

Appendix 9. Testing the responses of the GRAZPLAN model to increased atmospheric CO₂

Introduction

As part of the AWI project WP321 on impacts of climate change on pasture and livestock productivity, modifications were made to CSIRO's GRAZPLAN model (Donnelly *et al.* 2002) to simulate the response of pasture species to changes in atmospheric carbon dioxide concentration, [CO₂]. Response functions and parameters were developed based on a review of Australian and international literature on the effects of elevated [CO₂] on the growth and physiology of various pasture species (Project WP321 milestone TMS02 and TMS03 reports). In the reviewed studies elevated [CO₂] was imposed either in controlled environment growth chambers, greenhouses, open- and closed-top chambers in the field or free-air CO₂ enrichment in the field.

For the processes or factors listed below there were relatively consistent responses to elevated [CO₂] in the literature and these were incorporated in the GRAZPLAN model:

- increased assimilation rate;
- reduced transpiration rate;
- decreased specific leaf area (SLA) and
- reduced leaf nitrogen (N) concentration.

When assimilation is radiation limited it is modelled to increase as a function of increased [CO₂] relative to reference [CO₂] of 350 μmol mol⁻¹. The parameters required to model this are related to the CO₂ compensation point (CO₂ concentration at which net CO₂ assimilation is zero) and the variation of the compensation point with temperature; parameters were established for C3 and C4 grasses.

Reduced transpiration at elevated [CO₂] occurs because of the relationship of increasing stomatal resistance with increasing [CO₂]. Parameters for the relative change in stomatal resistance with a doubling of reference [CO₂] were derived for *Lolium* spp, other C3 grasses, C4 grasses and dicotyledons.

Observations in the literature of reduced SLA at increased [CO₂] were used to derive values for a proportional decrease in SLA at doubling of reference [CO₂] for the functional groups C₃ grasses, C₄ grasses, legumes and other dicotyledons.

Several studies showed that leaf N concentration decreased with elevated [CO₂]. Therefore a general function was introduced whereby the maximum and minimum N concentration of leaves decreased linearly to be 10% lower at double reference [CO₂].

Other responses to [CO₂] were observed in the literature, such as changes in assimilate allocation including root:shoot ratios, in nutrient allocation, in phenological development and in competitive interactions in mixed species communities. However, the responses were conflicting or inconsistent and general trends or relationships could not be drawn. Some of these factors may nevertheless have important implications for pasture growth under elevated [CO₂].

In order to test the test how well these modifications predicted pasture response to [CO₂] we used GRAZPLAN to simulate several experiments in which pasture was grown at elevated [CO₂]. Three initial studies were identified, by Lutze and Gifford (1998), Lilley *et al.* (2001) and Volder *et al.* (2004), chosen both because of relevance and potential availability of data. These experiments were included in the

literature review from which functions and generalised parameters were established for predicting pasture responses to increased [CO₂]. However, the response functions were of a general nature based on many studies and the details of any one study were not incorporated. We examined the above-mentioned studies in detail and compared GRAZPLAN predictions with observed data.

Elevated [CO₂] experiments chosen for model testing

Lutze and Gifford (1998) measured the effect of [CO₂] and nitrogen supply on the growth of *Danthonia richardsonii* in a glasshouse study at the Australian National University in Canberra, ACT. The plants were grown as “microcosms” in rectangular boxes in glasshouses; the aim was to simulate swards of pasture, considered more representative of field conditions than isolated plants. The microcosms were grown for four years at 360 or 720 μmol mol⁻¹ in combination with mineral nitrogen supply of 2.2, 6.7 or 19.8 g N m⁻² y⁻¹. Biomass was sampled every 6 months; some microcosms were non-destructively harvested with biomass above 8 cm height removed and weighed, while other microcosms were destructively sampled for total above- and below- ground biomass, carbon and nitrogen contents. Lutze and Gifford (1998) found significant growth enhancement under elevated [CO₂], with the highest growth under high N supply but enhanced growth even under restricted N supply. The effect of elevated [CO₂] did not diminish over the four years of the experiment.

