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Some effects of topographic aspect on grassland responses to elevated CO₂

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ABSTRACT

Grasslands are distributed globally across various topographies. In non-flat grasslands, aspect (the direction that a slope faces) influences the amounts of radiation and consequent effects on temperature and soil moisture, all of which are important drivers of plant growth. Aspect is important not only in hill and mountain areas but also in more moderate topographies such as plateaux, steppes and prairies. Here, we tested the aboveground growth response to an important driver of climate change – elevated carbon dioxide (eCO₂) – of two temperate grass species grown under simulated north (unshaded) and south (shaded) aspects. We used trellis-like structures to create the appropriate radiation regimes; irrigation ensured that only radiation and hence soil temperatures were different. We utilised the long-running New Zealand Free-Air Carbon Dioxide Enrichment (FACE) experiment and established turves of *Lolium perenne* L. and *Agrostis capillaris* L. The aboveground dry matter (DM) was regularly harvested over 10 months. For the main effects, there was no overall response to CO₂ but *Agrostis* produced about 50% more DM than *Lolium* while the north aspect produced about 15% more DM than the south. There was an interaction between CO₂ level and aspect: for both species production was about 20% greater under eCO₂ on the north aspect but had no effect on the south aspect. Given that a large proportion of the world's grasslands is on slopes, this aspect × CO₂ interaction causes us to reconsider the up-scaling of CO₂ responses from FACE experiments that have been universally carried out on flat terrain.

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Grasslands; aspect; radiation; soil temperature; elevated CO₂

Introduction

Grasslands are distributed globally across various topographies. In non-flat grasslands, aspect (i.e. the compass direction that a slope faces), characterised primarily by differences in radiation and consequent effects on temperature and soil moisture, becomes an important driver of plant growth and soil properties (Gong et al., 2008; Horvath et al., 1984; Lieffers & Larkin-Lieffers, 1987). While this is an obvious feature of hilly and mountainous areas, aspect is often an important feature of more modest topographies (Bennie et al., 2008) such as those described as plateau (Liu et al., 2006), steppe (Gong et al., 2008) and prairie (Lieffers & Larkin-Lieffers, 1987).

Elevated carbon dioxide (eCO₂) is a global change that is expected to have a significant impact on ecosystems but quantifying this response is associated with a high level of uncertainty (Finger et al., 2010) and is the topic of ongoing research. Field experiments, particularly those using Free Air Carbon Dioxide Enrichment (FACE) (e.g. Andresen et al., 2018; Hovenden et al., 2014; Mueller et al., 2016; Newton et al., 2014), provide the best experimental data on ecosystem responses to eCO₂ (Leakey et al., 2009). However, all grassland FACE experiments are on flat land and so the implications of

aspect have so far remained untested. There is good reason to expect an aspect × CO₂ interaction given likely interactions between CO₂ and irradiance and temperature (Poorter & Pérez-Soba, 2001).

Plants are able to respond to eCO₂ under low light conditions; in fact, the reduction in the light compensation point under eCO₂ suggests a stronger response as light levels decline (Long & Drake, 1991). Evidence for this effect has been found in experiments with shade, for example the work of Granados and Körner on lianas (Granados & Körner, 2002), but was not apparent in a study on wheat (Zhang et al., 2017). Differences in the CO₂ responses of shade and non-shade leaves have been observed (Eguchi et al., 2008) but this has not been widely investigated.

With a change in radiation, we expect an associated change in temperature. Temperature effects on the CO₂ response can be positive, negative or absent (Rawson, 1992) meaning that the effects of aspect (radiation and temperature differences) are likely to be difficult to predict. A further complication is that species can respond differently: Greer et al. (2000) grew five pasture species and found that the photosynthetic and plant growth responses to eCO₂ under short-term changes in

temperature and irradiation varied between species and growth conditions.

In this paper, we report on an initial study where 'aspect' was introduced to a FACE experiment on a flat site. This was achieved by installing a frame that held horizontal slats to create variations in shading throughout the year allowing us to create conditions of radiation and associated temperatures typical of north- and south-facing slopes (note that the experiment was located in the Southern hemisphere and hence south slopes receive less irradiance than north slopes). We then tested the aboveground growth response to eCO₂ of two temperate grass species and asked – does the CO₂ response of grasses differ depending on aspect?

