

THE IMPACTS OF GLOBAL CLIMATE CHANGE ON GRASSLAND ECOSYSTEMS

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ABSTRACT

Global climate change, induced by increase in the concentration of greenhouse gases in the atmosphere, can affect the growth and community structure of grassland ecosystems in two ways. The first is directly through changes in atmospheric concentration of CO₂ and the second is indirectly through changes in temperature and rainfall. At higher latitudes, where growth is largely temperature limited, it is probable that the direct effects of enhanced CO₂ will be less than at low latitudes. However, interactions with increasing temperature and water stress are complex. Grasslands range from intensively managed monocultures of sown species to species-rich natural and semi-natural communities whose regional distributions are controlled by variations in soil type and seasonal patterns of temperature and rainfall. The different species can show marked differences in their responses to increasing CO₂ concentrations, rising temperatures and water stress. This will probably result in major alterations in the community structure of grasslands in the future and possible shifts in ecosystem boundaries. In addition to impacts on primary productivity and community structure, a long-term effect of elevated CO₂ on grasslands is likely to be a significant increase in soil carbon storage. However, this may be counteracted by increases in temperature.

KEYWORDS

Primary production, community composition, C₃ and C₄ grasses, carbon dioxide, soil carbon, forage quality

INTRODUCTION

Rangelands, which include grasslands where the dominant vegetation consists of graminaceous species of plants, constitute over 50% of the Earth's land surface, carry most of the world's livestock, and support a significant human population (Chapin et al., 1996). In the northern hemisphere most of the grasslands are in cool temperate climates while in the southern hemisphere the greatest area is occupied by the savanna grasslands of the wet-and-dry tropics. Global climate change will affect the productivity of these lands in ways which are more difficult to assess than for cropping systems. This complexity arises from the scale at which these systems are used, the generally extensive form of management, the spatial heterogeneity typically incorporated in their management units and the potentially large number of species which may interact in the primary production system. Because of their large area and livestock numbers, grasslands play a significant role in biogeochemical and climatic feedback (Chapin et al., 1996). Grasslands play a positive role in the storage of carbon, but a negative role because of the emissions of methane (Mosier et al., 1991). They may also play an important role in the release of nitrous oxide (Minami et al., 1993; Bouwman, 1994).

Perhaps because of their complexity, the potential effects of climate change on grasslands have received much less attention than forests, although they clearly play an important part in the global carbon cycle and budget. For example it is estimated that grasslands contain more than 10% of the global soil carbon stocks and that changes in grasslands carbon storage have long-lived effects on the global carbon cycle (Solomon et al., 1993; Minami et al., 1994; Parton et al., 1995).

In this paper the aim is to review the knowledge of the impact of elevated atmospheric carbon dioxide (CO₂) on grassland species and the interactions with temperature and water stress. I also briefly review the problems of scaling from the level at which most

experiments are performed (single plants and small plots) to grassland ecosystems and the use of simulation models to predict responses to climate change. I work from the premise that the responses of grasslands to climate change variables will be the result of both the direct effects of increasing CO₂ and the indirect effects of rising temperature and changing patterns of rainfall. Further, there will also be interactions with other components of global change including an increase in nitrogen deposition and rising tropospheric ozone, but these are not discussed here.

THE FUTURE CLIMATE

Numerous studies in recent years (see IPCC, 1996b) have attempted to predict the consequences of global climate change for natural ecosystems, including grasslands. The effects of the projected changes in greenhouse gas concentrations on the global climate have been estimated using general circulation models (GCMs) (Viner et al., 1995). With the atmospheric concentration of CO₂ doubling from pre-industrial concentrations (about 280 μmol mol⁻¹) by the middle to late 21st Century, the predicted rise in global mean surface temperature is between 2°C and 4°C (Houghton et al., 1992). Global average temperature can provide some indication of the magnitude of likely climate change, but in terms of the regional implications, a global average conveys rather little information. However, it is at the regional level that the effects and impacts of global climate change on vegetation will be felt. While there is a good degree of confidence in the global estimates of future climate there is unfortunately, at present, much less agreement on projected changes at the regional level (Parry and Duncan, 1995). One important factor is that proximity to the oceans generally operates as a moderating influence and regions close to the oceans may warm more slowly than elsewhere at the same latitude (Carter, 1992). Another, is the uncertainty in estimating the effects of changes in cloud cover and type on the radiation balance and the role of clouds in the hydrological cycle (IPCC, 1996a).

In order to describe the future climate, most investigations have relied upon projections based on simulations with GCMs, in other words, climate change scenarios. Carter (1996) has argued that these scenarios have not been used effectively enough in past assessments, because of weaknesses in the methods adopted for selecting and applying climate change scenarios, with the result that there are problems of poor credibility of the projections, lack of representativeness of the results and inconsistencies within and between studies. A particular problem is that the majority of impact studies have used a scenario which represents the equilibrium climate under an equivalent doubling of CO₂ in the atmosphere. This scenario is unrealistic for two reasons. The first is that the climate is assumed to be in equilibrium with future changed atmospheric composition. In reality, the climate is continually responding to a gradual change in atmosphere composition (the so-called transient response). Second, because other atmospheric constituents as well as CO₂ also affect the climate, equivalent CO₂ doubling will occur before actual CO₂ doubling. The result has been confusion and inaccuracy in assessing impacts, especially in studies which have adopted scenarios of both climate change and elevated CO₂ concentration. Clearly, climate change scenarios need to be defined in terms of changes in both radiative forcing and atmospheric composition.

Because GCM outputs are most frequently available on a 250 km grid there is a necessity to downscale for vegetation impact studies.

Two methods have been used to downscale from the GCM grid box scale to the local scale: statistical methods and high resolution modelling. In the first of these, statistical relationships are derived between observed large-scale average climate and the observed local climate. Assuming that these observed relationships apply in the future, local climate is inferred from the projected large scale climate of a GCM. In the second method, a 'high resolution limited area climate model' (HIRLAM) is run over a geographical region using GCM outputs as boundary conditions. Of course, the results of the HIRLAM simulation are constrained by the performance of the bounding GCM in which it is nested. It should be recognised that different downscaling techniques can produce significantly different patterns of local climate in a region.

Another weakness of GCMs is their inability to reproduce the climate variability on the timescales experienced by vegetation. Various methods exist for generating daily climatological data using stochastic weather generators. Several studies, using these techniques, have shown that the impact of changes in climatic variability can be as significant as impacts caused by changes in mean climate (Semenov and Porter, 1995).