The experimental treatments as described by Lutze and Gifford (1998) were complicated, and changed over the duration of the experiment. Some of the environmental conditions are not well described, making the experiment difficult to simulate. To date we have not had access to data from the experiments; if the data becomes available simulation of the experiment may be more feasible.

Lilley *et al.* (2001) conducted an experiment to assess the effect of elevated [CO₂] and temperature on the growth of two pasture species, *Trifolium subterraneum* and *Phalaris aquatica*. The experiments were performed in enclosed controlled temperature gradient tunnels established on the Ginninderra Experiment Station near Canberra, ACT. We have had access to the raw data from this study, which has made simulation of this experiment relatively straightforward. This experiment and comparison of observed data with GRAZPLAN predictions are described in more detail below.

Volder *et al.* (2004) also examined the combined effect of elevated [CO₂] and warming on the growth of *Phalaris aquatica*, but considered both constant day/night warming as well as greater night-time warming (the latter considered more consistent with trends in global climate change). In addition, Volder *et al.* (2004) measured the effect of frequent versus infrequent cutting of above-ground biomass. Like the Lilley *et al.* (2001) study, Volder *et al.* (2004) performed the experiments in controlled temperature gradient tunnels at Ginninderra Experiment Station. In contrast to Lilley *et al.* (2001) who found little effect of [CO₂] on phalaris growth (see below), Volder *et al.* (2004) found higher above-ground growth, but only during spring when growth rates were generally highest. There was no effect of warming treatment and a negative effect of frequent cutting on total above-ground production.

Although we have not had access to the raw data from the Volder *et al.* (2004) experiment, the environmental conditions under the different treatments are relatively clearly presented. We have simulated the experiment in GRAZPLAN, but the predicted pasture growth rates are much lower than the observed data. Volder *et al.* (2004) commented that they observed high growth rates in comparison to other studies, which they attributed to the high rates of nitrogen fertilization and irrigation in their experiments. Despite simulating these conditions we have not predicted

similarly high production. Simulations have shown declining production during summer; this was not evident in the data presented by Volder *et al.* (2004) over two years of growth. Therefore there appears to be issues with the way GRAZPLAN predicts phenology of phalaris; this may be related to altered phenological development under frequent defoliation which is currently not represented by simulations, and could also be due to exposure of the plants to higher temperatures than those at which growth has previously been reported. To resolve this issue may require modification of certain parameters in GRAZPLAN.

Due to the issues in simulating the studies by Volder *et al.* (2004) and Lutze and Gifford (1998) we have not compared predicted and observed data in this report, although we are continuing to work on these simulations. Instead the report is focussed on the Lilley *et al.* (2001) study, which are confident in simulating accurately.

Description of Lilley *et al.* (2001) and simulation in GRAZPLAN

Lilley *et al.* (2001) conducted an experiment to assess the effect of elevated [CO₂] and temperature on the growth of two pasture species, *Trifolium subterraneum* and *Phalaris aquatica* in monoculture and as a mixed sward. The experiments were performed in enclosed controlled temperature gradient tunnels established on the Ginninderra Experiment Station near Canberra, ACT (149.10 E, 35.20 S). The tunnels were 1.25 m wide and high and 12 m long, with polycarbonate walls and a clear Teflon roof. Air was drawn into the tunnel from outside by fans and progressively heated as it travelled through the tunnel by radiation or heaters in periods of low radiation. Fan speed was altered to control the rate of air flow and achieve the target temperature. Each tunnel contained a “field” temperature section with temperature close to ambient and a “warmed” temperature experimental section. For elevated [CO₂] treatments CO₂ was injected into the air inlet section of the tunnel; the concentration was continuously monitored and this determined the injection rate as controlled by a solenoid valve.

The experimental conditions imposed by Lilley *et al.* (2001) were a factorial of the treatments in Table A9.1 to give 12 levels. The [CO₂] treatments were imposed on whole tunnels and replicated three times, the tunnels were split into warming treatments and each [CO₂] by temperature subplot contained the three sward types. Lilley *et al.* (2001) included replicate comparison plots with the three sward types growing outside the temperature gradient tunnels (Figure A9.1).



Figure A9.1. Temperature gradient tunnel imposing CO₂ and temperature treatments as described by Lilley *et al.* (2001). Photograph J. Lilley.

