

Sensitivity of temperate grassland species to elevated atmospheric CO₂ and the interaction with temperature and water stress

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The annual cycle of growth of many temperate grasses is limited by low temperatures during the winter and spring and water stress during the summer. Climate change, induced by increase in the concentration of greenhouse gases in the atmosphere, can affect the growth and community structure of temperate grasslands 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.

Temperate grasslands range from intensively managed monocultures of sown species to species-rich natural and semi-natural communities whose local distributions are controlled by variations in soil type and drainage. 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 temperate grasslands in the future.

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.

Key words: soil carbon, scaling, stomatal conductance, temperate grasses

Introduction

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). The atmospheric concentration of carbon dioxide (CO₂) is projected to double from pre-industrial concentrations (about 280 μmol mol⁻¹) by the middle to

late 21st Century (Carter 1996). Together, rising concentrations of CO₂ and other greenhouse gases are predicted to result in an increase in global mean surface air temperature of between 1°C and 3°C by 2100 (IPCC 1996). 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. Here, we will review the impact of predicted climate change on temperate grasses, and in particular those of the cool temperate climatic zones of Europe.

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 1996). However, in rather general terms, the predictions of greenhouse gas induced climate change in the higher latitudes of Europe suggest that (i) winter temperature increases will be greater than the annual global mean increase, (ii) summer temperature will increase by a similar or smaller amount than the global annual mean, and (iii) winter precipitation will increase while summer precipitation changes are less certain (Parry and Duncan 1995, Carter 1996).

Grasslands are a characteristic, important and widespread type of vegetation in Europe (Knapp 1979, Weissbach and Gordon 1992). They range from intensively managed, single species, sown swards to natural and semi-natural communities. Even the natural and semi-natural grasslands are maintained in this state by man's activities and those of his livestock, and their composition and structure has been determined by a combination of climatic, edaphic and anthropogenic forces. The result of this is a series of different grassland communities (Knapp 1979, Rodwell 1992). These grasslands are typically composed of a complex mixture of perennial grasses, nitrogen-fixing legumes and non-fixing dicots of different growth forms.

The complex composition of many grasslands and the possible differential responses of component species to changing climate makes the prediction of community responses very difficult. One possible simplification is that the species can be classified as different functional types (Grime 1974, Grime et al. 1988), which co-exist

to form the grassland vegetation, and it is the response of the functional type which is investigated (Körner 1993). 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 the carbon storage of grasslands have long-lived effects on the global carbon cycle (Parton et al. 1995).

The growth rate of plants is determined by a range of environmental variables and when any of these is less than optimal it imposes a limit on growth rate and may be considered to impose a stress on the plant. The term stress, when used in biology, has general connotations rather than a precise definition but each environmental variable can cause stress, such as low and high temperature stress and drought stress (Jones and Jones 1989). Temperate grasses typically experience low temperatures during winter and spring, and high temperatures and water stress during summer (Jones 1988, Parsons 1988). The impact of the changing climate on the occurrence of these extremes is of major importance in understanding how grassland vegetation will respond in a future climate.

In this paper our aim is to review the knowledge on the impact of elevated atmospheric CO₂ on temperate grassland species and the interactions with temperature and water stress. Virtually all of these species have the C₃ pathway of photosynthesis. We also briefly review the problems of scaling from the level at which most experiments are performed (single plants and small plots) to grassland ecosystems. We 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.

