Climate Change Risks to Pastoral Production Systems

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Summary Final Report

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Programme Title: Climate change risks to pastoral production systems

Goal: To determine whether additional evidence supports the initial observation that New Zealand's pastoral production systems may have a substantially reduced ability to cope with environmental stress under elevated CO_2 conditions likely to be encountered with global change.

Context of the project:

An initial study at New Zealand's only long-term elevated CO_2 site, in collaboration with AgResearch, has shown that ryegrass suffers substantially increased levels of stress compared with non-elevated CO_2 conditions, in the mature phase of the growth cycle under slower-growing autumn conditions (Guo et al. 2006). That is, higher stress levels exist when demand for photosynthetic products is low. This has raised a question about how New Zealand's future pastoral production systems may behave when already under additional environmental stress from other factors associated with climate change – particularly drought and temperature extremes.

Approach:

To help better understand the issue of elevated CO_2-induced stress, we analysed data available from an initial study on three grass species under two nutrient treatments at an elevated CO_2 site in the USA. It was thought the lower nutrient availability in one treatment might lead to a smaller total demand for photosynthetic products, and thus to initiation of CO_2-induced stress even when plants were actively growing.

Outcomes:

We found that:
- Long-term exposure to elevated CO_2 appears to confer no net long-term advantage to overall photosynthetic performance at the US site under low nutrient conditions. This is consistent with other results from the site, and also with New Zealand studies under elevated CO_2 but with considerably higher nutrient availability.
- Grasses adapted to lower nutrient environments under elevated CO_2 do not suffer stress levels beyond those under either non-elevated CO_2 conditions or higher nutrient conditions, when actively growing with the demand for photosynthetic products being relatively high (the conditions in the US study).
- Overall, taking also the previous New Zealand study (Guo et al. 2006) into account, it appears enhanced stress due to elevated CO_2 is likely to be present only towards the end of a growth cycle, in the mature growth phase. It is thus not expected to be a factor significantly limiting future pastoral production, because New Zealand pastures are not

expected to spend much time in the mature growth phase (i.e. they generally will be grazed at or before that point).

Recommendations

Future work, which could be completed as part of a PhD or postdoctoral project, should concentrate on determining:

- At what stage in the growth cycle does elevated CO_2-induced stress become apparent – in particular, could it affect production of silage or hay crops that develop further into the mature phase than encountered in a normal grazing situation?

- Is the capacity of grasses to tolerate normal environmental stress during the active phase of the growth cycle affected by the presence of elevated CO_2? Could reduced demand for photosynthetic products during environmental stress initiate additional elevated CO_2-induced stress, and result in damage to the plant's photosynthetic system?

1.   Introduction

An initial study at New Zealand's only long-term elevated CO_2 site, in collaboration with AgResearch, has shown that ryegrass appears to suffer substantially enhanced levels of stress compared with normal conditions when growth slows in autumn (Guo et al. 2006). Stated more precisely, enhanced stress levels appear when demand for photosynthetic products – i.e. photosynthetic sink demand – becomes small as the ryegrass enters the mature part of the growth cycle following an earlier grazing event. This goes strongly against the prevailing paradigm that elevated CO_2 levels encountered under global change are likely to be beneficial – or at least neutral – for plant growth. The New Zealand results also suggest higher stress levels could occur if nutrient availability is limited, as this would also be expected to lower total sink demand.

The finding that ryegrass, and quite possibly other C_3 grasses, under elevated CO_2 conditions may suffer from stress more when photosynthetic sink demand is low raises a significant question about the future viability of New Zealand's traditional pastoral production systems. Under expected future global change – especially in the presence of more severe drought and temperature extremes – it seems possible the (photoprotective) capacity of ryegrass to cope with stress may be compromised. Of equal concern is that current evidence suggests (Guo et al. 2006) that ryegrass may possess no genetic encoding to react to rising CO_2 levels as a (photoprotective) threat, thus limiting opportunities for adaptation, or amelioration of the impacts of elevated CO_2 through plant breeding.

In this report we examine photosynthetic performance and indicators of stress levels in three grass species at an elevated CO_2 site in the USA. Evidence is sought to help better understand the issue of elevated CO_2-induced stress, and to further establish whether it is likely to be important in relation to New Zealand pastoral production systems.

The work was carried out by Jianmin Guo and Craig Trotter, Landcare Research for the Ministry of Agriculture and Forestry between February and June 2008.

2.   Objectives

The goal of the project was to:

- Determine whether additional evidence supports the initial observation that New Zealand's pastoral production systems may have a substantially reduced ability to cope with environmental stress under elevated CO_2 conditions likely to be encountered with global change.