Table A9.1. Experimental treatments imposed by Lilley *et al.* (2001).

Sward type	CO ₂	Temperature
<i>Trifolium subterraneum</i> monoculture	Ambient 380 $\mu\text{mol mol}^{-1}$	Field
<i>Phalaris aquatica</i> monoculture	Elevated 690 $\mu\text{mol mol}^{-1}$	Warmed + 4°C
<i>T. subterraneum</i> / <i>P. aquatica</i> 1:1 mix		

Seeds were sown into the tunnels (except for the outside comparison plots) on the 14th December 1995 with a target density of 235 plants m⁻². The swards were harvested from 0.34 m² plots on 11 occasions between day 29 and day 348 after sowing, removing biomass above 7 cm height (herbage). On the two final harvests biomass from below 7 cm to ground level was also sampled (plant bases), and on the final harvest below ground root biomass was also measured to a soil depth of 20 cm. Julianne Lilley gave access to the raw biomass data and also provided some data on the environmental conditions inside the tunnels. However, not all conditions were monitored during the experiment and some assumptions were made when simulating the tunnel environment.

The soils were described by Lilley *et al.* (2001) as a yellow podzolic. We estimated soil water holding characteristics from descriptions of a yellow podzolic soil core taken from Ginninderra, given in Tables 5 and 6 in Sleeman (1979) and profile 33A in Stace *et al.* (1968). The profile consisted of a loamy sand A horizon to approximately 50 cm depth over a clay B horizon to 100 cm. The parameters in Table 2 were used.

The temperature for each treatment combination was logged hourly by Lilley *et al.* (2001), and we used this to derive daily minimum and maximum temperatures for the input weather files. Over the experimental period (16th December 1995 to 28th November 1996) the warmed treatment had an average daily maximum temperature approximately 3°C higher and a daily minimum approximately 4°C higher than in the

Table A9.2. Soil water holding characteristics used in GRAZPLAN simulations of Lilley *et al.* (2001).

Soil depth (mm)	Saturated water content	Drained upper limit water content	15 bar lower limit water content	Air dry water content	SWCON
0-100	0.45	0.30	0.05	0.01	1.0
100-200	0.45	0.30	0.05	0.01	1.0
200-300	0.45	0.30	0.05	0.01	1.0
300-400	0.45	0.30	0.05	0.01	1.0
400-500	0.45	0.30	0.20	0.02	1.0
500-700	0.43	0.30	0.20	0.02	0.5
700-900	0.43	0.30	0.20	0.02	0.5
900-1100	0.43	0.30	0.20	0.02	0.5

Table A9.3: Average daily minimum and maximum temperature (°C) over the experimental period (16th December 1995 to 28th November 1996) for different tunnel treatments measured by Lilley *et al.* (2001) and outside tunnel comparison plots (data obtained from Ginninderra weather station records).

[CO ₂]	Temperature	Max T	Min T
Ambient	Field	21.9	6.8
	Warmed	24.5	11.3
Elevated	Field	21.5	7.0
	Warmed	24.0	10.8
Outside comparison plot		17.5	6.1

field temperature treatment (Table A9.3). Even without the warming treatment the tunnel environment was warmer than outside; the daily maximum was approximately 4°C higher while the minimum was only approximately 1°C higher inside than outside.

The differences in temperature inside and outside the tunnel contributed to differences in vapour pressure deficit (D). It is important to correctly simulate D, as in conjunction with stomatal conductance this drives transpiration rates, therefore affecting the soil water balance and plant water status. There is also a parameter in GRAZPLAN that results in reduced stomatal conductance at increasing D, which results in reduced rates of photosynthesis and thus plant growth. Measurements of D were not presented by Lilley *et al.* (2001), but using the same formula as used in GRAZPLAN based on the daily minimum and maximum temperature, we estimated that the average D over the duration of the study was 0.90 kPa outside the tunnels, 1.42 kPa inside the tunnel with field temperature and 1.46 kPa inside the warmed sections of the tunnels. However, in the experiment by Volder *et al.* (2004) at the same location and with similar conditions, D increased inside the temperature gradient tunnels but the increase was not as high as we calculated from the corresponding temperature data. There may have been slightly higher humidity inside the tunnels; as we could not find data on this, we used the Volder *et al.* (2004) data to make adjustments to the D that was calculated from the minimum and maximum daily temperature recorded by Lilley *et al.* (2001).

