

Temperate grasslands and global atmospheric change: a review

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Summary

Recent reviews confirm and extend previous observations that elevated carbon dioxide (CO₂) concentrations stimulate photosynthesis, leading to increased plant productivity. Elevated CO₂ concentrations tend to reduce the sensitivity of grassland ecosystems to low levels of precipitation but induce progressive nitrogen (N) limitations on plant growth which can be alleviated by supplying a significant external input of N in the form of mineral fertilizer or through the increased use of N-fixing legumes. Other nutrients, such as phosphorus, can act as the main limiting factor restricting the growth response in legumes to atmospheric CO₂ concentration. The botanical composition of temperate grasslands is affected by the rise in atmospheric CO₂ concentration, possibly through a decline in the relative abundance of grasses. Elevated CO₂ concentration will also alter the feeding value of herbage to grazers both in terms of fine-scale (for example, crude protein concentration and C:N ratio) and coarse-scale (legumes vs. grasses and C₃- vs. C₄-species) changes. The management guidelines of grasslands will need to be adapted to global atmospheric and climatic changes and to increased variability in climate.

Keywords: atmospheric CO₂ concentration, climate change, carbon sequestration, legume, productivity, herbage quality

Introduction

Grassland covers about 0.70 of the world's agricultural area. Rising atmospheric carbon dioxide (CO₂) concentrations are likely to affect several important

aspects of grasslands, such as the quantity and quality of the herbage produced, plant species composition, soil fertility and the potential to sequester carbon (C) in the soil, to mitigate the rise in atmospheric CO₂ concentrations. Grasslands and their livestock production systems are extremely diverse. They occur over a large range of climatic and soil conditions from browse rangelands and very extensive pastoral systems where domestic herbivores graze, to intensive systems based on forage and grain crops, where livestock are mostly kept indoors.

Atmospheric CO₂ rise and C sequestration by grassland ecosystems

Anthropogenic combustion of fossil fuels has caused mean concentrations of CO₂ in the atmosphere to reach and exceed 380 µmol mol⁻¹, a level that is about 0.32 greater than that in pre-industrial times (Keeling and Whorf, 2005). Because CO₂ absorbs long-wave energy, it warms the Earth's atmosphere. Predictions of future atmospheric CO₂ concentration in the year 2100 range between 540 and 970 µmol mol⁻¹ (Houghton *et al.*, 2001). Additional inputs of C to the atmosphere will produce further warming (Houghton *et al.*, 2001) and may contribute to the occurrence of more intense, more frequent and longer spells of high temperatures (Meehl and Tebaldi, 2004).

The current increase in atmospheric CO₂ concentrations has, however, proved to be less marked than was previously anticipated from CO₂ emission records and oceanic uptake, which has led to the existence of a C 'sink' in continental ecosystems being postulated. The demonstration of this sink has made it possible to envisage its use and development to sequester C and thus slow down the current rise in the effects of greenhouse gases. The Marrakesh Accords allow biospheric C sinks and sources to be included in attempts to meet emission reduction targets for the first commitment period of the Kyoto protocol. Signatory Annex I countries may take into account any sequestration of C induced by 'additional human activities'. These activities

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principally target the storage of C in plant biomass and the soil.

Accumulation of C in grassland ecosystems occurs mostly below-ground and changes in soil organic C stocks may result both in land-use changes (e.g. conversion of arable land to grassland) and in grassland management (Soussana *et al.*, 2004). The soil organic-C sequestration potential is estimated to be 0.01–0.3 Gt C year⁻¹ on the 3.7 billion ha of permanent pasture worldwide (Lal, 2004). Thus soil organic-C sequestration by the world's permanent pastures could potentially offset proportionately up to 0.04 of the global emissions of greenhouse gases. In Europe, Vleeshouwers and Verhagen (2002), further quoted by Janssens *et al.* (2003), applied a semi-empirical model of land use-induced soil-C disturbances to the European continent, and inferred a C sink of 101 Gt C year⁻¹ over grasslands (0.52 t C ha⁻¹ year⁻¹) with uncertainties greater than the mean. Using the eddy covariance method, the average net C storage was estimated at -0.10 kg C m⁻² year⁻¹ (range -0.40 to +0.11) averaged over nine European grassland sites. However, part of this C sink was offset by the emission of non-CO₂ greenhouse gases (Soussana *et al.*, 2007).