Direct effects of elevated CO₂

The 'business-as-usual' scenario of the IPCC projects that the atmospheric CO₂ concentration will rise from 355 $\mu\text{mol mol}^{-1}$ in 1990 to 520 $\mu\text{mol mol}^{-1}$ in 2050 and will exceed 700 $\mu\text{mol mol}^{-1}$ by 2100 (see Carter 1996). Carbon dioxide is the substrate for photosynthesis for all terrestrial higher plants, with C₃ plants growing in adequate light requiring 800–1000 $\mu\text{mol mol}^{-1}$ 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 of between 500 and 1000 $\mu\text{mol mol}^{-1}$. Reviews by Kimball (1983) and Cure and Acock (1986) of experiments done under a wide range of conditions have shown that a doubling of atmospheric CO₂ from 330 to 660 $\mu\text{mol mol}^{-1}$ increases the productivity of C₃ crops 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 $\mu\text{mol mol}^{-1}$ increase in CO₂. This means that the CO₂ enrichment since the start of the industrial revolution, from 280 to 355 $\mu\text{mol mol}^{-1}$, would be expected to have increased dry matter production of C₃ crops by 7.5–9.0%. This increase will be very difficult to detect empirically, 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 for the direct stimulation in growth by increasing CO₂, there has been some reluctance to accept that prolonged growth in elevated CO₂ stimulates yield under normal agricultural conditions (Jenkinson et al. 1994). This is largely because 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). Also, there is much evidence 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, Bowes et al. 1996). There are, however, very few observations from field experiments to confirm these views.

Recently, results for well-fertilized and irrigated *Lolium perenne* swards, grown at elevated (700 $\mu\text{mol mol}^{-1}$) and ambient atmospheric CO₂ in open-top chambers in Dublin, Ireland for a three year period, showed marked seasonal variations in the aboveground stimulation in yield (Figure 1) (Jones et al. 1996a). During the growing season the grass was managed by harvesting at frequent intervals to simulate a frequently cut sward. The largest increases in yield were recorded in the early and late growing season, with an overall stimulation in yield from the elevated CO₂ treatments of about 20% in 1992, 28% in 1993 and 42% in 1994. Furthermore, after three years of exposure to elevated CO₂, there is no evidence of down-regulation in the form of a decline in the effect of CO₂ on aboveground harvestable dry matter production (Jones et al. 1996b).

In these experiments only aboveground growth was measured. However, in experiments conducted at the FACE (Free-Air CO₂ Enrichment) facility in Zurich, Switzerland well-fertilized *Lolium perenne* and *Trifolium repens* showed differential responses of above- and be-

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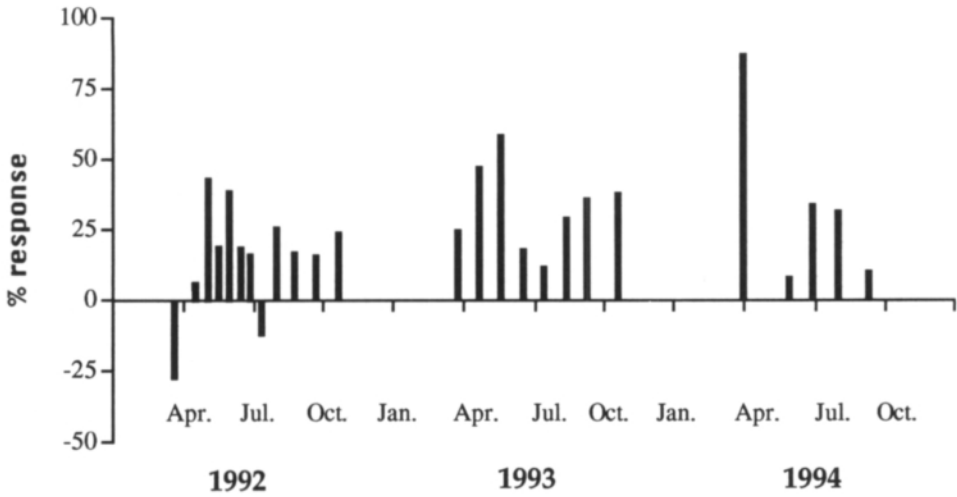


Fig. 1. The seasonal change in yield stimulation over a three year period for *Lolium perenne* swards grown in Dublin, Ireland in open-top chambers at elevated (700 $\mu\text{mol mol}^{-1}$) CO₂ compared with an ambient CO₂ treatment (from Jones et al. 1996b).

lowground biomass to elevated CO₂ (Jongen et al. 1995), with a much larger proportion of the extra dry matter produced at elevated CO₂ being allocated to the roots (Figure 2).