The objective of the project was to:

- Determine whether extra evidence exists to support the preliminary conclusion (Guo et al. 2006) that elevated CO_2 encountered under future global change may in some circumstances place grasses under additional stress, by:
- Completing plant biochemical analysis on existing dried leaf samples for three grass species grown under elevated CO_2 and control conditions
- Processing, analysing, and contrasting existing plant photosynthetic and fluorescence field data collected for three grass species under elevated CO_2 and control conditions
- Completing a brief report summarising the findings and data for the project; providing a comparison of results with the findings in Guo et al. (2006); and if consistent evidence of enhanced stress levels under elevated CO_2 is found, develop recommendations for future work.

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3. Methods

Abbreviations:

A	CO_2 fixation rate
A_{max}	photosynthetic capacity
$\Delta F/F_m'$	PSII photochemical efficiency
F_v/F_m	maximum PSII photochemical efficiency
NPQ	non-photochemical quenching
SLW	specific leaf weight

3.1 Study site, FACE environment, and experimental treatments

Data for this investigation were available for a study completed on three grass species (*Agropyron repens, Koeleria cristata*, and *Poa pratensis*) at the BioCON free-air elevated CO_2 site, University of Minnesota, Minnesota, USA. Details of site conditions and experimental design may be found in Lee et al. (2001). Briefly, the experiment is a split-plot arrangement of treatments in a completely randomised design. The CO_2 treatment is the whole-plot factor and is replicated three times among six rings at a concentration of 560 ppm. The subplot factors are species and nitrogen treatment. Half of the plots receive additions of nitrogen to approximately double current rates of atmospheric nitrogen deposition at the site[1]. In the other half of the plots, the available nitrogen is the ambient amount present in the soil at the start of the experiment. Species composition is controlled by hand-weeding the experiment 2–4 times per growing season. All measurements were made on intact, fully expanded leaves between 5 and 9 hours after sunrise on clear days in late May and early June 2005. At this time of the year, and under the conditions at the site, growth was expected to be

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[1] The higher nitrogen treatment under elevated CO_2 was not measured for *Agropyron repens.* However, the photosynthetic response of this species to a change in nitrogen levels under elevated CO_2 is similar to the response to nitrogen under non-elevated CO_2. Thus a small increase in A_{max}, and little change in g_s, are expected.

in the active phase (equivalent to late spring conditions in New Zealand), with growth and carbohydrate sinks unconstrained by other than average nutrient conditions (which were somewhat more constrained, for the lower nitrogen treatment, than for the previous New Zealand study by Guo et al. (2006)).

3.2 Leaf biochemical properties

Eight fully expanded leaves were taken from 2–3 sample plots. Leaf nitrogen and carbon content were determined on dried, ground material using a combustion furnace (LECO CNS 2000, LECO Corp., St Joseph, Michigan, USA). Specific leaf weight (SLW) was determined from the area of leaf segments measured soon after sampling, and oven-dry mass.

3.3 Photosynthetic gas exchange

Leaf CO_2 fixation rate (A) and stomatal conductance (g_s) under natural irradiance were measured in the middle of the day using a portable gas analysis system (Li-Cor 6400, Lincoln, NE) equipped with a CO_2 control module. Measurements were made on 4–5 fully expanded leaves in each of 2–3 sample plots. Leaf cuvette conditions were controlled for humidity, temperature and CO_2 concentration that were similar to field conditions. Each determination was made when A had stabilised. This process typically took 1–2 min.

The response of CO_2 fixation to intercellular CO_2 partial pressure (A/C_i response) was determined under saturating light (photosynthetic photon flux density (PPFD) of 1800 µmol m^{-2} s^{-1}). Cuvette CO_2 partial pressure (C_a) was increased in 13 steps from 5 to 140 Pa. Measurements were made at each C_a value when gas exchange had equilibrated, at which point the coefficient of variation (CV) for the CO_2 concentration differential between the sample and reference analysers was below 1%.

The values of light- and CO_2-saturated photosynthetic capacity (A_{max}) were calculated using Photosynthesis Assistant software (Dundee Scientific, Dundee, UK), which is based on the biochemical model proposed by Farquhar et al. (1980) and subsequently modified by Sharkey (1985).

3.4 Photochemical chlorophyll fluorescence

Chlorophyll fluorescence measurements were performed using a pulse-modulated fluorometer (Mini-PAM, Waltz, Effeltrich, Germany). Measurements were made on 4–5 fully expanded leaves in each of 2–3 sample plots. The experimental protocol of Genty et al. (1989) was followed. The fraction of absorbed light utilised in electron transport was calculated from the actual PSII photochemical efficiency $(F_m' - F)/F_m' = \Delta F/F_m'$, where F_m' is the lowered maximum yield during illumination with photosynthetically active radiation, and F is the fluorescence yield in light-adapted leaves. The potential PSII photochemical efficiency (F_v/F_m) was obtained from the ratio of maximal variable fluorescence to maximal fluorescence yield in dark-adapted leaves. The amount of energy dissipation activity in the pigment bed was estimated using the non-photochemical quenching (NPQ) of chlorophyll fluorescence, calculated as $F_m/F_m' - 1$.

