible fibre, CHO=water soluble carbohydrates (all significantly greater at elevated CO_2).

various. In the New Zealand FACE, one important mechanism is increased recruitment from seed (Edwards *et al.* 2000). The total seed rain of a number of species was greater at elevated CO_2, including grasses (*A. odoratum*, *L. perenne*, *Poa pratensis*); legumes (*T. repens*, *T. subterraneum*) and forbs (*H. radicata*, *L. saxatilis*). In the case of *A. odoratum*, *H. radicata*, *L. saxatilis* and *T. repens*, this was due to both more inflorescences m^{-2} and more seeds per inflorescence; for the other species it was due to increased inflorescence numbers. In successive seasons the greater seed rain resulted in greater seedling density of the forbs and legumes and greater abundance of these species (Fig. 1B). Edwards *et al.* (2000) make the point that recruitment from seed is an important mechanism of species compositional change in this environment and is perhaps an underestimated mechanism in other systems.

In common with many other experiments there has been some reduction in the protein content within species at elevated CO_2. However, because of increases in yield and in species composition towards greater legume content, the nutrients available for animal growth have actually increased at elevated CO_2 (Fig 1C).

Grazing by animals has the potential to interact with pasture responses to elevated CO_2 (Newton *et al.* 2000); this may occur as a result of selectivity in the diet of animals, physical damage to plants and canopy, or because of heterogeneity in nutrient returns. After 3 years, differences have started to develop between areas that are grazed by animals and areas in which grazing was simulated by cutting. The most striking difference has involved changes in species composition, with a stronger response of legumes to CO_2 in the grazed areas (Newton *et al.* 2000).

It is important to consider that the level of CO_2 enrichment in this experiment is quite modest (475 µL L^{-1}), equating to the concentration expected in 2030. Despite this small increase marked changes in ecosystem processes have been observed; in particular changes in species composition to favor dicot species. The increased legume content is beneficial to animal production. However, it will be important to determine whether the greater legume abundance can be sustained or whether the frequently observed oscillations in legume-grass balance will simply have a larger amplitude.

The longer-term consequences of elevated CO_2 for soil processes also needs to be included in our projections. Around a naturally occurring CO_2 spring in the north of New Zealand positive relationships are evident between atmospheric CO_2 concentration and net mineral-N production (Ross *et al.* 2000) and rates of infection of roots by arbuscular mycorrhizal fungi (Rillig *et al.* 2000). These results suggest nutrient availability to plants may change in the longer-term.

Grasslands of the North American Great Plains. As one travels west to east from the Rocky Mountains to the eastward extension of the Central Great Plains of North America, grasslands transition from short-grass steppe to mixed grass prairie and finally to tallgrass prairie. This transition corresponds to a precipitation gradient from the semi-arid regions on the lee side of the Rocky Mountains to areas of relatively high and more evenly-distributed rainfall in the sub-humid tallgrass prairie region.

Two CO_2 enrichment experiments have been conducted in this region utilizing open-top chambers of similar design and dimension, one on tallgrass prairie in Kansas (Owensby *et al.* 1999) and the other on shortgrass steppe in northeastern Colorado (Morgan *et al.* 2001).

Kansas Tallgrass Prairie OTC Experiment. The tallgrass prairie site is adjacent to the Kansas State University campus at Manhattan, KS, USA, lat. 39°12' N, long. 96°35' W (Owensby *et al.* 1993a,b). Long-term maximum/minimum temperatures (°C) are spring 19,6; summer 32,19; autumn 21,7; winter 5,-7. The 30-year average annual precipitation is 840 mm, with 520 mm falling during the growing season. A mixture of C_3 and C_4 vegetation occurs, with dominance by two C_4 grasses, *Andropogon gerardii* Vitman and *Sorghastrum nutans* (L.) Nash. Sub-dominants include a C_3 grass, *Poa pratensis* L., and two other C_4 grasses, *Bouteloua curtipendula* (Michx.) Torr. and *Sporobolus asper* var.asper (Michx.) Kunth. Average peak phytomass of this grassland occurs in early August at 435 g m^{-2}, with less than 10% contributed by herbaceous dicots.

Tallgrass prairie was exposed to elevated CO_2 over an 8-year period from 1989 to 1996. Open-top fumigation chambers (OTCs, 4.5 m in diameter by 4.0 m in height) were placed over the natural vegetation in late March, 1989 and retained on the same area for eight years (Owensby *et al.* 1999). Treatments replicated three times consisted of ambient CO_2-no chamber, ambient CO_2 with chamber, and twice ambient CO_2-enriched with chamber. A two-year study was conducted in separate chambers with elevated CO_2 and N fertilization.