Materials and methods

FACE experimental set-up

The New Zealand FACE experimental is fully described by Newton et al. (2014). Briefly, this long running (21 years) experiment consisted of three 12 m diameter 'rings' that had an eCO₂ atmosphere (target enrichment of 500 ppm) and three matching ambient CO₂ rings. During the experimental period, the 2-min average CO₂ concentration in the enriched rings was within 10% of the target 71% (Ring 1) to 86% (Ring 3) of the time; ambient CO₂ concentrations were about 395 ppm. The soil was a Mollic Psammaquent (black sand) and the pasture had not been re-sown for nearly 60 years; it consisted of a mixture of C3 and C4 grasses, legumes and forbs. The C4 species contributed little in terms of annual biomass (<1%). Annually P, K and S were applied to maintain soil concentrations at recommended levels for this type of pasture; note that the fertiliser regime did not include N, the only *de novo* input of this nutrient being from N fixation by legumes. The pasture was grazed by sheep when the aboveground biomass reached 180–200 g m⁻² dry matter (DM); the sheep were removed when the pasture was grazed down to 50–70 g m⁻². Typically, 10–12 grazing events occurred per year.

Shading treatment: irradiance and temperature

There were two irradiance levels set to mimic the difference between a north facing slope (unshaded) and the corresponding south facing slope (shaded) across different seasons. To manipulate the south slope's irradiance levels throughout the year a 7.2 m long and 1.5 m high trellis-type structure was constructed in each ambient and eCO₂ ring (see Figure 1 for

construction and placement in the rings). Requirements for the shading structure included minimal interference with the CO₂ enrichment process as well as being able to change the level of shading easily throughout the year to mimic seasonal changes in irradiance. To achieve this, horizontal slats were affixed to the frame; the width of the slats and their spacing could be changed over the year to give the required level of shading. The level of shading was changed monthly and the necessary amount calculated using the NIWA Solarview tool (<http://solarview.niwa.co.nz/>) was appropriate for a slope angle of 30°.

To check that the desired levels of shading were achieved, a photodegrading dye technique (Roales et al., 2013) was used. Five evenly spaced 30 ml glass vials containing the photodegradable fluorescent organic dye rhodamine WT (concentration 75 ppb) were placed on either side of each shading frame. Once a month, the vials were collected and replaced with new vials containing fresh 75 ppb rhodamine WT solution. The fluorescence of the rhodamine WT dye in the collected vials was determined; the relative difference in the fluorescence (i.e. amount of photodegradation) between the shaded and the unshaded plots is linearly related to the difference in irradiance.

Due to the proximity of the shaded and unshaded plots (c. 1 m apart) and the free mixing of the air, differences in irradiance will not result in measurable differences in air temperature. However, soil temperatures are usually very different for different aspects (e.g. Lambert & Roberts, 1976), especially so during clear-sky conditions (Gillingham & Bell, 1977). Obtaining an accurate record of differences in soil temperatures between the unshaded and the shaded plots proved problematic: it was difficult to non-destructively place an adequate number of temperature probes at varying depths for all the shading frames. Hence we modelled the likely soil temperatures using the Agricultural Production Systems Simulator (Keating et al., 2003).

Plot establishment and harvesting

Plots consisting of pure stands of either *Lolium perenne* L. (hereafter referred to as *Lolium*) or *Agrostis capillaris* L. (*Agrostis*) were established in both ambient and eCO₂ rings in October (spring) 2013. At this stage, the rings had been exposed to 16 years of CO₂ enrichment. Seed was obtained from the Margot Forde Forage Germplasm Centre (AgResearch Grasslands Research Centre, Palmerston North, New Zealand; <https://www.agresearch.co.nz/about/our-subsidiaries-and-joint-ventures/margot-forde-forage-germplasm-centre/>). For both



Figure 1. Construction and ring layout of the shading frames. (a) General view of a frame. (b) Frame in ring showing unshaded north plots (left side) and shaded south side (right). (c) Plots in winter. Note the frosted grass on the south/shaded side as well as the slats set in 'extended' mode to enhance the shading effect. (d) Placement of a frame in an elevated CO₂ ring.

species, six accessions were used with three of each originating from north and south aspects. In the experiment, in terms of growth there was no interaction between CO₂ level and the origin of the species. Hence these six accessions were treated as internal replicates. Plants were initially established in a glasshouse from seed in growing flats containing 5 cm depth of a compost-based growing media. When plants were approximately at the 3 leaf stage, 20 × 30 cm turves (including the initial 5 cm deep growing media) were transplanted into similarly sized areas excavated in the soil of the rings. The 12 turves (2 species × 6 accessions) were randomly placed in a line 10 cm apart on both the north and the south sides of the shading frames. To ensure that irradiance was the only factor affected by the shading treatment, a sprinkler irrigation system ensured that the turves were well watered. Weekly soil moisture measurements using a time domain reflectometer showed that there were no differences between turves of the two shading treatment (data not shown). The species composition of the turves was maintained by hand weeding of invasive grasses and the application of appropriate herbicides for control of broad leaved species. Throughout the experiment, the turves were protected from grazing by sheep and no fertiliser was added.