3.5 Statistical analysis

Where appropriate, data are reported as means with standard errors.

4. Results

4.1 Leaf biochemical properties

Leaf biochemical properties are given by species in Table 1, and mean relative change in properties with variation in CO_2 and nutrient treatments in Table 2. Mean foliar N contents were less than the previous New Zealand study (130 mmol m^{-2}; control conditions) for the lower N treatment (100 mmol m^{-2}), and slightly higher for the higher N treatment (138 mmol m^{-2}). Mean leaf nitrogen (N) content declined in plants grown under elevated CO_2 relative to ambient CO_2, with a greater relative decline for the higher N treatment. This is a common trend in FACE studies (e.g. Lee et al. 2001; Guo et al. 2006). As expected, mean leaf N content also increased under the higher N treatment. However, neither the mean increase in foliar N with higher N treatment, nor the mean decline in N content with elevated CO_2, were statistically significant when the species were combined as a group.

Mean specific leaf weight (SLW) was slightly greater in leaves grown under elevated CO_2 relative to ambient CO_2, although this difference was not statistically significant for the three species as a group.

4.2 Photosynthetic gas exchange

Figure 1 provides a comparison of midday leaf photosynthetic rate (A) and stomatal conductance (g_s). Values are given by species in Table 1, and mean relative change in properties with variation in CO_2 and nutrient treatments in Table 2. Rates of A tended to increase with elevated CO_2, compared with those under ambient CO_2, under low N conditions; and to decrease with elevated CO_2 under higher N conditions – though none of the individual changes was statistically significant. When the species were combined as a group, the only significant effect was that of elevated CO_2 resulting in a weakly significant decrease ($P \leq 0.1$) in A under the higher N treatment.

Stomatal conductance (g_s) showed similar trends to those for A (Fig. 1, Tables 1 and 2). That is, values of g_s tended to increase with elevated CO_2, compared with those under ambient CO_2, under low N conditions; and to decrease with elevated CO_2 under higher N conditions – though none of the individual changes was statistically significant. When the species were combined as a group, the only significant effect was due to the combination of elevated CO_2 under a higher N treatment, which resulted in a weakly significant decrease ($P \leq 0.1$) in g_s.

Photosynthetic capacity, A_{max}, showed practically no variation with elevated CO_2 or N treatment for other than *Agropyron repens*, which exhibited a mean increase with elevated CO_2 under lower N conditions (Table 1). However, the change was not statistically significant, nor was the mean response for the species as a group (Table 2).

Table 1 Comparison of leaf biochemical, photosynthetic and photochemical properties of leaves growing at ambient and elevated CO_2 partial pressures of 36 Pa (A) and 58 Pa (E), respectively; for lower N (LN) and higher N (HN) conditions. Results are means of measurements in 2 or 3 plots.

| | *Agropyron repens* | | | | *Koeleria cristata* | | | | *Poa pratensis* | | | |
| | LN | | HN | | LN | | HN | | LN | | HN | |
	A	E	A	E	A	E	A	E	A	E	A	E
N (μmol m^{-2})	77±4.5	87±2.7	101±3.4	-	117±15	103±3.4	207±6	131±3.4	108±17	65.2±3.8	100±7.9	79±8.2
C (mol m^{-2})	1.9±0.06	2.0±0.05	1.8±0.01	-	2.9±0.02	3.0±0.16	3.4±0.3	3.5±0.17	2.2±0.02	2.3±0.12	2.3±0.16	2.1±0.04
SLW (g m^{-2})	50±1.4	50±1.5	45±1.5	-	75±0.9	78±4.4	87±6.4	92±4.4	57±0.8	60±3.5	59±3.8	56±0.8
A (μmol m^{-2} s^{-1})	11.0±1.9	14.0±0.9	18.8±0.1	-	11.4±5.0	15.8±2.0	17.8±4.7	11.0±2.0	5.2±1.1	7.7±3.6	11.5±2.5	10.2±1.3
A_{max} (μmol m^{-2} s^{-1})	19±4.6	27±1.4	33±0.1	-	29±4.8	26±2.0	30±6.3	30±0.5	18±1.4	18±1.6	26±1.3	27±1.3
g_s (mol m^2 s^{-1})	0.12±0.05	0.12±0.0 (1)	0.20±0.0 (1)	-	0.13±0.0 (4)	0.21±0.0 (3)	0.17±0.0 (5)	0.12±0.0 (3)	0.08±0.0 (1)	0.11±0.0 (5)	0.13±0.0 (4)	0.11±0.0 (1)
$\Delta F/F_m'$	0.12±0.01	0.14±0.0 (1)	0.12±0.0 (1)	-	0.19±0.0 (3)	0.21±0.0 (1)	0.24±0.0 (2)	0.22±0.0 (1)	0.18±0.0 (2)	0.18±0.0 (2)	0.18±0.0 (1)	0.22±0.0 (1)
F_v/F_m	0.72±0.01	0.74±0.0 (1)	0.74±0.0 (1)	-	0.75±0.0 (1)	0.76±0.0 (1)	0.77±0.0 (1)	0.78±0.0 (1)	0.73±0.0 (4)	0.73±0.0 (1)	0.74±0.0 (2)	0.76±0.0 (1)
NPQ	4.79±0.26	5.34±0.1 (1)	4.82±0.0 (1)	-	4.94±0.0 (6)	3.77±0.6 (3)	3.56±0.1 (4)	4.03±0.6 (3)	5.1±0.5 (4)	5.22±0.0 (4)	4.43±0.0 (3)	4.73±0.4 (6)

