Modelled effects of rising CO_2 concentration and climate change on native perennial grass and sown grass-legume pastures

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ABSTRACT: Native perennial grass and sown grass-legume pastures are an important agricultural and environmental resource. We investigated the impact of rising carbon dioxide concentration ($[CO_2]$) and projected climate changes on these pasture ecosystems in southeastern Tasmania, Australia, using a biophysical simulation model, EcoMod. The model consists of interdependent modules that describe soil physicochemical and hydrological characteristics, and pasture growth and senescence, with fluxes described by empirical and mechanistic equations. Our simulations showed that in native pastures, projected climate change increased the biomass of C_4 grasses, with limited impact upon C_3 grasses, a trend reversed by rising $[CO_2]$. In sown pastures, projected climate change decreased the biomass of perennial rye grass *Lolium perenne* and total biomass markedly by 2070, whilst subterranean clover *Trifolium subterraneum* biomass increased. Subterranean clover biomass changed little with increased $[CO_2]$ alone, whereas perennial rye grass biomass increased. Responses across pastures reflected species' tolerances to environmental factors, with projected climate change generally having more of an impact on biomass than rising $[CO_2]$. Changes in both $[CO_2]$ and climate led to a reduction in protein content and digestibility. Soil inorganic nutrient concentrations decreased with increasing $[CO_2]$ and increased with projected climate change. Further simulations should investigate whether these patterns are robust for different sites and alternative environmental futures. Our results reinforce the need to pursue adaptation strategies in response to environmental change in order to maintain productive pasture ecosystems.

KEY WORDS: *Lolium perenne* · Ecosystem model · Simulation · Nutrient availability · Productivity · Tasmania

1. INTRODUCTION

Native perennial grasslands are an important, botanically diverse component of the Australian environment (Lodge & Garden 2000), providing important ecosystem services, such as the prevention of soil erosion and the provision of forage for grazing stock (Tubiello et al. 2007). Other grasslands have been 'improved' through fertilisation and irrigation, and sown with introduced species, including legumes ('sown pastures'). Management inputs increase the quantity and quality of the pasture, and thereby the economic value of the land (Tubiello et al. 2007). Both native perennial and sown pastures are likely to be impacted by changes in climate and atmospheric concentrations of carbon dioxide ($[CO_2]$). This may occur through physiological impacts on plant species within them (Drake et al. 1997, Ainsworth & Long 2005) and through impacts on soil re-

source availability, for water (Nowak et al. 2004) and nutrients (Luo et al. 2004). Actions occur directly — for instance, increasing temperature decreases water availability via increased evaporation — or indirectly, through changes in plant species composition influencing such factors as demand for water and nutrients (Suding et al. 2008). Changes have been demonstrated by manipulative experiments (Dukes et al. 2005, Hovenden et al. 2008); however, experimental sites can only provide a limited, site-specific insight into the potential effects of global changes (Norby & Luo 2004). Simulation models provide an avenue through which myriad impacts can be explored over longer timescales at many sites (Riedo et al. 2001, Gerten et al. 2008, Luo et al. 2008, Lazzarotto et al. 2010).

Here we used a detailed biophysical pasture simulation model (EcoMod; Johnson et al. 2003, 2008) to forecast potential future states of grasslands in southeastern Tasmania. EcoMod uses simple empirical and mechanistic equations based on generally accepted biophysical relationships to describe processes within the pasture system, and is the only model, to our knowledge, that attempts to integrate all facets of the pasture system: soil water, soil nutrients, animal metabolism, pasture management and plant growth. It has been extensively tested against a range of pasture systems and processes across Australia and New Zealand (Cullen et al. 2008b, Johnson et al. 2008). We concentrated on naturally senescing and cut pastures (with return of litter), consisting of native perennial grass, or sown annual legume and perennial grass species. We asked what potential impacts projected changes in climate and $[CO_2]$ will have on these pastures at 2 future instants in time. Our aim was to show how generic systems could potentially respond, in terms of species biomass, composition and soil nutrient dynamics, to changes in climate and $[CO_2]$, both singly and in combination. In our assessment of responses, we also examined the relative composition of the pasture in relation to its total biomass.

2. MODEL DESCRIPTION

EcoMod version 4.7.6 is a biophysical pasture simulation model that includes growth of multiple plant species, soil water and nutrient dynamics, animal intake and metabolism, and a range of management options (Johnson et al. 2008). It is amongst a suite of models, including the SGS Pasture Model (Johnson et al. 2003) and DairyMod (Johnson et al. 2008), that integrates all of the above facets of a pasture ecosystem. Simulations have been extensively tested against a range of systems in Australia and New Zealand (McCaskill et al. 2003, Sanford et al. 2003, White et al.

2003, Cullen et al. 2008b, Johnson et al. 2008). This testing has included accurate representations of water balance and deep drainage (White et al. 2003), pasture growth, senescence and herbage accumulation (Sanford et al. 2003, Cullen et al. 2008b, Johnson et al. 2008), inorganic nutrient leaching, particularly in native perennial pastures (McCaskill et al. 2003), and the representation of nitrous oxides emissions (Eckard et al. 2006). The model explained 85% of variation in annual herbage accumulation data for both native and sown pastures, when comparing 5 yr of experimental data with 31 yr of climate data, given observed annual rainfall. In particular, it accurately simulated the difference in herbage accumulation between sites due to their different environmental characteristics (Sanford et al. 2003). Most recently, EcoMod has described intra-annual pasture dynamics across New Zealand and Australia, where it has shown the capacity to simulate pasture growth rates and annual yields across a range of climatic zones and different species, over varying numbers of years of climate data (Cullen et al. 2008b, Johnson et al. 2008). The model has also been used for detailed drought analysis (Lodge & Johnson 2008a,b).

The model has modules for pasture growth in response to climate and nutrient constraints and pasture utilisation by grazers; animal physiology; and water and nutrient dynamics. Detailed descriptions of all of these modules and the mathematical formulations therein can be found at www.imj.com.au/consultancy/wfsat/wfsat.html. In brief, pasture management options can be implemented, including cutting, irrigation and fertiliser application. Daily climate and atmospheric data drive the model: rainfall, minimum and maximum temperature and relative humidity, average windspeed, incoming solar radiation, vapour pressure and atmospheric $[CO_2]$.

Pasture growth is calculated from canopy photosynthesis, scaling up from the leaf level where photosynthesis responds to irradiance using a non-rectangular hyperbola (Cannell & Thornley 1998b), adjusted to allow for the influence of soil water and nutrient status. Such an approach has been used by others (Cannell & Thornley 1998a, Wu & McGechan 1998, Riedo et al. 1999), although alternatives exist, such as the Farquhar–von Caemmerer–Berry (FvCB) scheme (e.g. Coughenour & Chen 1997, Zhou et al. 2008). Our description of photosynthesis is focused firmly at the canopy level and thus the FvCB model, although widely used, does not suit our purposes. FvCB uses Michaelis-Menten kinetics in response to sub-stomatal CO_2 concentration and therefore must be combined with a stomatal conductance model, which gives greater complexity than we regard as appropriate. Also, the treatment of temperature response is, in our

view, impractical for an eco- or agricultural-system model. In our scheme, temperature influences photosynthesis such that C_3 species peak at some optimum between a temperature minimum and maximum. C_4 species continue to photosynthesise at high temperatures given their ability to avoid photorespiration. Extreme cold and heat also prevent growth. Temperature, soil water and nutrient impacts in limiting growth can be understood with reference to their growth limiting factors (GLFs), which are defined as actual/potential with reference to the variable of interest; 0 means completely limited, and 1 indicates no limitation to growth. Thus, water limitation is actual evapotranspiration divided by potential evapotranspiration. Potential growth is scaled back according to these factors, as explained in the model documentation.

The specific impacts of elevated $[CO_2]$ on plant physiology were discussed fully by Cullen et al. (2009). In brief, as $[CO_2]$ rises, the light-saturated rate of leaf photosynthesis is assumed to respond to rising $[CO_2]$, according to a Michaelis-Menten relationship, with a more rapid response by C_3 species. In the model, the nitrogen (N) concentration of plants declines in response to elevated $[CO_2]$, again more rapidly for C_3 species, whilst the light-saturated rate of single leaf gross photosynthesis is proportional to the leaf N concentration. This allows for $[CO_2]$ downregulation of photosynthesis, e.g. through reduced carboxylation capacity due to declining leaf N as evidenced by Ellsworth et al. (2004). There is also a decline in stomatal conductance in response to elevated $[CO_2]$ that has the potential to affect plant water relations. These responses mirror those shown in experimental systems with increased $[CO_2]$ (Ellsworth et al. 2004, Ainsworth & Long 2005), and parameterisation of the model demonstrated that modelled responses to environmental stressors show good agreement with experimental results (Cullen et al. 2008a). Pasture protein content was calculated within the model from plant N concentration for both live and standing dead tissue, assuming that protein and water soluble carbohydrate were fully digestible. Prescribed values for the digestibility of cell wall material in both live and dead tissue (Johnson et al. 2003) were then used to calculate overall digestibility of the pasture.

