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Elevated CO₂ impacts on grazed pasture: long-term lessons from the New Zealand FACE

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Abstract. A grazed pasture Free Air CO₂ Enrichment (FACE) experiment has been operating for almost 15 years in the Rangitikei Region of New Zealand, following earlier work studying CO₂, temperature and moisture effects on pasture in growth chambers. The longer-term results are reviewed with a focus on primary productivity, pasture compositional dynamics, nutrient cycling feedbacks and soil carbon supply. In terms of the direct effects of CO₂ elevated to 475 ppm, increases in primary production were reflected in belowground allocation and legume stimulation, with the latter diminishing in the longer term and annual aboveground net herbage accumulation showing a low and variable response over time. The grazing animal has strongly influenced nitrogen (N) transformations, in terms of carbon (C) and N decoupling and return to soil, a feedback that appears to mitigate the recognized effects of increased C inputs on nitrogen limitation. Nevertheless, soil mineral N has decreased and labile fractions of soil carbon have increased – effects only detectable over a decade. Key lessons unique to this study include the animal and soil feedbacks that have driven longer-term effects differing from earlier growth chamber and the results of FACE in the first few years. Remaining questions for further investigation include mechanisms influencing legume responses and the effects of elevated CO₂ on N processes (biological fixation, microbial processing, mineral N losses). The facility is currently undergoing major refurbishment in order to explore the effects of elevated CO₂ and interactions with temperature and moisture availability.

Keywords: Free air CO₂ enrichment, nitrogen dynamics, primary production, soil nutrients, soil carbon.

Introduction

Free Air CO₂ Enrichment (FACE) studies represent our best attempt at simulating a key future environmental driver of the plant communities on which society depends for primary production and a host of other ecosystem services. The technology for studying the impacts of elevated CO₂ has developed from early use of indoor growth chamber studies, through outdoor closed chambers and open-topped chambers, to FACE studies which eliminate as far as possible the artefacts associated with confined systems, *i.e.* effects on temperature, moisture and radiation (Ross *et al.* 2004; Long *et al.* 2006). The other key benefit of FACE for grassland systems is the ability to operate the simulation over the long term and consider feedbacks on the plant community from the animal and soil sub-systems that are closely associated with it. Globally there have been numerous FACE studies conducted on various plant communities including plantation forest (*Pinus* and *Populus* spp.; Norby *et al.* 2005), crops (wheat, rice, sorghum, cotton, potato, grape; Kimball *et al.* 2002), natural grassland (Tasmania, Hovenden *et al.* 2006; Wyoming, Morgan *et al.* 2011) and sown pastures (Switzerland, Zanetti *et al.* 1997; Minnesota, Adair *et al.* 2009). None of these grassland studies have included mammalian grazing. This is important because of the known effects of animal diet selection on sward composition, the physical impact of the grazing animal

and the decoupling of carbon and nitrogen that occurs in the grazing animal through excreta return (Newton *et al.* 2001b).

A global change research programme relevant to New Zealand pastoral systems was initiated by AgResearch in the early 1990s and initially focused on the effects of elevated CO₂, as well as temperature and moisture interactions, on typical New Zealand pastures. These experiments were conducted using large turves in growth chambers under controlled conditions, enabling detailed physiological studies over season-long periods using different soil types and including a range of treatment levels (*e.g.* Ross *et al.* 1995; Newton *et al.* 1996; Ross *et al.* 1996; Clark *et al.* 1997; Clark *et al.* 1999). In the late 1990s the programme shifted to a field-based focus with the establishment of the New Zealand grazed pasture FACE experiment (Newton *et al.* 2001a).