Radiation is another factor that has a large impact on plant growth and that was different inside and outside the tunnels. Lilley *et al.* (2001) observed that the Teflon film used for the roof of the tunnels transmitted 96% of visible radiation; a small amount of data was provided from the study which indicated less radiation than this was transmitted. In Figure 2 of Volder *et al.* (2004) it was shown that between 20% and 50% of direct solar radiation was reflected or intercepted by the tunnel structure. This varied daily, but there also appeared to be a seasonal effect whereby a smaller proportion of radiation was transmitted during winter than in spring and summer. Based on these seasonal averages we reduced the radiation level recorded at the Ginninderra weather station by between 20% and 40% and used these values in the weather input files.

The swards inside the tunnels were irrigated; the irrigation frequency and amounts were not given by Lilley *et al.* (2001) except to say that swards were well-watered. We removed all soil water limitation to growth in the GRAZPLAN simulations by setting an irrigation event whenever the soil water content fell below the drained upper limit, with the irrigation amount being that required to return the soil water content to the drained upper limit.

The site was fertilized before the experiment was established and a green manure crop incorporated; prior to sowing the surface 30 cm of soil contained 111 kg ha⁻¹ of mineral N, and there was 18.3 kg ha⁻¹ of available phosphorous in the top 10 cm of soil. The plots were not fertilized during the experiment.

Comparison of predicted and observed data

Lilley *et al.* (2001) measured enhanced herbage production in the clover under elevated [CO₂], and reduced growth at warm temperature, while there were no treatment effects on herbage biomass in phalaris. The results of our simulations with GRAZPLAN were broadly consistent with these results.

Contrasting the observed and predicted data for the comparison plots outside the temperature gradient tunnels allows initial evaluation of model predictions without the

added complication of the treatment effects. In the mixture, cumulative herbage cut above 7 cm over the duration of the experiment was over-predicted in phalaris and under-predicted in clover (Figure 2); the observed and predicted combined cumulative herbage production of the mix was similar. Herbage growth of both monocultures was over-predicted (by 25% in clover and 60% in phalaris); however Lilley *et al.* (2001) noted that plants in the outside plots were slow to establish. This may have been due to the plants being established out of season (i.e. in summer as opposed to autumn), but for unknown reasons this effect was more pronounced in the outside plots than in the tunnels. Accurate predictions are therefore difficult to achieve given the stated uncertainty in experimental conditions.

Clover herbage production was enhanced by elevated $[CO_2]$ at field temperature, by 19% in the monoculture and by 31% in the mix (Figure 2). Warming reduced clover growth; when grown under higher temperature there was no significant difference between cumulative herbage biomass under ambient and elevated $[CO_2]$ and warming at ambient $[CO_2]$ resulted in a 28% decrease in production (Figure 2). Lilley *et al.* (2001) attributed the lower growth of clover at warm temperature to increased rates of respiration, especially during winter when photosynthesis was limited by radiation.

The model predictions of clover herbage growth were within the standard error of the observed data for ambient and elevated $[CO_2]$ at field temperature (Figure A9.2), indicating the $[CO_2]$ response functions in GRAZPLAN accurately simulated clover response to elevated $[CO_2]$. However, the model predictions were higher than observed when warming was simulated. There was a greater discrepancy in observed and predicted herbage biomass with warming at ambient $[CO_2]$ than at elevated $[CO_2]$ (the latter was predicted within two standard errors of the observed data). There was slightly greater over-prediction towards the end of the experiment in