Impacts of elevated CO₂ on photosynthesis and growth in grasslands

Recent reviews confirm and extend previous observations that elevated CO₂ concentrations stimulate photosynthesis, leading to increased plant productivity and modified water and nutrient cycles (e.g. Kimball *et al.*, 2002; Nowak *et al.*, 2004). Experiments under optimal conditions show that doubling the atmospheric CO₂ concentration increases leaf photosynthesis by 0.30–0.50 in C₃-plant species and by 0.10–0.25 in C₄-species, despite a small but significant down-regulation of leaf photosynthesis by elevated atmospheric CO₂ concentrations at some sites (Ellsworth *et al.*, 2004; Ainsworth and Long, 2005). Photosynthesis in a sward canopy has also been found to increase by 0.30 (Casella and Soussana, 1997; Aeschlimann *et al.*, 2005).

The stimulatory effect of elevated atmospheric CO₂ concentrations on above-ground grassland ecosystem production was found to average about 0.17 in two reviews of the subject (Campbell *et al.*, 2000; Ainsworth and Long, 2005), although responses for particular systems and seasonal conditions can vary widely. This value is about half that expected from consideration of the photosynthetic response to the elevation of atmospheric CO₂ concentrations alone. Under Free Air CO₂ Enrichment (FACE) fumigation, grassland production was increased by 0.15–0.20 (e.g. Hebeisen *et al.*, 1997; Ainsworth *et al.*, 2003; Nowak *et al.*, 2004). However, the long-term response to elevated atmospheric CO₂

concentrations may differ substantially from the short-term response. In the Swiss FACE experiment, the yield response of *Lolium perenne* to elevated atmospheric CO₂ concentration increased from 0.07 to 0.32 over a number of years under high applications of nitrogen (N) fertilizer. This increase was probably due to removing N limitation to plant growth through the application of N fertilizer (Lüscher and Aeschlimann, 2006). These results demonstrate that the immediate response of an ecosystem to a step increase in atmospheric CO₂ concentration at the start of the experiment may not represent an appropriate base on which to predict the response of a grassland ecosystem to an ongoing slow increase in the concentration of CO₂ in the atmosphere.

Interactions of elevated CO₂ with abiotic factors

As an increase in temperature enhances photorespiration in C₃-species (Long, 1991), the positive effects of atmospheric CO₂ enrichment on photosynthetic productivity are usually greater when temperature rises. The long-term ratio of dark respiration: photosynthesis in shoots was found to be approximately constant with respect to air temperature and CO₂ concentration (Gifford, 1995; Casella and Soussana, 1997). Although stomatal conductance is decreased under elevated atmospheric CO₂ concentration, the ratio of the intercellular CO₂ concentration: ambient CO₂ concentration is usually not modified and stomata do not appear to limit photosynthesis more in elevated compared to ambient CO₂ concentrations (Drake *et al.*, 1997).

The relative enhancement in growth due to elevated atmospheric CO₂ concentrations might be greater under drought conditions than in wet soil conditions because photosynthesis would be operating in a more CO₂-sensitive region of the response curve of growth to atmospheric CO₂ concentrations. In the absence of a water deficit, the C₄-photosynthetic pathway is believed to be CO₂-saturated at current atmospheric CO₂ concentrations. However, as a result of stomatal closure, it can become CO₂-limited under drought. An increased productivity from increased water-use efficiency is the major response to elevated atmospheric CO₂ concentrations in C₃- or C₄-crops that are exposed frequently to water stress (Casella and Soussana, 1997; Drake *et al.*, 1997; Aranjuelo *et al.*, 2005). Moreover, elevated atmospheric CO₂ concentrations can reduce depletion in soil moisture content in different natural and semi-natural temperate and Mediterranean grasslands (Morgan *et al.*, 2004). These results support a general view that elevated atmospheric CO₂ concentration reduces the sensitivity to low precipitation in grassland ecosystems (Volk *et al.*, 2000; Morgan *et al.*, 2004).