The primary responses to elevated CO_2 were mediated through reduced water use by the ecosystem due to reduced stomatal conductance, which improved water use efficiency (Owensby *et al.* 1993b; Knapp *et al.* 1993ab; Knapp *et al.* 1994; Knapp *et al.* 1995; Ham *et al.* 1995; Bremer *et al.* 1996; Owensby *et al.* 1996; Hamerlynck *et al.* 1997; Owensby *et al.* 1999). Volumetric soil water content of the 0-100 cm soil layer was determined using neutron scattering, and was generally higher in elevated CO_2 plots than ambient, mainly during periods when precipitation limited normal plant growth due to water stress. In four of the eight years, plots with elevated CO_2 had greater aboveground phytomass than those with ambient CO_2 (Fig 2). Root in-growth phytomass was greater under elevated CO_2 in three of the six years when it was measured. The basal cover and relative amount of warm-season perennial grasses (C_4) in the stand changed little during the 8-year period, but basal cover and relative amount of cool-season perennial grasses (C_3) in the stand declined in the elevated CO_2 plots and in ambient CO_2 plots with chambers. Forbs (C_3) and members of the Cyperaceae (C_3) increased in basal cover and relative amount in the stand at elevated compared to ambient CO_2.

Above- and belowground phytomass production and leaf area of fertilized plots

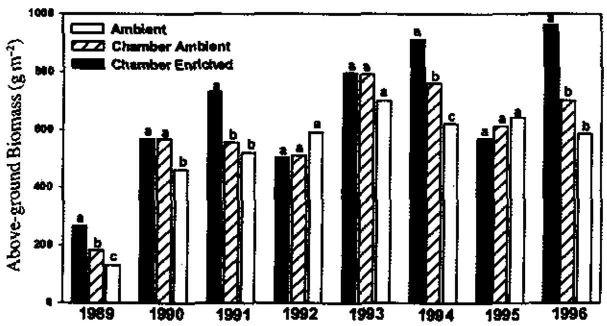

Figure 2 - Peak aboveground biomass (g m^{-2}) of Kansas tallgrass prairie exposed to ambient conditions, chambered ambient CO_2 and chambered elevated CO_2 from1989 to 1996. From Owensby et al. (1999).

were greater with elevated than ambient CO_2 in both years of the N/CO_2 study (Owensby *et al.* 1994). The increase in phytomass at high CO_2 occurred mainly aboveground in 1991, a dry year, and belowground in 1990, a relatively wet year. Nitrogen concentration was lower in plants exposed to elevated CO_2, but total standing crop N was greater at high CO_2. Increased root phytomass under elevated CO_2 apparently increased N uptake. The phytomass production response to elevated CO_2 was much greater on N-fertilized than unfertilized prairie, particularly in the dry year. Phytomass production response to elevated CO_2 was suppressed by N limitation in years with below-normal precipitation.

Stomatal conductance was reduced by as much as 50% under elevated CO_2 compared to ambient. The result was an improved water status for plants exposed to elevated CO_2, which was reflected by a less negative xylem pressure potential compared to plants exposed to ambient CO_2. At the canopy level, evapotranspiration (ET) was reduced by 22% under elevated CO_2. Increases in net carbon exchange (NCE) at the ecosystem level under elevated CO_2 were primarily caused by continued photosynthesis under elevated CO_2 when water stress had essentially stopped photosynthesis under ambient CO_2. Additionally, whole-chamber data collected on days with high evaporative demand showed that ecosystem quantum yield under elevated CO_2 remained high in the afternoon period (e.g. - 0.029 mmol CO_2 mmol PAR^{-1}), but decreased under ambient CO_2 (e.g. - 0.021 mmol CO_2 umol PAR^{-1}). Greater NCE and lower ET resulted in higher daytime water use efficiency under CO_2 enrichment vs. ambient (9.84 vs. 7.26 g CO_2 kg^{-1} H_2O).

Acid digestible fiber (ADF) and N values from the ambient and elevated CO_2 diet samples obtained from esophageally-fistulated sheep were used to estimate the growth response of yearling steers grazing tallgrass prairie. Estimated gain for steers consuming forage produced under elevated CO_2 in 1989 was lower than that produced under ambient CO_2 summed over the 150-day growth period (2X CO_2 - 80.6 kg; 1X CO_2 - 99.6 kg), with the greatest reduction in gain coming in the early season. Forage N concentrations were reduced under elevated CO_2 and fiber concentrations increased, both of which should reduce ruminant productivity. Since ruminant intake declines as forage quality decreases, there cannot be a compensatory intake response to maintain productivity levels comparable to current levels. For domestic livestock, diets can be supplemented to compensate for reduced forage quality, but with wild ruminants, or for ruminants in developing countries, diet supplementation likely will not be an option. The result will be reduced growth and reproduction.