The ability of the model to simulate both current native (see 'Simulation design: native pasture') and sown pasture dynamics, together with its well founded mechanistic and empirical equations that mirror physiological responses to environmental stressors found under field experimental conditions, allows us to utilise the model for environmental change projections with the confidence that the individual relationships used in the model correspond to best current understanding appropriate to the scale of the question.

3. METHODS

3.1. Environmental change scenarios

Meteorological data from the Australian Bureau of Meteorology SILO database (www.bom.gov.au/silo) were sourced for 1961 to 2000, at position 42.75° S and 147.25° E, using the Data Drill method (Jeffrey et al. 2001), thus providing our baseline climate data. The location allowed comparison with TasFACE (Hovenden et al. 2006), an ongoing experiment in native at Pontville, Tasmania that has increased temperature and $[CO_2]$ for 7 yr. Daily rainfall, vapour pressure, minimum and maximum relative humidity and temperature, and incoming radiation were downloaded. No trends were apparent, and as such, no scaling was required to make each year representative of 1990, the baseline year for climate scenarios. In effect, each year of data represented a 1990 climate.

Projected absolute changes in temperature, and percentage changes in rainfall for each month for 2030 and 2070, at position 42.75° S and 147.25° E, were sourced from OzClim (www.csiro.au/ozclim/home.do; Build Number 3.0.16), using the CSIRO Mk3 global circulation model with A1FI emission scenario (IPCC 2000) with associated high climate sensitivity, selected because emissions have thus far been at or above these projections (IPCC 2007). Qualitative biomass patterns were similar for alternative climate futures due to different emission scenarios (Cullen et al. 2008a). Changes were applied to the baseline temperature and rainfall data to provide climatic scenarios for 2030 and 2070 (Fig. 1). Consistent with continental projections (CSIRO 2007), southeast Tasmania is expected to show more marked warming by 2070 and changed seasonality in rainfall, although we predicted only a slight decrease in annual precipitation from 534 to 518 mm. Relative humidity was changed for 2030 and 2070 scenarios using the 50th percentile projections for Hobart (Table B8 in CSIRO 2007). TasFACE recorded an average windspeed of 2.7 m s^{-1} (Hovenden et al. 2006), which we included in the daily climate data file; we did not impose any changes on windspeed in the future climates. Potential evapotranspiration was internally calculated by Eco-Mod for all scenarios, according to the Penman-Monteith relationship.

$[CO_2]$ was increased from 380 ppm in baseline runs to 455 and 716 ppm for 2030 and 2070 projections, respectively, ignoring seasonal variations but consistent with emission scenarios. We use 'changed climate/climate change' to refer to varying climate data with the $[CO_2]$ unchanged, 'changed $[CO_2]$/$[CO_2]$ change' to refer to runs where climate data were left unaltered but $[CO_2]$ was increased, and 'changed environment/environmental change' to refer to simultaneous $[CO_2]$ and climate change.
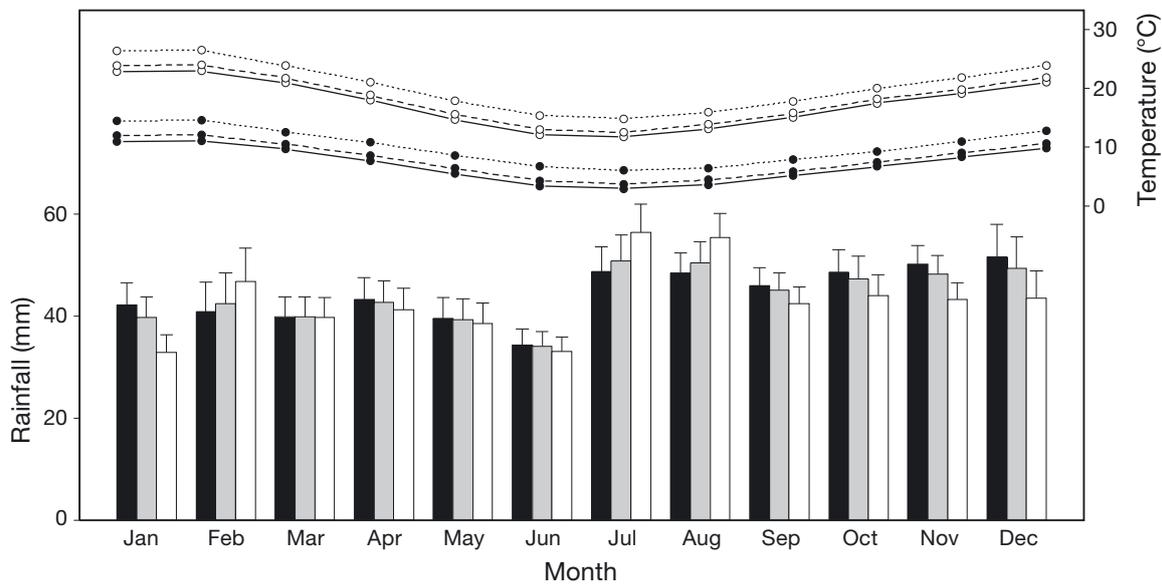
Fig. 1. Baseline and projected mean monthly rainfall (+ 1 SE), and minimum and maximum temperature at Pontville (SE not shown due to small magnitude). See Section 3.1 for data sources. For rainfall, black bars denote baseline conditions, grey bars are projections for 2030 and unfilled bars are projections for 2070. Baseline temperatures are denoted by solid lines, 2030 projections by dashed lines and 2070 projections by dotted lines. Filled (unfilled) symbols denote minimum (maximum) temperatures

3.2. Simulation design

3.2.1. Native pasture

Simulated native pastures were naturally senescing grassland and grassland cut once a year in early autumn (15 March) to 0.5 t ha^{-1}, cut biomass being returned as litter. Grasslands consisted of perennial C$_3$ and C$_4$ natives parameterised to represent *Austrodanthonia caespitosa* and *Themeda triandra*, respectively, the dominant species at TasFACE (Hovenden et al. 2008). The grassland was assumed to be flat and 50 ha in size. Thus, we used 3 climate scenarios, 3 [CO$_2$], and 2 cutting scenarios (Cut, Uncut; Table 1).

Parameters and initial conditions for TasFACE were sourced from data and using expert knowledge (see Tables A1–A3 in Appendix 1 for details of pasture and

soil parameters). The 1 m deep soil was characterised to represent the site as sandy-clay-loam at surface grading into clay by 20 cm depth. There were low levels of inorganic nutrients and organic matter. EcoMod ran for 40 yr of baseline climate data at 380 ppm [CO$_2$], either with or without cutting, allowing initial conditions to stabilise, as per previous rationales (Johnson et al. 2003). We then ran each year of climate data separately from these 'new' soil nutrient initial conditions, giving us 40 separate annual simulations from the same stable initial conditions.

The ability of EcoMod to simulate observed native pasture dynamics at Pontville was further tested by simulating the grassland using daily climate data (minimum and maximum temperature and relative humidity, rainfall, solar radiation and windspeed; vapour pressure was prescribed from generic patterns related to the site's latitude) downloaded from the weather station at the experimental site from 1 January 2005 to 31 December 2009 (for further details on the climate station see Hovenden et al. 2006). A cut was imposed on 15 March each year to a residual biomass of 1 t ha^{-1} to mirror the annual slash at the experimental site. Recorded biomass from clips in the 3 control plots at the Pontville experimental site from April 2007 to December 2009 (M. Hovenden unpublished data) were then compared to the simulated pasture (Fig. 2a), with the lines indicating the range of biomass recorded given the site's inherently patchy nature. The simulated biomass passes within the ranges recorded at Pontville at