The New Zealand FACE site is located 13 km southwest of the town of Bulls in the Rangitikei District at Flock House, a former agricultural research and training centre (40°14S, 175°16E, 9 m a.s.l.). Details of the site and methods are found in Newton *et al.* (2001a; 2006). The soil type is a Pukepuke black sand (Mollic Psammaquent) (Cowie and Hall 1965) and at the start of the experiment the 2.5 ha paddock had been in perennial pasture for the previous 30 years without re-sowing. At that time the pasture was dominated by perennial ryegrass (*Lolium perenne*) and white clover (*Trifolium*

repens) but also included numerous other C3 grasses (e.g. *Anthoxanthum odoratum*, *Agrostis capillaris*), other legumes (e.g. *Trifolium subterraneum*), forbs (e.g. *Hypochaeris radicata*, *Plantago lanceolata*) and C4 grasses (e.g. *Cynodon dactylon*, *Paspalum dilatatum*). Six circular plots of 12 m diameter were established in October 1997, with three being CO₂ enriched “rings” and three being ambient CO₂ control rings. The CO₂ is delivered to the rings through vertical tubes around the circumference with the flow controlled by solenoid valves and the CO₂ monitored at the centre of each plot. Wind speed and direction is also monitored to activate the upwind solenoids only, with an upper wind speed limit of 1 m s⁻². The atmosphere in the elevated CO₂ rings is enriched to a target of 475 ppm during the daytime. The plots are grazed by sheep 3-8 times per year during all seasons and during each grazing of 3-4 days the sheep are confined to individual plots. Pre-graze target pasture herbage mass is 2000 kg DM/ha and post-graze target pasture herbage mass is 800 kg DM/ha. Annual fertiliser inputs are on average 10 kg P/ha, 30 kg S/ha and 60 kg K/ha, with all N supplied by biological legume fixation.

A number of results relating to pasture production and composition after two years of FACE were reported in a multi-site comparison presented at the 2001 International Grassland Congress (Morgan *et al.* 2001). References to production, legume response and nutrient cycling results were also made in a paper presented at the 2005 International Grassland Congress (Luscher *et al.* 2005). This paper updates the key results focusing on primary production, pasture compositional dynamics, soil carbon supply and nutrient cycling feedbacks. The paper also notes some unresolved processes and includes discussion of new directions for the research programme.

Primary production

The earlier growth chamber studies at high levels of CO₂ enrichment (700 ppm) showed significant increases in photosynthetic rates for *T. repens*, *P. lanceolata* and *P. dilatatum* (>50%), which were even greater under low soil moisture levels (Clark *et al.* 1999). However this did not translate into increases in leaf extension or appearance rates in that study. This was consistent with observations in earlier work which instead attributed small increases in herbage yield (7-14%) to greater growing point densities in *T. repens* (Clark *et al.* 1997). While an aboveground response from the dominant C3 grasses was not observed, there were increases in root mass in the order of 50% (Ross *et al.* 1995; Newton *et al.* 1996). Initial measurements from the FACE over the first 27 months did show a significant (18%) increase in annual total herbage accumulation at elevated CO₂, this response being mainly in spring and attributable to forbs and legumes (Morgan *et al.* 2001).

The greatest effect of elevated CO₂ on C assimilation appeared toward the end of each pasture regrowth cycle, in that assimilation rates declined under ambient but remained high under elevated (Newton *et al.* 2006). This was attributed to the greater water use efficiency of swards at elevated CO₂, as soil moisture declined rapidly

during the regrowth cycle. The ability of plants at elevated CO₂ to maintain above- and below-ground growth through a simulated drought had been observed in an earlier simulated drought study with turves in growth chambers (Newton *et al.* 1996).

In the medium term an annual aboveground net herbage accumulation response has not been clearly seen. Over the first seven years of the FACE experiment, total herbage yields were consistently but not significantly greater (average +8%) under elevated CO₂ (Ross *et al.* 2004; Newton *et al.* 2006). This magnitude of herbage yield response was similar to that observed in growth chamber studies at higher levels of elevated CO₂ (Ross *et al.* 1996; Clark *et al.* 1997) and is low relative to other grassland FACE studies (0-30%, Campbell and Stafford Smith 2000). The prior growth chamber experiments showed that the greatest response to elevated CO₂ occurred at high temperatures and it was then suggested that this would limit the response of pastures in temperate regions where cool-season grasses dominate (Newton *et al.* 1994).