Effects of elevated CO_2 on the quantity and quality of belowground biomass and several soil organic matter pools were determined at the conclusion of the eight-year CO_2 enrichment experiment (Jastrow *et al.* 2000). Soil was sampled to a depth of 30 cm beneath and next to the crowns of C_4 grasses in these plots and in unchambered plots. Elevated CO_2 increased the standing crops of rhizomes (87%), coarse roots (46%), and fibrous roots (40%) but had no effect on root litter (mostly fine root fragments and sloughed cortex material >500 mm). Soil C and N stocks also increased under elevated CO_2, with accumulations in the silt/clay fraction over twice that of particulate organic matter (POM; >53 mm). The mostly root-like, light POM (density ≤1.8 Mg m^{-3}) appeared to turn over more rapidly, while the more amorphous and heavy POM (density >1.8 Mg m^{-3}) accumulated under elevated CO_2. Rhizome and root C:N ratios were not greatly affected by CO_2 enrichment. However, elevated CO_2 increased the C:N ratios of root litter and POM in the surface 5 cm and induced a small but significant increase in the C:N ratio of the silt/clay fraction to a depth of 15 cm. Eight years of CO_2 enrichment may have affected elements of the N cycle (including mineralization, immobilization, and asymbiotic fixation), but any changes in N dynamics were insufficient to prevent significant plant growth responses.

Starting in 1991 and ending in 1996, soil samples from 0 to 5 and 5 to 15 cm depths were taken for measurement of microbial biomass C and N, total C and N, microbial activity, inorganic N and soil water content. Soil microbial biomass C and N tended to be greater under elevated CO_2 than ambient CO_2 in the 5-15 cm depth during most years, and in the month of October, when analyzed over the entire study period. Microbial activity was significantly greater at both depths in elevated CO_2 than ambient conditions for most years. During dry periods, the greater water content of the surface 5 cm soil in the elevated CO_2 treatments increased microbial activity relative to the ambient CO_2 conditions. The increase in microbial activity under elevated CO_2 in the 5-15 cm layer was not correlated with differences in soil water contents, but may have been related to increases in soil C inputs from enhanced root growth and possibly greater root exudation. Total soil C and N in the surface 15 cm were, after 8 years, significantly greater under elevated CO_2 than ambient CO_2. Decomposition is likely enhanced under elevated CO_2 compared with ambient CO_2, but inputs of C are greater than the decomposition rates. Soil C sequestration in tallgrass prairie and other drought-prone grassland systems is, therefore, considered plausible as atmospheric CO_2 increases.

Colorado Shortgrass Steppe OTC Experiment. The shortgrass steppe is a semi-arid grassland along the western edge of the Great Plains of the United States, stretching from southeastern New Mexico and Western Texas north to the Colorado-Wyoming border at 41 °N latitude (Lauenroth and Milchunas, 1991). The study site is at the USDA-ARS Central Plains Experimental Range (CPER), lat. 40° 40' N, long. 104° 45' W, in the shortgrass steppe region of north-eastern Colorado (Lauenroth and Milchunas, 1991), about 56 km north-east of Fort Collins, CO. Twenty year season maximum/minimum temperatures (°C) are spring 17,2; summer 27,11; autumn 12,-3; winter 6,-8. Long-term (55 yr) mean annual precipitation averages 320 mm, with the majority occurring during May, June and July. Vegetation of the site is dominated by the warm-season, C_4 grass *Bouteloua gracilis* (H.B.K.) Lag., but contains an abundance of cool-season, C_3 grasses, most importantly *Pascopyrum smithii* (Rydb.) A. Love and *Stipa comata* Trin and Rupr, as well as a variety of C_3 forbs. Over the course of the study, C_3 grasses accounted for 61% of the aboveground vegetative dry matter, C_4 grasses (primarily *B. gracilis*) accounted for 35%, and the remaining 4% was in forbs. Average peak aboveground phytomass of this grassland occurs in late July at 70 g m^{-2} (Shoop *et al.* 1989), with similar production estimated in belowground organs. The soil at the experimental site is a Remmit fine sandy loam (Ustollic camborthids). Six hexagonal open-top chambers, 4.5 m diameter by 3.8 m high, were constructed with a galvanized steel tubing frame covered with clear, Lexan (Regal Plastics, Littleton, CO, USA) panels.

Three chambers were maintained at ambient CO_2 concentrations, three at approximately twice ambient (720 µL L^{-1}), and three other non-chambered experimental sites served as controls. After a baseline field season with no CO_2 enrichment (1996), chambers were placed over the experimental plots each growing season from mid-March until after plant senescence in late October from 1997 through 2000. Three more years of CO_2 enrichment are planned.

Recommended stocking rates are low on the shortgrass steppe due its low productivity. About half of the vegetation is defoliated only once during a growing season from cattle grazing, so a single defoliation, by species, at the approximate time of seasonal peak phytomass on half of the harvestable plot area was conducted to evaluate possible interactions of defoliation by grazers with the CO_2 response. A final harvest (after senescence) at the end of the growing season of previously defoliated as well as un-defoliated plants provided a seasonal measure of aboveground production.