Table 2 Comparison of mean differences in biochemical, photosynthetic and photochemical properties of leaves for three species of grasses grown at ambient and elevated CO_2 partial pressures of 36 Pa (A) and 58 Pa (E), respectively; for lower N (LN) and higher N (HN) conditions. Results are expressed as mean percentage change relative to the value at ambient CO_2; for 3 (LN) or 2 (HN species), ±SE.

	LN (%)	HN (%)
Nitrogen (mmol m^{-2})	−13±15	−29±8
Carbon (mol m^{-2})	3±1	−1±5
SLW (g m^{-2})	3±1	0±6
A (μmol m^{-2} s^{-1})	42±8	−24±15
A_{max} (μmol m^{-2} s^{-1})	11±16	1.9±1.9
g_s (mol^{-2} s^{-1})	33±18	−22±7
$\Delta F/F_m'$	9±5	7±15
F_v/F_m	1.4±0.8	2.0±0.7
NPQ	−3±10	10±3

4.3   Photochemical chlorophyll fluorescence

Figure 2 shows the leaf chlorophyll fluorescence parameters for the three species studied. Values of $\Delta F/F_m'$ indicate the efficiency of excitation capture of PSII (of a leaf at 1800 μmol m^{-2} s^{-1} PPFD in this case), and did not differ significantly among species under any treatment or treatment interaction (Table 1, Table 2). For the species as a group, mean values of $\Delta F/F_m'$ increased slightly, but not significantly, with elevated CO_2. The same overall pattern of a lack of variation was also observed for the values of F_v/F_m, which indicates the potential efficiency of excitation capture by PSII in a dark-adapted leaf.