From planting to April 2014 plants were allowed to establish; they were harvested periodically by using battery powered hand shears to cut the aboveground plant material to 2.5 cm; these initial harvests were not included in the analyses. Once the plants had established and the potential residual effect of the compost-based growing media was likely to be minimal, turves were regularly harvested with the interval between harvests depending on the season: it ranged from about 20 days in the spring and summer to 60 days in the winter.

There were a total of eight harvests with the experiment finishing in February 2015. The harvested material was dried for 72 h at 60°C and weighed to determine the amount of DM harvested. The data from all eight harvests were combined and expressed on a kg DM ha⁻¹ basis to give a total amount of DM grown over the 10 months of the experiment.

Statistical analyses

The total amount of DM grown over 10 months was analysed as a split-split plot design using the R (R Core Team, 2018) package 'agricolae' (de Mendiburu, 2017). The DM data from the six internal replicates for each

species were averaged. Hence, there were three replicates in the analysis. The main plot was CO₂, aspect (shading) the sub-plot and species the sub-sub-plot. Data satisfied the assumptions for analysis of variance and no transformations were carried out. *P*-values of less than 0.05 were regarded as statistically significant.

Results

Monthly climatic conditions during the experiment are shown in Table 1. All climatic variables were typical of the long-term averages for the site. In terms of the changes in environmental conditions induced by the shading frames, the rhodamine WT dye fluorescence data indicated that the desired levels of shading were achieved: in summer (November–January) the irradiance in the shaded ‘south’ plots was 70–80% of the unshaded ‘north’ plots while in winter (June–July) the values were about 10% (data not shown). The differential radiation resulted in differences in modelled soil temperatures: depending on the time of year, shaded plots were likely to be from 3°C to 6°C cooler than unshaded ones (Table 1).

Boxplots of the DM produced during the experiment in the *Lolium* and *Agrostis* curves grown under either ambient or elevated atmospheric CO₂ and two aspects (north/unshaded and south/shaded) are shown in Figure 2. In terms of the main effects, there was no overall response

to eCO₂ ($p = 0.35$) but *Agrostis* produced about 50% more DM than *Lolium* (11,408 vs. 7557 kg DM ha⁻¹; $p < 0.01$). Also, the north aspect produced about 15% more DM than the south (10,149 vs. 8816 kg DM ha⁻¹; $p = 0.02$). There was an interaction ($p = 0.05$) between CO₂ level and aspect. For both species, DM production was about 20% greater under eCO₂ on the north aspect but there was no CO₂ response on the south aspect.

Table 1. Monthly climatic variables over the course of the experiment from April 2014 to February 2015: average maximum temperature (Max. temp.), average minimum temperature (Min. temp.), total precipitation (Rainfall), average daily global solar radiation and modelled average soil temperature (10 cm depth) for the simulated North and South aspects.

Month	Max. temp. (°C)	Min. temp. (°C)	Rainfall (mm)	Solar radiation (MJ m ⁻²)	Soil temp. (°C)	
					North	South
April (2014)	20.6	11.6	109.2	10.3	22.3	16.3
May	16.7	7.9	95.5	7.3	19.7	13.7
June	15.8	7.1	73.8	5.9	15.9	11.3
July	13.3	3.8	24.0	6.9	13.0	9.1
August	14.0	4.9	89.1	9.8	13.5	8.5
September	16.2	7.7	82.4	13.3	14.9	10.1
October	17.2	8.4	60.2	17.8	16.0	11.7
November	17.8	10.0	61.3	21.5	17.4	13.6
December	21.5	12.6	80.4	22.8	19.0	15.9
January (2015)	25.3	13.6	0.0	28.0	21.2	17.4
February	22.8	12.9	63.5	22.2	23.0	17.6

All data except the modelled soil temperatures were obtained from the NIWA Virtual Climate Station Network (Tait, Henderson, Turner & Zheng, 2006).