Interactions of elevated CO₂ with soil nutrients

Over a number of studies it has been found that plants grown in conditions of high nutrient supply respond more strongly to elevated atmospheric CO₂ concentrations than nutrient-stressed plants (Poorter, 1998). FACE experiments confirm that high N soil contents increase the relative response to elevated atmospheric CO₂ concentrations (Nowak *et al.*, 2004). With *L. perenne*, in the Swiss FACE experiment, the response in above-ground dry matter (DM) yield to elevated atmospheric CO₂ concentrations increased from being not significant to a significant positive proportional response of 0.17 (range 0.07–0.32) when the rate of application of N fertilizer was increased from 14 to 56 g N m⁻² year⁻¹ (Schneider *et al.*, 2004; Lüscher and Aeschlimann, 2006). Under elevated atmospheric CO₂ concentrations, *L. perenne* showed a significant reduction in the concentration of shoot N (Soussana *et al.*, 1996; Zanetti *et al.*, 1997). With a non-limiting N fertilizer supply, the concentration of leaf N (N, mg g⁻¹ DM) declined with the DM yield of shoots (DM, g) according to highly significant power models in ambient ($n = 49$ DM^{-0.38}) and in elevated ($n = 53$ DM^{-0.52}) atmospheric CO₂ concentrations. The difference between both regressions was significant and indicated a lower critical concentration of leaf N in elevated than in ambient atmospheric CO₂ concentrations for high, but not for low, values of shoot biomass. With a sub-optimal supply of N fertilizer, the nitrogen nutrition index of the grass sward, calculated as the ratio of the actual: critical leaf N concentrations, was significantly lowered under elevated atmospheric CO₂ concentrations (Soussana *et al.*, 1996; Zanetti *et al.*, 1997). This indicates a lower availability of inorganic N for the grass plants under elevated atmospheric CO₂ concentrations, which was also apparent from the significant declines in the annual N yield of the grass sward and in the nitrate leaching during winter (Soussana *et al.*, 1996).

Over the 10 years of fumigation in the Swiss FACE experiment, the most important change was the increasing response in the annual N yield to elevated atmospheric CO₂ concentrations (proportionately from -0.13 to +0.29) in monocultures of *L. perenne* in the high N-fertilizer treatment but not in the low N-fertilizer treatment (Daepf *et al.*, 2000; Schneider *et al.*, 2004). Changes observed in the high N-fertilized swards of *L. perenne* may be summarized as decreasing N limitation (Lüscher *et al.*, 2006) in reference to the concept of progressive N limitation in natural systems (Luo *et al.*, 2004). The CO₂-induced N limitation was alleviated in the high N-fertilizer treatment only by supplying a significant external input of N. These results confirm

that N is a major limiting factor in the response of grasslands to elevated atmospheric CO₂ concentrations.

When other nutrients are not strongly limiting, a decline in N availability may be prevented by an increase in biological N₂-fixation under elevated atmospheric CO₂ concentrations (Gifford, 1994). Indeed, in fertile grasslands, legumes benefit more from elevated atmospheric CO₂ concentrations than non-fixing species (Hebeisen *et al.*, 1997; Lüscher *et al.*, 1998) resulting in significant increases in symbiotic N₂ fixation (Soussana and Hartwig, 1996; Zanetti *et al.*, 1997). An experiment with N₂-fixing and non-fixing alfalfa (*Medicago sativa*) showed that the uptake of mineral N from the soil did not increase under elevated atmospheric CO₂ concentrations (Lüscher *et al.*, 2000). The additionally harvested N under high atmospheric CO₂ concentrations derived solely from increased activity of symbiotic N₂ fixation. This is in line with the results for *Trifolium repens* in the Swiss FACE experiment (Zanetti *et al.*, 1996, 1997) and from an experiment conducted with micro-swards (Soussana and Hartwig, 1996). Nevertheless, other nutrients, such as phosphorus, may act as the main limiting factor restricting growth and responses in yield in legumes to atmospheric CO₂ concentrations. This has been demonstrated both in calcareous grasslands (Stöcklin *et al.*, 1998) and under controlled environmental conditions (Almeida *et al.*, 2000). N₂ fixation does, however, not limit the growth of *T. repens* experiencing P deficiency (Hogh-Jensen *et al.*, 2002), as a low P status (below a P content in soil of 27 mg g⁻¹) induces changes in the relative growth of roots, nodules and shoots rather than changes in the rates of resource uptake per unit mass or area of these organs.