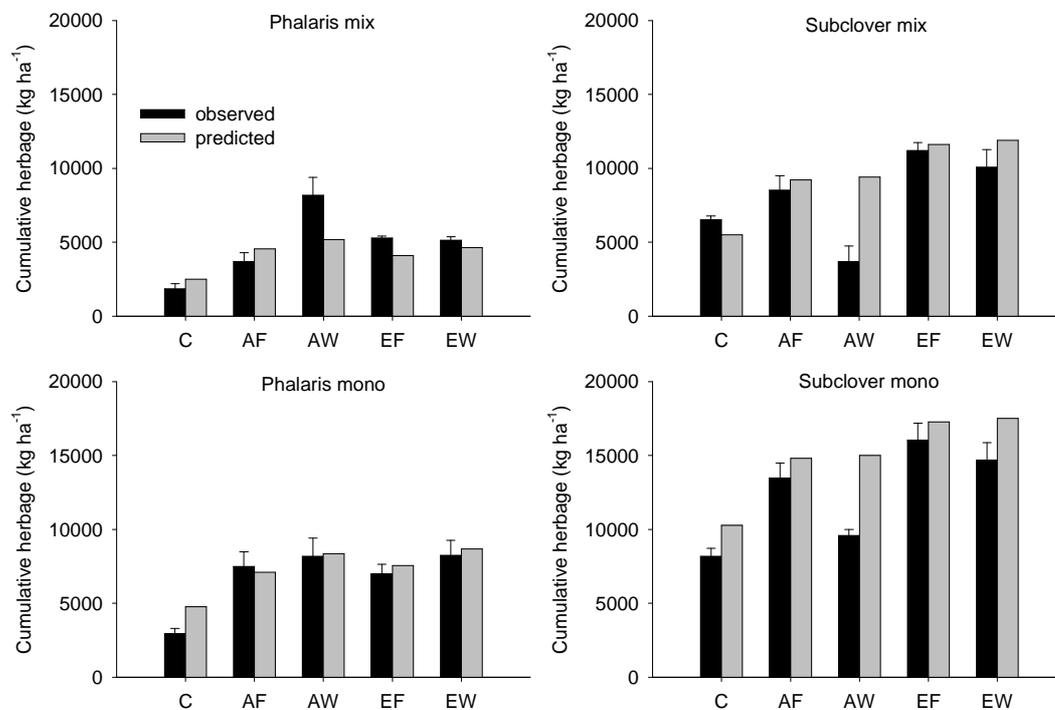


Figure A9.2. Final observed cumulative herbage biomass (greater than 7 cm height) measured by Lilley *et al.* (2001) and predicted with GRAZPLAN on 11 occasions between December 1995 and November 1996. Treatments are C = outside tunnel comparison plots; AF = ambient $[CO_2]$ field temperature; AW = ambient $[CO_2]$ warm temperature; EF = elevated $[CO_2]$ field temperature; EW = elevated $[CO_2]$ warm temperature.

summer (Figures A9.3 and A9.4). Lilley *et al.* (2001) noted that the clover began to senesce in early summer; the model predicted the start of senescence in early December in the field temperature treatment and late October for the warm treatment. It is possible that the timing or rate of senescence was not accurately predicted, but observed data is not available to verify this. It is also possible that temperature effects on respiration or responses to increased vapour pressure deficit at high temperature were not accurately represented by the model. The GRAZPLAN model does include temperature effects on phenology, assimilation, respiration and aging of tissue, and considers plant response to D. However, the increased temperature measured by Lilley *et al.* (2001) in the warmed treatments relative to outside the tunnels (7 °C higher average maximum temperatures, Table A9.3, and up to 42°C) are beyond the range considered in GRAZPLAN.

There was no effect of [CO₂] or warming on the cumulative herbage biomass of the phalaris monoculture observed by Lilley *et al.* (2001); the GRAZPLAN simulations produced the same result, with the exception of the outside comparison plots the predicted results were within one standard error of observed data for all treatments (Figure A9.2). Lilley *et al.* (2001) attributed this lack of [CO₂] and warming response to a mild nitrogen limitation. GRAZPLAN results showed a growth limitation by nitrogen during the latter half of the experiment in phalaris monoculture for all treatments.

In contrast to the monoculture, herbage production of phalaris in mixture was enhanced by both elevated [CO₂] and temperature. GRAZPLAN simulations were similar in trend but smaller in magnitude than the observed data (Figure A9.2). In particular, the response to warming at ambient [CO₂] was significantly under-predicted; the observed reduction in clover growth with warming conferred a competitive advantage to phalaris that was not predicted. There was no observed change to the mixture composition with [CO₂] treatment and this was reflected in the model simulations. Treatment effects on the combined phalaris and clover herbage production were accurately simulated.