Aboveground plant productivity has been consistently enhanced in shortgrass steppe vegetation under a double ambient CO_2 regime, as indicated by increases in standing aboveground peak phytomass ranging from 20% (ns) to 71% (Fig. 3A). Root in-growth bag and minirhizotron data suggest similar CO_2-induced production responses in belowground plant organs (D.G. Milchunas, unpublished data). The greatest relative increase occurred in a dry year (2000) in which production at mid-season was about half of the long-term average for the site. Results from the first two years of CO_2 enrichment indicate no significant interactive effect of defoliation on the CO_2 growth enhancement. After 4 years of CO_2 enrichment, no relative differences in growth responses to CO_2 have been detected between C_3 and C_4 grasses, although a trend (P=0.11) in 1997 suggested a slightly higher CO_2-induced production increase for the forb group. A significant chamber effect in most years resulted in higher production inside than outside chambers, a result we believe was due to chamber warming and earlier green-up in the spring.

Measurements of leaf gas exchange from the OTC study as well as from previous controlled environment work (Morgan *et al.* 1994a; Read *et al.* 1997) indicate that short-term increases in CO_2 stimulate photosynthesis in the C_3 *P. smithii*, but long-term (greater than a few days to a week) exposure of *P. smithii* leaves to elevated CO_2 results in consistent and significant downward photosynthetic acclimation. Consequently, leaf photosynthetic activity per unit leaf area conducted under chamber

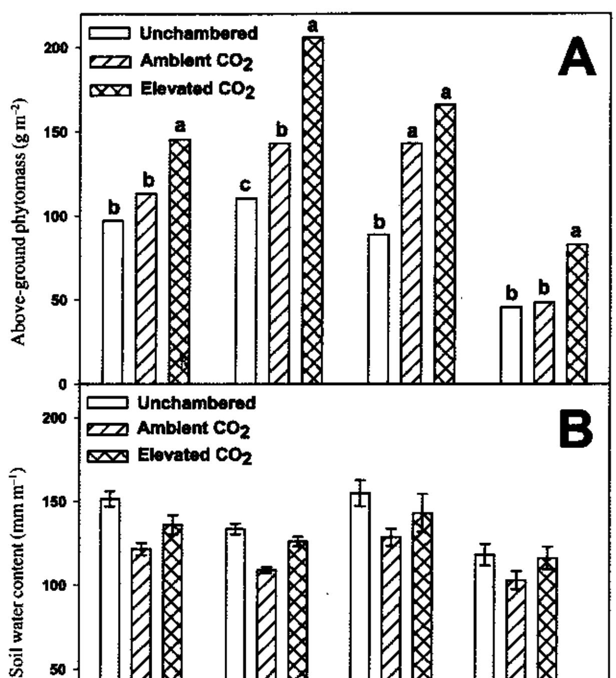

Figure 3 - A) Above-ground phytomass on the Colorado shortgrass steppe determined at the approximate time of peak seasonal biomass production in unchambered, ambient (370 µL L^{-1}) and elevated (720 µL L^{-1}) CO_2 plots. Significant treatment differences ($P < 0.05$) determined from Analysis of Variance, with different letters within year indicating significantly different ($P < 0.05$) treatment means as determined by Fisher's LSD. B) Average growing season soil water content as determined by neutron probe for unchambered, ambient and elevated CO_2 plots. Bars are standard errors of seasonal means.

conditions often is similar between ambient and elevated CO_2 chambers, and enhancements under elevated CO_2 are generally less than 15% compared to leaves in ambient chambers. The decline in photosynthetic capacity of CO_2-enriched *P. smithii* leaves often is associated with reduced forage N concentrations and enhanced leaf carbohydrate levels (Read *et al.* 1997; Morgan *et al.* 2001). We found that photosynthesis in leaves of the dominant C_4 grass, *B. gracilis*, as well as other C_4 grasses, are not CO_2-saturated at present ambient CO_2 concentrations of 360 mmol mol^{-1} (LeCain and Morgan, 1998; Morgan *et al.* 1994a), suggesting that some direct photosynthetic enhancement is possible in *B. gracilis* as a result of rising CO_2 concentrations (see also Ghannoum *et al.* 2000). Consequently, both C_3 and C_4 grasses of the shortgrass steppe exhibit some photosynthetic enhancement due to CO_2 enrichment, but because of significant photosynthetic acclimation in the C_3, *P. smithii*, differences in CO_2 responses are not great.

The consistent and strong responses of this grassland to CO_2 enrichment appear to result as much from improvements in water relations as from any other factor. Weekly measurements of leaf water potential and soil water content have revealed a very strong influence of elevated CO_2 on water in the shortgrass steppe, with higher leaf water potentials (Morgan *et al.* 2001) and soil water contents (Fig. 3B) in CO_2-enriched chambers compared to ambient chambers. These wetter conditions in CO_2-enriched chambers are likely due to partial stomatal closure, which improves leaf level as well as system level water use efficiency (Lapitan *et al.* 2000; Morgan *et al.* 1994a, 1998), indirectly enhances photosynthesis and maintains significant photosynthetic activity later in the growing season as soil water is depleted (Morgan *et al.* 2001; see also Chiarielle and Field, 1996). Increased infection of roots with vesicular-arbuscular mycorrhizae and increased partitioning of phytomass to belowground organs may also contribute to improved plant water relations of CO_2-enriched shortgrass steppe grasses through more efficient mining of soil water (Morgan *et al.* 1994b).