More recent biomass production data from years 6-10 indicate an increase in the annual herbage production response to elevated CO₂, though still non-significant (Ross *et al.* 2013). A relevant result in considering the lack of above-ground response is the good evidence for below-ground allocation of the additional C fixed. Both root production (Allard *et al.* 2005) and root exudation (Allard *et al.* 2006) have been shown to increase significantly under FACE.

Pasture compositional dynamics

As noted above, annual aboveground net herbage accumulation was not significantly greater under elevated CO₂, largely because the most dominant plant functional group (C3 grasses) did not respond strongly. However, both the legume and forb components of the sward did respond, a result consistent with the interaction between their recognized warm-season growth peak and the known greater effect of elevated CO₂ at higher temperatures (Newton *et al.* 1994). As a result, the proportion of legumes in harvested biomass was two-fold greater under elevated CO₂ in the first four years of the experiment, and the proportion of forbs showed a similarly marked increase over the first six years (Ross *et al.* 2004). This was consistent with the results of the earlier growth chamber studies showing a 63% response in clover yield at 525 ppm (Clark *et al.* 1997). Elevated CO₂ has also been shown to affect sward botanical composition via seedling recruitment at this site, in that while most species showed increased seed production, only legume and forb species showed greater seedling establishment (Edwards *et al.* 2001).

However, more recent data has shown that the legume response observed in the first five years of the experiment has not persisted, with no significant difference in harvested legume biomass in years 6-10 (Ross *et al.* 2013). The reasons for this remain unclear and are the subject of ongoing investigation. Possible explanations include phosphorus limitation (Gentile *et al.* 2012), despite seemingly adequate plant available P

levels; or a shift in the balance between legume stimulation and animal selection for legumes (Newton *et al.* 2001b).

Nutrient cycling

Changes in botanical composition in favour of legumes as a result of elevated CO₂ should result in increased N inputs, since N fixation is usually proportional to legume production (Ledgard *et al.* 1987). While the total amount of N harvested in above-ground biomass was initially greater under elevated CO₂ due to greater legume content, this declined over time to be the same as ambient after five years, attributed to a decline in total biomass production rather than bulk tissue N concentrations (Newton *et al.* 2010). The increase in photosynthetic N use efficiency associated with elevated CO₂ (Leakey *et al.* 2009) results in the production of plant tissue with a lower N content. Individual species in the sward did show reduced tissue N concentration relative to that observed in ambient CO₂ (-11% in C3 grasses, Allard *et al.* 2003) but changes in botanical composition toward species with higher tissue N concentration (legumes and forbs) during the first five years mitigated this at the whole-sward level (Newton *et al.* 2010).

In terms of the return of N to soil, in a grazed system the fate of N in above-ground biomass depends on both litter return and on cycling via animal intake and the decoupling of C and N associated with excretion. The return of higher C:N litter would be expected to encourage N immobilization in soil organic matter, but the analysis of litter tissue quality showed no difference in C:N ratio between ambient and elevated CO₂, likely the result of re-mobilization during senescence (Allard *et al.* 2004). That study estimated that the differences in litter C:N between species, combined with changes in botanical composition, resulted in an 18% increase in the rate of N release from direct plant tissue inputs to soil at elevated CO₂. With regard to cycling through the animal, Allard *et al.* (2003) observed a higher proportion of legume in the diet at elevated CO₂, but the associated decline in tissue C:N of species meant no difference in dietary N. Decomposition rates of dung were lower under elevated CO₂, which reduced the estimation of a higher rate of N return to soil to 9% (Allard *et al.* 2004). Another potential outcome of the animal cycling pathway is an increase in soil N losses via volatilization and leaching due to the greater partitioning of N to urine resulting from an increase in legume proportion in the diet (Allard *et al.* 2003) but this has not been confirmed by direct measurement.