Elevated CO₂-induced changes in C and N cycling below-ground

Plants grown under elevated atmospheric CO₂ concentrations generally increase the partitioning of photosynthates to roots which increases the capacity and/or activity of below-ground C sinks. In monocultures of *L. perenne* under elevated atmospheric CO₂ concentrations, the imbalance between a strongly increased C uptake in the shoot zone and a relatively reduced N uptake from the soil leads to an increased partitioning (proportionately up to a 1.08 increase) in growth to the root system (Soussana *et al.*, 1996; Hebeisen *et al.*, 1997; Suter *et al.*, 2002). This was demonstrated from the strong negative relationship between the N concentration in the root fraction and in the shoots (Soussana *et al.*, 1996; Daepf *et al.*, 2001). The ratio between leaf area index: total plant (root and shoot) biomass varied with the N supply, the atmospheric CO₂ concentration and the temperature (Calvet and Soussana, 2001).

Soil organic-C stocks result from the balance between inputs and decomposition of soil organic matter. An increased allocation below-ground may lead to an increment in soil organic-C content. In a mesocosm experiment with monocultures of *L. perenne*, continuous CO₂-exchange measurements indicated an increased C storage below-ground (Casella and Soussana, 1997). The same trend was obtained in the Swiss FACE experiment but the corresponding difference was not statistically significant (Aeschlimann *et al.*, 2005; Xie *et al.*, 2005). The supplemental C input at elevated atmospheric CO₂ concentrations was mainly due to the less protected soil particles >50 µm in size (Loiseau and Soussana, 1999a; Allard *et al.*, 2004; Xie *et al.*, 2005). This may imply a greater sink capacity for atmospheric CO₂ but could also be accompanied by a more rapid turnover of the older, finer and more recalcitrant pools (Cardon *et al.*, 2001). The increase in C storage in the particulate soil organic matter with atmospheric CO₂ concentration was found to be non-linear and declining at above ambient CO₂ concentrations, which may indicate that the soil C sink in grasslands will become saturated in a high atmospheric CO₂ concentration world (Gill *et al.*, 2002). Due to the large variability in soil C content, significant differences in total soil organic-C content are very hard to detect in individual studies and are usually not significant (Loiseau and Soussana, 1999a; Gill *et al.*, 2002).

Studies (Newton *et al.*, 1996; Cardon *et al.*, 2001) have suggested a higher C turnover rather than a substantial net increase in soil C under elevated atmospheric CO₂ concentrations. In a ¹³C labelling experiment, the ¹³C isotopic mass balance method was used to calculate the C turnover in the stubble and roots and in the soil particulate organic matter above 200 µ. With monocultures of *L. perenne*, raising atmospheric CO₂ concentrations stimulated the turnover of organic C in the roots, stubble and particulate soil organic matter (OM) fractions at high but not at low N-fertilizer supply (Loiseau and Soussana, 1999b).