Table 1. Simulation runs for native perennial and sown pastures

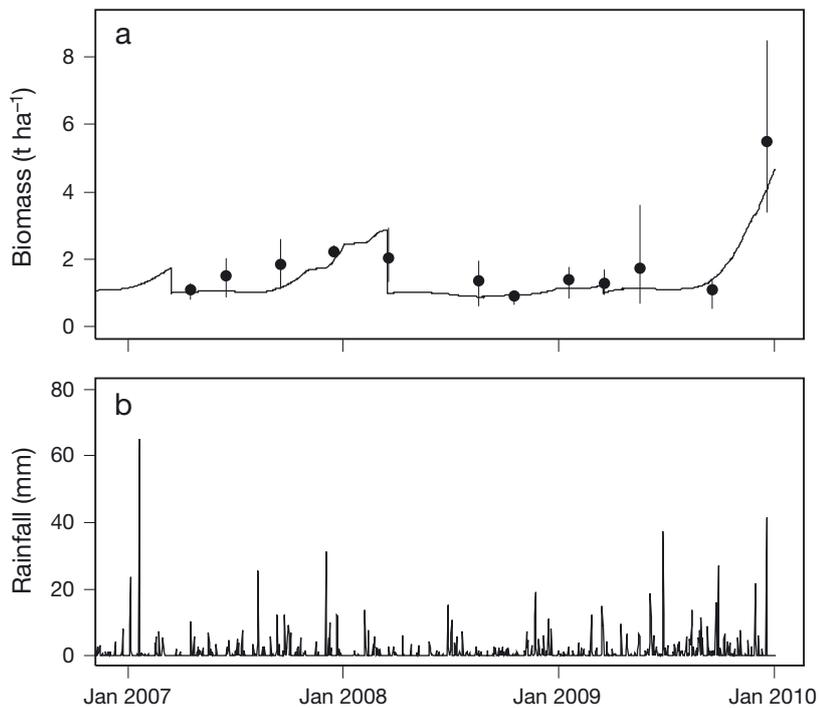| Climate | [CO$_2$] | | |
	Baseline 380 ppm	2030 455 ppm	2070 16 ppm
Baseline (1990)	Cut Uncut	Cut Uncut	Cut Uncut
2030	Cut Uncut	Cut Uncut	–
2070	Cut Uncut	–	Uncut Cut

Fig. 2. (a) Simulated total biomass (thick black line) and mean observed biomass (black dots; lines indicate the range) from 3 control plots at the Pontville experimental site (M. Hovenden unpubl. data). (b) Recorded daily rainfall at the Pontville experimental site

3.2.3. Data recorded

Root, live and dead shoot, and stolon (where relevant) biomasses were recorded, together with ecosystem N properties (ammonium and nitrate in the top 10 cm of soil, and from 10 to 30 cm), and pasture digestibility and protein content. We recorded the GLF for temperature, water and nutrients in the native pasture, thus assessing relative strengths of growth limitations. We did not record GLFs in sown pastures since they should be limited by temperature given management, but did record irrigation and fertiliser amounts. EcoMod records on a daily basis, so yearly averages or totals, as appropriate, were calculated for each of the simulated variables.

3.2.4. Data analyses

Since variation was in the climate data, and not the simulated variables given that we used a deterministic model, a full factorial analysis of variance (ANOVA) or other statistical test was inappropriate. Instead, we presented our results in table form and assessed general patterns and whether changed [CO_2] exacerbated or countered trends due to changed climate. We assessed the sensitivity of our results to initial conditions of the pasture in terms of its percentage composition and absolute amount of biomass. Qualitative results were generally unchanged by varying the initial pasture species composition; further details on the simulation design for variation in initial species composition are provided in Tables A4 and A5 in Appendix 2. Results were robust to a cutting date change from March to October.

all times, barring a slight under-prediction compared to records in September 2007. These results suggest that the model adequately describes the pattern of growth and senescence with appropriate accuracy, as well as simulating the response of the pasture to rainfall events (Fig. 2b), particularly given our stated aim of exploring how generic systems could potentially respond to environmental change, as opposed to a precise description of Pontville itself (e.g. Zhou et al. 2008).

3.2.2. Sown pasture

The same set of simulations (Table 1) was applied to sown pasture that consisted of subterranean clover *Trifolium subterraneum* and perennial rye grass *Lolium perenne*. Sown pasture was irrigated and N fertilised to minimise soil resource limitation. Irrigation was added in response to soil water deficit throughout the year, such that, whenever deficit in the top 50 cm of soil exceeded 20 mm, water was added so that field capacity was reached. Water was canopy-applied between 09:00 h and midday, with at least 1 d between applications. N fertiliser was applied, as urea at 30 kg N ha^{-1}, when either (i) the soil test value became <5 mg N kg^{-1}, or (ii) the GLF for N was ≤0.75.

4. RESULTS

4.1. Biomass and composition

4.1.1. Native pasture

Native perennial pasture biomass showed relatively minor effects with changes in climate, [CO_2] or both (absolute amounts in Table 2). Increased [CO_2] increased overall pasture biomass, particularly in the uncut scenario, due to a 14% increase in live C_3 biomass by 2070, whilst C_4 biomass remained relatively

Table 2. Native pasture species biomass responses to environmental change. Baseline: 1990 climate and 1990 [CO_2] scenario; 2030 and 2070 [CO_2]: increased [CO_2] in line with scenarios but no change of climate; 2030 and 2070 climate: projected changes in climate but no change in [CO_2]; 2030 and 2070 env: simultaneous changes in both [CO_2] and climate. Data are mean total above ground biomass (AG) and the percentage of this which is alive over 40 different weather years, with a maximum SE across all scenarios given at the base of each column. The final 2 columns give the percentage of biomass in the pasture, both above- and below-ground, that is C_3

Scenario	Uncut				Cut				Pasture composition (% C_3)	
	C_3		C_4		C_3		C_4			
	Total AG (t ha^{-1})	Live (%)	Total AG (t ha^{-1})	Live (%)	Total AG (t ha^{-1})	Live (%)	Total AG (t ha^{-1})	Live (%)	Uncut	Cut
Baseline	0.90	41	0.82	43	0.45	50	0.32	52	50.8	55.3
2030 [CO_2]	0.93	41	0.84	43	0.46	51	0.32	52	51.1	55.5
2070 [CO_2]	1.01	42	0.87	44	0.47	51	0.32	53	52.4	56.2
2030 climate	0.91	40	0.87	42	0.48	49	0.35	52	49.7	55.1
2070 climate	0.99	38	1.09	44	0.60	47	0.46	54	46.0	53.1
2030 env	0.94	40	0.89	42	0.49	49	0.35	52	50.0	55.2
2070 env	1.09	39	1.12	44	0.61	48	0.44	54	47.5	54.2
Max. SE	0.04	0.01	0.02	0.01	0.04	0.01	0.01	0.01	0.6	1.2

unaffected, although it still grew by 9% (results calculated from baseline figures in Table 2). These differences were due to the species-specific responses to [CO_2] included in the model parameterisation. Changed climate had negligible impacts upon total C_3 biomass, whereas total C_4 biomass increased markedly, by 33 and 44% in the uncut and cut scenarios by 2070 (results calculated from baseline figures in Table 2). Changed climate and increased [CO_2] acted additively, such that overall environmental change led to increased total pasture biomass with increased C_3 and C_4 biomass (Table 2). Changed climate outweighed the impact of changed [CO_2], such that the C_3 composition of the pasture decreased with overall environmental change (Table 2), although cutting ameliorated the reduction in the proportion of C_3 biomass.

4.1.2. Sown pasture

Changed [CO_2] increased perennial rye grass biomass by 24 and 32% in uncut and cut pastures, respectively, by 2070 compared to the baseline, whilst subterranean clover biomass changed negligibly (Table 3). Changed climate reduced perennial rye grass biomass slightly by 2030, which, however, declined substantially (60% in uncut, 53% in cut pastures) by 2070 (results calculated from baseline in Table 3). Conversely, biomass of subterranean clover increased in response to changed climate by 2070, doubling in cut pastures and increasing by 180% in uncut pastures (results calculated from baseline in Table 3). Effects of changed [CO_2] and climate were again additive: overall environmental change led to a decline in perennial rye grass and an increase in subterranean clover bio-

Table 3. Sown pasture species biomass responses to environmental change. Other details as in Table 2

Scenario	Uncut				Cut				Pasture composition (% *L. perenne*)	
	Lolium perenne		*Trifolium subterraneum*		*L. perenne*		*T. subterraneum*			
	Total AG (t ha^{-1})	Live (%)	Total AG (t ha^{-1})	Live (%)	Total AG (t ha^{-1})	Live (%)	Total AG (t ha^{-1})	Live (%)	Uncut	Cut
Baseline	3.56	82	0.31	81	2.67	83	0.50	83	90.8	82.0
2030 [CO_2]	3.89	82	0.33	81	2.98	83	0.51	83	91.1	83.3
2070 [CO_2]	4.47	81	0.36	80	3.49	82	0.52	82	91.4	84.9
2030 climate	3.24	82	0.34	81	2.44	83	0.57	83	89.0	78.3
2070 climate	1.54	80	0.87	81	1.26	81	0.99	81	59.0	51.7
2030 env	3.58	81	0.36	81	2.73	82	0.58	83	89.6	80.0
2070 env	2.39	78	0.82	80	1.92	79	1.03	80	70.5	61.0
Max. SE	0.10	0.001	0.05	0.002	0.06	0.001	0.04	0.001	2.3	1.6

mass, but not to the extent of the responses induced by changed climate alone (Table 3). Overall environmental change led to a reduction in the domination of the sward by perennial rye, with a decline in total community biomass compared to the baseline (Table 3).