In terms of the soil N outcome of these processes, earlier studies in turves (Ross *et al.* 1995; Ross *et al.* 1996) and results from the FACE (Ross *et al.* 2004) showed no consistent effect of elevated CO₂ on total or mineral N. However, in the longer term, the total amount of N in soil has increased under elevated CO₂ (Newton *et al.* 2010; Ross *et al.* 2013) but the plant-available forms (as indicated by resin strips, Newton *et al.* 2006; Newton *et al.* 2010) are lower, supporting the concept of progressive nitrogen limitation (PNL) proposed

elsewhere (Luo *et al.* 2004).

Soil carbon supply

Studies of soil turves in growth chambers indicated higher rates of C turnover but could show no consistent effects of elevated CO₂ on soil C fractions (Ross *et al.* 1995; Ross *et al.* 1996). In addition, early results from the FACE showed no significant effect on total, extractable and microbial C but did indicate greater respiratory CO₂ production (Ross *et al.* 2004). The recent longer-term results have confirmed the increase in heterotrophic respiration and detected significantly greater microbial C pools and labile C fractions under elevated CO₂ (Ross *et al.* 2013).

Furthermore, Ross *et al.* (2013) have summarized the results of the FACE in terms of effects on the three routes of C input to the soil, showing that the balance of inputs shifts from aboveground to belowground inputs under elevated CO₂. Elevated CO₂ led to an increase in below-ground plant inputs to soil via both root exudation (Allard *et al.* 2006) and the turnover of greater root tissue growth - root in-growth core methods showed an increase in root growth and decrease in root residence time, particularly in the summer-autumn period (Allard *et al.* 2005). Yeates and Newton (2009) have also shown a 3-4 fold increase in populations of root feeding nematodes under elevated CO₂ which has likely contributed to the increased root turnover.

By contrast, aboveground litter inputs were lower under elevated CO₂ (Allard *et al.* 2005). There were no differences in the decomposition rates of shoot or root tissue from individual plant species under ambient and elevated CO₂, but higher rates for legumes and forbs indicated that the greater contribution of these species to aboveground tissue turnover would increase overall rates of mass loss (Allard *et al.* 2004). This effect, combined with the changes in above/below-ground allocation initially indicated a 15% greater input of plant organic matter to soil. Dung inputs were also lower under elevated CO₂, resulting from lower dung decomposition rates in summer (Allard *et al.* 2004) and this effect serves to reduce those early estimates of greater organic matter inputs to approximately 10% (Newton *et al.* 2006).

The greater belowground C inputs under elevated CO₂ were initially expressed in a 15% greater accumulation of soil coarse particulate organic matter with a lower C:N ratio (Allard *et al.* 2005). The lack of observed soil C gains in other fractions may reflect the low level of clay and micro-aggregate formation in the coarse-textured soil type at the FACE site. The most recent analysis of total soil C, accounting for variation at the start of the experiment, indicates a greater rate of soil C accumulation of 1.2%/yr under elevated CO₂ over the 2003-07 period (Ross *et al.* 2013), which is in the middle of the range of other rates reported in the literature (De Graaff *et al.* 2006).

Key long-term lessons

As indicated above, a number of results arising from the earlier growth room studies were consistent with results appearing in the first five years of the FACE study, i.e.

individual species growth responses, herbage yield, soil C. However, some of the effects of elevated CO₂ observed in the early period of the FACE experiment have not held up in the longer term, in particular the increase in herbage accumulation in the first two years and the stimulation of legume growth (with likely implications for N fixation inputs) in the first four years. Conversely, some effects have not revealed themselves until later in the experiment, in particular soil C and N increases and the decline in plant-available N.

Five years into the experiment, the site went through a major summer-autumn drought, which enabled observation of soil moisture interactions and also the nutrient dynamics following rewetting. Re-wetting after the drought led to an N mineralization flush and temporarily higher N harvested in yield (Newton *et al.* 2010). Clearly short-term studies run the risk of missing the impact of such events on system dynamics, which may indeed be of greater significance given projections of increasing frequency and severity of droughts for some regions in New Zealand under global change scenarios (Baisden *et al.* 2008).