Although the predicted cumulative herbage production of phalaris was similar to the

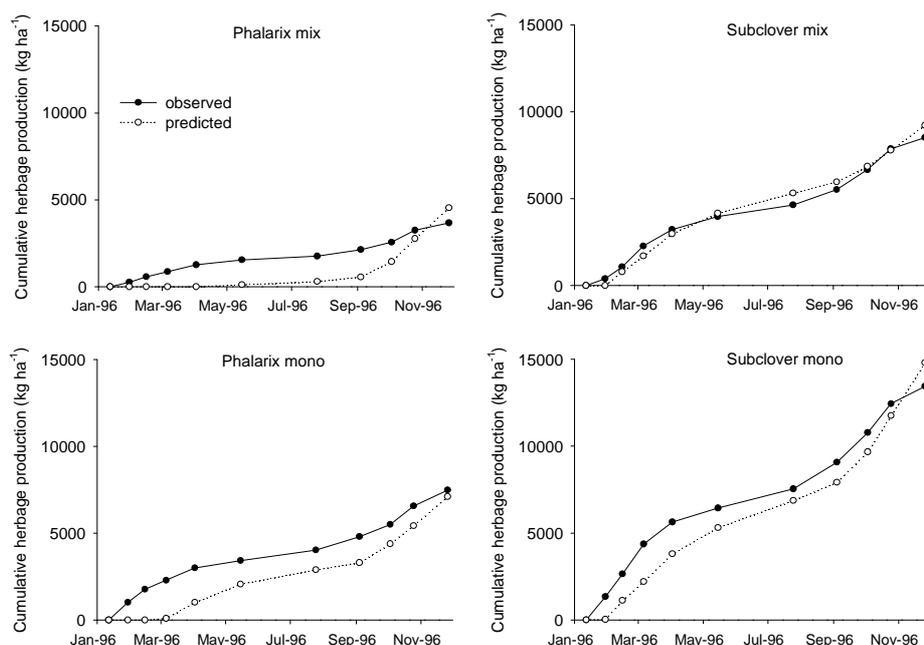


Figure A9.3. Observed cumulative herbage biomass (greater than 7 cm height) over time measured by Lilley *et al.* (2001) and predicted with GRAZPLAN between December 1995 and November 1996, in the ambient [CO₂] field temperature treatment.

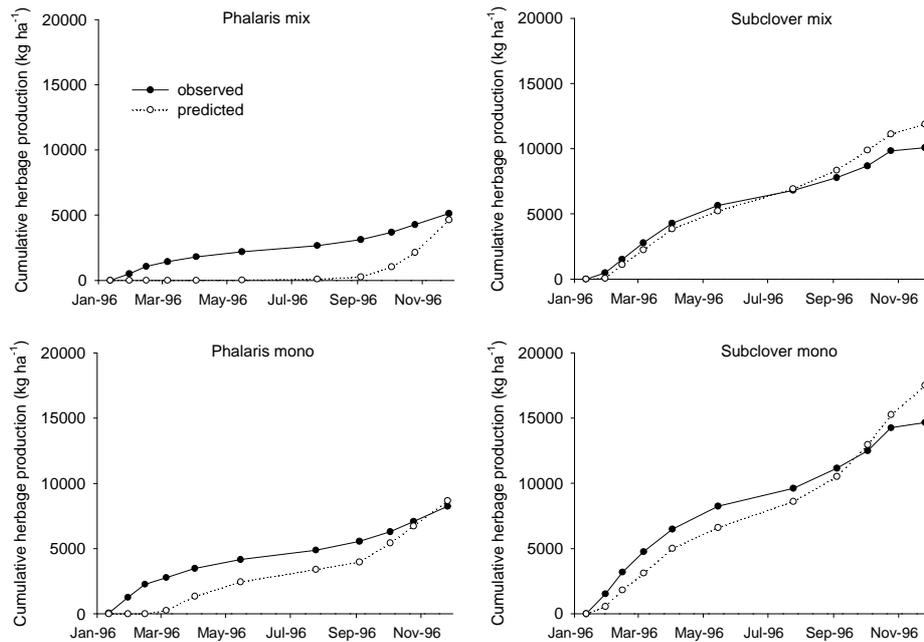


Figure A9.4. Observed cumulative herbage biomass (greater than 7 cm height) over time measured by Lilley *et al.* (2001) and predicted with GRAZPLAN between December 1995 and November 1996 in the elevated $[CO_2]$ warm temperature treatment.