4.2. Ecosystem soil N responses and GLFs

Changes in the environment and management affected soil N properties in native and sown pastures (Table 4), which generally exhibited directional trends with changed climate and changed $[CO_2]$. Native pastures had low nitrate ($[NO_3^-]$) and ammonium ($[NH_4^+]$) concentrations under current environmental conditions, particularly at depth (Table 4). Total inorganic N decreased with changed $[CO_2]$, but only at the surface. In contrast, changed climate increased both $[NO_3^-]$ and $[NH_4^+]$, at the surface and at depth. Climate change dominated the signal, and inorganic N concentrations increased with overall environmental change (Table 4). Applying fertilisation and irrigation in sown pastures produced a clearer simulation of the response of nutrient contents to environmental change, with similar responses at the surface and at depth (Table 4). Increased $[CO_2]$ decreased both $[NO_3^-]$ and $[NH_4^+]$, whereas changed climate had the opposite effect (Table 4). Changed climate dominated the signal such that overall environmental change led to increased inorganic N.

Nutrient levels were higher in cut pastures, whether native or sown, perhaps due to cutting allowing nutrient accumulation and preventing plant nutrient uptake. GLFs varied with environmental change and between species (Table 5). N predominantly limited growth of C_3 species under all environments, whilst temperature was most limiting for C_4 species with baseline climate. N became limiting for C_4 species with the 2070 climate, and environment, as increased temperatures ameliorated the temperature limitation. Water tended to be the least limiting factor, although temperature barely limited C_3 growth.

4.3. Ecosystem and management implications

In native pastures, digestibility and protein content responded with small declines to changed $[CO_2]$, changed climate and environmental change (Table 6). This mirrored the relatively minor effects of the stressors on biomass dynamics and reflected the lower digestibility of C_4 material given the biomass response to climate change, and the lower digestibility of C_3 material under conditions of increased $[CO_2]$ due to the simulated dilution of N within the biomass. The 2070 environment in sown pasture led to only a 5% reduction in digestibility, which reflected changes in pasture composition, with subterranean clover compensating for the reduction in perennial rye grass. Protein content in the sward declined with changed $[CO_2]$, by

Table 4. Mean soil nutrient concentrations in native and sown pasture under changed environmental conditions. Surface: 0–10 cm depth; Depth: 10–30 cm depth. Inorg: total inorganic N ($[NO_3^-]$ (nitrate) + $[NH_4^+]$ (ammonium)) ($\times 10^{-2}$ for native, $\times 10^0$ for sown). Data are mean nutrient concentrations for 40 different weather years, with the base of each column giving the maximum SE over those 40 yr for the given measured variable. For scenarios, see Table 2 caption

| Scenario | Uncut | | | | | | Cut | | | | | |
| | Surface (kg ha⁻¹) | | | Depth (kg ha⁻¹) | | | Surface (kg ha⁻¹) | | | Depth (kg ha⁻¹) | | |
	NO_3^-	NH_4^+	Inorg	NO_3^-	NH_4^+	Inorg	NO_3^-	NH_4^+	Inorg	NO_3^-	NH_4^+	Inorg
Native pasture												
Baseline	5.4	19.3	24.7	0.12	0.10	0.22	9.6	31.7	41.2	0.14	0.08	0.22
2030 $[CO_2]$	5.1	18.5	23.6	0.12	0.11	0.22	9.1	30.5	39.7	0.14	0.08	0.21
2070 $[CO_2]$	5.4	18.3	23.7	0.13	0.11	0.24	9.8	30.2	40.0	0.14	0.08	0.22
2030 climate	8.1	21.6	29.7	0.16	0.11	0.27	13.8	35.4	49.2	0.23	0.08	0.31
2070 climate	15.9	27.0	42.8	0.36	0.11	0.47	26.7	42.6	69.4	1.04	0.19	1.23
2030 env	7.7	20.6	28.3	0.16	0.11	0.27	13.3	33.9	47.2	0.21	0.08	0.29
2070 env	17.6	24.5	42.2	0.40	0.11	0.50	29.7	39.5	69.1	0.97	0.08	1.05
Max. SE	0.94	1.02	1.89	0.05	0.006	0.05	0.88	0.85	1.55	0.24	0.04	0.27
Sown pasture												
Baseline	14.0	20.1	34.1	14.5	3.4	18.0	25.5	22.6	48.1	31.6	5.8	37.4
2030 $[CO_2]$	11.8	19.6	31.3	10.7	2.9	13.6	21.7	21.6	43.3	24.6	5.0	29.6
2070 $[CO_2]$	10.7	18.7	29.4	9.0	2.5	11.5	18.6	19.8	38.5	19.8	4.1	23.4
2030 climate	24.3	21.8	46.1	32.6	5.2	37.8	36.8	23.2	60.0	53.8	7.5	61.3
2070 climate	69.9	22.3	92.3	135	11.6	147	71.3	20.6	92.0	136	11.7	148
2030 env	20.1	20.7	40.8	24.5	4.4	28.9	32.2	22.5	54.8	43.5	6.6	50.1
2070 env	59.2	20.4	79.6	103	9.5	113	63.0	19.1	82.0	110	9.9	120
Max. SE	2.8	0.4	2.7	7.1	0.3	7.3	2.2	0.3	2.2	5.5	0.2	5.7

Table 5. Mean growth limiting factors (GLFs) in native pasture over 40 different weather years for C_3 and C_4 species, together with maximum SE associated with each variable across all scenarios. GLFs are defined in Section 2, and are unitless, with 0 indicating growth is completely limited, and 1 indicating no limitation to growth. Scenarios as in Table 2

| Scenario | Uncut | | | | | | Cut | | | | | |
| | Nitrogen | | Temperature | | Water | | Nitrogen | | Temperature | | Water | |
	C_3	C_4	C_3	C_4	C_3	C_4	C_3	C_4	C_3	C_4	C_3	C_4
Baseline	0.22	0.50	0.84	0.38	0.78	0.89	0.21	0.50	0.84	0.38	0.75	0.94
2030 [CO_2]	0.20	0.49	0.84	0.38	0.79	0.89	0.19	0.49	0.84	0.38	0.75	0.95
2070 [CO_2]	0.20	0.50	0.84	0.38	0.81	0.91	0.19	0.49	0.84	0.38	0.76	0.96
2030 climate	0.23	0.46	0.86	0.43	0.77	0.88	0.22	0.46	0.86	0.43	0.74	0.93
2070 climate	0.27	0.34	0.90	0.58	0.75	0.83	0.26	0.35	0.90	0.58	0.72	0.88
2030 env	0.21	0.45	0.86	0.43	0.78	0.88	0.20	0.45	0.86	0.43	0.74	0.93
2070 env	0.25	0.34	0.90	0.58	0.77	0.86	0.23	0.34	0.90	0.58	0.73	0.90
Max. SE	0.004	0.005	0.002	0.004	0.01	0.01	0.005	0.005	0.002	0.004	0.01	0.01

Table 6. Pasture quality indicators. Data are mean quality indicators (%) over 40 different weather years, together with maximum SE associated with each variable across all scenarios. Scenarios as in Table 2

| Scenario | Native | | | | Sown | | | |
| | Protein | | Digestibility | | Protein | | Digestibility | |
	Uncut	Cut	Uncut	Cut	Uncut	Cut	Uncut	Cut
Baseline	3.4	3.3	37.7	41.2	25.4	25.4	69.4	69.9
2030 [CO_2]	3.1	3.0	37.6	41.0	24.7	24.7	68.9	69.4
2070 [CO_2]	2.2	2.1	37.1	40.4	20.9	20.8	65.9	66.5
2030 climate	3.4	3.3	37.3	40.9	25.4	25.3	69.3	69.6
2070 climate	3.3	3.4	37.3	41.0	25.0	24.8	68.5	68.5
2030 env	3.1	3.0	37.1	40.7	24.7	24.6	68.7	69.1
2070 env	2.1	2.2	36.6	40.0	20.6	20.4	64.9	65.0
Max. SE	0.04	0.03	0.27	0.36	0.04	0.03	0.06	0.08

5. DISCUSSION

We aimed to show how generic pasture systems might respond to changes in climate and [CO_2] in southeastern Tasmania, including whether rising [CO_2] would exacerbate or counter the impacts of shifts in climate. The responses we simulated were generally consistent among cut and naturally senescing, native perennial and sown annual legume-perennial grass pastures, and the response to changed climate generally outweighed the response to changed [CO_2]. Our results also indicated that pasture quality and the need for irrigation and fertiliser are likely to change in the future. Overall these results have implications for future pasture use and the wider environment.