There are, unfortunately, few other examples of long-term exposure of temperate plant communities to elevated CO₂, but the picture emerging from these studies is of rather complex responses which depend on interactions with other climatic conditions. For example, an estuarine marsh community in Chesapeake Bay, Maryland, USA showed sustained carbon gain

(Drake and Leadley 1991) but an arctic tundra community exhibited marked down-regulation of photosynthesis after only three weeks at elevated CO₂ (Oechel et al. 1994). Furthermore, Owensby et al. (1993) showed that in a tallgrass prairie ecosystem, C₄ tallgrass species had increased production under elevated CO₂, but C₃ grass species had not. They concluded that, in water-stressed environments dominated by C₄ species, increased water-use-efficiency resulting from elevated CO₂ was responsible for increased productivity.

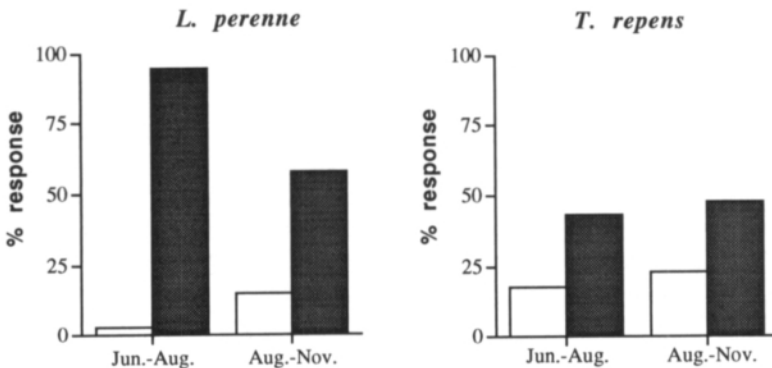


Fig. 2. The response of above-ground (□) and belowground (■) biomass production of *Lolium perenne* and *Trifolium repens* swards grown in a FACE (Free Air CO₂ Enrichment) facility near Zürich at elevated CO₂ (600 $\mu\text{mol mol}^{-1}$) compared with an ambient CO₂ treatment (data from Jongen et al. 1995).

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, Gifford 1992, Ziska et al. 1990). 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 crops grown 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.

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 temperature 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

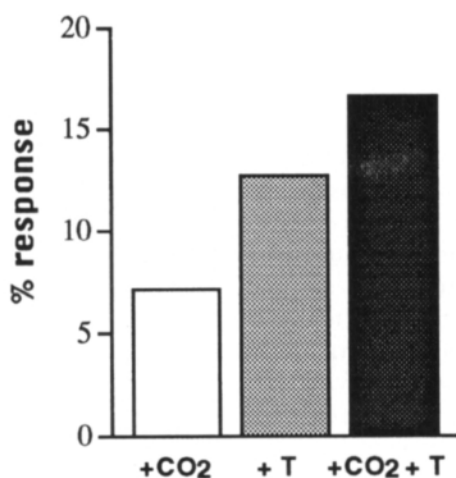


Fig. 3. The yield response of *Lolium perenne* swards grown in Solardomes at the Institute of Terrestrial Ecology, Bangor, Wales to elevated CO₂ (+CO₂) and/or elevated temperature (+T) as compared with an ambient CO₂ and ambient temperature treatment. The elevated CO₂ treatment was 700 μmol mol⁻¹, elevated temperature was ambient +3 °C (data from Ashenden pers. comm.).

plant 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 (Figure 3) (Ashenden pers. comm.). 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 curves taken from a ryegrass/white clover based pasture, found that ryegrass growth rates declined as temperature increased from 10/4 °C (day/night) to 22/16 °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. In higher latitudes there is evidence that the largest effect of rising temperatures is mediated through the longer growing season rather than increased growth rate at higher temperatures (Bergthórsson et al. 1988). Furthermore, because of the seasonal response to elevated CO₂ (mentioned above) we might expect a changing interaction between CO₂ and temperature during the season as indicated by Newton et al. (1994). The response is more complex in mixed-species grass swards where individual species show different responses to temperature (Newton et al. 1994). When the seasonal change in CO₂ effectiveness is put together with seasonal changes in temperature/CO₂ interactions and changes in species composition, an even more complex pattern of response to CO₂ becomes likely.