observed data, the timing of growth was different. The predicted early growth was lower than observed, while the later growth was higher. This was observed in all treatments, (for example in the ambient $[CO_2]$ field temperature, Figure A9.3, and elevated $[CO_2]$ warm temperature treatments, Figure A9.4), in both mixture and monoculture. This is unrelated to the CO_2 response functions and may be an issue with simulation of the phenology of phalaris sown out of season (during summer), and with frequent defoliation.

In comparison with herbage biomass, plant base (below 7 cm) and root biomass at the end of the experiment were poorly predicted by GRAZPLAN. The plant base biomass was significantly under-predicted in nearly all cases (Figure A9.5). In addition, while Lilley *et al.* (2001) noted similar treatment effects as occurred for herbage production, there were no or limited treatment effects simulated. After establishment the plant base biomass remained relatively constant over time; this appears to be a general issue with the way allocation was modelled under frequent defoliation and requires further investigation.

Similarly, root biomass was also underestimated by GRAZPLAN and treatment effects were not simulated (Figure A9.6). The discrepancy between predicted and observed data was greatest in the phalaris monoculture. Lilley *et al.* (2001) observed higher root growth under elevated $[CO_2]$ and reduced root growth under warm temperatures. This was attributed partly to phalaris having a greater proportion of total biomass in roots and therefore growth responses being more easily discerned. It was also suggested that the partitioning of biomass to roots increased under elevated $[CO_2]$, which may have explained the lack of response of above-ground biomass. As stated above, changes in allocation and differences in root:shoot ratio have been reported elsewhere in the literature (e.g. Volk *et al.* 2000, Marchi *et al.* 2004). However, the response was variable which made it difficult to extract general relationships; until further data is available this cannot be accurately simulated. The low root biomass predicted by GRAZPLAN was unrelated to treatments. The model predicted sharply declining root biomass at the end of the experiment (summer),

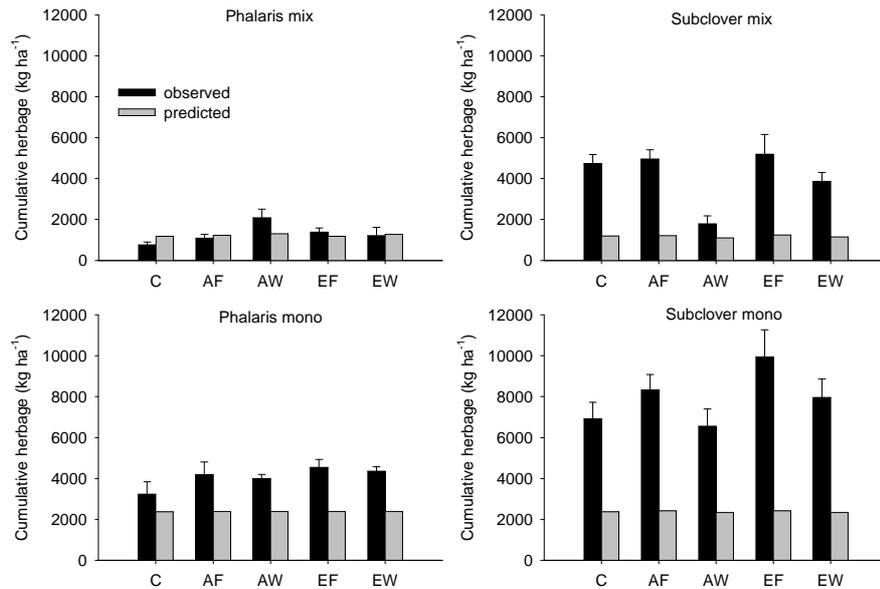


Figure A9.5. Plant base biomass (less than 7 cm height) measured by Lilley *et al.* (2001) and predicted with GRAZPLAN at the end of the experiment in November 1996. Treatments are C = outside tunnel comparison plots; AF = ambient [CO₂] field temperature; AW = ambient [CO₂] warm temperature; EF = elevated [CO₂] field temperature; EW = elevated [CO₂] warm temperature.

