



Tomorrow's pastures: subtropical grass growth under climate change

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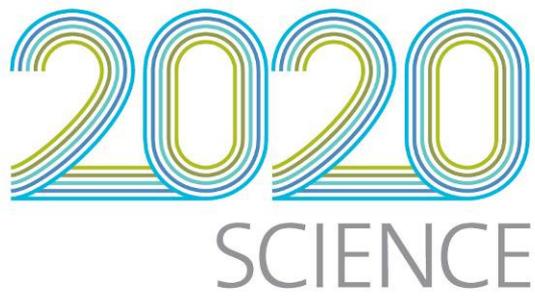
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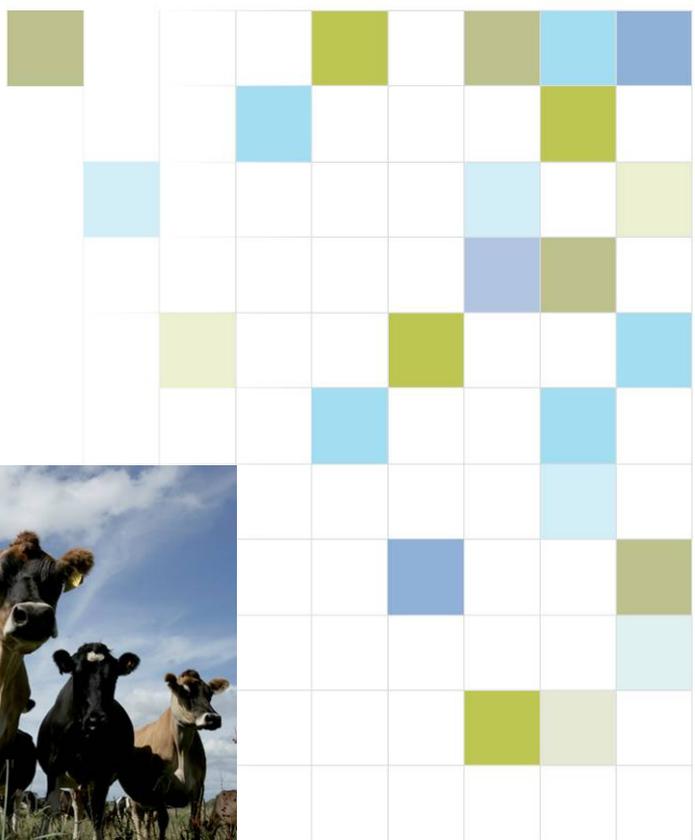
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SLMACC Project C10X0826

December 2009



New Zealand's science. New Zealand's future.



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Contract Report to MAF/FRST

December 2009

Mike Dodd, Mark Lieffering, Paul Newton and Dongwen Luo

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1. Executive Summary

We conducted experimental work and modelling to assess the impact of global change (increased temperature and elevated atmospheric CO₂) on the germination and growth of C4 grass species relevant to New Zealand. While we conducted experiments with *Digitaria sanguinalis*, *Paspalum dilatatum* and *Pennisetum clandestinum* the report focuses most strongly on *Pennisetum* (kikuyu). The experimental work was carried out at the NZ FACE experiment which simulates the atmospheric CO₂ concentration and temperature change expected in 25-30 year's time (475 ppm CO₂ and + 0.5-1.0 °C warming during nighttime). The results showed a strong response, particularly of the kikuyu, to temperature largely through an increased mineralisation of N for plant growth. The effect of elevated CO₂ was to dampen the mineralisation response thus leading to a CO₂ × warming interaction reducing the stimulatory effect of temperature change.

We used the data to parameterise and verify an ecosystem model that we then ran to simulate future conditions for a hypothetical farm in the Manawatu region. The financial cost of climate change due to increased C4 growth and thus reduced herbage quality was \$25,000 per annum in additional purchased feed for a 100 ha farm for the temperature only scenario and \$7,500 per annum for the increased temperature and elevated CO₂ scenario.

These results cause us to revise our view of the likely impact of C4 grasses and will allow us to make more robust predictions for pastoral agriculture across a range of systems in New Zealand.

2. Introduction

Pastoral agriculture, producing about 40% of New Zealand's exports by value, is potentially very vulnerable to climate change (MAF 2007) by virtue of its overwhelming reliance on immediate forage supply. The industry is founded on pastures based on ryegrass and white clover, both of which use the C3 photosynthetic pathway, which makes them eminently suited to our historically temperate climatic conditions. However, projected future global change scenarios for New Zealand indicate warmer temperatures combined with less rainfall in the north and east of the country and more rainfall in the south and west (Mullan et al., 2008). Warmer temperatures, especially when combined with drier conditions, are

likely to shift the competitive balance toward subtropical grasses having the C4 photosynthetic pathway (e.g. kikuyu and paspalum, Collatz et al. 1998). These types of grasses are already present in northern New Zealand (distributed approximately north of a line from Taranaki to the Waikato to the Bay of Plenty; Field, (1989)) but low winter temperatures generally restrict their growth elsewhere. Given the projections of warmer temperatures and drier summers, there is an expectation that the C4 species will spread and/or increase in dominance over large areas of the North Island as a result of climate change (Field & Forde 1990).

The spread and increasing dominance of C4 species with climate change has the potential to negatively affect productivity and profitability of farming enterprises currently based on C3 pasture species. Pastures dominated by C4 grasses can produce more dry matter on an annual basis when grown under conditions favourable to them (Crush & Rowarth 2007) but this material is usually of a lower feed quality compared to the C3 grasses (Barbehenn et al 2004). In addition, the marked seasonality of the C4 grasses (their lack of winter and spring growth and a large peak of material of low quality in the summer), means that the amount of metabolisable energy available for animal production at crucial times of the year can be much lower.

Though C4 species are widespread in New Zealand, under current climatic conditions their dominance is confined to Northland and coastal areas of the Northern North Island (Edgar and Connor 2000).. Given the potential economic losses with increasing dominance (see below) it is surprising that there is very little information on the potential of C4 species to spread and dominate New Zealand pastures as a result of climate change. Climatic “envelopes” for occurrence (but not growth and dominance) in relation to selected parameters have been determined for a number of C4 species in New Zealand (Campbell et al., 1999). However, elevated CO₂ was not able to be included in generating the envelopes. Recent work ranging from single leaf to meta-analyses has shown that C4 species can and do respond to elevated CO₂, and especially under warmer conditions, more so than C3 species (Wand et al., 1999; Sage and Kubien, 2003). In order to forecast C4 dominance in response to changing climate and elevated CO₂, the interactions with other factors must also be considered, namely competitiveness with other species in the pasture, selection effects of grazing animals and soil biogeochemical feedbacks. To make progress in this we used a unique experimental facility that enables large areas of intact vegetation to be grown (and

grazed) under ambient or elevated CO₂ combined with control or warming regimes. The facility is located in a region where a number of C4 species occur at relatively low abundance and provides an ideal opportunity to test how C4 abundance might alter under global change.

3. Objectives

The objective of this project was to investigate the effect of elevated CO₂ and increased temperatures on the germination, emergence and early growth of C4 subtropical grasses within a region currently dominated by C3 pastures. The results were aimed to provide the information necessary to evaluate the C4 threat and enable the development of strategies to deal with it.

4. Methods

The study consisted of two elements: a) a series of field experiments designed to assess the germination and early growth of three C4 grass species under varying conditions of temperature and CO₂. This experiment was located at the NZ FACE facility at Flock House, Bulls; and b) a modelling exercise examining the potential effect of elevated CO₂ and warming interactions on pasture growth and forage quality using the pastoral simulation model EcoMod (Johnson et al. 2008).