DIRECT EFFECTS OF ELEVATED CO₂

The IPCC 'business-as-usual' scenario predicts that the atmospheric CO₂ concentration will rise from 354 μmol mol⁻¹ in 1990 to 530 μmol mol⁻¹ in 2050 and will exceed 700 μmol mol⁻¹ by 2100 (Watson et al., 1990). Carbon dioxide is the substrate for photosynthesis for all terrestrial higher plants, with C₃ plants growing in adequate light requiring 800-1000 μmol mol⁻¹ CO₂ for saturation of photosynthesis (Lawlor, 1993). As a consequence, increasing atmospheric CO₂ concentrations will directly increase the rate of photosynthesis and dry matter production of terrestrial C₃ plants. Among the wide range of C₃ crops and non-agricultural species that have been examined almost all show significant increases in photosynthesis and dry matter production in response to an increase in atmospheric CO₂ to between 500 and 1000 μmol mol⁻¹. Reviews by Kimball (1983) and Cure and Acock (1986) of experiments done under a wide range of conditions, but mainly on pot-grown plants, have shown that a doubling of atmospheric CO₂ from 330 to 660 μmol mol⁻¹ increases the productivity of C₃ species by an average of 33%. Poorter (1993) found the growth stimulation of 156 species of C₃ plants, produced by a doubling of the atmospheric CO₂ concentration, to be 41%. Assuming a linear response to rising CO₂, these observations suggest that dry matter production increases by between 0.10 and 0.12% per 1 μmol mol⁻¹ increase in CO₂. If these observations are extrapolated to the field, this means that the CO₂ enrichment since the start of the industrial revolution (from 280 to 355 μmol mol⁻¹) would be expected to have increased dry matter production of C₃ herbaceous plants by 7.5-9.0%. This increase would be very difficult to detect empirically, even for crop species, particularly because new varieties have been selected throughout this period for higher yields independent of CO₂ effects, but also because of massively increased inputs such as fertilisers. Furthermore, the assumption of a linear response between approximately present day CO₂ concentrations and twice present day values is almost certainly erroneous, although at present we do not know at what CO₂ concentration whole plants or whole ecosystems will be saturated (Körner, 1995).

Despite the consistent evidence, from short term experiments on pot-grown plants, for the direct stimulation in growth by increasing CO₂, there has been some reluctance to accept that prolonged growth in elevated CO₂ stimulates productivity under normal field conditions (Körner and Miglietta, 1994). Indeed, data from grasslands ungrazed for 100 years at Rothamsted, UK, suggest that rising CO₂ has not

affected dry matter production (Jenkinson et al., 1994). There are several additional reasons for this scepticism. First, it has been assumed that photosynthesis is often limited by other environmental variables such as temperature, water and nutrient availability during much of the year, so that plants do not respond to increased atmospheric CO₂ (Melillo et al., 1990). Second, the effects of long-term trends in climate change can easily be overridden by interannual variation in the complex interactions among environmental factors that determine the growth of plants, e.g. nitrogen and water availability. Third, there is much evidence, particularly from pot experiments, that the initial CO₂ stimulation of photosynthesis is not maintained and that down-regulation of photosynthesis occurs after prolonged exposure to high CO₂ concentration (Bowes, 1993). There are, however, very few observations from field experiments on grasses to confirm these views, although results from a small number of long-term studies using open-top chambers or Free Air CO₂ Enrichment (FACE) have been published recently (Hebeisen et al., 1997). The limited information from field experiments (Table 1) suggests that there is indeed a sustained response to elevated CO₂ but that for a doubling of present day concentrations the increase in productivity is in the region of 15-20% rather than the 30-40% reported for pot-grown plants (Jones et al., 1996; Hakala and Mela, 1996).

Another feature of the prolonged field experiments with grasses has been the evidence for greater allocation of assimilates to roots rather than shoots at elevated CO₂ (Jongen et al., 1995). In some cases there is evidence that the root fraction increased in elevated CO₂ even though there was no increase in growth above ground (Hebeisen et al., 1997). This indicates that in many grasslands much of the increased carbon assimilated at elevated CO₂ is entering the soil initially through enhanced growth but also possibly via increased tissue turnover or root exudation. The fate of this extra carbon entering the below-ground compartment is still unclear. It may be incorporated by soil organisms including bacteria and fungi, accumulated in soil organic matter, or released back to the atmosphere as increased soil or root respiration. The quantification of these pathways for carbon present a formidable technical challenge but they must be determined if accurate carbon budgets are to be developed for grassland ecosystems. There is evidence that the CO₂ and nitrogen concentrations at which the grass roots had been grown affects decomposition rates (Van Ginkel et al., 1996) and there are also differences between species (Jongen et al., 1995). In general, root decomposition decreased under elevated CO₂ concentrations but the effect was greater in clover than in ryegrass (Jongen et al., 1995). It is likely that the combination of higher root yields at elevated CO₂, combined with a decrease in root decomposition, will lead to longer residence time of carbon in the soil and probably to higher soil carbon storage. Indeed, Casella and Soussana (1997) have recently shown that annual below-ground carbon storage of perennial ryegrass swards was increased by 32 and 96% in 2 x ambient CO₂ at low and high nitrogen supplies, respectively.

INTERACTIONS OF ELEVATED CO₂ AND TEMPERATURE

In higher latitudes, where grass growth is largely temperature limited throughout much of the growing season, it is probable that the direct effects of enhanced CO₂ will be less than at low latitudes. Here, temperatures are no longer limiting and growth is consequently more likely limited by available CO₂ (Lemon, 1983). There are, however, many experimental observations that run contrary to this argument and show that optimal conditions are not a prerequisite for enhanced growth at elevated CO₂. In fact, the enhancement can be maintained when other factors are co-limiting. For example, some temperate

crops growing under low irradiance have been found to have a larger response to CO₂ than those growing at higher irradiance (Sionit et al., 1982; Ziska et al., 1990; Gifford, 1992). This is thought to be due to the suppression at increasing CO₂ concentrations of photorespiration, which is proportionately more significant at low irradiance, and could be important for plants growing in overcast conditions during the spring at high latitudes (Long, 1991). Also, there is some evidence that elevated CO₂ may lower the minimum temperature at which some plants grow and complete their life-cycle (Potvin, 1985). This response could be very important in temperature-limited growing conditions, especially if most of the observed and predicted warming is due to increases in minimum (night-time) temperatures (IPCC, 1996a).