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 rainfall projected in some climatic scenarios would be expected to increase this effect under climate change. However, a direct effect of increasing CO₂ concentrations is to decrease stomatal conductance in many 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). With the temperate grasses the reduction in conductance varies from 43% for *Triticum aestivum* (Tuba et al. 1994) to 50% for *Avena barbata* (Jackson et al. 1994) and 51% for *L. perenne* (Jones et al. 1996a).

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. Field et al. (1995) suggest 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 above-ground 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.

Species specific responses to elevated CO₂

As already made clear, temperate grasslands are typically composed of a complex mixture of perennial grasses, nitrogen-fixing legumes and non-fixing dicots of different growth forms. Most studies so far have concentrated on the response of single plant 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.

As an example, Figure 4 shows the response of four species representative of the Lolio-Cynosuretum grassland association (Rodwell 1992) to elevated CO₂. These results show large differences between species in the sensitivity of aboveground biomass production to elevated CO₂. In addition the sensitivity alters during the growing season. The most marked difference is between *Cynosurus cristatus*, which shows no significant growth response at elevated CO₂ and *Lolium perenne*, showing an almost 150% increase in aboveground biomass at elevated CO₂ during September. Further, differential responses at elevated CO₂ were also recorded for the C:N ratio of aboveground biomass and the specific leaf area (Figure 4).

Baxter et al. (1994) have also found large differences in sensitivity to elevated CO₂ be-

tween component species for montane *Agrostis-Festuca* grassland in Snowdonia, N. Wales. They have demonstrated that, whereas whole plant dry weight of *Agrostis capillaris* and *Poa alpina* increased at elevated CO₂, there was a decrease in growth rate of *Festuca vivipera* under similar conditions. *F. vivipera* also partitioned more assimilates to roots at elevated CO₂ and the leaves showed marked discoloration and senesced faster (Baxter et al. 1994).

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.

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 leads 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 are therefore complex on a temporal scale and require more detailed studies. Future studies must address this issue by carry-

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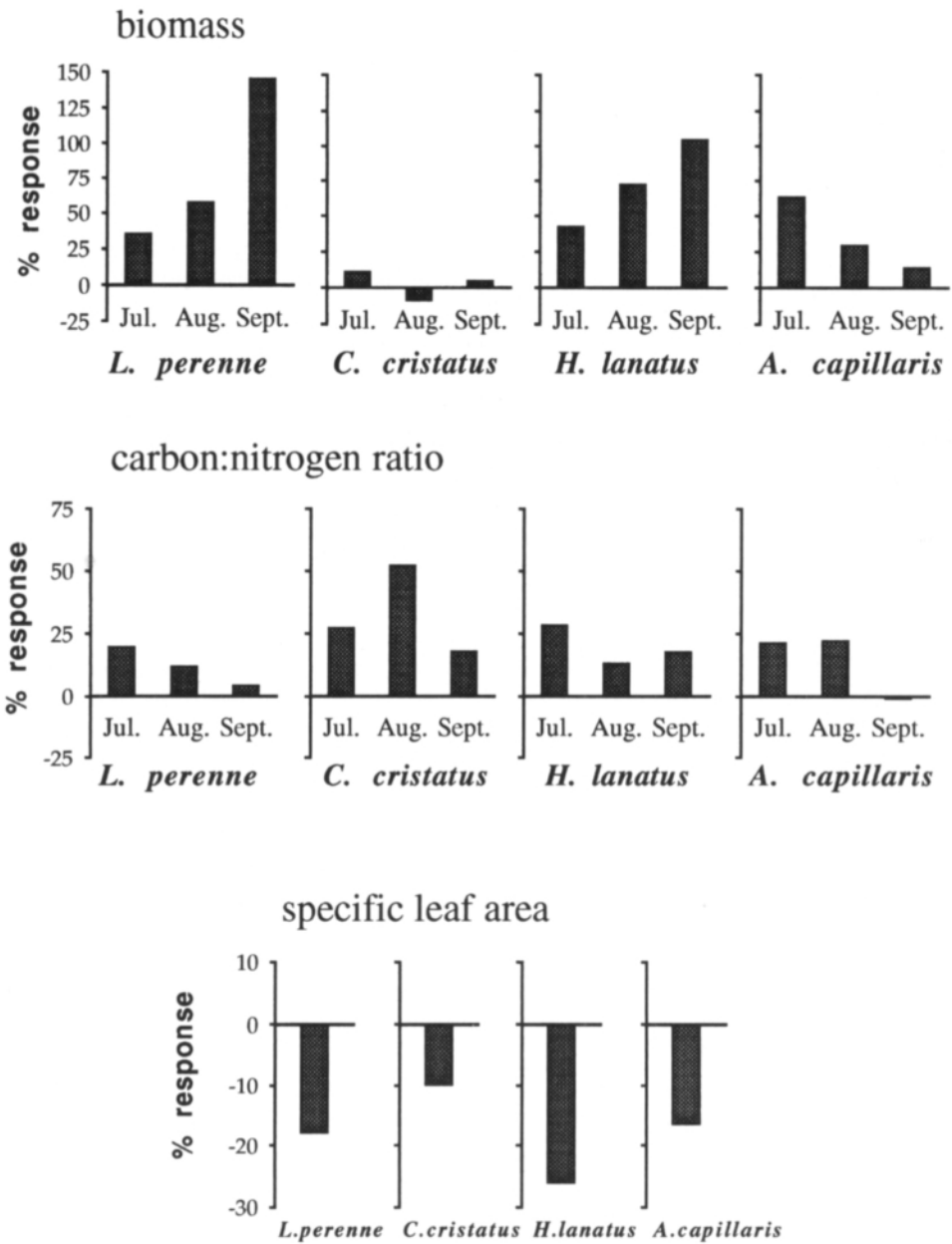