Figure 3 shows the values of the parameter NPQ obtained for the three species studied. NPQ is an indicator of the amount of thermal energy dissipation in the pigment bed, and can be interpreted as a measure of the demand for dissipation of excess light energy – which increases when plants become stressed. Differences between treatments were not significant for any species (Table 1), nor for the species as a group.
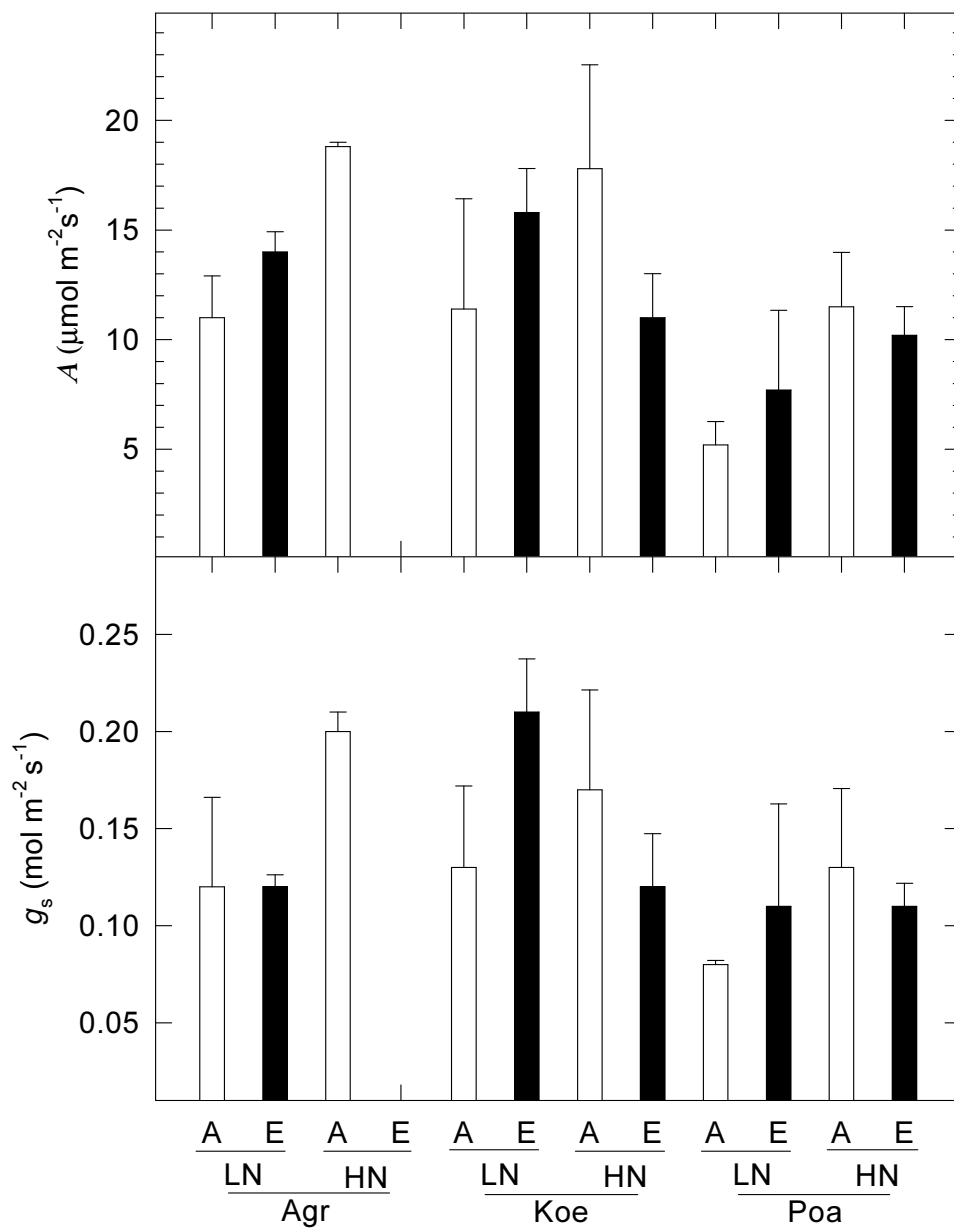
Fig. 1 Comparison of leaf net photosynthetic rate (A) and stomatal conductance (g_s) for leaves grown at an ambient CO_2 partial pressure of 36 Pa (A) and an elevated CO_2 partial pressure of 58 Pa (E), under lower N (LN) and higher N (HN) conditions. Results are means of measurements on 4–5 leaves in each of 2–3 plots, for each species (Agr – *Agropyron repens*; Koe – *Koeleria cristata*; Poa – *Poa pratensis)*. For *Agropyron repens*, the expected response to higher nitrogen levels under elevated CO_2 is for a small increase in A, and a small decrease in g_s (Lee et al. 2001).