Future elevated atmospheric CO₂ concentrations will probably be associated with warmer temperatures. Unfortunately, limited experimental evidence is available on the interactive effects of enriched CO₂ and elevated temperatures but the observed and predicted responses are generally complex and varied. Using a mechanistic model of carbon exchange, Long (1991) has shown that elevated CO₂ concentrations could alter both the magnitude of the response of leaf and canopy carbon gain to rising temperature, and sometimes, the direction of response. Newton et al. (1994) suggested that, because of the modifying effects of temperature, the influence of CO₂ on grass growth in temperate regions will be different during the changing seasons. Experiments carried out in solardomes, which allow studies on the effects of both changes in CO₂ and temperature on vegetation (Jones et al., 1993), show that exposure to an increase in temperature of 3°C above present ambient has a larger effect on the annual aboveground biomass production of *Lolium perenne* than does a doubling of present day CO₂ concentrations. However, the combined effects of elevated CO₂ and elevated temperature are less than additive, indicating a decline in response to elevated CO₂ as temperature increases. Newton et al. (1994), using turves taken from a ryegrass/white clover based pasture found that ryegrass growth rates declined as temperature increased from 10/4½°C (day/night) to 22/16½°C and furthermore, this decline was greater at elevated CO₂. In contrast, white clover growth rate increased with temperature and was stimulated by elevated CO₂. The interactions between elevated CO₂ and elevated temperature will be further complicated by the fact that the effects of temperature on grass growth are the results of both an increase in the length of the growing season and higher growth rates as temperatures rise. Phenology of the grassland species and its coincidence with weather conditions is of crucial importance to the understanding of the response of these ecosystems to elevated CO₂ (Campbell et al., 1995).

INTERACTIONS OF ELEVATED CO₂ AND WATER STRESS

The seasonal pattern of growth of temperate grasses generally shows a decline during the summer months, which is partially developmentally related to the onset of flowering (Parsons, 1988), but can in many cases be attributed to developing water stress (Jones, 1988). The stress is due to an excess of evapotranspiration over rainfall and is a consequence of the increase in the soil water deficit. The decline in summer soil moisture content in temperate regions, predicted by most climate scenarios (IPCC, 1996a), would be expected to increase this effect under climate change. The growth of tropical grasses is already severely limited by water stress and it is unlikely that this will change significantly under predicted climate change. However, a direct effect of increasing CO₂ concentrations is to decrease stomatal conductance in most species. A reduction in stomatal conductance will be expected to reduce transpiration and increase water-use efficiency at the leaf scale, and in effect conserve

water for continued plant growth.

There have been many experimental demonstrations of reduced stomatal conductance at elevated CO₂ (Morison, 1985; Eamus, 1991) and for a doubling of present day CO₂ concentrations the reduction in conductance frequently varies from 20 - 50% (Eamus, 1991; Field et al., 1995). It is likely however that a number of processes interact at the ecosystem scale to reduce the magnitude of the response of ecosystem evapotranspiration to increasing CO₂ as compared with transpiration at the leaf scale (Eamus, 1991). This difference arises from the effect of stomatal closure on leaf temperature and the drying of the boundary layer in response to decreasing stomatal conductance, which increases the driving gradient for transpiration (Jarvis and McNaughton, 1986; McNaughton and Jarvis, 1991; Field et al., 1995). Furthermore, the effects of increasing CO₂ on canopy evapotranspiration are likely to be smallest in aerodynamically smooth canopies such as grasses (Jarvis and McNaughton, 1986). Field et al. (1995) suggests that the decrease in evapotranspiration in this type of canopy may be only 25% as large as the decrease in leaf conductance. Also, the increase in leaf area associated with greater aboveground biomass at elevated CO₂ will diminish the effect of reduced single leaf conductance.

However, a small number of ecosystem measurements of evapotranspiration of grasses at elevated CO₂ have shown that although canopy evapotranspiration may not, as predicted, decline significantly at elevated CO₂, there is nevertheless an increase in the water-use efficiency (expressed as the ratio of canopy CO₂ uptake/water vapour loss) which is a consequence of higher CO₂ assimilation rates (Nijs et al., 1989; Diemer, 1994). Despite an increase in instantaneous water-use efficiency, if canopy evapotranspiration does not decline at elevated CO₂, water stress may develop at the same rate compared with ambient conditions. Also, in circumstances where leaf area increases at elevated CO₂, we might expect water stress to develop more rapidly.

Overall, we therefore expect that the effect of elevated CO₂ on grassland ecosystem evapotranspiration, and therefore on developing water stress, will be rather small. A significant exception however may be C₄-dominated grasslands. There is clear evidence that in both annual grasslands of California and tallgrass prairies of Kansas, soil moisture was higher at elevated CO₂ and this has important implications for the duration of the growing season in seasonally droughted systems (Owensby et al., 1996). The consequence of this is that in tallgrass prairies at elevated CO₂ the C₄ grass species had increased biomass production (Table 1) while the C₃ grass species were unaffected (Owensby et al., 1996).

INTERACTIONS OF ELEVATED CO₂ AND NUTRIENT AVAILABILITY

It has frequently been suggested that increased biomass production under elevated CO₂ will not be sustained in natural and semi-natural ecosystems due to nutrient limitations, particularly nitrogen. Indeed, Owensby et al. (1993b) have shown that in tallgrass prairie the response of biomass production to elevated CO₂ over two years in nitrogen fertilised plots was much greater than in unfertilised plots. Here, in natural grasslands with inherently low nitrogen availability, the response to elevated CO₂ was suppressed by nitrogen limitation.

In the short-term, the impact may be reduced by increased nutrient use efficiency and increased nutrient uptake due to higher root biomass at elevated CO₂. In the longer term there may be less nitrogen available due to slower decomposition of litter because of reduced litter quality. However, Gifford (1992) has argued that while in the

short-term of a single season, productivity is strongly limited in many ecosystems by the amount of nitrogen that is newly mineralised or fixed, over the longer term of decades the nitrogen cycle does the opposite and follows the carbon cycle. The mechanisms for increasing nitrogen inputs into ecosystems could be increased nitrogen fixation due to increased availability of energy sources (carbon), through better competition by roots over denitrifying and heterotrophic organisms for available nitrogen, or reduced losses of nitrogen as gaseous emissions or leaching, or combinations of these mechanisms (Gifford, 1992). Anthropogenic addition of nitrogen will also have regional effects in N. America and Europe.