N fertilization is not economically feasible and therefore not an important issue in shortgrass steppe rangelands of the Western Great Plains, nor are legumes an important feature of the landscape. Nevertheless, the dynamics of soil N cycling plus the seasonality of plant growth can result in a variable available soil N pool, so interactions of N with CO_2 may be important. Further, N is considered the most growth-limiting nutrient in grasslands. Results from our OTC study indicate that production increases under elevated CO_2 are accompanied by reductions in shoot N concentrations, most notably in the C_3 species (Morgan *et al.* 2001). This confirms what we have observed in these species and grassland soils in controlled environment experiments (Hunt *et al.* 1996; LeCain and Morgan, 1998; Morgan *et al.* 1994b; Read and Morgan, 1996; Read *et al.* 1997). One of the adaptations sometimes seen in plants exposed to elevated CO_2, increased partitioning of phytomass to belowground organs (Rogers *et al.* 1994,1996), has been observed in some of our studies with shortgrass steppe grasses and soils, and appears to be driven by reductions in plant N concentration (Morgan *et al.* 1994b,1998, 2001). We suspect that much of the reduced plant N concentration under elevated CO_2 is due to enhanced growth in a N-limited system, resulting in a dilution of plant N (Hunt *et al.* 1998). These N-deficiency effects of CO_2 enrichment are less evident or non-existent under conditions of high N fertility (Morgan *et al.* 2001).

SYNTHESIS

CO_2 Enrichment Experiments. The results of these four field CO_2-enrichment experiments support our first hypothesis that elevated CO_2 will enhance grassland production. However, a comparison both within and between studies revealed large differences in the relative responses (Table 2). In the Swiss pasture, production responses to elevated CO_2 (600 µL L^{-1}) increased over time, up to maximal enhancements of 25% for *T. repens* and fertilized *L. perenne*, but CO_2 had considerably less effect on production in non-fertilized *L. perenne* swards. Production was stimulated 18% in the New Zealand pasture under 475 µL L^{-1} CO_2, compared to growth enhancements of up to 3[illegible]% in tallgrass prairie and 71% in shortgrass steppe under doubled ambient CO_2 concentration. In the two C_4-dominated native grasslands, CO_2-induced growth responses were greatest in the driest years, with no significant CO_2 growth enhancements in half of the measurement years in the sub-humid tallgrass prairie, but only one year in the semi-arid shortgrass steppe when significant and large CO_2 enhancements in growth were not observed. These results support our third hypothesis that the relative responses of grasslands will tend to be greater as water becomes more limiting. Gas exchange and water balance research in Kansas (Ham *et al.* 1995; Nie *et al.* 1992; Owensby *et al.* 1999) and Colorado (Lapitan *et al.* 2000; Morgan *et al.* 1998, 2001) indicate that the primary effect of CO_2 on production of the tallgrass prairie and shortgrass steppe is through improved water relations that result in higher water use efficiency.

All four projects confirm that the capability of these systems to respond to CO_2 and the nature of those responses is conditioned by N (Table 2). Extensive investigations of monoculture and bi-species responses of *T. repens* and *L. perenne* plus N fertilizer studies provide compelling evidence that responses of plants to elevated CO_2 is limited by N, and that growth enhancements in grasslands will be greatest when legumes are present or adequate N fertilization occurs. The Swiss and New Zealand FACE experiments indicate that N-fixing legumes may be competitively favored in many systems as CO_2 increases. Other responses, like the tendency of CO_2-enriched plants to partition more phytomass to belowground organs (Rogers *et al.* 1994,1996), appear to be one of several N deficiency responses that develop in plants subjected to high CO_2 concentrations when available soil N is insufficient to meet the increased demands of CO_2-enriched plants. These responses will have an important effect on how different species respond to elevated CO_2, and will certainly impact forage quality. These results support the notion that legumes should become more competitive in grasslands as atmospheric CO_2 concentration rise.