Fig. 4. The response of biomass production, carbon to nitrogen (C:N) ratio and specific leaf area of four grass species from the Lolio-Cynosuretum association exposed to elevated (700 $\mu\text{mol mol}^{-1}$) CO₂ compared with an ambient CO₂ treatment. Plants were grown as monocultures in pots in open-top chambers (from Jongen 1996).

ing out experiments on complete grassland ecosystems (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. It has been hypothesised that nitrogen fixers may benefit more from elevated CO₂ than non-fixers, and there is some evidence to support this (Stewart and Potvin 1996).

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 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. Many of the results reported above have

been obtained using either single plants or small plots which have been grown for periods of, most frequently, a few weeks and, very rarely, as much as 2–3 years.

In order to understand how large geographical areas, such as northern Europe, 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 (see above). 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 consist of 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).

Predicting the response of European temperate grasslands to climate change on a spatial scale of landscape and region presents particularly difficult problems because of the marked patchiness of different grassland ecosystems (Knapp 1979). On a temporal scale, the difficulties are possibly greater, because most experimental work on which the predictions are based has been done over very short time periods. However, mechanistic models of vegetation growth and carbon fluxes, which can be run to simulate changes over decades and centuries, provide a valuable tool to predict long term changes.

To illustrate, the Hurley-Pasture model of

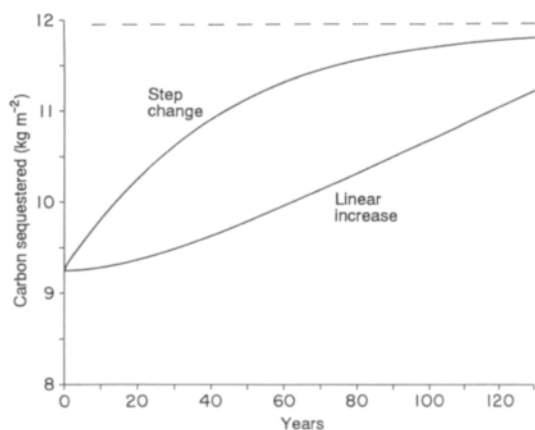


Fig. 5. Carbon sequestration in grassland soils estimated using the Hurley Pasture Model. The sequestered carbon is plotted against time for two scenarios. In the first, a step change in the atmospheric CO₂ concentration from 280 to 350 $\mu\text{mol mol}^{-1}$; in the second, it is assumed that the atmospheric CO₂ concentration increases linearly from 280 to 350 $\mu\text{mol mol}^{-1}$ over 130 years. The dashed line indicates the asymptote for the step change (from Thornley et al. 1991).