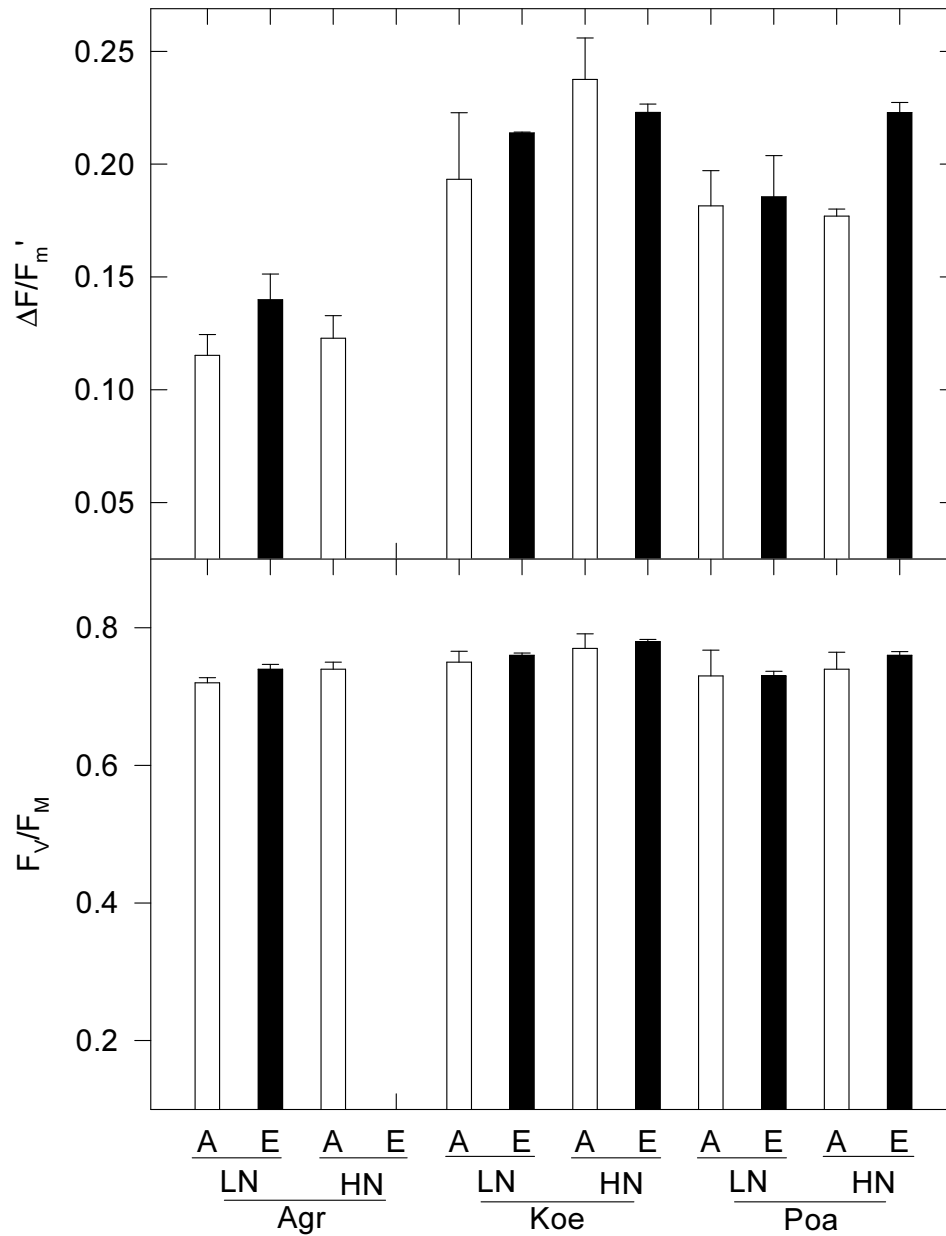
Fig. 2 Comparison of actual PSII photochemical efficiency, $\Delta F/F_m'$ measured on light-adapted leaves, with the maximum PSII photochemical efficiency (F_v/F_m) measured on dark-adapted leaves – at midday for the plants grown at ambient CO_2 of 36 Pa (A) and elevated CO_2 of 58 Pa (E), under lower nitrogen (LN) and higher nitrogen (HN) conditions. Results are means of measurements on 4–5 leaves in each of 2–3 plots, for each species (Agr – *Agropyron repens*; Koe – *Koeleria cristata;* Poa – *Poa pratensis*).
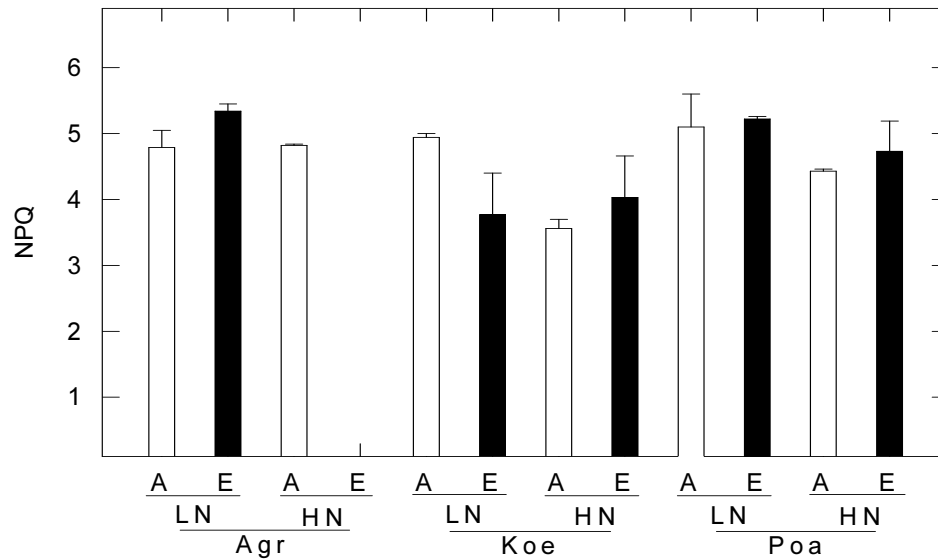
Fig. 3 Comparison of NPQ for plants grown at ambient CO_2 of 36 Pa (A) and elevated CO_2 of 58 Pa (E), under lower nitrogen (LN) and higher nitrogen (HN) conditions. Results are means of measurements on 4–5 leaves in each of 2–3 plots, for each species (Agr – *Agropyron repens*; Koe – *Koeleria cristata*; *Poa – Poa pratensis*