Perhaps the most surprising result has been the lack of any evidence to indicate a superior growth response in C_3 compared to C_4 grasses. In tallgrass prairie, long-term CO_2 enrichment resulted in a decline in basal cover for C_3 grasses, while cover of C_4 grasses remained unchanged (Table 2). In the New Zealand pasture a wide range of responses among C_3 grasses was reported resulting in little stimulation overall, while, in contrast the major C_4 grass (*Paspalum dilatatum*) was stimulated by CO_2. The reasons for the range of C_3 responses is not understood, but as abundance in the New Zealand pasture appears to relate strongly to recruitment processes as well as vegetative growth (Edwards *et al.* 2000) there are a range of possible influences (allocation to seed, predation/grazing, availability of microsites) that might modify plant response to elevated CO_2. The basis for the response of the dominant C_4 species is also unclear, but a number of potential mechanisms can be suggested (Ghannoum *et al.* 2000) including the improved shoot water relations described below. In the shortgrass steppe, production of C_3 and C_4 grasses respond similarly and strongly to elevated CO_2. The decline in C_3 grass basal cover in the tallgrass prairie could have resulted because of the strong CO_2 responses of the tall C_4 grasses *A. gerardii* and *S. nutans* which tower above and shade the C_3 dominant, *P. pratensis* (Owensby *et al.* 1999). Similar CO_2-induced growth enhancements of C_3 and C_4 grasses in the shortgrass steppe occurred because they were driven primarily by the effects of CO_2 on water relations (Morgan *et al.* 1998, 2001), which benefited C_3 and C_4 grasses alike. The results of these three field experiments are contrary to earlier predictions of greater responses

Table 1 - Changes in the effect of elevated CO_2 on different parameters of pure *L. perenne* swards from the Swiss FACE experiment (1993 - 1998) at high N fertilisation (A; 560 kg N ha^{-1} y^{-1}) and at low N fertilisation (B; 140 kg N ha^{-1} y^{-1}) over six years. (according to Daepp et al. 2000)

	Six Year Mean at 350 µL L^{-1} CO_2	CO_2 Effect 1st year	CO_2 Effect 6th year	Annual Effect (% y^{-1})	Change of CO_2 r^2
			A - High N		
DM yield	1400 g m^{-2}	+ 7%	+ 25%	3.1 *	0.67
SLA	21.4 cm^{-2} g^{-1}	- 18%	0%	6.2 **	0.91
[N]	33.0 mg g^{-1}	- 20%	- 14%	1.2 ns	0.20
N yield	46.1 g m^{-2}	- 13%	+ 8%	4.0 *	0.59
N(soil)	29%	- 1%	+ 22%	6.0 **	0.86
			B Low N		
	Six Year Mean at 350 µL L^{-1} CO_2	CO_2 Effect 1st year	CO_2 Effect 6th year	Annual Effect (% y^{-1})	Change of CO_2 r^2
DM yield	720 g m^{-2}	+ 5%	+ 9%	1.2 ns	0.09
SLA	15.8 cm^{-2} g^{-1}	- 20%	- 13%	1.6 ns	0.39
[N]	20.7 mg g^{-1}	- 16%	- 21%	-0.3 ns	0.07
N yield	14.6 g m^{-2}	- 13%	- 15%	0.6 ns	0.03
N(soil)	68%	0%	- 2%	0.1 ns	0.01

CO_2 effect = (annual mean at 600 µL L^{-1} CO_2 / annual mean at 350 µL L^{-1} CO_2) x 100.
Annual change of CO_2 effect = the slope of the linear regression analyzing the CO_2 effect as affected by the year of CO_2 enrichment. Significance of the slope (ns = not significant; * = $p<0.05$; ** = $p<0.01$) and r^2 of the linear regression are given.
DM yield: annual dry mass yield harvested above a cutting height of 5 cm.
SLA: specific leaf area.
[N]: concentration of N in the harvested herbage.
N(soil): proportion of N yield derived from uptake of mineralized N from soil organic matter (SOM) and not from fertilizer N (measured with the ^{15}N dilution method).

Table 2 - Site descriptions and grassland responses to increases in CO_2.