In the same study, the soil-N cycle was investigated using ¹⁵N-labelling. Elevated atmospheric CO₂ concentrations reduced to a greater extent the harvested N derived from soil than that derived from fertilizer, and significantly increased the recovery of fertilizer-N in the roots and in the particulate soil organic matter fractions (Loiseau and Soussana, 1999b). The increase in the immobilization of fertilizer-N in the soil fractions was associated with a decline in fertilizer-N uptake by the grass sward, which supported the hypothesis of a negative feedback of elevated atmospheric CO₂ concentrations on the N yield and uptake of swards. Raising atmospheric CO₂ concentrations had little effect on nitrifying and denitrifying enzyme activity in four European grasslands (Barnard *et al.*, 2004). Nevertheless,

an increased greenhouse gas emissions of N₂O was found in response to elevated CO₂ (Baggs *et al.*, 2003) in the Swiss FACE experiment, which may exacerbate the forcing effect of elevated atmospheric CO₂ concentrations on the global climate.

As a result of these interactions with soil processes, experiments which impose sudden changes in temperature or atmospheric CO₂ concentrations, and which last only few years, are unlikely to predict the magnitude of the long-term responses in crop productivity, soil nutrients (Thornley and Cannell, 2000) and C sequestration. This may imply that the actual impact of elevated atmospheric CO₂ concentrations on yields in farmers' fields could be less than earlier estimates which did not take into account limitations in availability of nutrients and plant-soil interactions.

Plant species dynamics and diversity

Much of the world's grasslands are characterized by pastures that are botanically diverse. In a field experiment with varying levels of plant species diversity, the biomass accumulation in response to elevated levels of atmospheric CO₂ concentrations was greater in species-rich than in species-poor assemblages (Reich *et al.*, 2001). In some studies grassland communities grown in elevated CO₂ concentrations have displayed higher plant species diversity than controls under ambient CO₂ concentrations (Teyssonneire *et al.*, 2002a) but this was not confirmed by Zavaleta *et al.* (2003).

The relative growth responses to elevated atmospheric CO₂ concentrations obtained for isolated plants cannot be used to predict the response in multi-species mixtures but the CO₂ response of monocultures may be a better predictor (Poorter and Navas, 2003). In the Swiss FACE experiment, the inter-specific differences in the response to elevated atmospheric CO₂ concentrations resulted in a consistent and significant increase in the proportion of *T. repens* in the binary mixtures at both levels of N supply (Lüscher *et al.*, 2005; Lüscher and Aeschlimann, 2006). Similarly, in more complex mixtures containing other grass, legume and non-legume dicotyledonous species, the proportion of legumes was significantly higher at elevated atmospheric CO₂ concentrations (Lüscher *et al.*, 1996). This effect was also observed in diverse permanent plant communities in FACE and mini-FACE experiments (Teyssonneire *et al.*, 2002a; Harmens *et al.*, 2004; Ross *et al.*, 2004). In a mini-FACE experiment, elevated atmospheric CO₂ concentrations significantly increased the proportion of dicotyledonous species (forbs and legumes) and reduced that of the monocotyledons (grasses). Management differentiated this response as elevated atmospheric CO₂ concentrations increased the proportion of forbs when the plants were defoliated

infrequently and of legumes when frequently defoliated (Teyssonneyre *et al.*, 2002a).

However, not all grass species responded negatively to high atmospheric CO₂ concentrations. In subsequent studies of between-species competition among three grasses, it was observed that grasses that capture relatively more light per unit leaf area in mixtures than their competitors become increasingly dominant under elevated atmospheric CO₂ concentrations (Teyssonneyre *et al.*, 2002b). Moreover, a high N-use efficiency can confer a competitive advantage under elevated atmospheric CO₂ concentrations to mixed grasses (Soussana *et al.*, 2005). Such experiments show that the diversity and botanical composition of temperate grasslands is likely to be affected by the current rise in atmospheric CO₂ concentrations, and that guidelines on grassland management will need to be adapted to a future world of high atmospheric CO₂ concentrations.