There were small responses of native pasture biomass to environmental stressors. This was due to the differential limitation of the C_3 and C_4 perennial grass

1.2% in native pastures and 4.5% in sown pastures. Climate change had negligible impacts on digestibility and protein, but in this case, the [CO_2] impact was retained with overall environmental change (Table 6).

Environmental alterations also led to changes in the amount of N and water applied to sown pastures. Plant demand for N increased with increased [CO_2] due to increased growth, and thus increased [CO_2] led to increased fertiliser application (Table 7). Conversely, water use efficiency was increased under higher [CO_2] due to the decline in canopy conductance, and hence irrigation declined. In contrast, the large increase in inorganic N availability with climate change reduced the need for fertiliser application. Irrigation was also projected to decline, although negligibly by 2030, as physiological mechanisms prevented the growth of the sown pasture at higher temperatures. Again, impacts were additive, such that the decline in fertiliser use with changed climate was ameliorated at high [CO_2], whilst irrigation declined more with environmental change given that both changed [CO_2] and changed climate alone led to reductions in water application (Table 7).

Table 7. Sown pasture management indicators. Data are mean amounts of fertiliser and irrigation applied over 40 different weather years, together with maximum SE associated with each variable across all scenarios. Scenarios as in Table 2

| Scenario | Fertiliser (kg ha^{-1}) | | Irrigation (mm yr^{-1}) | |
	Uncut	Cut	Uncut	Cut
Baseline	317	272	624	551
2030 [CO_2]	383	332	620	552
2070 [CO_2]	427	378	557	509
2030 climate	250	217	620	546
2070 climate	48	45	523	476
2030 env	307	275	620	551
2070 env	138	134	499	450
Max. SE	12.8	12.2	14.3	14.2

species (Table 5) under the different conditions. This meant that both species could only respond with limited increased growth to increased $[CO_2]$, with C_3 species having a greater response, in line with experimental findings (Ainsworth & Long 2005) and our parameterisation of carbon fixation in the model. Changed climate increased the growth of C_4 species far more than that of C_3 grasses because of the mechanism within the model by which their response to temperature was regulated. Temperature constraints on C_4 perennial grass growth were thus reduced (Table 5), and allowed C_4 perennial grasses to increase, as shown experimentally elsewhere (Wan et al. 2005, Luo 2007). Our simulated change mirrors the current distribution of C_4 grasses, which show strong correlations with warmer summer temperatures in Australia (Hattersley 1983) as elsewhere (von Fischer et al. 2008), and reflects the findings by Cullen et al. (2009) in simulating herbage accumulation over a wider area of Australia. An empirical modelling approach that related C_3, C_4 and shrub abundance to climatic parameters also indicated that changed climate would lead to C_4 increase, although this was at the expense of C_3 grasses. However, such a change was not universal, with some native grass areas maintaining C_3 relative abundance (Epstein et al. 2002). Neither changed climate nor changed $[CO_2]$ markedly reduced the already limited growth of the C_3 and C_4 perennial species, and thus simultaneous environmental change led to a small increase in overall pasture biomass because of the positive impacts of changed $[CO_2]$ and climate alone on C_3 and C_4 species, respectively. Other modelling studies have shown decreased net primary productivity in *Themeda triandra* grasslands with climate change, whilst $[CO_2]$ was shown to offset these decreases (Coughenour & Chen 1997). Our results confirm the importance of the relative degree of water and nutrient limitation in determining pasture responses (Riedo et al. 2001), which may also partly explain mixed responses of field experiments to warming in general (Rustad et al. 2001, Reich et al. 2006b, Luo 2007).

In contrast to the response in native pasture, changed climate and changed $[CO_2]$ had opposite impacts on pasture biomass in sown pasture, which led to an overall decline in biomass with simultaneous change of climate and $[CO_2]$. The opposing influences of temperature and $[CO_2]$ have also been revealed through the FvCB approach to modelling photosynthesis in tall grass prairie in the United States over long timescales (Zhou et al. 2008), grasslands elsewhere (Coughenour & Chen 1997), and at broader spatial scales (Levy et al. 2004). The rectangular hyperbola model of photosynthesis used here has also shown opposing effects of climate and $[CO_2]$ change in previous model simulations (Thornley et al. 1991). In our simulations, although

$[CO_2]$ increased perennial rye grass biomass, as shown experimentally elsewhere (Schneider et al. 2004), this could not compensate for the large reduction in growth engendered by changed climate due to temperatures that are beyond the physiological tolerance of perennial rye grass. The limited responsiveness of subterranean clover to $[CO_2]$ meant that although it increased in response to changed climate, simultaneous environmental change decreased pasture biomass overall. The limited responsiveness of the legumes to raised $[CO_2]$ may at first appear surprising given that some experiments and simulation models have shown positive responses to increased $[CO_2]$ (Teyssonneyre et al. 2002, Ross et al. 2004, Lazzarotto et al. 2010). In our simulations, however, competition from perennial rye grass (Arnone 1999), and prevention of N limitation to growth given the urea fertilisation within the sown pastures, prevented increased subterranean clover growth. In contrast, other simulation models run in sites with low amounts of soil N had increased clover growth given reduced competition from perennial rye grass with increased $[CO_2]$ (Lazzarotto et al. 2010). In common with sown and native pasture field experiments (Schneider et al. 2004, Reich et al. 2006a), the $[CO_2]$ fertilisation effect was more apparent at the higher levels of N supply found in the sown pasture compared to the nutrient-deficient native pasture.

The N balance of the pasture system was also influenced by changed $[CO_2]$ and climate and their impacts upon plant growth. The idiosyncratic responses of individual inorganic N species to changed $[CO_2]$ in native pastures were not surprising, given the low quantities involved and dynamic nature of the nutrient simulations. Increased biomass due to changed $[CO_2]$ led to declines in N at baseline climate, as has been shown in other modelling studies using various approaches to the simulation of pasture growth (Thornley et al. 1991, Cannell & Thornley 1998a, Shen et al. 2009). This is consistent with the first stage of the progressive nutrient limitation mechanism of Luo et al. (2004), as demonstrated in some experimental ecosystems (Schneider et al. 2004, Reich et al. 2006a). Declines in mineral N were experimentally induced at TasFACE by increased $[CO_2]$, but this occurred in the absence of biomass increases (Hovenden et al. 2008). Hovenden et al. (2008) attributed the decrease to plant allocation shifting in response to $[CO_2]$ that then affected microbial community composition and function, although the exact mechanism remains unknown.

Simultaneous change of $[CO_2]$ and climate led to the simulation of increased mineral N pools across the different pastures, as did changed climate alone. Simultaneous increased temperature and $[CO_2]$ at TasFACE showed the potential for warming to overturn declines in mineral N due to rising $[CO_2]$ (Hovenden et al. 2008).

Experimental warming alone did not alter mineral N pools at TasFACE (Hovenden et al. 2008), although more recent observations are revealing an increase in mineral N with warming alone (M. Hovenden unpublished data). Other warming experiments in sub-arctic heath have also shown the potential to increase mineral N pools despite biomass also increasing (Jonasson et al. 1999, Rinnan et al. 2007). As well as being broadly in agreement with experimental studies, our model results have also been mirrored by previous simulation studies (Thornley et al. 1991, Schimel et al. 1994, Shen et al. 2009). In our work, temperature limitation to plant growth, as shown by the GLF values for C_4 species in native pasture (Table 5) and the modelled prevention of perennial rye grass growth due to excessive temperatures, allowed further nutrient accumulation under changed climate scenarios. In cut simulations, increased N may also be aided by the return of litter to the surface that then allows increased transfer of N to the mineral pool with increased heterotrophic activity, in line with experimental observations of increased N mineralisation following warming (Rustad et al. 2001). Further experimental work is required to elucidate the sensitivities of autotrophs and heterotrophs to environmental stressors and determine whether plant uptake is affected to a greater or lesser extent than processes that increase mineral N availability. This will further aid development of our, and other, ecosystem models, given that the results we simulated depended on our parameterisation of such processes (see also Luo 2007).