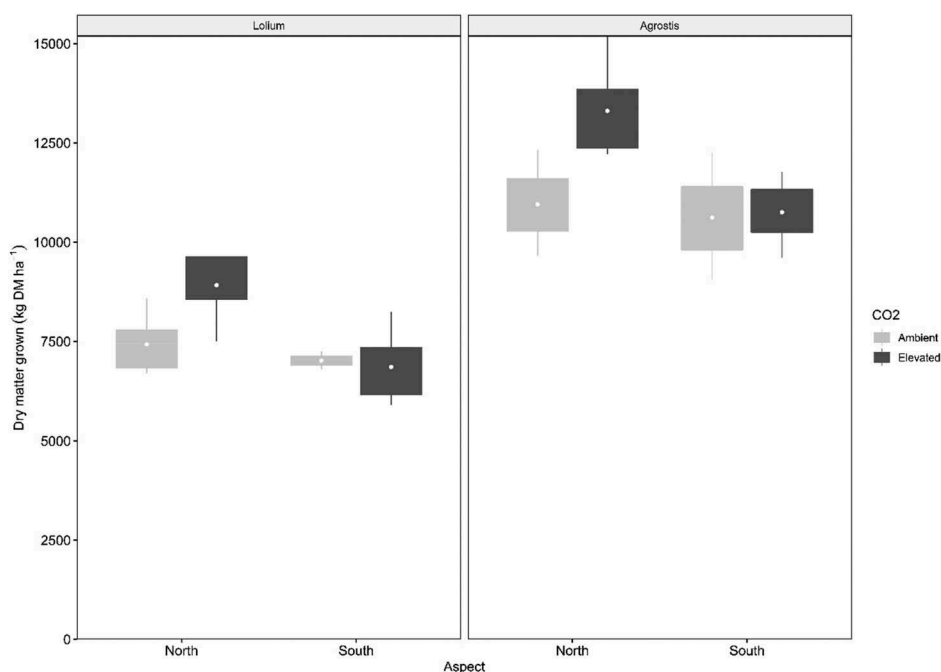


Figure 2. Boxplots of total dry matter (DM) production (kg DM ha⁻¹) of curves of *Lolium perenne* L. (*Lolium*) and *Agrostis capillaris* L. (*Agrostis*) grown under either ‘Ambient’ or ‘Elevated’ atmospheric CO₂ and two mimicked aspects (‘North’/unshaded or ‘South’/shaded). See text for experimental details. The lower bound of the boxplot is the data’s first quartile (Q1) and the upper bound the third quartile (Q3). The upper whisker shows Q3 + 1.5 × the interquartile range (IQR; Q3 – Q1) and the lower whisker Q1 – 1.5 × IQR. The solid white point denotes the mean of the data.

Discussion

In this research, we mimicked a difference in aspect in a flat experimental area by creating shade conditions that represented north (unshaded) and south (shaded) facing slopes. Our intention was to see if the CO₂ response of grasses was likely to differ with aspect; if this was the case we would need to revise our view of grassland responses to CO₂ which, until this point, have been exclusively measured on flat areas. If there is a differential eCO₂ response for different aspects, it would clearly lead to errors in scaling up experimental data from flat terrain as a considerable proportion of the world's grasslands are on slopes. For example, for New Zealand land on slopes accounts for approximately 50% of the country's pastoral area (Kemp & Lopez, 2016). In the Tibetan grasslands around the headwaters of the Yellow River (China), sloping land accounted for about 80% of all grasslands (calculated from Figure 3 in Liu et al., 2006). Also in China, for the extensive Xilingol steppe grasslands, which would traditionally be considered 'flat', it is estimated that 40% of the pastures are on hill slopes (Chen, 1988 cited in Gong et al., 2008). Similarly, for the United States of America, grassland dominant eco-regions that would normally be considered as having low relief such as the Great Plains and Prairies can have from 20% to 40% of their areas on slopes (calculated from Table 3 in Theobald et al., 2015).

In the initial analyses of the data in our experiment, we examined responses to shading and eCO₂ on a seasonal basis. Despite the seasonal differences in radiation and soil temperature during the experimental period (Table 1), we did not find a significant interaction between season, aspect and CO₂ in terms of the biomass grown (data not shown). However, the accumulated biomass over 10 months did show that there was a difference in the CO₂ response that depended on the aspect. There was a significant stimulation of growth by eCO₂ on the north facing aspect but no CO₂ effect on the south slope leading to a significant CO₂ × aspect interaction. This result was consistent for both *Lolium* and *Agrostis*.