The long-term nature of the experiment has allowed for the expression of nutrient cycling feedbacks such as PNL (Newton *et al.* 2010) for which there was little evidence from growth room studies or early FACE results (Ross *et al.* 1996; Ross *et al.* 2004). In an adaptive pasture management context, lower mineral N status of pastures may reinforce the recent trend of increased fertilizer N inputs (MacLeod and Moller 2006), which will have negative implications for persistence of the legume component that has been for many decades the mainstay of intensively managed New Zealand pastures.

Figure 1 attempts to summarise the key direct and indirect effects and longer term feedbacks demonstrated in the FACE study. In particular the direct effects include increased primary production, particularly of the legume and below-ground components, as well as the change in tissue quality. Indirect effects relate to increased water use efficiency and nitrogen use efficiency which slow the depletion of these resources. The major negative feedback on NPP involves the effect of increased C inputs to soil on N immobilization and N limitation to primary production. The other pathway of N sequestration in biomass identified by Luo *et al.* (2004) is not relevant to grassland systems where there is minimal biomass accumulation in persistent tissue. Additionally, in a grazed legume-based system the positive feedback loop that counters N limitation is the stimulation of legume production, cycling of fixed N through the animal and return of mineral N in urine. These effects appear to mitigate PNL in such systems.

Remaining questions and new directions

As indicated above, the mechanisms driving the transient legume stimulation remain unclear, warranting further investigation of the potential impact of animal selection and plant P nutrition. Indeed, there is plenty of scope for deeper investigation of the effects of elevated CO₂ on N transformations and processes, including fixation rates,

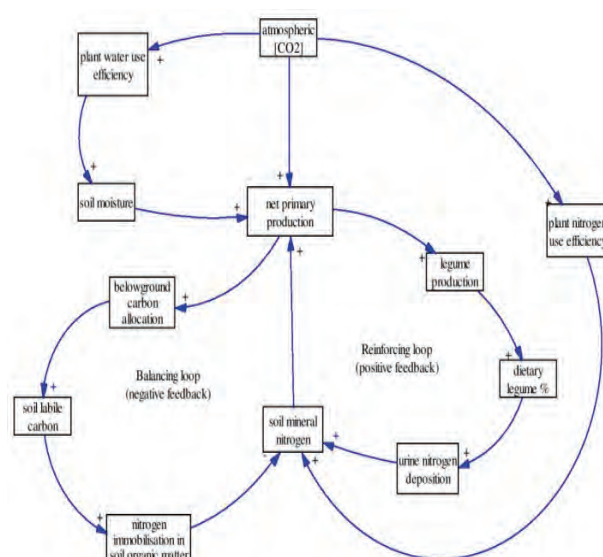


Figure 1. Cascading effects of elevated CO₂ in grazed grass-legume pastures using a causal loop diagram. Arrows indicate positive (+) or negative (-) effects of changes in one variable on another. Positive or reinforcing feedbacks are indicated by a loop where the multiplied signs are overall positive (e.g. positive feedback on NPP via N fixation and cycling through the animal); negative or balancing feedbacks are indicated by loop where the multiplied signs are overall negative (e.g. negative feedback on NPP via C inputs to soil and N immobilization).

nitrification and losses of N₂O, NH₃ (to atmosphere) and NO₃⁻ (to groundwater). The fluxes of C and N (*i.e.*, shoot senescence, root senescence and exudation) have been measured in various short-term studies but the outcome in terms of inputs to soil at the annual timescale is not well quantified. Figure 2 presents a coarse attempt at this, based on extrapolation of the data from several studies and attempting to preserve the measured treatment effects. However, the balance calculations (white boxes) are not necessarily consistent with other short term measurements, *e.g.* soil respiration is approximately 25% greater under elevated CO₂ (Ross *et al.* 2013). Quantification of these fluxes with well-validated models may be a better approach, with the added benefit of then being able to use such models for projecting the ecosystem service outcomes of future environmental drivers.