Environmental stressors decreased pasture nutritional quality, in both sown and native pastures. In native pastures this was mostly due to the increased dominance of C_4 grasses, which are nutritionally inferior to C_3 grasses, even at elevated [CO_2], due to their lower protein content (Barbehenn et al. 2004). Rising [CO_2] has also been shown to lead to decreased protein and N contents of a variety of species across a range of temperatures (Zvereva & Kozlov 2006, Taub et al. 2008), further reducing pasture quality. Our simulated decline in sown pasture digestibility and protein (approximately 5%) was slightly less than the 10 to 15% protein decline found in crop plants (Taub et al. 2008) and the decline in digestibility in some experiments (Milchunas et al. 2005). However, absolute values will depend on the specific pasture species that we simulated, and we are not aware of the existence of such knowledge. The limited response of protein to temperature change whilst it declined with [CO_2] agreed with a recent meta-analysis (Zvereva & Kozlov 2006). Increased legume biomass, as we simulated in later climates, with or without changed [CO_2], has been shown to lead to increased pasture quality experimentally (Allard et al. 2003); the exact response will depend on the nutrient composition of the pasture species, their

partitioning of biomass under environmental change, and change in their abundance (Howden et al. 2007).

Our simulations highlight the requirement for farmers to adapt to environmental stressors if they wish to maintain yields and forage quality (Karing et al. 1999, Howden et al. 2007). In particular, our results highlight the importance of breeding programs in selecting and distributing pasture genotypes most suited to projected future conditions. Our results may also have implications for ecosystems downstream of the pastures. Increased mineral N from climatic change poses a risk of greater leaching and surface runoff and thus eutrophication of watercourses (Carpenter et al. 1998), particularly if rainfall events become more intense (CSIRO 2007).

Notwithstanding uncertainties in projections of future climate change (Beaumont et al. 2008), our results provide testable hypotheses for future experimentation and also show responses to environmental stressors consistent both internally and with the results of other workers (Gerten et al. 2008, Luo et al. 2008). The compositional changes we have simulated may be modified by altered precipitation patterns (Pitman & Perkins 2008) as well as changes in rainfall quantity. However, other modelling studies have shown that changes in temporal rainfall distribution had little impact on biomass in comparison to changes in rainfall quantity (Cullen et al. 2008a, Gerten et al. 2008). Predictive confidence would also be improved by an exploration of parameter space for soil environments and pasture species, over a range of future climates and [CO_2] (e.g. Brassard & Singh 2007, Challinor et al. 2009).

In common with experiments (Norby & Luo 2004), the model was run with a step change in environmental parameters, and only for 1 yr at a time. This allowed a rigorous evaluation of responses to these step changes. However, the reality of future environmental change is that this will occur gradually, with some ecosystem effects taking time to become apparent, through compositional change or long-term dynamic responses in soil organic matter (Luo et al. 2004, Suding et al. 2008), as opposed to the short-term physiological responses characterised well in our model parameterisations. Some authors have argued that general conclusions may not be altered when looking at gradual versus step changes (e.g. Thornley et al. 1991), whereas more recent work has shown different responses when abrupt versus gradual changes are imposed (Shen et al. 2009). Examining dynamics for longer than 1 yr may also influence the results; for example, Schimel et al. (1996) showed opposite responses in net primary productivity when comparing first versus second year simulation results to environmental changes, and Thornley & Cannell (1997) showed that short-term responses could be different in sign or at least magnitude from long-term

responses. Future simulations using longer time frames would therefore be a useful next step in furthering our understanding of how environmental change will likely impact pasture ecosystems and the processes operating in them.

6. CONCLUSION

Our simulations have shown that for native and sown pastures, projected climate change is likely to have far more of an impact than rising $[CO_2]$ in determining the future biomass, composition and nutrient dynamics of these grasslands. C_4 species increased in biomass under changed climates in native perennial pastures, whereas C_3 species remained unaffected in native pastures whilst they underwent a large decline in sown pastures, responses due to temperature sensitivities in their growth and other limiting factors in the native pasture. Sown grass-legume pastures partially compensated for the grass species decline with increased legume biomass. Soil N declined in response to increased $[CO_2]$ but increased in response to changed climate, a response that dominated the environmental change signal. Nutrient dynamics depended upon management practices and the prevention of plant nutrient uptake in future environments. Declines in forage quality across pasture types with environmental change can only be partially ameliorated by management practices. Farmers must pursue adaptation strategies for soil water and nutrient levels and pasture species composition, if they wish to maintain current stocking levels. The incorporation of longer-term feedbacks through compositional change and microbial dynamics may ameliorate or worsen our projected outcomes, the investigation of which should be a priority in further research.

LITERATURE CITED

Ainsworth EA, Long SP (2005) What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO_2. New Phytol 165: 351–372

Allard V, Newton PCD, Lieffering M, Clark H, Matthew C, Soussana JF, Gray YS (2003) Nitrogen cycling in grazed pastures at elevated CO_2: N returns by ruminants. Glob Change Biol 9:1731–1742

Arnone JA III (1999) Symbiotic N_2 fixation in a high Alpine grassland: effects of four growing seasons of elevated CO_2. Funct Ecol 13:383–387

Barbehenn RV, Chen Z, Karowe DN, Spickard A (2004) C_3 grasses have higher nutritional quality than C_4 grasses under ambient and elevated atmospheric CO_2. Glob Change Biol 10:1565–1575

Beaumont LJ, Hughes L, Pitman AJ (2008) Why is the choice of future climate scenarios for species distribution modelling important? Ecol Lett 11:1135–1146

Brassard JP, Singh B (2007) Effects of climate change and CO_2 increase on potential agricultural production in Southern Québec, Canada. Clim Res 34:105–117

Cannell MGR, Thornley JHM (1998a) N-poor ecosystems may respond more to elevated $[CO_2]$ than N-rich ones in the long term. A model analysis of grassland. Glob Change Biol 4:431–442

Cannell MGR, Thornley JHM (1998b) Temperature and CO_2 responses of leaf and canopy photosynthesis: a clarification using the non-rectangular hyperbola model of photosynthesis. Ann Bot (Lond) 82:883–892

Carpenter SR, Caraco NF, Correll DL, Howarth RW, Sharpley AN, Smith VH (1998) Nonpoint pollution of surface waters with phosphorus and nitrogen. Ecol Appl 8:559–568

Challinor AJ, Wheeler T, Hemming D, Upadhyaya HD (2009) Ensemble yield simulations: crop and climate uncertainties, sensitivity to temperature and genotypic adaptation to climate change. Clim Res 38:117–127

Coughenour MB, Chen DX (1997) Assessment of grassland ecosystem responses to atmospheric change using linked plant-soil process models. Ecol Appl 7:802–827

CSIRO (Commonwealth Scientific and Industrial Research Organisation) (2007) Climate change in Australia. Tech Rep 2007, CSIRO (www.climatechangeinaustralia.gov.au/)

Cullen B, Eckard R, Johnson I, Lodge G and others (2008a) Climate change impacts on Australian grazing systems. University of Melbourne, Parkville

Cullen BR, Eckard RJ, Callow MN, Johnson IR and others (2008b) Simulating pasture growth rates in Australian and New Zealand grazing systems. Aust J Agric Res 59:761–768

Cullen BR, Johnson IR, Eckard RJ, Lodge GM, Walker RG, Rawnsley RP, McCaskill MR (2009) Climate change effects on pasture systems in south-eastern Australia. Crop Pasture Sci 60:933–942

Drake BG, Gonzalez-Meler MA, Long SP (1997) More efficient plants: a consequence of rising atmospheric CO_2? Annu Rev Plant Physiol Plant Mol Biol 48:609–639

Dukes JS, Chiariello NR, Cleland EE, Moore LA and others (2005) Responses of grassland production to single and multiple global environmental changes. PLoS Biol 3:e319

Eckard RJ, Johnson IR, Chapman DF (2006) Modelling nitrous oxide abatement strategies in intensive pasture systems. Int Congr Ser 1293:76–85

Ellsworth DS, Reich PB, Naumburg ES, Koch GW, Kubiske ME, Smith SD (2004) Photosynthesis, carboxylation and leaf nitrogen responses of 16 species to elevated pCO_2 across four free-air CO_2 enrichment experiments in forest, grassland and desert. Glob Change Biol 10:2121–2138

Epstein HE, Gill RA, Paruelo JM, Lauenroth WK, Jia GJ, Burke IC (2002) The relative abundance of three plant functional types in temperate grasslands and shrublands of North and South America: effects of projected climate change. J Biogeogr 29:875–888