It is worthwhile to note that our use of a flat site to represent a north aspect underestimates the actual differences in radiation received between aspects; this is because a flat site receives less radiation than a slope with a north aspect. This difference is especially so in winter: for a slope of 30°, up to 80% more radiation will be received by the north slope than flat land. This means that the interaction between aspect and eCO₂ in terms of biomass grown may be underestimated in our study.

Our initial hypothesis was that the more shaded areas could show a stronger growth response to CO₂.

This was based on the evidence that the positive effect of eCO₂ on photosynthesis should be greater as irradiance gets close to a species' light compensation point (e.g. Kubiske & Pregitzer, 1996). However, in the event, the more shaded south aspect showed no response to CO₂. It may be that our shading treatment did not reduce the light levels close enough to the CO₂ compensation point. Even in the middle of winter, at mid-day, the irradiance of the south/shady plots (c. 200 μmoles m⁻² s⁻¹) was substantially higher than the typical light compensation points of temperate pasture species (e.g. *L. perenne* c. 20 μmoles m⁻² s⁻¹; Huylbroeck & Bockstaele, 1999). It may also be the case that differences in soil temperature as a result of the shading treatments modified the CO₂ response. Our modelled soil temperatures suggest lower temperatures of up to 6°C on the south aspect. While positive CO₂ × temperature interactions are not universal, they have often been reported and may be responsible for the aspect effect we observed.

Agrostis DM production was about 50% more than that of *Lolium* although the latter would be regarded as a higher producing species in the right conditions (e.g. Peeters, 2004). No visible disease or pest damage was evident in the *Lolium* swards, so the likely reason for the greater production of *Agrostis* is soil nutrient status. *Agrostis* can grow better than *Lolium* at low levels of soil N availability (Bradshaw et al., 1964) and it seems likely that soil N was low in the plots as legumes were weeded out and no N fertiliser was applied.

It should be pointed out that our results are for the aboveground DM production only. There is evidence that the above- and belowground components of plant growth can respond differently to eCO₂. Using turves with the same soil as in our experiment, Ross et al. (2004) and Newton et al. (1996) found only modest increases in aboveground pasture production but 50% greater root mass with eCO₂. Further evidence for a differential response comes from data collected earlier in the New Zealand FACE experiment: though there was no increase in aboveground biomass, both root production measured using an in-core growth technique (Allard et al., 2005) and root exudation (Allard et al., 2006) were higher under eCO₂. It is also the case that our mimicking of different aspects is incomplete as the change in irradiance is very likely to be associated with a change in soil moisture. A more complex experiment that includes this factor would be very desirable.

There are several implications of our finding that the CO₂ response differs depending on aspect. First, where modelling of CO₂ effects by both earth system and ecosystem models is validated against experimental data then the validation set is almost certainly

from experiments on flat land. This would be an inappropriate comparison if the modelling was designed to capture CO₂ responses of anything other than flat land. Second, we only looked at plant growth in this experiment; our results suggest that other soil and plant properties sensitive to eCO₂ might also change depending upon aspect. Third, land managers often take advantage of aspect-driven differences in plant growth and seasonality in the provision of fodder for their livestock. Our finding suggests the relationship between aspects is likely to change in the future which in turn may produce new challenges for livestock managers.

Conclusions

We found that radiation levels typical of 'north' (unshaded) and 'south' (shaded) slopes resulted in different plant growth responses to eCO₂. There was a positive effect of eCO₂ on the north aspects but no effect of CO₂ on south aspects. Given that a large proportion of the world's grasslands is on slopes, this interaction causes us to reconsider scaling of the CO₂ responses from experiments that have been universally carried out on flat terrain. Further exploration of impacts of aspect on eCO₂ responses, particularly the inclusion of a soil moisture treatment, is recommended.

Authors' Contributions

All authors contributed to this study. Mark Lieffering and Paul Newton conceived and designed the experiment; Mark Lieffering, Paul Newton, Shona Brock and Phil Theobald carried out the experiment; Mark Lieffering analysed the data; and Mark Lieffering and Paul Newton wrote the paper.

Disclosure statement

No potential conflict of interest was reported by the authors.

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