4.1 Field experiments

4.1.1 FACE Site

The NZFACE facility consists of six circular grazed pasture plots of 12 m diameter, three of which have the atmospheric CO₂ content enriched from current ambient levels (385 ppm) to 475 ppm. The facility and the general pasture measurement protocols are described by Newton et al. (2006). Each ambient and elevated CO₂ plot has a passive warming system installed. This consists of covering a 3m × 3m area of the experimental plot at night with a long wave radiation blocking cover raised 500 mm above the surface to reduce the heat lost by infra red (IR) radiation. The method raises both day and night soil temperatures, but air temperatures are raised only at night and for a period during the early part of the photoperiod (day time) at canopy height. In our testing phase we showed that our system resulted in warming of about 1°C at 5 cm soil depth across the day (Lieffering and Newton, 2008). The design for this project will therefore include a

total of 12 experimental units: two CO₂ levels (ambient and elevated) × two temperature regimes (control and warmed) × three replicates.

4.1.2 C4 grass germination/emergence

For the germination/emergence experiment, seeds of four accessions of three C4 species present in the vicinity of the FACE (Table 1) were selected. Laboratory germination tests were conducted on the seed to establish % viability (tetrazolium stain).

Table 1: Species/accessions used in the study.

Botanical name	Common name	Life form	Accession ¹
<i>Digitaria sanguinalis</i>	summer grass	annual	BZ4724
<i>Paspalum dilatatum</i>	paspalum	perennial	cv. Raki
<i>Paspalum dilatatum</i>	paspalum	perennial	BO445
<i>Pennisetum clandestinum</i>	kikuyu	perennial	cv. Whittett

¹Margot Forde Germplasm Centre, Palmerston North

Within each experimental unit, four soil cores of 120 mm diameter and 50 mm depth were taken from the pasture, the plant material removed and the soil replaced to create a gap in the sward. Sowing lots of each accession, sufficient to include twenty viable seed, were hand sown into the gaps on June 16, 2009. Grazing in the main experiment was carried out at periodic intervals when pasture mass reached approximately 2000 kgDM ha⁻¹. The small plots of sown seed were protected from grazing by cages and the resident vegetation harvested to grazing height with electric shears at the same time as the grazing events.

A visual assessment of emergence above the soil surface was made every 7 days from August 6 until November 3, 2009. Emerging seedlings that were identified as non-sown species were removed. Cumulative germination curves were developed based on the sum of positive seedling increments over time.

4.1.3 Autumn growth

Seed of the three species in Table 1 were germinated in incubators in December 2008 for transplanting into the FACE in January 2009. Despite the application of alternating diurnal temperatures (30/20°C) and KNO₃ solution as indicated in the literature (Hsu et al. 1985, White et al. 2001) to the seed lots, insufficient seedlings of paspalum and digitaria germinated and hence these species were not transplanted.

In each experimental unit, an area of 500 x 500 mm was sprayed with glyphosate (10 ml L⁻¹) in mid-January 2009 and the herbage residue removed. On February 16, twenty-one kikuyu seedlings were transplanted into the sprayed plots. Survival was monitored on March 6. Ten surviving plants were tagged with plastic rings around the main tiller/stolon on March 19 as resident vegetation recovered. On each plant, one unfolded leaf was marked on March 26 and its length measured 7 days later to assess leaf extension rate. Leaf numbers on the marked stolon were counted weekly from April 9 until May 21 and mean weekly leaf appearance rates were calculated from the average of the 10 duplicate plants in each experimental unit.

4.1.4 Spring growth

Seven genotypes of kikuyu and five genotypes of paspalum were selected for transplanting into the FACE in spring 2009. The kikuyu genotypes were sourced from plant material collected in Northland in 1997 and subsequently maintained in pots outside at Palmerston North and the paspalum genotypes were sourced from plant material collected from pastures at Grasslands Research Centre, Palmerston North. Rooted stolon (for kikuyu) and rhizome (for paspalum) cuttings were transplanted into plastic sleeves of 50 mm diameter and 120 mm depth and the sleeves transferred to excavated holes in the experimental units of the FACE on August 20 (see Plate 1). Each experimental unit included one plant of each genotype (i.e. 12 plants per experimental unit without duplication).



Plate 1: A transplanted kikuyu stolon.

At weekly intervals from September 2 until November 3, each plant was measured for the number of growing points, the number of emerged leaves on a marked tiller (the oldest tiller) and the length of a marked leaf on the marked tiller (the oldest green leaf). On November 3, all green tissue was harvested from each plant, dried at 65°C and weighed for dry mass accumulation.

4.1.5 Soil moisture, temperature and plant available nitrogen

Volumetric soil moisture to 120 mm depth was measured at weekly intervals using time domain reflectometry (TDR 300, Spectrum Technologies Inc., Plainfield, Illinois, USA); eight measurements per ring were taken in warmed and unwarmed treatments. We measured air temperatures in every control and warmed plot in all ambient and elevated CO₂ rings at 20 cm above the soil surface using a solar radiation shielded USB temperature/humidity datalogger. Samples were taken every 5 minutes; these were averaged to give hourly values. To determine the level of warming, the hourly differences in temperature between the warmed and control plots were calculated and averaged for the ambient and elevated CO₂ rings. Plant nutrient availability was measured using ion exchange membranes (Bowatte et al. 2008); membrane sheets (50 mm x 10 mm, VWR International Ltd, Poole, England) were

fixed to plastic plant labels (100 mm x 15 mm) and inserted in the soil in the centre of the circular sampling area to leave the top of the sheet at the soil surface so that the effective depth sampled was 50 mm. Membranes were removed and replaced at a two-weekly interval. After removal, membranes were washed with distilled water, extracted with 25 ml of 0.05M HCl and analysed for nitrate and ammonium content using a FIAstar 5000 flow injection analyser (Foss Tecator, Hoganas, Sweden)

4.1.6 Statistical analysis

Where plants were measured at intervals the data were analysed as a split-plot repeated measures design; CO₂ was taken as the whole plot and temperature as the sub-plot. Mixed models were used in REML variance components analysis using Genstat (Payne et al. 2008). Seedling emergence data were square root transformed, modelled with a logistic equation and the three parameters analysed in R.

4.2 Simulation modelling

While a number of C4 species occur in the Manawatu , they make a limited contribution to pasture mass (at our Flock House experimental site, a maximum of 5% of pasture dry matter, Newton et al. 2006). As such, it is a useful location to explore the effects of global change (increasing atmospheric CO₂ levels and temperatures) on not only C4 growth but also the interactions between the currently dominant C3 grasses. To understand the long term effects of global change on these dynamics, we used a biophysical simulation model (EcoMod; described in Johnson et al., 2008) that mechanistically simulates most of the plant, soil and animal processes in multi-species grazed grasslands.

We ran simulations 1) under current conditions of temperature and CO₂; 2) with future projected warming and current CO₂ levels or 3) with future projected warming and CO₂ levels. For the present day simulations EcoMod's stochastic weather generator was used to produce weather that matched the long term mean of the weather in the Manawatu; for the change scenarios a stepwise change of 2 °C to the mean minimum and mean maximum temperatures with or without an increase to 600 ppm CO₂ were used. Rainfall and other climatic parameters were not changed.