Gerten D, Luo Y, Le Maire G, Parton WJ and others (2008) Modelled effects of precipitation on ecosystem carbon and water dynamics in different climatic zones. Glob Change Biol 14:2365–2379

Hattersley PW (1983) The distribution of C_3 and C_4 grasses in Australia in relation to climate. Oecologia 57:113–128

Hovenden MJ, Miglietta F, Zaldei A, Van der Schoor JK, Wills KE, Newton PCD (2006) The TasFACE climate change impacts experiment: design and performance of combined elevated CO_2 and temperature enhancement in a native Tasmanian grassland. Aust J Bot 54:1–10

Hovenden MJ, Newton PCD, Carran RA, Theobald P and others (2008) Warming prevents the elevated CO_2-induced reduction in available soil nitrogen in a temperate, perennial grassland. Glob Change Biol 14:1018–1024

Howden SM, Soussana JF, Tubiello FN, Chhetri N, Dunlop M, Meinke H (2007) Adapting agriculture to climate change. Proc Natl Acad Sci USA 104:19691–19696

IPCC (Intergovernmental Panel on Climate Change) (2000) IPCC special report on emissions scenarios. Cambridge University Press, Cambridge

IPCC (2007) Climate Change 2007: synthesis report: Contribution of Working Groups I, II and III to the Fourth Assessment Report of the IPCC. IPCC, Geneva

Jeffrey SJ, Carter JO, Moodie KB, Beswick AR (2001) Using spatial interpolation to construct a comprehensive archive of Australian climate data. Environ Model Softw 16: 309–330

Johnson IR, Lodge GM, White RE (2003) The Sustainable Grazing Systems Pasture Model: description, philosophy and application to the SGS National Experiment. Aust J Exp Agric 43:711–728

Johnson IR, Chapman DF, Snow VO, Eckard RJ, Parsons AJ, Lambert MG, Cullen BR (2008) DairyMod and EcoMod: biophysical pasture-simulation models for Australia and New Zealand. Aust J Exp Agric 48:621–631

Jonasson S, Michelsen A, Schmidt IK, Nielsen EV (1999) Responses in microbes and plants to changed temperature, nutrient, and light regimes in the Arctic. Ecology 80: 1828–1843

Karing P, Kallis A, Tooming H (1999) Adaptation principles of agriculture to climate change. Clim Res 12:175–183

Lazzarotto P, Calanca P, Semenov M, Fuhrer J (2010) Transient responses to increasing CO_2 and climate change in an unfertilized grass-clover sward. Clim Res 41:221–232

Levy PE, Cannell MGR, Friend AD (2004) Modelling the impact of future changes in climate, CO_2 concentration and land use on natural ecosystems and the terrestrial carbon sink. Glob Environ Change 14:21–30

Lodge GM, Garden DL (2000) Grazing management studies in the Temperate Pasture Sustainability Key Program: site descriptions, treatments and data collection. Aust J Exp Agric 40:133–141

Lodge GM, Johnson IR (2008a) Agricultural drought analyses for temperate Australia using a biophysical pasture model. 1. Identifying and characterising drought periods. Aust J Agric Res 59:1049–1060

Lodge GM, Johnson IR (2008b) Agricultural drought analyses for temperate Australia using a biophysical pasture model. 2. Relationship between rainfall and the start and end of predicted droughts. Aust J Agric Res 59:1061–1067

Luo Y (2007) Terrestrial carbon-cycle feedback to climate warming. Annu Rev Ecol Syst 38:683–712

Luo Y, Su B, Currie WS, Dukes JS and others (2004) Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. Bioscience 54:731–739

Luo Y, Gerten D, Le Maire G, Parton WJ and others (2008) Modeled interactive effects of precipitation, temperature, and [CO_2] on ecosystem carbon and water dynamics in different climatic zones. Glob Change Biol 14:1986–1999

McCaskill MR, Ridley AM, Okom A, White RE and others

(2003) SGS nutrient theme: environmental assessment of nutrient application to extensive pastures in the high rainfall zone of southern Australia. Aust J Exp Agric 43:927–944

Milchunas DG, Mosier AR, Morgan JA, LeCain DR, King JY, Nelson JA (2005) Elevated CO_2 and defoliation effects on a shortgrass steppe: forage quality versus quantity for ruminants. Agric Ecosyst Environ 111:166–184

Norby RJ, Luo Y (2004) Evaluating ecosystem responses to rising atmospheric CO_2 and global warming in a multifactor world. New Phytol 162:281–293

Nowak RS, Ellsworth DS, Smith SD (2004) Functional responses of plants to elevations of CO_2: Do photosynthetic and productivity data from FACE experiments support early predictions? New Phytol 162:253–280

Pitman AJ, Perkins SE (2008) Regional projections of future seasonal and annual changes in rainfall and temperature over Australia based on skill-selected AR4 models. Earth Interact 12:1–50

Reich PB, Hobbie SE, Lee T, Ellsworth DS and others (2006a) Nitrogen limitation constrains sustainability of ecosystem response to CO_2. Nature 440:922–925

Reich PB, Hungate BA, Luo Y (2006b) Carbon-nitrogen interactions in terrestrial ecosystems in response to rising atmospheric carbon dioxide. Annu Rev Ecol Syst 37:611–636

Riedo M, Gyalistras D, Fischlin A, Fuhrer J (1999) Using an ecosystem model linked to GCM-derived local weather scenarios to analyse effects of climate change and elevated CO_2 on dry matter production and partitioning, and water use in temperate managed grassland. Glob Change Biol 5:213–223

Riedo M, Gyalistras D, Fuhrer J (2001) Pasture responses to elevated temperature and doubled CO_2 concentration: assessing the spatial pattern across an alpine landscape. Clim Res 17:19–31

Rinnan R, Michelsen A, Baath E, Jonasson S (2007) Fifteen years of climate change manipulations alter soil microbial communities in a subarctic heath ecosystem. Glob Change Biol 13:28–39

Ross DJ, Newton PCD, Tate KR (2004) Elevated [CO_2] effects on herbage production and soil carbon and nitrogen pools and mineralization in a species-rich, grazed pasture on a seasonally dry sand. Plant Soil 260:183–196

Rustad LE, Campbell JL, Marion GM, Norby RJ and others (2001) A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. Oecologia 126:543–562

Sanford P, Cullen B, Dowling PM, Chapman DF and others (2003) SGS pasture theme: effect of climate, soil factors and management on pasture production and stability across the high rainfall zone of southern Australia. Aust J Exp Agric 43:945–959

Schimel DS, Braswell BH, Holland EA, McKeown R and others (1994) Climatic, edaphic, and biotic controls over storage and turnover of carbon in soils. Global Biogeochem Cycles 8:279–293

Schimel DS, Braswell BH, McKeown R, Ojima DS, Parton WJ, Pulliam W (1996) Climate and nitrogen controls on the geography and timescale of terrestrial biogeochemical cycling. Global Biogeochem Cycles 10:677–692

Schneider MK, Luscher A, Richter M, Aeschlimann U and others (2004) Ten years of free-air CO_2 enrichment altered the mobilization of N from soil in *Lolium perenne* L. swards. Glob Change Biol 10:1377–1388

Shen W, Reynolds JF, Hui D (2009) Responses of dryland soil respiration and soil carbon pool size to abrupt vs gradual and individual vs combined changes in soil temperature,

precipitation and atmospheric [CO_2]: a simulation analysis. Glob Change Biol 15:2274–2294

Suding KN, Lavorel S, Chapin FS III, Cornelissen JHC and others (2008) Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. Glob Change Biol 14:1125–1140

Taub DR, Miller B, Allen H (2008) Effects of elevated CO_2 on the protein concentration of food crops: a meta-analysis. Glob Change Biol 14:565–575

Teyssonneyre F, Picon-Cochard C, Falcimagne R, Soussana JF (2002) Effects of elevated CO_2 and cutting frequency on plant community structure in a temperate grassland. Glob Change Biol 8:1034–1046

Thornley JHM, Cannell MGR (1997) Temperate grassland responses to climate change: an analysis using the Hurley Pasture Model. Ann Bot (Lond) 80:205–221

Thornley JHM, Fowler D, Cannell MGR (1991) Terrestrial carbon storage resulting from CO_2 and nitrogen fertilization in temperate grasslands. Plant Cell Environ 14: 1007–1011