SPECIES SPECIFIC RESPONSES TO ELEVATED CO₂

As already made clear, most grasslands are typically composed of a complex mixture of annual and perennial grasses, nitrogen-fixing legumes and non-fixing dicots of different growth forms. Most studies so far have concentrated on the response of single plants and/or single species at elevated CO₂. However, there is a major concern that it will not be possible to extrapolate to community responses from the results of these experiments (Pitelka, 1994). This is because the different species are likely to show marked differences in their responses to increasing CO₂ (Kimball, 1983; Cure and Acock, 1986; Poorter, 1993) and climatic stresses, and this will probably result in major alterations in community structure in the future. Campbell et al. (1995) identified considerable variation in the response of 13 different forage species to increases in CO₂. The response was strongly determined by temperature, the greatest response being observed at warm temperatures in C₃ species with the highest potential growth rate at these temperatures. These results suggest that community composition should change most rapidly in response to elevated CO₂ in warm seasons. However, if water stress occurs at the same time then C₄ species may be favoured over C₃ species (Campbell et al., 1995).

Little information is available on the responses of mixed species communities when exposed to elevated CO₂, where competition between the different species will interact with the differential responses to elevated CO₂. Preliminary results from experiments in which this type of interaction has been investigated have shown that it is unlikely to be possible to predict the response of a mixed community from the observed responses of species grown in monoculture (Jongen, 1996). Recently, Stewart and Potvin (1996) have investigated the effect of CO₂ enrichment on plant-plant interactions in an artificial grassland community dominated by *Trifolium repens* and *Poa pratensis*. Their results show that elevated CO₂ increased the strength and number of plant-plant interactions and that *Trifolium*, a nitrogen-fixing legume, exploited the CO₂-enriched atmosphere more effectively than *Poa*, a non-fixing C₃ grass.

Many grasslands contain C₄ species which are expected to respond less to increasing CO₂ than C₃ species. This should translate into higher primary production for C₃ vs. C₄ species if other resources are not more limiting than CO₂. However, as mentioned above, studies by Owensby et al. (1993a; 1996) on a tallgrass prairie community with a mixture of C₃ and C₄ perennial species have yielded some unexpected results. They show that in mixed C₃-C₄ communities, the resource limits that currently maintain plant composition have a greater impact than the direct CO₂ fertiliser effect on C₃ photosynthesis. In the tallgrass prairie, water stress and time of nitrogen availability favour C₄ species and the partial alleviation of water stress under elevated CO₂ probably gives the C₄ species a greater competitive advantage. As a consequence, when a tallgrass prairie community was exposed to elevated CO₂ for a five year period the content of the C₃ grasses continued to decline (Owensby et al., 1996).

In addition to differential responses to elevated CO₂, component species of grasslands show species specific responses to ambient temperature and stress factors, including water stress (Jones, 1988). The different temperature responses are the result of each species having its own optimum temperature regime for growth, which lead to a different seasonal pattern of growth for the component species. For example in mixed grass-clover swards, grasses may be dominant early in the season with clover forming a significant component during mid-season. The effects of increasing CO₂ concentration and rising temperature on the composition of these swards is therefore complex on a temporal scale and requires more detailed studies. Future studies must address this issue by carrying out experiments on complete grassland ecosystems (e.g., Wolfenden and Diggle, 1995). Because of the additional interactions in ecosystems between plant and soil, these experiments will need to be carried out either *in situ* or using monoliths representative of the natural communities transferred to controlled environments. One approach which may help to simplify these studies is to determine whether the growth response to elevated CO₂ and its interaction with temperature and water stress can be predicted on the basis of ecological functional types. Different functional types can be identified, based on the established growth phase of the plants; for example competitors, ruderals and stress tolerators (Grime, 1974; Grime et al., 1988). Hunt et al. (1991) predicted a high CO₂ responsiveness within the competitive functional type, with the ruderal strategy showing a smaller response. In the case of grasslands, alternative functional types may be more relevant; for example, nitrogen fixers and non-fixers, and C₃ or C₄ photosynthetic types. It has been hypothesised that nitrogen fixers may benefit more from elevated CO₂ than with non-fixers and there is some evidence to support this (Stewart and Potvin, 1996).

FORAGE QUALITY AND HERBIVORY

Although the productivity of grassland ecosystems is an important indication of their response to climate change, the accompanying changes in forage nutritive value (forage quality) are crucial in determining grazing animal production efficiency. Forage quality depends on digestibility, protein and energy content, palatability, concentrations of minerals and anti-nutritional factors. These factors are all sensitive to the growing conditions for grassland and elevated CO₂; warmer weather and changed rainfall patterns will have possibly conflicting effects on components of quality. Forage quality will probably decline at elevated CO₂ because of higher C:N ratios and possible higher concentrations of unpalatable and/or toxic compounds in plants (Chapin et al; 1996). Plants grown at elevated CO₂ also tend to have reduced mineral concentrations (except phosphorus) relative to those grown at ambient CO₂ concentrations (Owensby et al., 1993a).

Herbivory is an integral part of grassland ecosystems and the effect of elevated CO₂ on diet quality, as well as the feedback to carbon acquisition and nutrient cycling, will play an important role in ecosystem function in a high-CO₂ world. Although forage consumption may increase as quality declines, because herbivores will need to eat more to meet nutritional demands, ruminants and functional caecum animals will likely have reduced consumption and productivity because intake is controlled largely by the rate of passage of ingesta, which is reduced as diet quality decreases (Owensby et al., 1993a).

Herbivory affects nutrient cycling by changing the rate at which the plant tissues are broken down and the nutrients are released. Ruminants in grassland systems cycle as much as 25% of the aboveground biomass through rumen fermentation, which has

degradation times measured in hours compared to years for surface litter decomposition. As the reduced nitrogen concentration of plant tissue at elevated CO₂ is likely to reduce the rate of decomposition, thereby slowing nutrient cycling and energy flow (Schimel et al., 1994), the influence of herbivory on nutrient cycling at elevated CO₂ requires further investigation.

SCALING UP

Processes in vegetation occur over a wide range of spatial and temporal scales but because of the current interest in *global* change there is a need to scale upwards to predict the responses to change (Wessman, 1992; Jarvis, 1995). There may be general agreement that increasing global carbon dioxide concentrations and the changing climate will have direct physiological effects on plants, but the duration of these effects and their impact at the level of the population and ecosystem is still relatively unknown. This is largely because much of the experimental work on plant responses to climate change has involved investigation of single plant responses over time periods of days to weeks. Most of the results reported to date have been obtained using either single plants or small plots which have been grown for periods between, most frequently a few weeks and, very rarely, as much as 2-3 years. Recently, however, more results from prolonged exposure of grass ecosystems in the form of small plots have been reported (Jones et al., 1996, Owensby et al., 1996, Jongen et al., 1995) (Table 1).