Simulations were run for a hypothetical paddock composed of a representative C3 species (ryegrass) and C4 species (kikuyu). To simplify interpretation of the results, no animals were used (all harvesting was done through cutting with the herbage returned uniformly as dung and urine). Cutting was carried out when the dominant species (usually ryegrass) reached the 3-leaf stage of growth; the pastures were cut to a residual of 1500 kg DM ha⁻¹. The soil type was Ecomod's default clay-loam. No nutrients were exported from the system as milk or meat though N could be lost by leaching and/or volatilisation. In addition, for simplicity, no legumes were included in the pasture and N fertiliser was added at each cutting episode. This amounted to about 100 – 140 kg N ha⁻¹ year⁻¹ which is typical of the amounts of N fixed by legumes in NZ pastures. All other nutrients were assumed to be non-limiting. We kept most model parameters at their default values. However, we changed some of the kikuyu parameters based on the experimental results and to better reflect reports in the literature on kikuyu growth and performance in Northland. For example, the sensitivity of kikuyu to low temperatures was increased: the onset of low temperature stress was increased from 6 to 13 °C while the occurrence of full stress was increased from the default of 2 °C to 7 °C (i.e. there was no kikuyu growth when the average daily temperature fell below 7 °C). Similarly, kikuyu was made more tolerant to water stress and was given a deeper rooting depth. Finally, because there is no option to change seasonal digestibility, as happens with kikuyu, we decreased the digestibility of the live plant material to an annual average of 50%.

Simulations were run for 100 years to enable sufficient “spin-up” of the model variables, particularly those relating to the soil organic pools. Daily output from the last 20 years were averaged to give monthly and annual outputs of the variables of interest: total annual dry matter (DM) yield, monthly DM yields as well as percentage of kikuyu in the pasture and seasonal metabolisable energy (ME) content. Because data from our long-term free air CO₂ enrichment experiment suggests that mineral N becomes less available under elevated CO₂, we also determined average annual levels of nitrate and ammonium in the soil solution of the profile.

To explore the financial implications of changes in pasture composition with warming and future CO₂ levels, we performed an analysis involving ME availability and requirement. Average monthly ME requirements were determined for a high producing dairy cow (600 kg MS yr⁻¹). Based on the available literature, the maximum intake was set at 20 kg DM d⁻¹: multiplying this by the nutritive value of the pasture on offer in any month sets the upper limit to the amount of energy

that could be obtained from the pasture. Any deficit to this requirement was assumed to be made up by supplementary feed with an energy content of 10 MJME kg DM⁻¹ costing \$0.2 kg DM⁻¹ (Chaston 2008). We assumed the cost was for buying extra feed, rather than saving feed and making hay/silage on-farm. This cost was then extrapolated to a 100 ha farm carrying 250 cows.

5. Results

5.1 Field experiments

5.1.1 Passive warming treatment

In the passive night-time warming plots, air temperatures at 20 cm above ground level were 0.8-1.3°C higher compared to unwarmed plots (Fig. 5.1).

Warming was slightly greater and more consistent in the autumn (average across CO₂ levels of + 1.18 °C) due to extensive periods of rainy and cloudy conditions in the spring making the passive warming less effective (+0.93 °C). In the autumn, warming was 0.34 °C higher in the future CO₂ plots compared to the current CO₂ plots while the difference was only 0.15 °C in the spring.

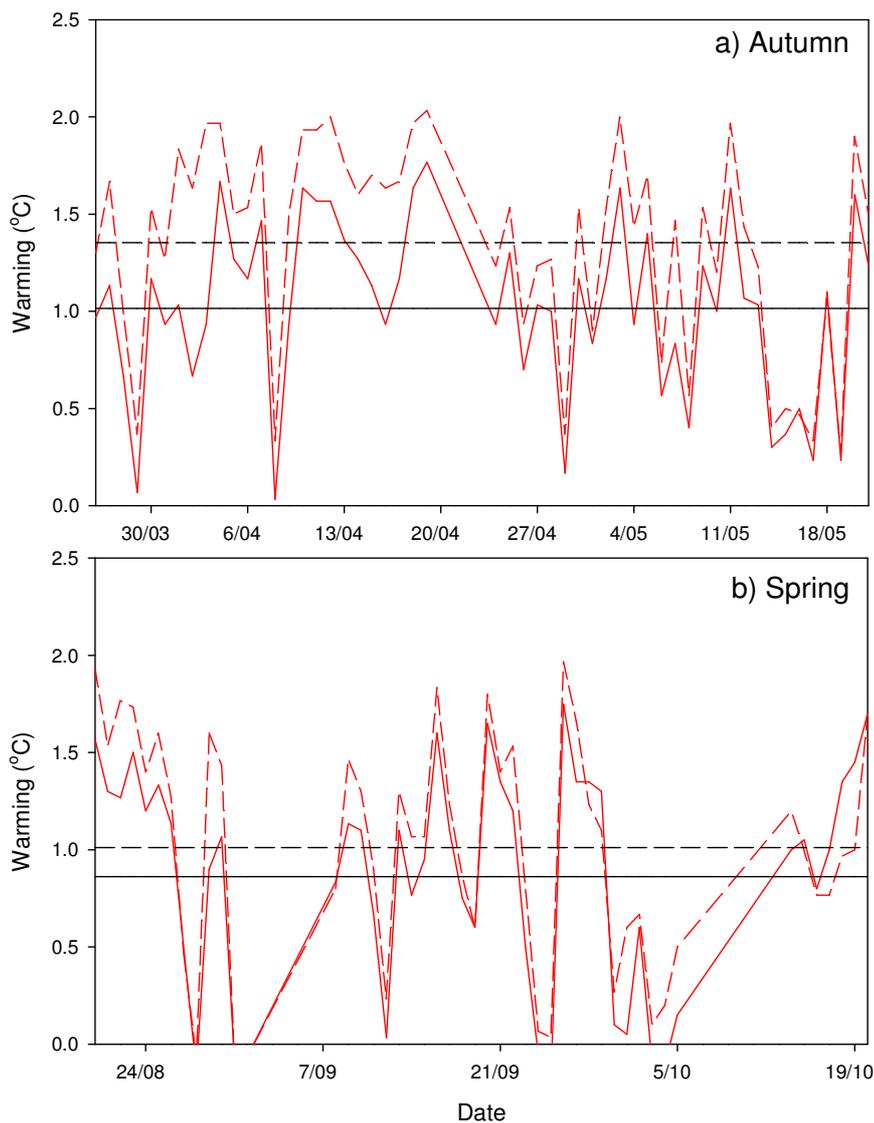


Fig. 5.1: Daily difference in minimum night-time air temperatures at 20 cm above the ground for the current (solid red lines) and future (dashed red lines) CO₂ levels in (a) autumn and (b) spring 2009. Individual data points not shown. The horizontal black lines are the averages for the current (solid) and future (dashed) CO₂ levels.

5.1.2 Germination/emergence

Viability according to the tetrazolium test was high for the kikuyu cultivar, moderate for the paspalum cultivar “Raki” and the digitaria, and low for the paspalum accession (Table 2). Total cumulative seedling emergence was highest in the two paspalum accessions, followed by kikuyu and very low numbers for digitaria (Table 2). These relativities were similar throughout the period of measurement.

Table 2: Viability (tetrazolium test) and field emergence of four C4 genotypes.