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5. Discussion

It is well documented that increased CO_2 enhances the photosynthetic rate and growth of most C_3 plants in the short term (e.g. Bowes 1993; Ainsworth et al. 2003). However, it is increasingly apparent that the extent of this response is variable, and its persistence over the long term is questionable (e.g. Foyer 1988; Griffin and Seemann 1996; Drake et al. 1997; Lee et al. 2001). The persistence of the response is particularly in doubt when there is significant nutrient limitation (Reich et al. 2006), although little response has also been observed in ryegrass in New Zealand even under conditions where nutrients are not expected to be significantly limiting production (Newton et al. 2006).

The results for photosynthetic performance obtained in this study are largely consistent with the significant body of work published for this site. This indicates that adaptation of plant systems to long-term exposure to elevated CO_2 results in little long-term net photosynthetic response, and that:

- Mean rates of light-saturated leaf net photosynthesis (A) show little overall change between ambient and elevated CO_2 conditions. Mean rates tended to increase with elevated CO_2 for lower nitrogen conditions, and decrease under higher nitrogen conditions, but the changes were not statistically significant.

- Mean values of photosynthetic capacity (A_{max}) show little overall change between ambient and elevated CO_2 conditions. Mean rates increased slightly with elevated CO_2 for lower nitrogen conditions, and decreased slightly under higher nitrogen conditions, but the changes were not statistically significant.

- Stomatal conductance showed little overall response between ambient and elevated CO_2 conditions for this study. Mean reductions of about 20% are usually seen in larger studies at the site (Lee et al. 2001). In this study mean rates tended to increase with elevated CO_2 for lower nitrogen conditions, and decrease with elevated CO_2 under higher nitrogen conditions, but the changes were not statistically significant.

- Mean foliar nitrogen content declined under elevated CO_2 conditions, both in the lower and (substantially; by 30%) in the higher nitrogen treatments, but the changes are not statistically significant. Mean reductions in nitrogen content of up to about 10%, though not in every year, have been seen in sampling over a wider range of herbaceous species at the site (Lee et al. 2001).

Given the above changes, it is not surprising that mean biomass production at the site shows no significant difference between ambient and elevated CO_2 conditions (Reich et al. 2004). A similarly insignificant change, under considerably higher nutrient conditions, has been observed for long-term studies at the New Zealand pastoral FACE site (Newton et al. 2006). Further discussion on the trends in photosynthetic performance, for a wider range of herbaceous species at the Minnesota BioCON site, can be found in Lee at al. (2001).

The new data of primary interest in this project are those obtained through measurement of chlorophyll fluorescence (which has not previously been reported for the Minnesota BioCON site). When plants are not able to use all incoming light energy, the excess must be dissipated, much of it via the xanthophyll cycle which converts excess light energy into heat in the pigment bed of the leaf. The parameter NPQ is a measure of this energy dissipation. When plants are under environmental stress (e.g. drought) and rates of photosynthesis are low, the demand for energy dissipation is larger, and NPQ increases. Plants may also respond in the medium term (days to weeks) by increasing their total energy dissipative capacity (their photoprotective capacity). Damage to the plant's photosynthetic system – either temporary or permanent depending on the severity and persistence of environmental stressors – can occur if the total photoprotective capacity of plants is exceeded. In this case values of maximum PSII photochemical efficiency (F_v/F_m) measured in dark-adapted leaves are either temporarily, or permanently, reduced – termed photoinhibition and photodamage, respectively.

Surprisingly little work has yet been done on the changes in light energy dissipation and photoprotective capacity of plants under elevated CO_2 conditions. Guo et al. (2006) found that NPQ in ryegrass was greatly enhanced under elevated CO_2 during New Zealand autumn growth conditions, when the demand for photosynthetic products was low in mature pasture (i.e. when pasture was well-recovered from the previous grazing event). The substantially

larger values of NPQ observed under these conditions imply considerably increased requirements for photoprotection – i.e. the same response as when plants are under stress. By contrast, no significant changes with NPQ were observed in the New Zealand study with elevated CO_2 in the early part of the growth cycle, soon after grazing in autumn, when demand for photosynthetic products was still high and the ability of the plant to supply products was limited by reduced leaf area.