In order to understand how large geographical areas occupied by grasslands will respond to climate change, there is clearly a need to scale up from single plants and plots with dimensions in the order of 1 to 100 m², to patches (100-10000 m²), to landscapes (1-100 km²) and ultimately to regions (10000 km²) as well as from relatively short-term to long-term time scales (years to centuries). The scaling process involves taking information at one scale and using it to derive processes at another scale (Wessman, 1992; Jarvis, 1995). A major problem with this approach is the non-linearity between processes and variables; for example transpiration at any spatial scale is non-linearly related to stomatal conductance (Field et al., 1995). Also, there are heterogeneities in properties that determine the rate of processes. Heterogeneity may be random or exist as patches, for example a grass sward may exist as a strictly random arrangement of grass and clover plants or it may consist of patches where the species composition and dominance of individual species varies over a given area. Ultimately however, the key to scaling is determining what to ignore. The object is not to analyse all of the smaller scale aspects of a process under observation, but to focus instead only on those that have direct importance to the scale under consideration (Wessman, 1992). Bridging the gap between site-level ecological understanding and global scale phenomena is probably best achieved using a combination of remote sensing studies, the use of geographic information systems and simulation modelling.

MODELLED PREDICTION OF CLIMATE CHANGE IMPACTS

There have been a wide variety of models developed to explore the response of grassland vegetation and soils to climate change. These models range from the purely statistical, to models which simulate basic ecophysiological and demographic processes (Smith et al., 1993). Biogeography models are used to predict changes in the distribution of vegetation types in response to elevated CO₂ and climate change while biogeochemistry models predict changes in global fluxes of water, carbon, and nitrogen. On the basis of our understanding of physiological and ecological responses we can expect that elevated CO₂ and changes in climate will affect both the structure and function of grassland ecosystems. Structural responses

include changes in species composition and a variety of vegetation characteristics such as canopy density and rooting depth. Functional responses include changes in the cycling of carbon, nutrients and water. A recent comparison of three biogeography and three biogeochemistry models have been made (VEMAP Members, 1995). The VEMAP study shows that while both classes of models present rather consistent simulations of current conditions, their predictions diverge substantially when climate and CO₂ are altered. Key areas of divergence between the models arise from the formulation of the effects of CO₂ on water and nutrient use, on allocation of net primary production to different plant components and on long-term coupling of carbon and nitrogen storage. The models also differ in the degree to which canopy processes are coupled to the atmosphere and the feedbacks which result from this coupling.

The CENTURY (biogeochemistry) model, developed by Parton et al. (1993) has been used extensively to investigate the regional responses of grasslands to climate change (Schimel et al., 1990; 1991) and recently Parton et al. (1995) have modelled the impact of climate change and increasing atmospheric CO₂ for 31 temperate and tropical grassland sites using the CENTURY model. They also compared equilibrium and transient responses. A '2 x CO₂' climate change scenario increased net primary production everywhere except in cold desert steppe regions but caused soil carbon to decrease overall with a loss of 4 Pg from global grasslands after 50 years. Combined climate change and elevated CO₂ increased production and reduced global grassland C losses to 2 Pg, with tropical soils becoming small sinks for soil C. The year to year variability in plant production was high, such that a 16% increase in net production would be required before it could be detected. Predicted changes in soil carbon stocks made by CENTURY are substantially lower than other estimates made by Van den Pol Van Dasselaar and Lantiga (1995) using the carbon cycle model CCGRASS and Thornley et al. (1991) using the Hurley Pasture Model.

Several biogeographic models have suggested that there will be significant changes in the distribution of grasslands worldwide in response to climate change (Prentice et al., 1992; Neilson, 1993; Ojima et al., 1993a; Henderson-Sellers and McGuffie, 1995). However, because many grasslands are not in equilibrium with present climatic conditions it is probable that although individual species may change distribution there is unlikely to be any synchronised movement of entire vegetation belts (Chapin et al., 1996). The semi-arid grassland may be among the first to show the effects of climate change. This may manifest itself through changes in grassland-woody species boundaries as C₄ grasslands become increasingly populated by C₃ woody plants which are favoured by increasing CO₂ concentrations (Chapin et al., 1996). Ojima et al. (1993b) using a 2 x CO₂ climate change scenario suggest that this will lead to an approximate 40% increase in the area of warm grasslands and a 50% decrease in cool grasslands.

FUTURE RESEARCH NEEDS

It is clear that future changes in atmospheric composition, climate and human land use have the capacity to exert large effects on the distribution and functioning of terrestrial vegetation, including grasslands. There is at present a concerted effort, largely coordinated under Global Change and Terrestrial Ecosystems (GCTE), a core project of the International Geosphere Biosphere Programme (IGBP) (Steffen et al., 1992), to investigate and predict the nature of vegetation responses to future global change. It is recognised that it is necessary to address the global-scale nature of changes in terrestrial vegetation, but this imposes very important restrictions on the scientific approach to the problem. In order to make predictions for

the future, further modelling is necessary and this should be increasingly concerned with the rates at which vegetation structure and function change in response to relatively slow changes in climate and atmospheric CO₂ concentration, as well as changes in human land use.

Because of the uncertainties in predictions made by existing global models it is essential that modellers and experimentalists communicate new results suggesting mechanisms not included, or poorly described, in existing models (Hall and Scurlock, 1991). In order to reduce the range of predicted responses and to determine which models are most accurate it is necessary to collect appropriate measurements from grassland ecosystems that can confirm or validate the projections of the models. In particular, these include flux measurements of carbon and water exchange over large areas of major grassland types. Measurements over the seasonal cycle and, periodically, over several years to determine fluxes during years with different temperatures and amounts of precipitation are essential. These data can be used to determine whether measured carbon and water fluxes are consistent with values predicted by particular models (Baldocchi et al., 1996). Model sensitivity to different climates may be examined by simulating ecological responses to Holocene climates or more distant past warm periods for which palaeoecological data exists.

It is still widely recognised that modelling efforts are currently constrained by inadequate databases of ecosystem responses to elevated CO₂ and altered climate. Consequently, experimental ecophysiology and ecosystem studies need to investigate the response of natural and agricultural grassland ecosystems, above and below ground, across broad climate gradients to elevated CO₂, with particular emphasis on changes in relationships among environmental variables such as temperature, moisture and nutrients. Particular emphasis should be placed on carbon pool quantification over time and space. Also, in mixed C₃-C₄ ecosystems, determination of the differential responses among species (functional types) that affect productivity and interspecific competition leading to composition shifts requires investigation. Because past experiments have only been conducted over relatively short periods in the context of the ecological timescale, important aspects of the vegetation response have not been identified. These changes are not only the result of changes in the relative proportions of genotypes due to differences in responsiveness but include invasion or extinction of species and perhaps most importantly human interaction altering the genetic makeup of communities. Clearly, modelling activities must not ignore the composition of communities and we must therefore develop a better understanding of functional characteristics to incorporate genetic variation into predictive models.