Botanical name	Accession	Viability (%)	Mean total seedlings emerged (of 20 viable)
<i>Digitaria sanguinalis</i>	BZ4724	68	3.5
<i>Paspalum dilatatum</i>	cv. Raki	63	10.3
<i>Paspalum dilatatum</i>	BO445	12	10.0
<i>Pennisetum clandestinum</i>	cv. Whittett	92	7.2

There was a significant effect of the CO₂ enrichment treatments, but not of the warming treatments, on the pattern of emergence for all accessions combined (Fig. 5.2). Emergence followed a typical asymptotic pattern in the current CO₂ rings but a more linear pattern in the elevated CO₂ rings. Consequently, total percentage emergence was not different between treatments but was reached at an earlier stage in current CO₂ conditions (i.e. the half-maximum parameter in the logistic model was significantly lower). The patterns for all species combined were largely a reflection of the patterns for the two paspalum accessions.

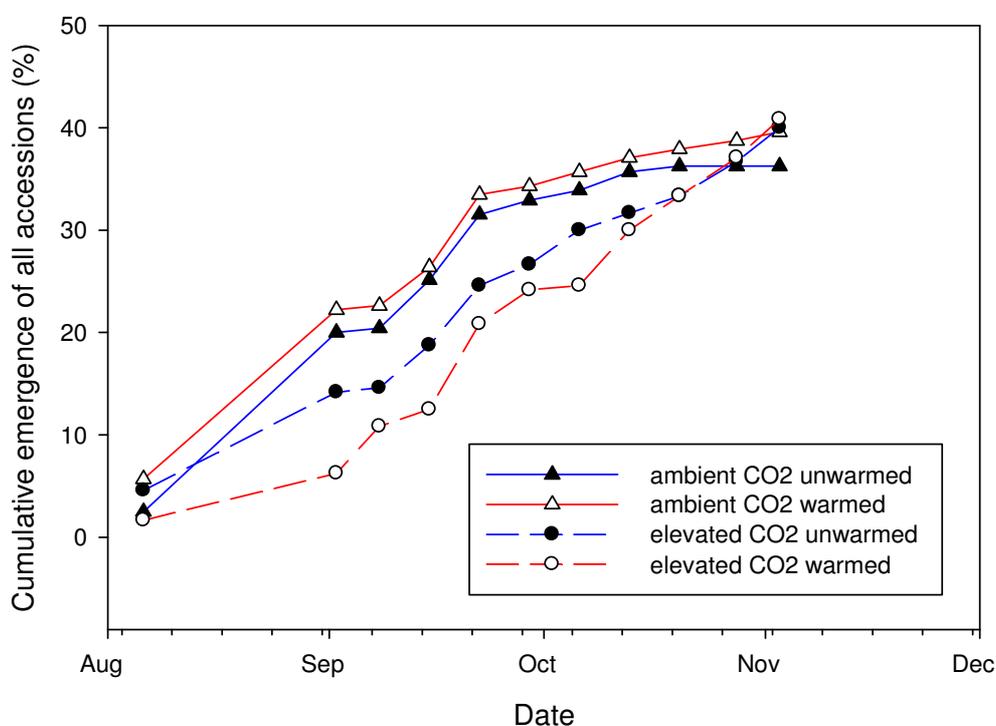


Fig. 5.2: Cumulative emergence (percent of viable seed) of seedlings for all four C4 accessions combined.

5.1.3 Autumn growth and soil conditions

Survival of the autumn-transplanted kikuyu seedlings averaged 70% overall between planting in mid February and the first leaf measurements in late March. This level varied between the rings (one as low as 20%) but was fairly consistent between the treatments.

Leaf extension of the autumn-transplanted kikuyu was minimal and showed no differences between the CO₂ and warming treatments. It was apparent that most of the extension occurred as the youngest leaf was emerging, which makes measurement difficult as the base of the lamina is often obscured at this point. Substantial leaf tip damage from unidentified sources also complicated these measurements.

Weekly mean leaf appearance rates varied from 0.25 to 1.3 leaves/week during April and May (Fig. 5.3a). The pattern of leaf appearance showed an initial decline during April, a brief resurgence in late April – early May before declining again in May. There was a significant CO₂ × warming effect (p=0.008) with the fastest rate of appearance under warming in current CO₂ and the slowest under warming at elevated CO₂. By the end of May few new leaves were appearing and many plants showed extensive senescence. There was no evidence that the different CO₂ and warming treatments had any effect on the maintenance of the growth of kikuyu into the cool season, and all plants died over the winter.

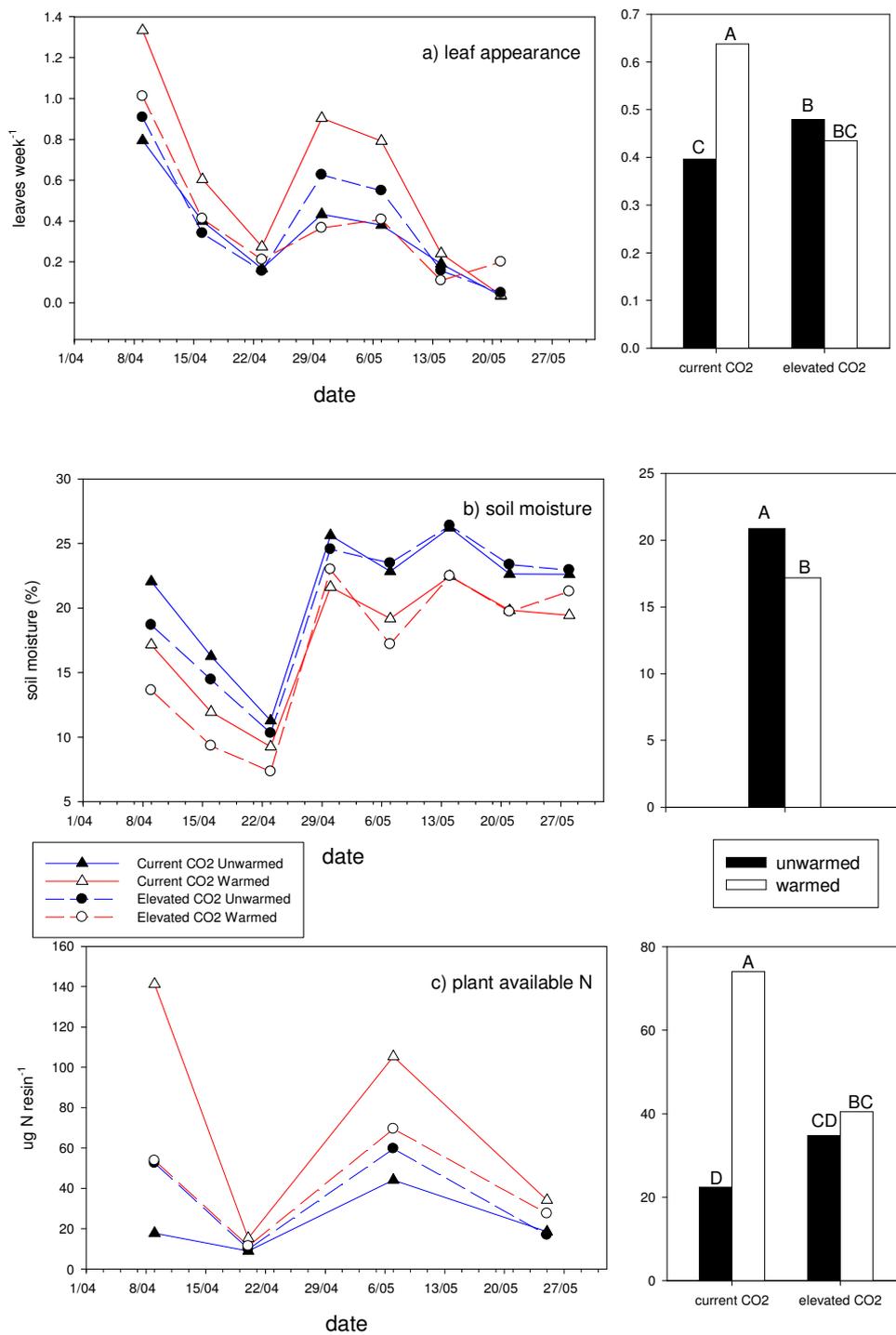


Fig. 5.3: a) leaf appearance rate of kikuyu, b) soil moisture content and c) plant available nitrogen during autumn 2009. Line graphs show the data over time and bar graphs the main effects from a repeated measures analysis; in no cases was there an interaction over time. Bars with different letters represent means that are significantly different ($p < 0.05$).