In this study, no changes in NPQ were observed between control and elevated CO_2 treatments. However, values of NPQ were considerably larger in this BioCON study – more than 5 times larger – than those found for the New Zealand study. The reasons for this are quantitatively not understood, although rates of both A and A_{max} in the BioCON study were about 25% lower than in the earlier New Zealand study and so a higher demand for photodissipation at equivalent light levels would be expected (and thus higher values of NPQ). Unfortunately it could not be determined whether the total photoprotective capacity – and not just the percentage being used – had increased for the grasses in the Minnesota study, as the equipment necessary to do this was not available. However, it is usual for plants to at least partially adapt to lowered nutrient conditions by increasing the total pool of xanthophyll cycle products, and thus increase photoprotective capacity (e.g. Verhoeven et al. 1997).

The results of the study on the Minnesota grasses, while not conclusive because measurements could only be acquired under good growth conditions, are nonetheless consistent with our current working hypothesis for the mechanism of elevated CO_2-induced 'stress'. That is, a requirement for increased photoprotection occurs when short-term demand for photosynthetic products, relative to unconstrained rates of production, is low. It appears that even with lower nutrient conditions under elevated CO_2 there remains a largely balanced state in which the reduced rate of photosynthetic production that occurs remains – under otherwise good growth conditions – not only less than the demand for photosynthetic products but also with any increased photodissipative demand able to be met. As such, the greater photosynthetic efficiency afforded by elevated CO_2 under otherwise good growth conditions does not result in a requirement for photoprotection that is unable to met, and so 'stress' is not increased. This result is effectively the same as that found for the same growth phase in our earlier New Zealand study.

Taken overall to date, the findings from the Minnesota and New Zealand studies continue to suggest that elevated CO_2-induced stress is unlikely to be present during the active part of the growth cycle, occurring only as a short-term effect within a growth cycle when grasses are close to maturity. It therefore seems unlikely to pose a threat to pastoral production systems, since pastures are purposefully managed to avoid prolonged periods in a mature state. There do remain, however, several questions to be answered before the effect can be completely dismissed as unimportant. These are:

- At what stage in the growth cycle does elevated CO_2-induced stress become apparent – in particular, could it affect production of silage or hay crops that develop further into the mature phase than encountered in a normal grazing situation?

- Is the capacity of grasses to tolerate normal environmental stress, during the active phase of the growth cycle, affected by the presence of elevated CO_2? Could reduced demand for photosynthetic products during environmental stress initiate additional elevated CO_2-induced stress, and result in damage to the

plant's photosynthetic system?

The latter question arises because water and temperature stress impose extra demands on the photoprotective capacity of plants, but it remains unclear whether reduced demand for photosynthetic products under these circumstances will also initiate additional elevated CO_2-induced stress.

6. Conclusions and Future Work

6.1 Conclusions

When considering the results of this study alongside those of recent New Zealand work (Guo et al. 2006), it appears that even lowered nutrient conditions are not likely to affect the way grasses respond to the potential for elevated CO_2-induced stress. Overall, the present evidence is that grasses in both lower and higher nutrient environments adapt in ways that do not increase stress levels beyond plant photoprotective capacity when actively growing. Thus, elevated CO_2-induced stress would seem to be a factor that is only evident – if at all – in the mature phase of the growth cycle, when demand for photosynthetic products is small, and the potential for supply is large due to there being a large leaf area.

The conditions available at the time of the Minnesota study did not allow examination of the question of whether stress levels under elevated CO_2 become substantially enhanced in the mature part of the growth cycle. However, it may not be especially important even if this does occur, because agricultural grasslands are generally managed to avoid prolonged periods in the mature growth phase, i.e. they are generally grazed at or before that point. There are, nonetheless, several issues that need to be clarified before CO_2-elevated stress can be dismissed as unimportant:

- Is there any effect on production for silage or hay, when grasses may spend longer in a more mature phase?

- Is the capacity of grasses to tolerate normal environmental stress, during the active phase of the growth cycle, affected by the presence of elevated CO_2?

6.2 Future work

The issues that yet need investigation are:

- Can further work confirm the preliminary results found in New Zealand that elevated CO_2-induced stress is present when grasses approach the mature growth phase? This is being investigated as part of current work funded by the Foundation for Research, Science and Technology.

- At what stage in the growth cycle does elevated CO_2-induced stress become apparent – in particular, could it affect production of silage or hay crops that develop further into the mature phase than encountered in a normal grazing

situation?

- Is the capacity of grasses to tolerate normal environmental stress, during the active phase of the growth cycle, affected by the presence of elevated CO_2? Could reduced demand for photosynthetic products during environmental stress initiate additional elevated CO_2-induced stress, and result in damage to the plant's photosynthetic system?

7.   Acknowledgements

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