REFERENCES

Baldocchi, D., R. Valentini, S. Running, W. Oechel and R. Dahlman. 1996. Strategies for measuring and modelling carbon dioxide and water vapour fluxes over terrestrial ecosystems. *Global Change Biology* **2**: 159-168.

Bouwman, A.F. 1994. Computing land use emissions of greenhouse gases. *Water, Air, and Soil Pollution* **76**: 231-258.

Bowes, G. 1993. Facing the inevitable: plants and increasing atmospheric CO₂. *Annual Review of Plant Physiology and Plant Molecular Biology* **44**: 309-332.

Campbell, B.D., W.A. Laing, D.H. Greer, J.R. Crush, H. Clark, D.Y. Williamson and M.D.J. Given. 1995. Variation in grassland populations and species and the implications for community responses to elevated CO₂. *Journal of Biogeography* **22**: 315-322.

Carter, T.R. 1992. The greenhouse effect and Finnish agriculture.

National Board of Agriculture. *The First Hundred Years*. pp. 31-57.

Carter, T.R. 1996. The role of scenarios in climate impact and adaptation assessment. ECLAT Workshop, Sissi, Greece (in press).

Casella, E., J.-F. Soussana and P. Loiseau. 1996. Long-term effects of CO₂ enrichment and temperature increase on a temperate grass sward. I. Productivity and water use. *Plant and Soil* **182**: 83-99.

Casella, E. and J.-F. Soussana. 1997. Long-term effects of CO₂ enrichment and temperature increase on the carbon balance of a temperate grass sward. *Journal of Experimental Botany*. **48**: 1309-1321.

Chapin, F.S., S. Diaz, M. Howden, J. Fuigdefábregas and M. Stafford Smith. 1996. Rangelands in a changing climate: Impacts, Adaptations, and Mitigation. Pages 134-158 in Watson et al., eds. *Climate change 1995. Impacts, Adaptations, and Mitigation of Climate Change: Scientific-Technical Analysis*. Cambridge University Press, Cambridge.

Cure, J.D. and B. Acock. 1986. Crop responses to carbon dioxide doubling: a literature survey. *Agricultural and Forest Meteorology* **38**: 127-145.

Diemer, M.W. 1994. Mid-season gas exchange of an alpine grassland under elevated CO₂. *Oecologia* **98**: 429-435.

Eamus, D. 1991. The interaction of rising CO₂ and temperature with water use efficiency. *Plant, Cell and Environment* **14**: 843-852.

Field, C.B., R.B. Jackson and H.A. Mooney. 1995. Stomatal responses to increased CO₂: implications from the plant to the global scale. *Plant, Cell and Environment* **18**: 1214-1225.

Gifford, R.M. 1992. Interaction of carbon dioxide with growth-limiting environmental factors in vegetation productivity: implications for the global carbon cycle. Pages 24-58 in G. Stanhill, ed. *Advances in Bioclimatology Vol 1*. Springer-Verlag, Berlin/Heidelberg/New York.

Grime, J.P. 1974. Vegetation classification by reference to strategies. *Nature* **150**: 26-31.

Grime, J.P., J.G. Hodgson and R. Hunt. 1988. *Comparative Plant Ecology: A functional approach to common British species*. Unwin Hyman, London, 742 p.

Hakala, K. and T. Mela. 1996. The effects of prolonged exposure to elevated temperatures and elevated CO₂ levels on the growth, yield and dry matter partitioning of field-sown meadow fescue. *Agricultural and Food Science in Finland* **5**: 285-298.

Hall, D.O. and J.M.O. Scurlock. 1991. Climate change and productivity of natural grasslands. *Annals of Botany* **67**: (suppl.) 49-55.

Hebeisen, T., A. Lüscher, S. Zanetti, B.U. Fischer, U.A. Hartwig, M. Frehner, G.R. Hendry, H. Blum and J. Nösberger. 1997. Growth responses of *Trifolium repens* L. and *Lolium perenne* L. to free air CO₂ enrichment and management. *Global Change Biology*. **3**: 149-160.

Henderson-Sellers, A. and K. McGuffie. 1995. Global climate models and 'dynamic' vegetation changes. *Global Change Biology* **1**: 63-75.

Houghton, J.T., B.A. Callander and S.K. Varney (eds.) 1992. *Climate Change 1992: The Supplementary Report to the IPCC Scientific Assessment*. Cambridge University Press, 200 p.

Hunt, R., D.W. Hand, M.A. Hannah and A.M. Neal. 1991. Response to CO₂ enrichment in 27 herbaceous species. *Functional Ecology* **5**: 410-421.

Hunt, H.W., E.T. Elliott, J.K. Detling, J.A. Morgan and D.-X. Chen. 1996. Responses of a C₃ and a C₄ perennial grass to elevated CO₂ and temperature under different water regimes. *Global Change Biology* **2**: 35-47.

IPCC. 1996a. *Climate Change 1995 - The Science of Climate Change. Contribution of Working Group I to the Second Assessment Report of the Intergovernmental Panel on Climate Change*, J.T.