Tubiello FN, Soussana JF, Howden SM (2007) Crop and pasture response to climate change. Proc Natl Acad Sci USA 104:19686–19690

von Fischer JC, Tieszen LL, Schimel DS (2008) Climate controls on C_3 vs C_4 productivity in North American grasslands from carbon isotope composition of soil organic matter. Glob Change Biol 14:1141–1155

Wan S, Hui D, Wallace LL, Luo Y (2005) Direct and indirect effects of experimental warming on ecosystem carbon processes in a tallgrass prairie. Global Biogeochem Cycles 19:GB2014

White RE, Christy BP, Ridley AM, Okom AE and others (2003) SGS water theme: influence of soil, pasture type and management on water use in grazing systems across the high rainfall zone of southern Australia. Aust J Exp Agric 43: 907–926

Wu L, McGechan MB (1998) Simulation of biomass, carbon and nitrogen accumulation in grass to link with a soil nitrogen dynamics model. Grass Forage Sci 53:233–249

Zhou X, Weng E, Luo Y (2008) Modeling patterns of non linearity in ecosystem responses to temperature, CO_2 and precipitation changes. Ecol Appl 18:453–466

Zvereva EL, Kozlov MV (2006) Consequences of simultaneous elevation of carbon dioxide and temperature for plant-herbivore interactions: a metaanalysis. Glob Change Biol 12:27–41

Appendix 1. Pasture and soil parameters for pontville

Table A1. *Themeda triandra* and *Austrodanthonia caespitosa.* Pasture parameters. Values changed from the defaults given for C_3 and C_4 plants are shown in **bold**; no parameters were changed on mass flux or shoot partitioning tabs within EcoMod and thus parameters from these tabs are not shown. C_3 plants are assumed not to have low or high temperature effects. Defaults were used for sown pasture simulations. GLF: growth limiting factor; Phys/resp: photosynthesis and respiration

Tab	Parameter	C_3	C_4	Tab	Parameter	C_3	C_4
General	Initial shoot dry weight (t ha^{-1})	**0.5**	**0.5**	CO_2	CO_2 scale parameter (ppm)	**1770**	700
	% green dry weight	50	50		Plant N composition		
	Initial root dry weight (t ha^{-1})	1.0	1.0		CO_2 scale parameter	600	600
					Curvature	**1.7**	1.7
Growth	Leaf appearance interval (%)	20	20		Minimum value for function	**0.5**	0.5
	Live leaves tiller^{-1}	4.0	**6.0**				
	Light extinction coefficient	**0.75**	**0.9**	Temperature	Onset (°C)	n/a	7.0
	Dead to litter (% d^{-1})	1.0	**0.5**		Full (°C)		−5.0
	Optimum leaf % N	2.0	**1.0**		T_{sum} (°D)		75
	Max. leaf % N	**2.2**	**1.3**				
	Remobilisation (%)	**85**	**85**	Roots	Root depth (cm)	**40**	100
	Shoot nutrient composition as % of leaf nutrient composition	50	50		Depth for 50% reduction in root biomass (cm)	**13**	25
	Root nutrient composition as % of root nutrient composition	50	**40**		Scale factor	3.0	3.0
					Root partitioning parameter (%)	20	**30**
Phys/resp	Leaf reference P_{max} (mg CO_2 m^{-2} s^{-1})	**2.2**	**2.8**	Transpiration	Scale factor between wilting point and field capacity	**0.4**	**0.3**
	Minimum temperature for photosynthesis (°C)	**0.0**	**5.0**		GLF at saturation	**0.9**	**0.9**
	Optimum temperature (°C)	20.0	**30.0**				
	Curvature	**1.3**	1.5	Nutrient uptake	N (mg N kg^{-1})	**4**	**4**
	Respiration growth efficiency	0.75	0.75				
	Maintenance coefficient (% d^{-1})	3.00	3.00				

Table A2. Soil water module and soil nutrient module parameters for Pontville grassland. Values changed from default are shown in **bold**; some soil water tab (evaporation, wet up, dry down, infiltration time-step, initial soil water content, canopy and litter, leaching) and nutrient tab (temperature, N transformations, nutrient adsorption, plant inputs, animal inputs, nitrification inhibition) parameters are not shown as they were not changed from default

Soil physical properties	Horizon	Depth (cm)	Soil type
	Surface	**5**	**Sandy-clay-loam**
	A	**20**	**Clay-loam**
	B1	**30**	**Clay**
	B2	**100**	**Clay**
Profile inclination (%)		**0**	

Table A3. Soil nutrient module parameters for Pontville grassland. **Bold:** changed from the default

Initial organic status Carbon	Labile	Inert
Surface C (% mass)	**0.5**	**1.5**
Basal C (% mass)	0	0.25
Depth (cm) for 50% decline	5	20
Curvature	3	3
Nutrient composition		C/N
Microbial biomass		**8.0**
Inert pool		**14.4**
Total soil organic matter		**14.4**
Fast pool		**30.0**
Initial inorganic status Factor	Nitrate	Ammonium
Surface (mg kg^{-1})	0	**4**
Depth for 50% decline (cm)	20	20
Curvature	5	5
Bulge (mg kg^{-1})	3	0
Bulge depth (cm)	30	100
Spread	30	30
Organic matter dynamics Factor	% d^{-1}	Efficiency
Fast decay	**6**	0.6
Slow decay	0.012	0.1
Transfer from fast to slow	10	na
Atmospheric inputs Factor		kg ha^{-1} yr^{-1}
N		10

Appendix 2. Sensitivity of results to initial conditions

Given the design of our simulations, and that once the model had been spun up, we only examined 1 yr at a time, we also undertook an examination of how sensitive the results we report are to changes in the initial composition of the pasture. As our discussion further outlines, the generality of these results should be assessed against a broader range of soil types and background climates, and over longer timeframes.

Table A4. Initial conditions for C$_3$ and C$_4$ biomass. *Italics*: simulation initial conditions used for results reported in the main text. Below and Above refer to below- and above-ground biomass

C$_3$ biomass			C$_4$ biomass			Total biomass
Below (t ha^{-1})	Above (t ha^{-1})	Live (%)	Below (t ha^{-1})	Above (t ha^{-1})	Live (%)	
1	*0.5*	*50*	*1*	*0.5*	*50*	*3*
3	2	75	3	2	75	10
0.1	0.2	50	1.5	1.2	50	3
0.5	0.5	50	4	5	50	10
1.5	1.2	50	0.1	0.2	50	3
4	5	50	0.5	0.5	50	10

Native pastures

Given time constraints, we examined responses of C$_3$ and C$_4$ biomass, and nitrate and ammonium, under 1990 and 2070 conditions. We graphically assessed whether responses in these variables were similar to the major responses reported in the main text. We started the experiment under conditions of high total sward biomass (10 t ha^{-1}) or low total sward biomass (3 t ha^{-1}), with either equal C$_3$-C$_4$ mixtures, or a 10% versus 90% mix. Table A4 presents the full simulation design.

Sown pastures

As subterranean clover is an annual, the initial conditions parameter tab was changed such that subterranean clover had a longer or shorter growth period than originally simulated (Table A5). We also maintained subterranean clover with the values used in the main text but altered the initial amount of perennial rye grass, and the percentage alive. In the default simulations, subterranean clover had an initial biomass that would immediately collapse given the starting point of the simulations and the growth characteristics of subterranean clover. We examined a simulation with no initial subterranean clover biomass; there were no obvious or biologically meaningful differences between the simulation with no initial biomass and with default initial biomass. Cut and uncut simulations were carried out under 1990 and 2070 conditions, with cutting applied on 15 March to a residual biomass of 0.5 t ha^{-1}.

Table A5. *Lolium perenne* and *Trifolium subterraneum*. Initial conditions for perennial rye grass and subterranean clover biomass. All different rye simulations were run with default clover, and vice versa. Defaults are shown in *italics* (these results are presented and discussed in the main text). Below and Above refer to below- and above-ground biomass

Lolium perenne			*Trifolium subterraneum*		Initial biomass
Below (t ha^{-1})	Above (t ha^{-1})	Live (%)	Start	Anthesis	(t ha^{-1})
0.5	1	20	*1 Apr*	*1 Nov*	*1*
0.5	1	80	*1 Apr*	*1 Nov*	*1*
1	2.5	20	*1 Apr*	*1 Nov*	*1*
1	*2.5*	*80*	*1 Apr*	*1 Nov*	*1*
1	*2.5*	*80*	1 Mar	15 Nov	1
1	*2.5*	*80*	1 Mar	1 Oct	1
1	*2.5*	*80*	1 May	1 Oct	1
1	*2.5*	*80*	*1 Apr*	*1 Nov*	*1*
1	*2.5*	*80*	1 Apr	1 Nov	0