Grassland	Precip. and Temp.	Production Response to Elevated CO_2	Plant Community and Species Changes/Responses	N fertility & legumes	Forage quality	Defoliation and Grazing Interactions
Swiss Pasture *L. perenne* & *T. repens* in mono- cultures & bi-species.	*Ann. Precip.* 853 mm	Monoculture: *L. perenne* production under elevated CO_2 increased over 6 yr, from 7 – 25% with high N fertilizer, and from negative responses to 9% with low N. *T. repens*: 25% higher production over 6 yrs.	Bi-species: Productivity and N yield greater under elevated CO_2 with *T. repens*. Higher proportion of *T. repens* in mixed swards under elevated CO_2. Plant community composition influenced more by N fertility and defoliation than by CO_2.	Greatest production responses occur with N fertilizer input and legumes. N reduction in monocultures of CO_2-enriched *L. perenne*. N fixation enhanced 66% in grass/legume mixture under elevated CO_2. Growth enhancement of *L. perenne* dependent on N supply.	Forage [N] lower in CO_2 enriched *L. perenne*, but no N deficiency when grown in association with *T. repens*. Higher N yield under CO_2 enrichment. Increased carbohydrates under CO_2 enrichment.	Frequent defoliation of *L. perenne* increased root/shoot ratios, but no interaction with CO_2.
New Zealand Grazed Pasture C_3 and C_4 grasses; forbs; legumes; annuals & perennials	*Ann. Precip.* 875 mm *Temp. (° C) (max/min)* Sp 17/8 Su 21/12 Au 18/9 W 13/4	18 % higher aboveground phytomass harvested from plant community over 27 months CO_2 enrichment.	Relative change in aboveground biomass after 27 months CO_2 enrichment: C_3 grasses: 7% C_4 grasses: 65% Legumes: 92% Forbs: 105%.	Absolute and relative increases in abundance of legumes.	Decline in forage [N] in individual species but higher total digestible organic matter, protein, and water soluble carbo-hydrates under high CO_2 on a ground area basis.	Greater CO_2 enrichment enhancement of legumes under grazing compared to cutting.
Kansas Tallgrass Prairie C_3 and C_4 grasses; dominants are *A. gerardii*, *S. nutans*, *P. pratensis*, <10% forbs	*Ann. Precip.* 840 mm *Temp. (° C) (max/min)* Sp 19/6 Su 32/19 Au 21/7 W 5/–7	Productivity affected little in wet years, and enhanced up to 36% under elevated CO_2 in normal or dry years.	Little long-term effect of elevated CO_2 on cover and relative amount of C_4 grasses. Basal cover and relative amount of forbs (all C_3) and members of Cyperacea increased, but decreased for C_3 grasses.	Response to elevated CO_2 limited by N. Total soil N in upper 15 cm higher after eight years of CO_2 enrichment.	Reductions in shoot N, but total N either unchanged or higher in aboveground tissues because of production increases under elevated CO_2. Increased fiber and lower digestibility under elevated CO_2	Interaction of defoliation with CO_2 dependent on soil water. In dry year, elevated CO_2 enhanced re-growth. In wet year, no effect of CO_2 on re-growth.
Colorado Shortgrass Steppe C_3 and C_4 grasses, dominated by C_4 *B. gracilis*, with C_3s *P. smithii* and *S. comata*; <7% forbs	*Ann. Precip.* 320 mm *Temp . (° C) (max/min)* Sp 17/2 Su 27/11 Au 12/-3 W 6/-8	Seasonal aboveground production consistently enhanced by CO_2, with highest relative responses (71%) occurring in driest growing seasons.	After 4 years of CO_2 enrichment, no differences in responses of C_3 or C_4 grasses aboveground phytomass to elevated CO_2. A trend suggesting greater growth responses of forbs in one year.	Responses to elevated CO_2 limited by N. The tendency to increase biomass partitioning to belowground organs under elevated CO_2 declines as soil N increases. Native legumes not important in the shortgrass steppe.	Reductions in shoot [N] when elevated CO_2 leads to production increases. N yield generally greater under elevated CO_2.	The relative enhancement of aboveground plant production is similar in plots defoliated once compared to non-defoliated plots.

of C_3 species to elevated CO_2 (e.g. Bazzaz, 1990). The complexity of ecosystem character likely modifies the CO_2 responses of species in the field, so the assessment of different species responses, most of which have been examined previously in monocultures and in controlled environments, may differ substantially in the field, especially in native grassland ecosystems composed of numerous species (Owensby *et al.* 1999). Further, the importance of water relations in the responses of plants to elevated CO_2 has probably not been appreciated, and may be particularly important in the substantial growth responses of C_4 species (Ghannoum *et al.* 2000; Wand *et al.* 1999).

Both the Kansas and New Zealand studies indicate significant growth responses of forbs to elevated CO_2, and there was limited proof of a strong forb response to elevated CO_2 in the Colorado shortgrtass steppe. Forbs are a small fraction of phytomass in all three of these grasslands, but their responsiveness to elevated CO_2 (Table 2) suggests the possibility that they may become more important in future CO_2-enriched grasslands.

A common theme across all four studies was a decline in shoot N concentration at elevated CO_2 unless supplemental N was provided via N fertilization or with N-fixing legumes. This has several important implications for grasslands and for foraging ruminants. First, as mentioned above, it suggests that legumes may become more competitive in grasslands. It also means that the use and introduction of legumes into grasslands may become more important as forage quality declines. While it appears that the N yield of many grasslands may increase under elevated CO_2, due to significantly enhanced production, the utilization of forage may decline since intake by ruminants goes down with forage quality. In more intensively-managed improved pastures, N fertilization and the introduction of legumes may be economically viable means by which to respond to rising atmospheric CO_2. In rangelands, N fertilization is not economically feasible, and the inter-seeding of legumes is difficult at best with today's technology. The responses of native legumes to elevated CO_2 may be an import factor in how these grasslands will evolve to support grazing by both domesticated and wild animals.

The evaluation of how CO_2 enrichment interacts with defoliation responses were obtained primarily from mechanical defoliation. There was no interaction of CO_2 with defoliation response in the shortgrass steppe study, although a single mid-summer cutting stimulated production (Table 2). In the tallgrass prairie, the response to CO_2 was greater when defoliation occurred in a dry year, but made little difference in seasonal production in an unusually wet years. Frequent defoliation of *L. perenne* increased root/shoot ratio in the Swiss pasture, but had no impact on the CO_2 response. The only study to utilize grazing animals, the New Zealand FACE experiment, indicated that sheep grazing enhanced the CO_2 response of legumes. These results are too few and differences between experiments too great to effectively summarize across grasslands, but they clearly indicate a possibility for defoliation of pastures to interact with the CO_2 response through various mechanisms (e.g. water, N, plant reserves).