- Houghton, L.G. Meira Filho, B.A. Callander, N. Harris, A. Kattenberg and K. Maskell, eds. Cambridge University Press, Cambridge and New York, 572 p.
- IPCC.** 1996b. Climate Change 1995 - Impacts, Adaptations and Mitigation of Climate Change: Scientific-Technical Analyses. Contribution of Working Group II to the Second Assessment Report of the Intergovernmental Panel on Climate Change, R.T. Watson, M.C. Zinyowera and R.H. Moss, eds. Cambridge University Press, Cambridge and New York, 879 p.
- Jarvis, P.G. and K.G. McNaughton.** 1986. Stomatal control of transpiration: Scaling up from leaf to region. *Advances in Ecological Research* **15**: 1-49.
- Jarvis, P.G.** 1995. Scaling processes and problems. *Plant, Cell and Environment* **18**: 1079-1089.
- Jenkinson, D.S., J.M. Potts, J.N. Perry, V. Barnett, K. Coleman, and A.E. Johnston.** 1994. Trends in herbage yields over the last century on the Rothamsted long-term continuous hay experiment. *Journal of Agricultural Science, Cambridge* **122**: 365-374.
- Jones, M.B.** 1988. Water relations. Pages 205-242 in M.B. Jones and A. Lazenby, eds. *The Grass Crop: the physiological basis of production.* Chapman and Hall, London.
- Jones, M.B., T. Ashenden and H.D. Payer.** 1993. Enrich - a European network of research on the impact of elevated carbon dioxide on herbaceous plants. Pages 231-236 in E.D. Schulze and H.A. Mooney, eds. *Design and Execution of Experiments on CO₂ Enrichment.* Ecosystem Research Report No. 6, CEC Brussels.
- Jones, M.B., M. Jongen and T. Doyle.** 1996. Effects of elevated carbon dioxide concentrations on agricultural grassland production. *Agricultural and Forest Meteorology* **79**: 243-252.
- Jongen, M, M.B. Jones, T. Hebeisen, H. Blum and G. Hendry.** 1995. The effects of elevated CO₂ concentrations on the root growth of *Lolium perenne* and *Trifolium repens* grown in a FACE system. *Global Change Biology* **2**: 361-371.
- Jongen, M.** 1996. The effect of elevated atmospheric carbon dioxide on pasture species. PhD thesis, Trinity College Dublin.
- Kimball, B.A.** 1983. Carbon dioxide and agricultural yield: an assemblage and analysis of 430 prior observations. *Agronomy Journal* **75**: 779-788.
- Körner, C. and F. Miglietta.** 1994. Long-term effects of naturally elevated CO₂ on Mediterranean grassland and forest trees. *Oecologia* **99**: 343-351.
- Körner, C.** 1995. Towards a better experimental basis for upscaling plant responses to elevated CO₂ and climate warming. *Plant, Cell and Environment* **18**: 1101-1110.
- Lawlor, D.W.** 1993. Photosynthesis; molecular, physiological and environmental processes. Longman, Harlow. 318 p.
- Lemon, E.R.** (ed.) 1993. CO₂ and Plants: The Response of Plants to Rising Levels of Atmospheric Carbon Dioxide. Westview Press, Boulder, Colorado. 280 p.
- Long, S.P.** 1991. Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO₂ concentrations: Has its importance been underestimated? *Plant, Cell and Environment* **14**: 729-739.
- McNaughton, K.G. and P.G. Jarvis.** 1991. Effects of spatial scale on stomatal control of transpiration. *Agriculture and Forest Meteorology* **54**: 279-302.
- Melillo, J.M., T.V. Callaghan, F.I. Woodward, E. Salati and S.K. Sinha.** 1990. Effects on ecosystems. Pages 283-310 in J.T. Houghton et al., eds. *Climate Change: The IPCC Scientific Assessment.* Cambridge University Press, Cambridge.
- Minami, K., J. Goudriaan, E.A. Lantinga and T. Kimura.** 1993. The significance of grasslands in emission and absorption of greenhouse gases. Pages 1231-1238 in *Proceedings of the 17th International Grassland Congress, Palmerston North.*
- Morison, J.I.L.** 1985. Sensitivity of stomata and water use efficiency to high CO₂. *Plant, Cell and Environment* **8**: 467-474.
- Mosier, A.R., D. Schimel, D. Valentine, K. Bronson and W. Parton.** 1991. Methane and nitrous oxide fluxes in native, fertilized and cultivated grasslands. *Nature* **350**: 330-332.
- Neilson, R.P.** 1993. Vegetation redistribution: a possible biosphere source of CO₂ during climatic change. *Water, Air and Soil Pollution* **70**: 659-673.
- Newton, P.C.D., H. Clark, C.C. Bell, E.M. Glasgow and B.D. Campbell.** 1994. Effects of elevated CO₂ and simulated seasonal change in temperature on the species composition and growth rates of pasture turves. *Annals of Botany* **73**: 53-59.
- Newton, P.C.D., H. Clark, C.C. Bell, E.M. Glasgow, K. Tate, D.J. Ross, G.W. Yeates and S. Saggars.** 1995. Plant growth and soil processes in temperate grassland communities at elevated CO₂. *Journal of Biogeography* **22**: 235-240.
- Nijs, I., I. Impens and T. Behaeghe.** 1989. Leaf canopy responses of *Lolium perenne* to long-term elevated atmospheric carbon dioxide concentrations. *Planta* **177**: 312-320.
- Ojima, D.S., B.O.M. Dirks, E.P. Glenn, C.E. Owensby and J.O. Scurlock.** 1993a. Assessment of C budget for grasslands and drylands of the world. *Water, Air, and Soil Pollution* **70**: 95-109.
- Ojima, D.S., W.J. Parton, D.S. Schimel, J.M.O. Scurlock and T.G.F. Kittel.** 1993b. Modeling the effects of climate and CO₂ changes on grassland storage of soil C. *Water, Air and Soil Pollution* **70**: 643-657.
- Owensby C.E., P.I. Coyne, J.M. Ham, L.M. Auen and A.K. Knapp.** 1993a. Biomass production in a tallgrass prairie ecosystem exposed to ambient and elevated CO₂. *Ecological Applications* **3**: 644-653.
- Owensby, C.E., L.M. Auen and P.I. Coyne.** 1993b. Biomass production in a nitrogen fertilized tall-grass prairie ecosystem exposed to ambient and elevated levels of CO₂. *Plant and Soil* **165**: 105-113.
- Owensby, C.E., J.M. Ham, A. Knapp, C.W. Rice, P.I. Coyne and L.M. Auen.** 1996. Ecosystem-level responses of tallgrass prairie to elevated CO₂. Pages 147-162. in G.W. Kock, H.A. Mooney, eds. *Carbon Dioxide and Terrestrial Ecosystems.* Academic Press Inc., San Diego, California.
- Parry, M. and R. Duncan.** (eds.) 1995. *The Economic Implications of Climate Change in Britain.* Earthscan, London. 133 p.
- Parsons, A.J.** 1988. The effects of season and management on the growth of grass swards. Pages 129-177 in M.B. Jones and A. Lazenby, eds. *The Grass Crop: the physiological basis of production.* Chapman and Hall, London.
- Parton, W.J., J.M.O. Scurlock, D.S. Ojima, T.G. Gilmanov, R.J. Scholes, D.S. Schimel, T. Kirchner, J.G. Menaut, T. Seastedt, E. Garcia Moya, A. Kamnalrut and J.I. Kinyamario.** 1993. Observations and modelling of biomass and soil organic matter dynamics for the grassland biome worldwide. *Global Biogeochemical Cycles* **7**: 785-809.
- Parton, W.J., J.M.O. Scurlock, D.S. Ojima, D.S. Schimel, D.O. Hall and SCOPEGRAM group members.** 1995. Impact of climate change on grassland production and soil carbon worldwide. *Global Change Biology* **1**: 13-22.
- Pitelka L.** 1994. Ecosystem response to elevated CO₂. *Trends in Ecology and Evolution* **9**: 204-206.
- Poorter, H.** 1993. Interspecific variation in the growth response of plants to an elevated CO₂ concentration. *Vegetatio* **104/105**: 77-97.
- Potvin, C.** 1985. Amelioration of chilling effects by CO₂ enrichment. *Physiol. Veg.* **23**: 345-352.
- Prentice, K.C., W. Cramer, S.P. Harrison, R. Leemans, R.A. Monserud and A.M. Solomon** 1992. A global biome model based on plant physiology and dominance, soil properties, and climate.