Thornley and Verberne (1989) has been used by Thornley et al. (1991) to estimate the terrestrial carbon storage resulting from an increase in CO₂ concentration and temperature in temperate grasslands. The results suggest that the CO₂ fertilization that has occurred since the industrial revolution, and which will continue in the future, has resulted in increased carbon sequestration in soils and may contribute appreciably to the so-called missing carbon sink (Figure 5). However, a rise in temperature tends to act in the reverse direction, and it may be that increasing temperature will counteract the CO₂ effect. Similar model predictions have been made by Parton et al. (1995) using the CENTURY model. The outcome of these modelling exercises are further examples of the important interactions between rising CO₂ and increasing temperature as climate change occurs.

Conclusions

Temperate grassland productivity shows a significant, but variable, positive response to increasing ambient CO₂ concentrations. There appears to be a larger response of belowground growth compared to aboveground and if this is sustained it suggests that grassland soils will become an increasing sink for carbon in the future, unless higher temperatures counteract the effect. There are important interactions between rising CO₂ and increased temperatures which in some cases are not simply additive. If the temperature increase reaches 3°C globally, as projected in some scenarios, it is likely that the temperature effects will exceed the CO₂ effects in temperate grasslands (Parton et al. 1995). However, elevated CO₂ has important differential effects on the component species of grasslands and as a consequence we are likely to see significant changes in sward composition. Similar conclusions have been reached by Wolfenden and Diggle (1995) working with upland grassland vegetation in Britain.

In order to predict responses of grasslands to climate change over Europe there is a need to scale up from the experimental work which has been done at the single plant and small plot scale. There are considerable difficulties associated with this scaling and preliminary analysis shows that some effects seen at the plot scale, such as a reduction in evapotranspiration at elevated CO₂, will not be seen or will be reduced in magnitude at the landscape and regional scale. Modelling is the most likely solution to many of these difficulties, as experiments are impossible on the large spatial and temporal scales required to answer many of the questions about the consequences of climate change for grasslands.

Acknowledgements. Trevor Ashenden and John Thornley are thanked for kindly providing some of the results presented here.

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SELOSTUS

Kohonneen hiilidioksidipitoisuuden, lämpötilan ja kuivuuden vaikutus nurmikasveihin

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Monien lauhkean vyöhykkeen nurmikasvien kasvua rajoittavat talvella ja keväällä kylmyys ja kesällä kuivuus. Ilmaston muutos, jonka aiheuttaa ilmakehän kasvihuonekaasujen pitoisuuden kasvu, voi vaikuttaa suoraan ja epäsuorasti nurmien kasvuun ja niiden lajikoostumukseen. Ilmakehän hiilidioksidipitoisuuden muutos vaikuttaa suoraan kasvien kasvuun. Toisaalta ilmaston lämpeneminen ja sademäärän muutokset vaikuttavat epäsuorasti. On todennäköistä, että hiilidioksidipitoisuuden nousu vaikuttaa enemmän matalilla leveysasteilla kuin korkeammilla leveysasteilla, missä lämpötila usein rajoittaa kasvua. Lämpötilan ja veden saannin muutosten yhteisvaikutukset ovat kui-

tenkin monimutkaisia.

Lauhkean kasvuvyöhykkeen nurmet vaihtelevat voimaperäisesti viljellyistä monokulttuureista monilajisiin kasvustoihin, joiden paikalliseen esiintymiseen vaikuttavat maalaji ja maan kuivatusolosuhteet. Kohonnut hiilidioksidipitoisuus, lämpötila ja kuivuus voivat vaikuttaa hyvin eri tavoin eri nurmikasveihin, mikä todennäköisesti tulee muuttamaan suuresti nurmien lajikoostumusta tulevaisuudessa.

Kohonnut hiilidioksidipitoisuus saattaa pitkällä aikavälillä merkittävästi lisätä maahan varastoituneen hiilen määrää. Lämpötilan kohoaminen voi kuitenkin kumota tätä ilmiötä.