Changes in species composition are also an important mechanism altering production of herbage and its value for grazing livestock in drier rangelands with the invasion of woody shrubs and in warm humid climates with the invasion of C₄-species. Proliferation of woody plant species in grasslands and savannas in recent history has been widely reported around the world. The causes for this shift in vegetation are controversial and centre around changes in livestock grazing, fire, climate and atmospheric CO₂ concentrations (Hibbard *et al.*, 2001). Increased atmospheric CO₂ concentrations are predicted to increase C₃-species over C₄-species but the projected increase in temperature will favour C₄-species. Results from White *et al.* (2001) indicate that competition is highly important in limiting the invasion of C₃-grasslands by C₄-species.

Forage quality

To meet the maintenance requirements of livestock for crude protein implies that the concentration of crude protein in herbage from pastures should be 70–80 g kg⁻¹ DM and to meet the requirements of the highest producing dairy cows it should be up to 240 g kg⁻¹ DM. In conditions of very low soil N status, the reduction in crude protein concentrations of herbage under elevated atmospheric CO₂ concentrations may put a system into a sub-maintenance level for animal performance. C₄-grasses are a less nutritious food resource than C₃-grasses both in terms of a reduced crude protein concentration of herbage and in higher C:N ratios. Elevated atmospheric CO₂ concentrations will likely alter food quality to grazers both in terms of fine-scale (crude protein concentration and C:N ratio) and coarse-scale (C₃-species vs. C₄-species) changes (Ehleringer *et al.*, 2002). However, when legume development is not restricted by adverse factors (such as low

soil phosphorus content and low soil moisture content), an increase in the proportion of legumes in swards may compensate for the decline in the crude protein concentration of non-fixing plant species (Hartwig *et al.*, 2000; Allard *et al.*, 2003; Picon-Cochard *et al.*, 2004).

Interactions between elevated CO₂ and climate change

Experiments with elevated atmospheric CO₂ concentrations and increases in temperature and precipitation have shown increased net primary production with strong multi-factor interactions, including changes in species distribution and litter composition (e.g. Shaw *et al.*, 2002; Zavaleta *et al.*, 2003; Henry *et al.*, 2005). In a Mediterranean annual grassland, the largest increase in diversity of plant species was found in response to the combination of increased temperatures, elevated atmospheric CO₂ concentrations and increased precipitation (Zavaleta *et al.*, 2003). Increases in climatic extremes may suppress the dominance of C₃-species and promote C₄-species, including weeds, due to faster migration rates, greater production of seeds, better ability to colonize many habitats and rapid maturity (White *et al.*, 2001). Combined with elevated atmospheric CO₂ concentrations, climate change is, therefore, likely to cause profound changes in the diversity, productivity and stability of grassland ecosystems.

Conclusions

There are three critical issues for the fate of temperate grasslands in a high atmospheric CO₂ concentration world with an altered climate. First, the production and the quality of herbage will be affected by climatic variation and by the frequency of extreme climatic events (Porter and Semenov, 2005). To some extent, elevated atmospheric CO₂ concentrations will reduce the vulnerability of pasture and forage production to climatic variation and climatic change. However, for a number of sub-optimal environmental and soil conditions, the increased resource-use efficiency of plant growth under high atmospheric CO₂ concentrations will not prevent a decline in productivity and quality.

Second, global environmental change, e.g. rising temperatures, changing precipitation and rising atmospheric CO₂ concentrations, will become a major driver of changes in plant diversity and loss in the 21st century. A recent modelling study of 1350 European plant species predicted that half of these species will become classified as 'vulnerable' or 'endangered' by the year 2080 due to rising temperatures and changes in precipitation (Thuiller *et al.*, 2005). Although such model predictions are highly uncertain, experiments do support the concept of rapid changes in species

composition and diversity under elevated atmospheric CO₂ concentrations with complex interactions with other drivers of global change.

Third, the net C exchange by terrestrial ecosystems will be affected by projected global warming, and by the increased incidence of extreme climatic events, such as heat-waves and droughts (Ciais *et al.*, 2005). The conservation of grassland C stocks and the role of grasslands as C sinks will become increasingly difficult to preserve in an altered climate with a high temporal variability and under high atmospheric CO₂ concentrations which may saturate the C sink in soils.

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