Journal of Biogeography **19**: 117-134.

Schimel, D.S., W.J. Parton, T.G.F. Kittel, D.S. Ojima and C.V.

Cole. 1990. Grassland biogeochemistry: links to atmospheric processes. *Climate Change* **17**: 13-25.

Schimel, D.S., T.G.F. Kittel, and W.J. Parton. 1991. Terrestrial biogeochemical cycles: global interactions with the atmosphere and hydrology. *Tellus* **43A**: 188-203.

Schimel, D.S., B.H. Braswell Jr., E.A. Holland, R. McKeown, D.S. Ojima, T.H. Painter, W.J. Parton and A.R. Townsend. 1994. Climatic, adaphic, and biotic controls over carbon and turnover of carbon in soils. *Global Biogeochemical Cycles* **8**: 279-293.

Semenov, M.A. and J.R. Porter. 1995. Climate variability and modelling of crop yields. *Agriculture and Forest Meteorology* **73**: 265-283.

Sionit, N., H. Hellmers and B.R. Strain. 1982. Interaction of atmospheric CO₂ enrichment and irradiance on plant growth. *Agronomy Journal* **74**: 721-725.

Smith, T.M., W.P. Cramer, R.K. Dixon, R. Leemans, R.P. Neilson and A.M. Solomon. 1993. The global terrestrial carbon cycle. *Water, Air, and Soil Pollution* **70**: 19-37.

Solomon, A.M., I.C. Prentice, R. Leemans and W.P. Cramer. 1993. The interaction of climate and land use in future terrestrial carbon storage and release. *Water, Air and Soil Pollution* **70**: 595-614.

Steffen, W.L., B.H. Walker, J.S. Ingram and G.W. Kock. 1992. Global Change and Terrestrial Ecosystems: The Operational Plan. International Geosphere-Biosphere Programme. IGBP-Report, No 21, Stockholm, 95 p.

Stewart, J. and C. Potvin. 1996. Effects of elevated CO₂ on an artificial grassland community: competition, invasion and neighbourhood growth. *Functional Ecology* **10**: 157-166.

Thornley, J.H.M., D. Fowler and M.G.R. Cannell. 1991. Terrestrial

carbon storage resulting from CO₂ and nitrogen fertilization in temperate grasslands. *Plant, Cell and Environment* **14**: 1007-1011.

Van den Pol Van Dasselaar, A. and E.A. Lantinga. 1995. Modelling the carbon cycle of grassland in the Netherlands under various management strategies and environmental conditions. *Netherland Journal of Agricultural Science* **43**: 183-194.

Van Ginkel, J.H., A. Gorissen and J.A. van Veen. 1996 Long-term decomposition of grass roots as affected by elevated atmospheric carbon dioxide. *Journal of Environmental Quality* **25**: 1122-1128.

VEMAP Members. 1995. Vegetation/ecosystem modelling and analysis project: Comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate change and CO₂ doubling. *Global Biogeochemical Cycles* **9**: 407-437.

Viner, D., M. Hulme and S.C.B. Raper. 1995. Climate change scenarios for the assessments of the climate change on regional ecosystems. *Journal of Thermal Biology* **20**: 175-190.

Watson, R.T., H. Rodhe, H. Oescheger and U. Siegenthaler. 1990. Greenhouse Gases and Aerosols. Pages 1-40 in J.T Houghton et al., eds. *Climate Change: The IPCC Scientific Assessment*. Cambridge University Press, Cambridge.

Wessman, C.A. 1992. Spatial scales and global change: Bridging the gap from plots to GCM grid scales. *Annual Review of Ecology and Systematics* **23**: 175-200.

Wolfenden, J. and P.J. Diggle. 1995. Canopy gas exchange and growth of upland pasture swards in elevated CO₂. *New Phytologist* **130**: 369-380.

Ziska, L.H., B.G. Drake and S. Chamberlain. 1990. Long-term photosynthetic response in single leaves of a C₃ and C₄ salt marsh species grown at elevated atmospheric CO₂ *in situ*. *Oecologia* **83**: 469-472.

Table 1

The effect of prolonged exposure to elevated (2 x ambient) CO₂ concentration on the productivity of grassland species

Dominant Grass Species ^z	Exposure System	Measurement	Conditions	% Change	Source
<i>Lolium perenne</i> / <i>Trifolium repens</i>	controlled environment rooms	Harvestable yield	simulated seasonal T ^y cycle	+7.2	Newton et al., 1994
<i>Lolium perenne</i>	open-top chambers	Harvestable yield	ambient T	+16 (year 1) +28 (year 2)	Jones et al., 1996
<i>Lolium perenne</i>	ventilated plastic tunnels	Harvestable yield	ambient T-N ^x ambient T+N ambient T+ 3/2C-N ambient T+ 3/2C+N	+18 +14 +16 +17	Casella et al., 1996
<i>Festuca pratensis</i>	open-top chambers inside greenhouse	Harvestable yield	ambient T ambient T+3°C	0 (year 1) 0 (year 2) +29 (year 1) +22 (year 2)	Hakala & Mela, 1996
<i>Bouteloua gracilis</i> (C ₄) <i>Pascopynum smithii</i>	phytotron	Total plant biomass	ambient T ambient T +4°C ambient T ambient T+4°C	+35 +3 +13 +23	Hunt et al., 1996
<i>Andropogon gerardii</i> (C ₄)	open-top chambers	Standing peak biomass	dry ^w 1989 norm. 1990 dry 1991 wet 1992 wet 1993	+81 +63 +31 0 +27	Owensby et al., 1996

^zC₃ photosynthetic types unless stated otherwise ^yTemperature ^xLow N supply -N, High N supply +N

^wDry, norm. and wet refer to growing season precipitation