The long-term responses of these grasslands will be controlled to a large extent by soil processes. Results of these studies all indicate a decline in N concentration of CO_2-enriched foliage when soils are not supplemented with N. These results suggest available soil N may limit the long-term responses of grasslands to rising CO_2. However, a New Zealand experiment conducted at a naturally occurring CO_2 spring indicated long-term CO_2 enrichment led to increased soil mineral N. And eight years of CO_2 enrichment on the tallgrass prairie resulted in higher total N in the surface 15 cm of the soil profile. Work in all four of the grasslands featured in this paper indicate enhanced microbial activity under elevated CO_2. These results suggest elevated CO_2 will alter belowground biological processes that will affect the availability of soil nutrients, but the results are too sketchy to speculate exactly how those changes will control grassland responses in future CO_2-enriched environments.

Interactions of CO_2 with Global Warming. This report has focused on CO_2 responses, but a few comments on global warming, its impact on grasslands and interactions with CO_2 seem warranted. The latitudinal distribution of plant functional types has been described, in part, through long-term temperature patterns (Terri and Stowe, 1976), so it seems likely that predicted increases in global temperatures will have important impacts on plant species production, distribution and plant community composition. In general, relatively large increases in temperature should favor warm-season plants (however, see Alward *et al.* 1999). However, there may be interactions with CO_2 that modify or even cancel temperature effects on vegetation. For instance, while warming may favor warm-season C_4 species, some of the effects of CO_2 enrichment on C_3 photosynthesis will tend to counter that response, rendering C_3/C_4 distribution changes relatively insensitive to increases in temperature (Polley *et al.* 2000). Further, while warmer temperatures may enhance the CO_2 production response, differences in plant development may lead to complicated interactions between CO_2 and species response as temperature increases (Newton *et al.* 1994).

The effect of warming on hydrology introduces other uncertainties. By itself, a warming trend will increase potential evapotranspiration, leading to desiccation. However, the improved water use efficiency under elevated CO_2 will tend to counter that response. In semi-arid grasslands, significant increases in both temperature and CO_2 may eventually shift the competition more in favor of C_4 grasses because of 1) the overriding benefit of CO_2 to improving plant water relations of most plant species, regardless of photosynthetic pathway, and 2) the adaptation of C_4 species to warm temperatures.

Warmer temperatures will no doubt shift plant communities with elevation. At very high mountain elevations where plant response to CO_2 is presently limited or completely absent due to cold temperatures, global warming may push temperatures high enough to elicit a significant plant growth response to CO_2 (Nösberger *et al.* 2000). Extreme temperatures will likely impact species distributions and abundance through reproduction, competition or survivorship, although species response differences are diverse and difficult to predict (Polley *et al.* 2000).

Changes in climate will likely impact foraging by ruminants. High daytime air temperatures currently reduce total grazing time for cattle with little or no compensatory nighttime grazing. Experiments and computer simulation models have suggested that in general, the potential for animal production will be increased in northern regions of the Great Plains with moderate global warming, but could be reduced in some cattle breeds in southern regions due to protracted periods of high temperatures (Hanson *et al.* 1993). For domestic livestock enterprises, increased stocking rates may be recommended because of the reduced intake of lower quality forage which will further reduce animal gains. Dietary supplementation may be used to maintain current production levels, but that will increase cost of production. Wild ruminant diet quality will be affected, and it is likely that they will have reduced growth and reproduction.

CONCLUSIONS

A comparison of results among four field CO_2 enrichment experiments conducted in contrasting grasslands suggests that productivity of grasslands should increase as CO_2 concentration rises. However, the ultimate responses of these grasslands to CO_2 and other aspects of global change will involve more complex changes in species dominance and survival along with alterations in soil biogeochemistry, much of which is still poorly understood. Collectively, these four projects do provide strong evidence that soil N will figure importantly in the CO_2 responsiveness of grasslands, and a strong case can be made, based on the Swiss and New Zealand FACE experiments, that legumes will be 1) important in supporting CO_2-induced production responses and 2) more competitive in future CO_2-enriched environments. The results from the two native grasslands also support the notion that water limitations will enhance the CO_2 production response through improved water use efficiency. But the hypothesized competitive advantage of C_3 over C_4 plants, based on differences in photosynthetic metabolism, is not borne out in these field studies. Further, feedbacks of soil processes to CO_2-induced plant responses are only beginning to be understood, and while there is now sufficient information to confirm significant soil-based biological responses, the long-term trajectory of those responses on whole ecosystems is poorly understood. The consequences for animal production are even less understood. Long-term global change studies, conducted in field environments, combined with modeling exercises will be required to unravel the complexities of how grasslands ecosystems will respond to increased CO_2 and climate change.

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