In 2012 the FACE was suspended for a major renovation, in order to conduct maintenance of the gas supply system, upgrade the control systems and install irrigation to enable soil moisture manipulation. The additional irrigation infrastructure will add to the earlier inclusion of passive warming treatments using thermal covers, and enable studies of CO₂, temperature and moisture interactions (Dodd *et al.* 2010), with a particular focus on the responses of new plant germplasm. Experiments are also planned to examine nitrogen dynamics (N fixation, nitrification and nitrous oxide emissions). Recent associated work also includes parameterization of a pasture ecosystem module within the APSIM framework (AgPasture, Li *et al.* 2011) that has the ability to simulate CO₂ effects on photosynthesis rate, nitrogen demand and stomatal conductance.

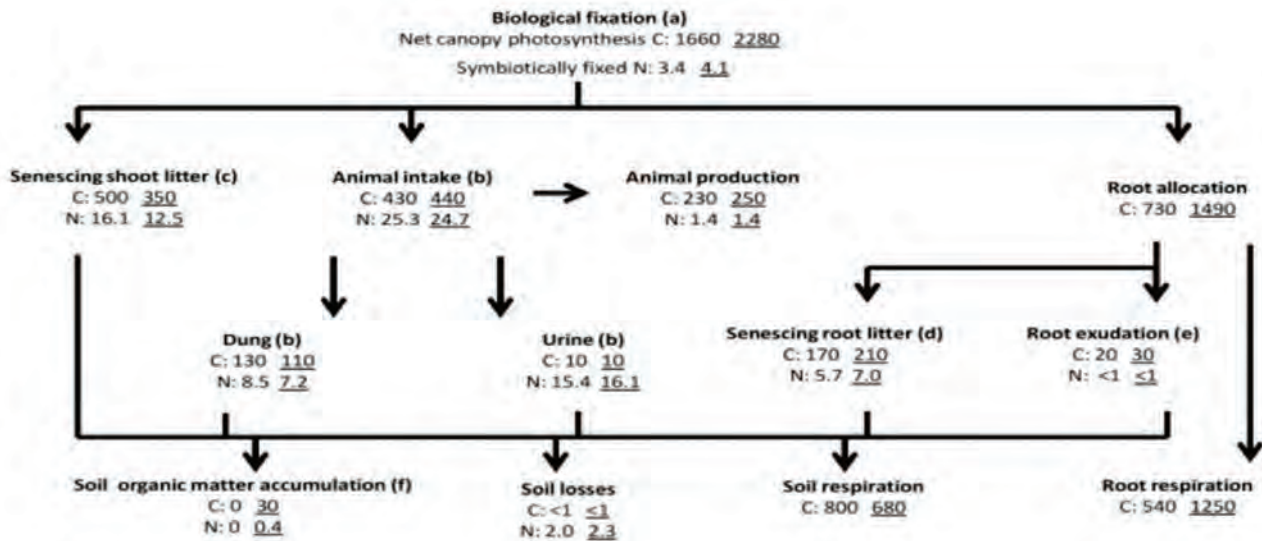


Figure 2. Coarse estimates of carbon (C) and nitrogen (N) fluxes ($\text{g/m}^2/\text{y}$) in ambient and elevated (underlined numerals) CO₂ situations for the New Zealand grassland FACE site. Estimates labelled are based on data from various publications: (a) Newton *et al.* 2001a; (b) Allard *et al.* 2003; (c) Allard *et al.* 2004; (d) Allard *et al.* 2005; (e) Allard *et al.* 2006; (f) Ross *et al.* 2013. Calculations unlabelled are calculated by difference.

Another new dimension will be the use of the biophysical data from the FACE to analyse the impacts of a future CO₂ enriched atmosphere on a range of pastoral ecosystem services, *i.e.* forage supply, nutrient regulation, water regulation, climate regulation and carbon sequestration using a recently developed soil ecosystem service analysis framework dominant (Dominati *et al.* 2010).

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