Volumetric soil moisture content (Fig. 5.3b) ranged from less than 10% to greater than 25%. There was significantly ($p < 0.001$) lower soil moisture in the warmed treatments at both current and elevated CO_2 .

There was a significant $\text{CO}_2 \times$ warming effect on plant available nitrogen (N) (Fig 5.3c) ($p = 0.008$); most nitrogen was available under warming at current CO_2 but the warming impact was absent under elevated CO_2 . Figure 5.4 shows the rate of leaf appearance plotted together with plant available N. The similarity in these curves within treatments suggests a strong influence of N availability on leaf appearance rates.

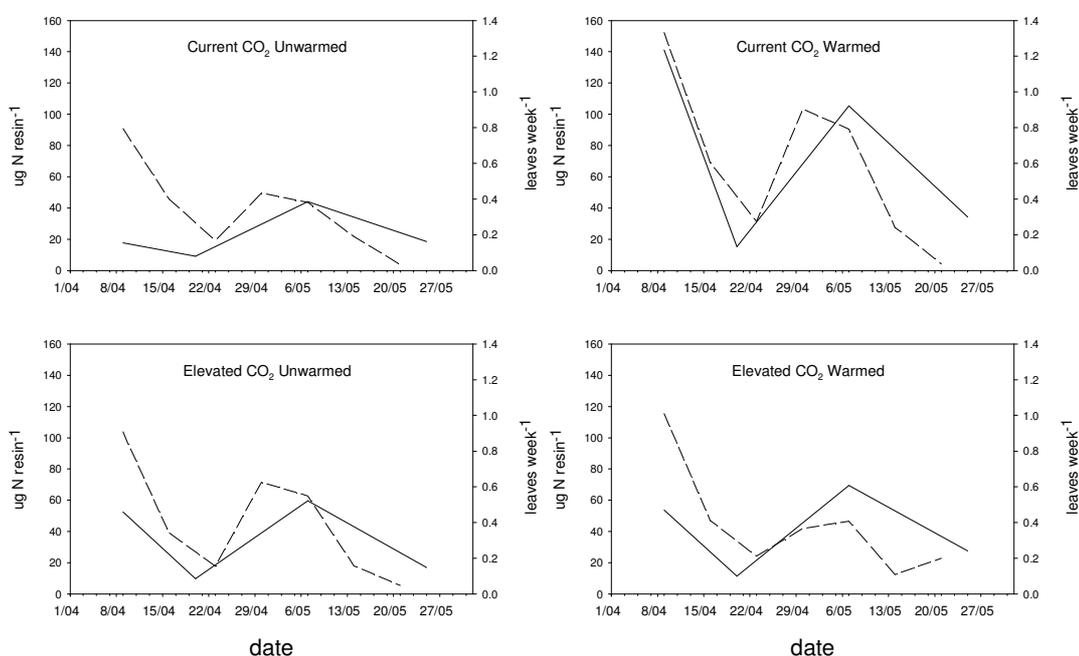


Fig. 5.4: The data for leaf appearance of kikuyu (dashed line) and plant available nitrogen (solid line) by treatment in autumn 2009.

5.1.4 Spring growth and soil conditions

Survival of the spring-transplanted kikuyu was approx. 60%, again variable between rings but largely consistent between treatments. All transplanted paspalum survived.

Mean leaf appearance rates for kikuyu varied between 0.27 and 1.2 leaves/week during the spring, being highest in mid-September, declining from then until mid-October and increasing rapidly after that (Fig. 5.4a). Mean leaf

appearance rates for paspalum (data not shown) varied much less, being fairly consistently between 0.2 and 0.6 leaves per week over most of the spring period except for one week in late September when they averaged 1.2 leaves per week. There was no significant effect of the treatments on leaf appearance rate for either species.

Soil moisture in spring was high throughout, increasing from 30% to over 45% with no difference between treatments (Fig. 4b). Plant available N showed a similar response as in the autumn with the highest N availability in the current CO₂ warmed treatment (Fig. 4c), although the absolute levels were much lower than those measured in autumn.

As was observed in autumn, leaf extension was minimal on the measured kikuyu leaves. Only during the second week did we measure an increase in length substantially greater than the estimated operator measurement error associated with the callipers (~3mm). During this period the extension rate was approx. 10 mm, with no significant effect of the CO₂ and warming treatments. For paspalum, we measured extension rates of 5-7 mm/week for the first three weeks before the estimates dropped below the estimated measurement error. Again there was no significant effect of the CO₂ and warming treatments and these data are not shown.