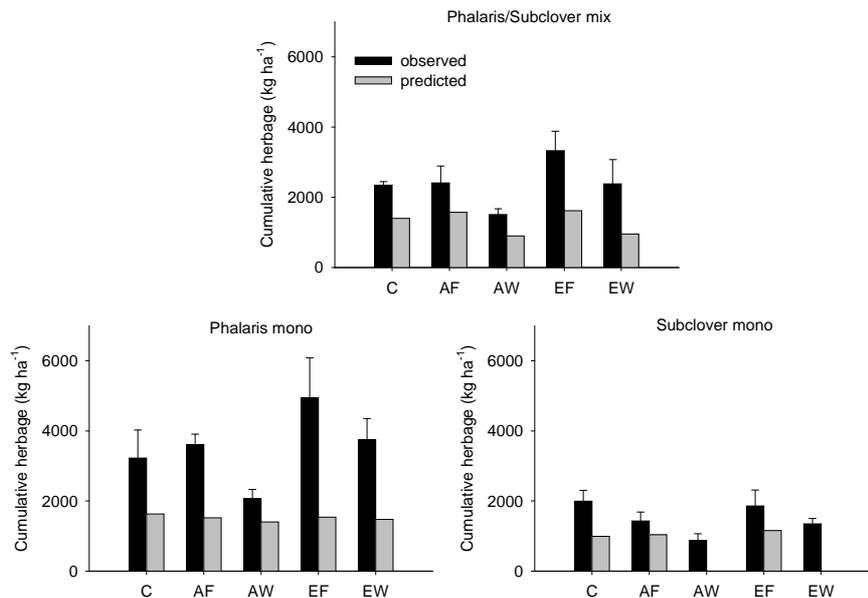


Figure A9.6. Root biomass to 20 cm depth measured by Lilley *et al.* (2001) and predicted with GRAZPLAN at the end of the experiment in November 1996. Treatments are C = outside tunnel comparison plots; AF = ambient [CO₂] field temperature; AW = ambient [CO₂] warm temperature; EF = elevated [CO₂] field temperature; EW = elevated [CO₂] warm temperature.

which may again indicate inconsistencies in the way phenology was modelled for this study.

Conclusions

Application of the [CO₂] response functions incorporated in GRAZPLAN to simulate the study by Lilley *et al.* (2001) resulted in predictions that were relatively consistent with observed data, at least for above-ground biomass. Many of the differences in the

predicted and observed data were unrelated to [CO₂] treatment effects and therefore not due to the [CO₂] response functions. Some of the discrepancies occurred due to artefacts of the experimental treatments resulting in different conditions to what would normally be observed in the field. For example, the frequent defoliation may have altered phenological development and simulation of this requires some further modification. In addition, deviation of observed and predicted data was found at high temperatures. Temperature functions are incorporated in GRAZPLAN simulating the responses of phenology, assimilation, respiration and aging of tissue. However, the maximum temperatures in the warmed tunnel treatments were extreme, up to 42°C in Lilley *et al.* (2001) and 47 °C in Volder *et al.* (2004). This is beyond the limits of the GRAZPLAN temperature response functions and indeed observations of pasture physiology responses to temperature. This is likely to be important given that elevated [CO₂] is predicted to occur with warmer temperatures in future climate scenarios.

Responses that are poorly or inconsistently represented in the literature, such as allocation of assimilate and particularly root:shoot ratios, may have large effects on growth. Root turnover may also change under elevated [CO₂] which has significant implications for production (Norby and Jackson 2000). These and other uncertainties make predicting production in future climates challenging. Although the applicability of the [CO₂] response functions appears promising, this work represents only an initial testing of these functions and more rigorous testing is desirable.

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