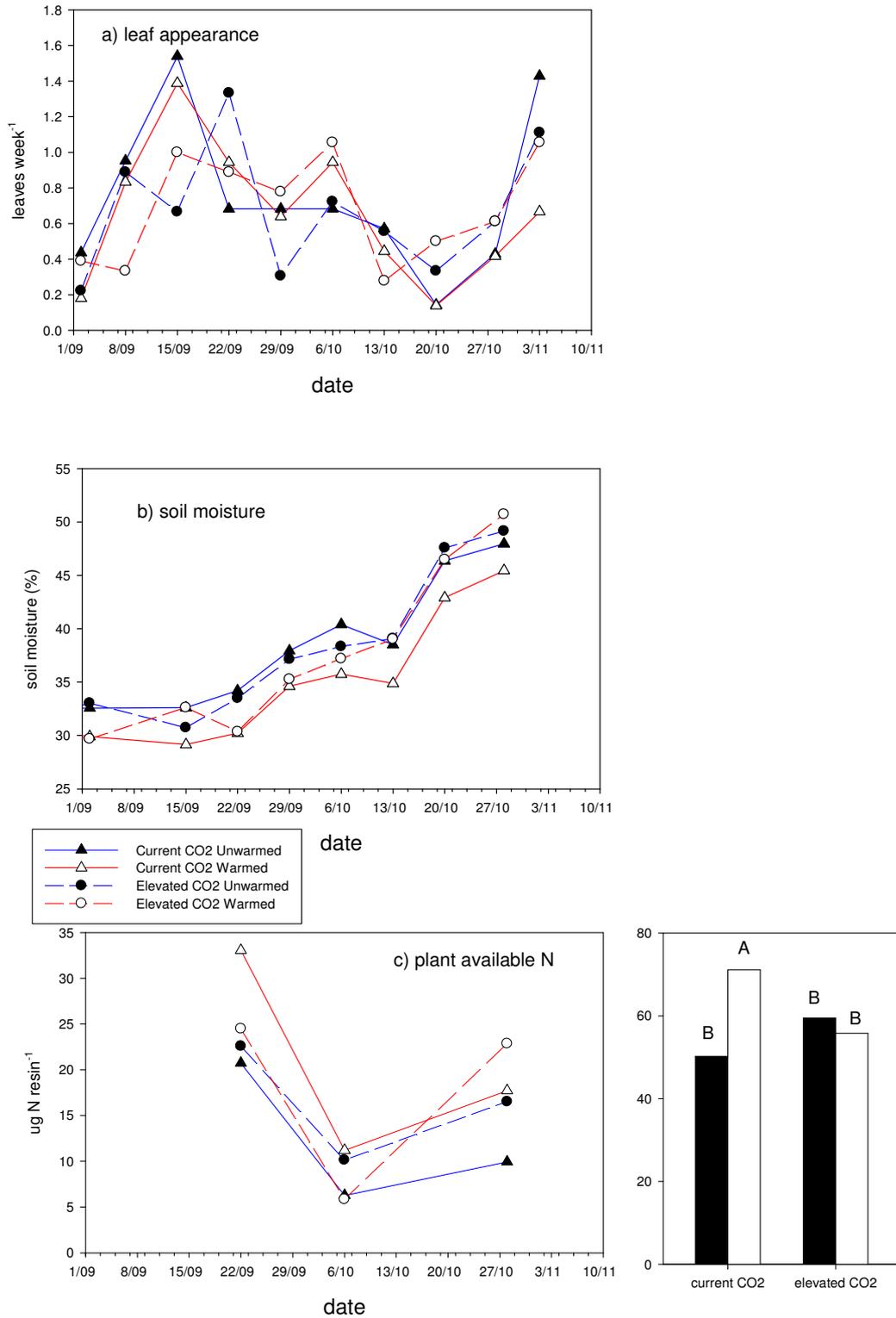


Fig 5.4: a) leaf appearance rate of kikuyu, b) soil moisture content and c) plant available nitrogen during spring 2009. Line graphs show the data over time and bar graphs the main effects from a repeated measures analysis; in no cases was there an interaction over time. Bars with different letters represent means that are significantly different ($p < 0.05$).

The plants were harvested on 3 November, 75 d after transplanting. There was no difference between the mass harvested by species or treatments. However, when mass was expressed per growing point there was a significant CO₂ × warming interaction (p=0.018) with the elevated CO₂ plus warmed growing points showing the greatest mass (Fig 5.5).

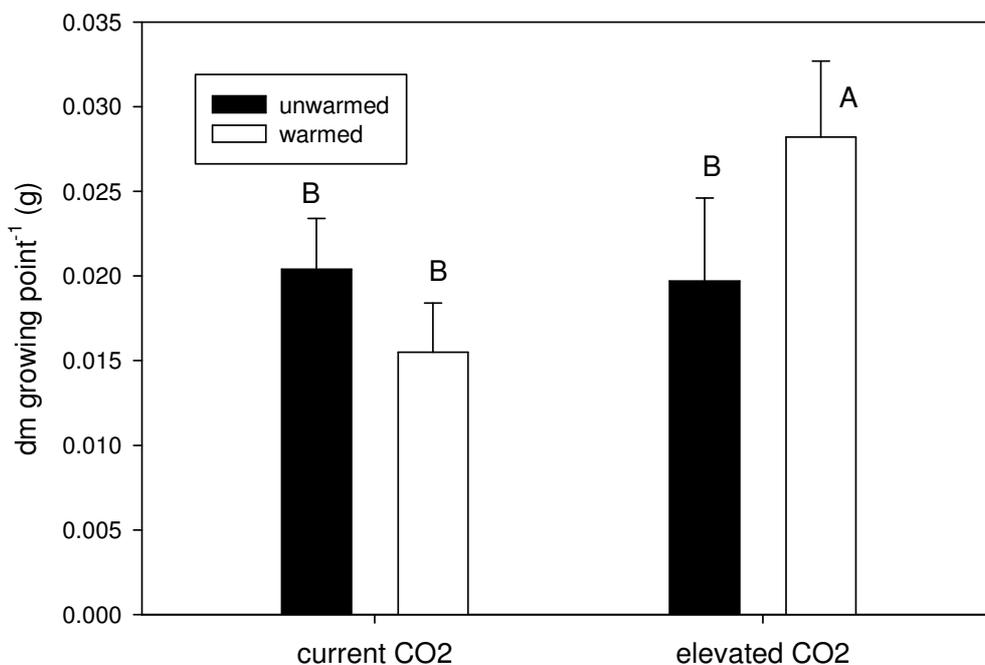


Fig 5.5: Mass per growing point for paspalum and kikuyu plants on 3 November, 75 d after transplanting.

We examined the relationship between N availability and leaf appearance and found a strong positive linear relationship for the autumn data (regression $p < 0.001$; adjusted $R^2 = 0.58$) (Fig 5.6a). The data for spring (Fig 5.6b) showed no relationship but values for the resin N were much lower than those measured during autumn (see Fig 5.3c cf. 5.4c).

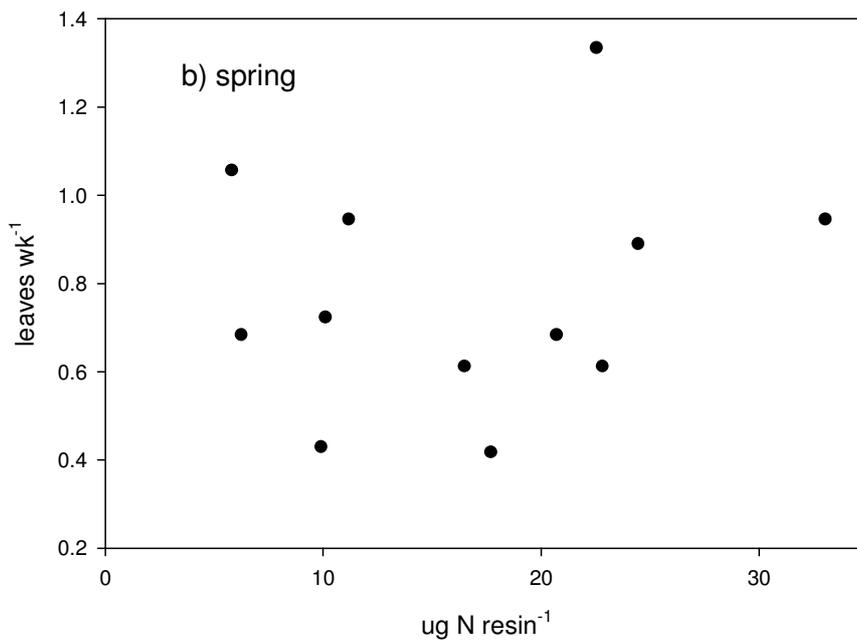
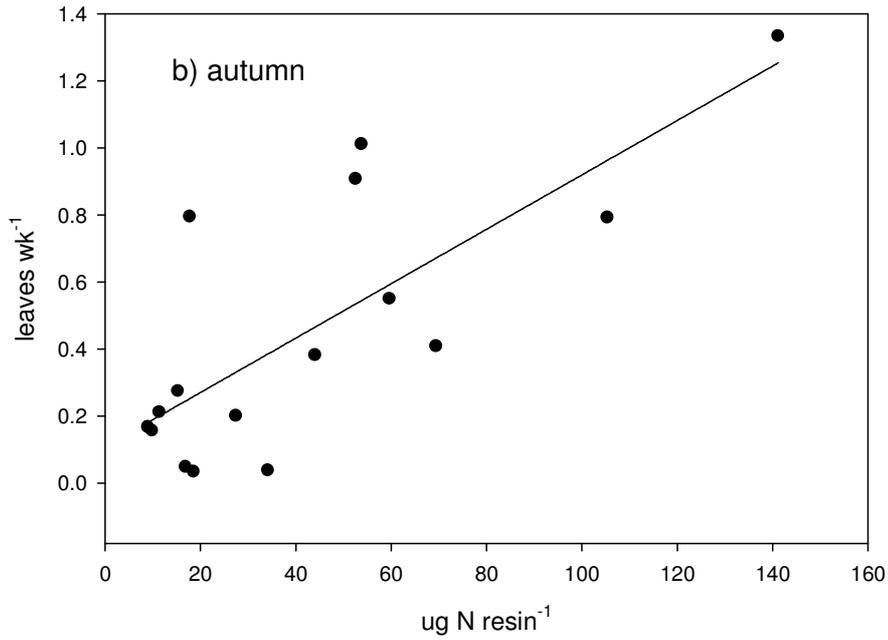


Fig 5.6: Leaf appearance rate of kikuyu plotted against plant nitrogen availability for a) autumn and b) spring 2009.

5.2 Simulation modelling

The key results of the simulations run to determine the effects of future warming only or future warming and elevated CO₂ are shown in Fig. 5.7.

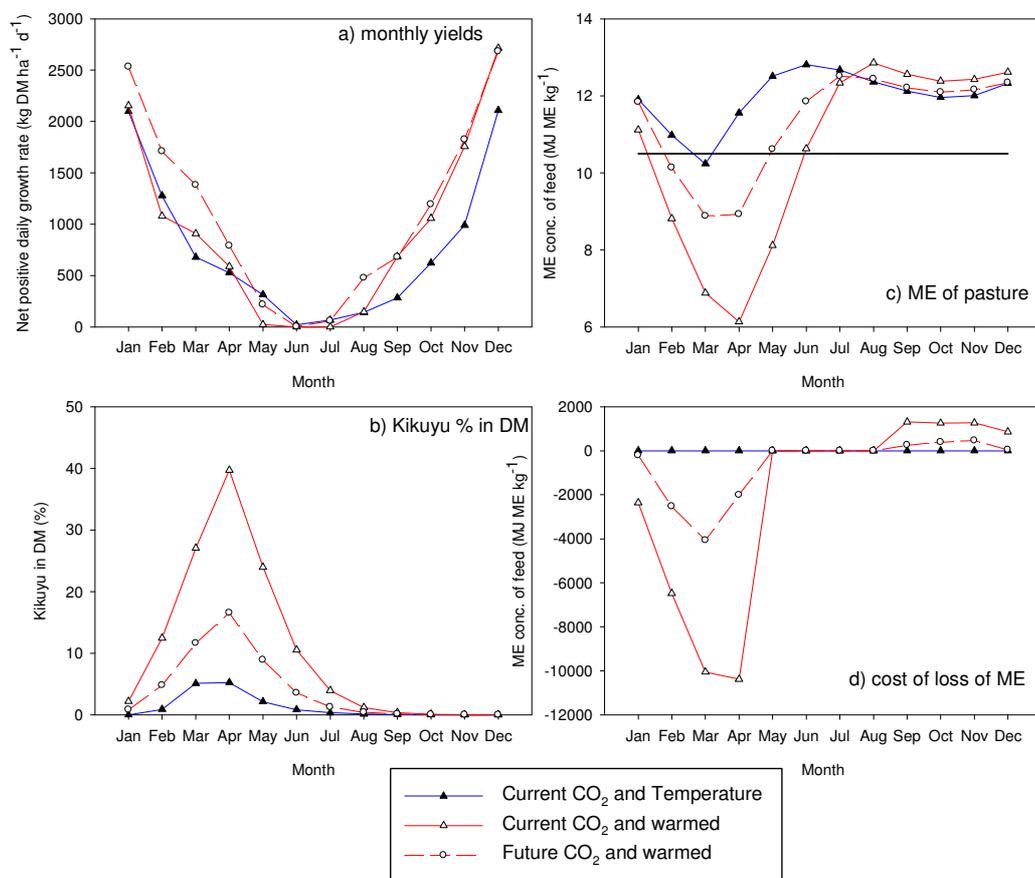


Fig 5.7: Simulated monthly a) yield, b) kikuyu % in DM; c) metabolisable energy (ME) content of the pasture and d) additional costs to maintain ME intake for a 250 cow farm (see text for details) for three scenarios. Solid horizontal line in c) indicates the ME requirement for milk production.

Warming alone increased total annual DM yields from about 9 to 11 t ha⁻¹ (+22%). It is worth noting that annual DM yields for the NZ FACE site over the last 5 years have been 8-9 t ha⁻¹. The greater annual yield with warming was due mainly to increases in ryegrass spring growth rates (Fig. 5.7a). The warming doubled mineral N content in the soil in the spring, most likely due to increased mineralisation rates (data not shown). The combination of greater N availability, warmer temperatures and the lack of competition from kikuyu (Fig. 5.7b) led to enhanced growth of ryegrass.

With warming alone there was little or no increase in yield for either the autumn or winter. The most marked effect was the large increase in kikuyu

content of the pasture over the late summer and autumn, from about 5% to 40% (Fig. 5.7b). In the late summer-autumn, warming did not increase ryegrass growth rates, probably due to competition for soil moisture from the kikuyu. Kikuyu responded strongly to the increase in temperature and is more tolerant of the lower soil moisture levels at that time of year. Hence the increase in kikuyu growth compensated for the decrease in ryegrass growth leading to no change in overall yield at this time of year.

The increase in kikuyu content over autumn with warming resulted in decreases in the ME content of the pastures from about 10.5 to 6 MJME kg DM⁻¹ (Fig. 5.7c). Although annual total ME produced was greater under warmed conditions (data not shown), for much of the year the pasture was of very low nutritional value relative to the requirements of lactating cattle.

The combination of warming and future CO₂ levels increased yields to about 13 t ha⁻¹ (48% greater than current CO₂ and temperatures). This increase was due to increases in pasture growth rates in both spring and autumn (Fig. 5.7a). Because kikuyu was almost absent in the spring, the increase in pasture growth rates in spring can only be attributed to greater ryegrass growth. However, because pasture growth rates in the spring were similar to warming alone, the response was likely to have been due almost entirely to the warming rather than the elevated CO₂. A factor that may have restricted the ryegrass response to elevated CO₂ was that compared to warming alone, the addition of elevated CO₂ decreased spring soil mineral N levels (data not shown).

In contrast to the spring, in the late summer-autumn pasture growth rates were appreciably higher under future CO₂ and warming. This can be attributed largely to the change in pasture composition: kikuyu responded less strongly to elevated CO₂ than ryegrass. Hence kikuyu growth was depressed relative to warming only and its contribution to the pasture DM fell from 40% to about 15% (Fig. 5.7b). This then led to less competition for soil moisture (data not shown) and greater ryegrass growth rates. Along with the decrease in kikuyu percentage with future CO₂ levels there was a concomitant increase in pasture ME content from 6 to about 9 MJME kg DM⁻¹; though this level is still less than optimal for milk production.

Figure 5.7d shows the results of the simple financial analysis, with the effect of warming by itself or in combination with future CO₂ levels being shown as the differential cost or benefit relative to the base scenario. The increase in kikuyu

content of the pasture in the late summer and autumn led to extra feeding costs in the order of \$10,000 per month for warming by itself. For both scenarios, there was a slight benefit in the spring from the extra growth. The overall cost of the extra kikuyu was about \$25,000 and \$7,500 a year for warming by itself and warming plus future CO₂ respectively.

6. Discussion

6.1 Field experiments

Our experimental data are the first to document climate change impacts on C4 grasses in a grazed field experiment. Treatment effects, where they occurred, were largely interactions between CO₂ concentration and temperature showing how important it is to consider both of these aspects of our future environment rather than just temperature. The aim of the experimental work was to find parameter values and insights that would enable us to model a range of future scenarios involving C4 grasses.

Germination and emergence are not life history stages included in physiologically based models such as EcoMod; however, these are crucial stages in the spread and establishment of plant populations. Establishment was poor with a maximum of 40% emergence (Fig. 5.2). This response was not unexpected for the perennial species *Paspalum* and kikuyu which are notoriously poor germinators (Hsu et al. 1985 Schrauf et al. 1995). Day-night soil surface temperature amplitudes (White et al. 2001) may have been insufficient at this site during the period studied. The annual *Digitaria* might be expected to have higher germination, but the result here (17% of viable seed sown despite apparently good soil moisture conditions) confirms other work (White et al. 1997). Embryo dormancy is a possible explanation (Gallart et al. 2008) though a lab germination test we carried out using the dormancy-breaking methods shown to be successful in that study failed to improve germination in this accession.

A more surprising result was that there was a CO₂ effect on emergence with elevated CO₂ suppressing emergence (Fig 5.2). A germination and emergence response to warming was anticipated, but not observed and the effect of CO₂ was unexpected. One explanation for this may well be the lower availability of mineral N in the elevated CO₂ treatment (Fig. 5.4c) with nitrate being known to have a stimulatory effect on germination (Hsu et al. 1985; White et al.

2001). However again, a laboratory germination test we carried out on kikuyu and paspalum seed using a range of nitrate solutions equivalent to observed soil levels (1-50 mmol L⁻¹) also failed to show a response in germination rate. This indirect effect of climate change on germination and emergence is potentially important as we have previously shown in this grassland that recruitment from seed is a powerful influence on species composition (Edwards et al. 2001), that species composition influences many ecosystem processes such as feed quality (Allard et al. 2003) and litter decomposition rates (Allard et al. 2004). The result also bears on the potential for the spread of C4 species under climate change, in terms of a potential germination/establishment limitation mechanism under elevated CO₂.

There was a marked difference in treatment effects on vegetative growth between the autumn and the spring (Figs. 5.3, 5.4). In autumn, leaf appearance was stimulated by warming at current but not elevated CO₂ levels, consistent with previous studies with kikuyu at ambient CO₂ (Ivory & Whiteman 1978) and *Andropogon* at ambient and elevated CO₂ (Kakani & Reddy 2007). However, there were no treatment effects in spring. In autumn, the impact was aligned with treatment effects on soil N availability (rather than soil moisture or temperature) and leaf appearance could be modelled as a linear function of N availability (Fig. 5.6). In spring, this relationship was not evident despite a higher N availability in the current CO₂ + warmed as found in autumn. As we have no *a priori* expectation of a different relationship between leaf appearance and N availability in autumn compared to spring it seem likely that the much lower levels of N found in spring (compare Figs 5.3c and 5.6c), and the consequent smaller differences in absolute amounts between treatments, were not sufficient to drive differences in leaf appearance.

The major finding of our experimental work was the strong dependence of C4 responses on N availability. While previous studies have shown C4 responses to CO₂ can be N limited (Ghannoum & Conroy 1996) just as C3 responses can (Daepf et al 2000), these are the first field data to show this in a 'natural' situation. We then proceeded to use simulation modelling to explore the long-term interactions between climate, CO₂ and soil biogeochemical cycles; this is a powerful tool that can provide insights into possible responses that are outside of our current experience. In particular we wanted to make sure that the N dependence of C4 responses was captured in the model. The results were encouraging. Warming by itself increased mineral N levels in the spring, and because temperatures were below the growth threshold for kikuyu, the lack of

competition for N led to greater growth of ryegrass. In contrast, in the autumn, when kikuyu growth was not constrained by temperature, ryegrass growth was suppressed by competition for water with the kikuyu and there was no increase in overall growth. Additional feedbacks were evident under future CO₂ levels and warming: there was no enhancement in spring ryegrass growth because of lower available N levels. This is consistent with the “progressive nitrogen limitation” (PNL) effect whereby the addition of extra carbon from the elevated CO₂ effect on plant growth decreases the mineralisation of N and hence the level of plant availability (Luo et al. 2004; Newton et al. 2006). Also, because kikuyu responded less to elevated CO₂ than ryegrass, there was a boost to late summer-autumn growth because the ryegrass had less competition for water.

6.2 Model simulations

Though we found ‘realistic’ patterns of growth in our simulations we are conscious that further refinement of the model is possible. For example, there is no provision in the model to deal with the changing digestibility (and hence ME content) of kikuyu as it matures leading us to choose an average digestibility that reflected the seasonal range. Experience in Northland has shown that digestibility and ME content can be improved by fast rotations that maintain the sward in a leafy state (Jagger et al. 2006) and thus the model represents a relatively poorly managed kikuyu pasture. Also, it was difficult to model the build up of kikuyu stolons that results in the formation of a “mat” by the end of autumn which then slows down the regrowth of the temperate grasses in the springtime. This is likely to have underestimated the effects of increasing kikuyu dominance in the pasture.

We used the results from our simulation to estimate the effects of warming only and warming plus future CO₂ levels on the costs to maintaining productivity of a high producing dairy farm with a substantial kikuyu component in its pastures. We found that with warming only, because of the loss of pasture quality, there could be an additional cost of about \$25,000 per year to buy in extra feed for an average dairy farm. Most of the additional costs occurred in late summer-autumn, when the kikuyu content increased and simulated ME values fell to nearly 6 MJME kg DM⁻¹. Animals cannot eat enough of this material (i.e. there is a bulk limitation) and will also decrease voluntary food intake, and hence milk production and liveweight gains will become severely restricted (Geenty & Rattray 1987, Jagger 2009). The cost of additional feed under the future warming and elevated CO₂ scenario was \$7,500; the reduction reflecting a reduced availability of soil N resulting in reduced C4 response to the temperature change.

The approximate cost of \$250 ha⁻¹ year⁻¹ for extra feed if the kikuyu is not managed can be compared to the costs of managing kikuyu. The Northland Kikuyu Action Group (KAG) has done research on developing management strategies to deal with this autumn dominance of kikuyu. This involves mulching the kikuyu dominant pasture and broadcasting annual ryegrasses at a cost of \$370 ha⁻¹ (Jagger et al. 2006), although this may have limited application to the Manawatu, where establishment & winter growth of annual ryegrass may be slower. Nevertheless, the calculation does indicate a lower cost of using supplementary feed and retaining kikuyu pastures compared to regrassing.

7. Conclusions

Previous studies of C4 distribution and performance under climate change in New Zealand have focused on the impact of changes in temperature (e.g. Campbell et al 1999). Here we show in field experiments that the increase in elevated CO₂, which is more certain than changes in temperature, interacts with temperature change indirectly through modifying plant N availability. With this response captured in an ecosystem model we are able to show that the outcome of increasing atmospheric CO₂ is to reduce the future stimulation of C4 growth expected to result from global warming. In regions where C3 grasses dominate we show that this effect reduces the costs to a farming operation by two thirds. However, it is also important to recognise that in areas where C4 grasses dominate the CO₂ × warming interaction will limit the potential benefits of increasing temperature unless additional N fertiliser is applied. These results are particularly useful as we move to complete detailed impact studies of climate change impacts on farming systems throughout New Zealand.

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