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Interacting effects of vegetation, soils and management on the sensitivity of Australian savanna rangelands to climate change

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Abstract There is an increasing need to understand what makes vegetation at some locations more sensitive to climate change than others. For savanna rangelands, this requires building knowledge of how forage production in different land types will respond to climate change, and identifying how location-specific land type characteristics, climate and land management control the magnitude and direction of its responses to change. Here, a simulation analysis is used to explore how forage production in 14 land types of the north-eastern Australian rangelands responds to three climate change scenarios of +3°C, +17% rainfall; +2°C, −7% rainfall; and +3°C, −46% rainfall. Our results demonstrate that the controls on forage production responses are complex, with functional characteristics of land types interacting to determine the magnitude and direction of change. Forage production may increase by up to 60% or decrease by up to 90% in response to the extreme scenarios of change. The magnitude of these responses is dependent on whether forage production is water or nitrogen (N) limited, and how climate changes influence these limiting conditions. Forage production responds most to changes in temperature and moisture availability in land types that are water-limited, and shows the least amount of change when growth is restricted by N availability. The fertilisation effects of doubled atmospheric CO_2 were found to offset declines in forage production under 2°C warming and a 7% reduction in rainfall. However, rising tree densities and declining land condition are shown to reduce potential opportunities from increases in forage production and raise the sensitivity of pastures to climate-induced water stress. Knowledge of these interactions can be applied in engaging with stakeholders to identify adaptation options.

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1 Introduction

The impacts of climate change on primary industries are likely to vary between regions (Sivakumar et al. 2005). Areas that are potentially most vulnerable need to be identified so that adaptation responses can be tailored to individual situations (Howden et al. 2007). In order to prepare for climate change it is, therefore, essential to understand what makes some locations more sensitive to impacts than others, and what challenges and opportunities are likely to arise (Fuhrer 2003). For rangelands, this requires building knowledge of how different land types will respond to climate change, and identifying how location-specific land type and climate characteristics control the magnitude and direction of their responses to change (Heisler-White et al. 2009).

The world's rangelands are set to experience elevated carbon dioxide (CO_2) concentrations, rising temperatures and changing precipitation patterns (IPCC 2007). Increasing atmospheric CO_2 concentrations have been shown to have a number of effects on rangelands, influencing plant physiological responses to changes in temperature, rainfall and evaporative demand (Tubiello et al. 2007). Such changes will induce a variety of system responses, including changes in forage production and quality (Wand et al. 1999; Barbehenn et al. 2004), changes in the distribution of C_3 and C_4 plant species (Howden et al. 1999a), altered competition between grasses and trees (Bond and Midgley 2000), and changes in erosion and land condition (Rounsevell et al. 1999). These responses will have a range of positive and negative effects on livestock production and the viability of farming enterprises, and will be moderated by adaptive practices (McKeon et al. 2009).

Spatial variability in the responses of agro-ecological systems to climate change can be attributed to patterns of soil characteristics, vegetation types, climate and management (Pan et al. 1996). Such controls vary at a range of spatial scales, and interact through multiple feedback mechanisms that complicate interpretations of how any one landscape or climate characteristic influences system responses to climate change (Fuhrer 2003). The individual and interactive effects of atmospheric CO_2, temperature, rainfall and nutrients on the sensitivity of plant growth to climate change have received considerable attention in cropping and rangeland systems around the world (Parry et al. 2004). For example, numerous sensitivity studies have explored the effects of these controls on primary production and farming systems across the North American grasslands, South African veld, Asian steppe, and the Australian rangelands (e.g. Riedo et al. 1999; Christensen et al. 2004; Sivakumar et al. 2005; McKeon et al. 2009). Nonetheless, the interacting effects of location-specific land type and climatic controls on the sensitivity of rangelands to climate change are yet to be resolved sufficiently to inform management and policy (Fuhrer 2003). This raises the question: for a given amount of climate change, to what extent and why, will rangeland ecosystems at some locations be more sensitive than others?

In Australia, a number of studies have sought to identify the potential impacts of climate change on agro-ecological systems (Harle et al. 2007; Howden et al. 2008). These studies have employed mechanistic pasture growth and animal production models to determine how combinations of changes in CO_2, temperature and rainfall influence forage production and livestock carrying capacity (Hall et al. 1998; Howden et al. 1999b; White et al. 2003; Cullen et al. 2009; McKeon et al. 2009). The studies have demonstrated the effects of CO_2 fertilisation on pasture growth in both C_3 and C_4 pasture communities (Cullen et al. 2009). They have shown that the magnitude of forage production responses to CO_2, temperature and rainfall change is spatially heterogeneous (Crimp et al. 2002). Further, changes in forage production may exceed the magnitude of climate changes (Hall et al. 1998), and are influenced by nutrient availability (McKeon et al. 2009). However, the principal contribution of these studies has been in identifying the sensitivity of rangeland responses to step changes in various climate factors (e.g. temperature and rainfall). Research is now required to explore the contribution of location-specific characteristics of rangelands to their vulnerability to climate change. Building research in this area will provide a basis for understanding the diversity of climate change impacts across savanna rangelands, and focussing adaptation efforts to cope with this diversity of change.

This research seeks to identify underpinning controls on the sensitivity of savanna rangelands to climate change in a case study of north-eastern Australia. Here, we analyse simulations of forage production from a daily time-step pasture growth model run for a range of land types under a suite of climate change scenarios to: 1) identify which functional characteristics of rangeland land types control their sensitivity to climate change; 2) identify what effect the presence of trees has on the climate change sensitivity; 3) evaluate the influence of climate type (including rainfall amount and variability) on the sensitivity of rangelands to a given step change in climate; and 4) determine what effect land condition has on rangeland sensitivity to climate change.

2 Study area

The study area is the savanna rangelands of Queensland, Australia, covering an area of 172.8 Mha within the state (Fig. 1). The dominant land use is extensive livestock (beef and wool) production.

The study area covers four Köppen-Geiger climate zones. These include hot arid desert and steppe in the centre and south-west, a temperate zone with hot summer to the east, and tropical savanna in the far-north (Peel et al. 2007). Mean annual rainfall ranges from >1,000 mm in the north, to <150 mm in the south-west. Rainfall seasonality decreases from north-to-south, with the highest rainfall occurring during the summer months (November to March) and influenced by the Australian summer monsoon (Sturman and Tapper 2001). Summertime daily maximum air temperatures lie in the mid-thirties in the north and east, and can exceed 40°C in the south-west. During the winter months (June to August), maximum air temperatures lie in the mid-twenties across the study area, while mean monthly minimum air temperatures are <12°C (Bureau of Meteorology 2010). Frosts may occur in the southern rangelands, with Charleville (S26° 24′, E146° 15′) recording on average 30–40 days per year with minimum temperature <2°C (Bureau of Meteorology 2010).

At the landscape scale the study area can be divided into a number of land types, which are defined by groupings of geomorphic features (e.g. hills, floodplains) and vegetation communities (DPI&F 2009). This study evaluates controls on the sensitivity of 14 representative land types to climate change. Land types selected for the study covered: 1) the range of soil fertility levels (low to high) that are found in the study area; 2) the dominant soil textures and geomorphic features; and 3) the dominant vegetation groups (C_4 pasture communities) and therefore the range of forage quality and productivity levels. A list of the land types selected for the study and their functional characteristics is provided in Online Resource 1.

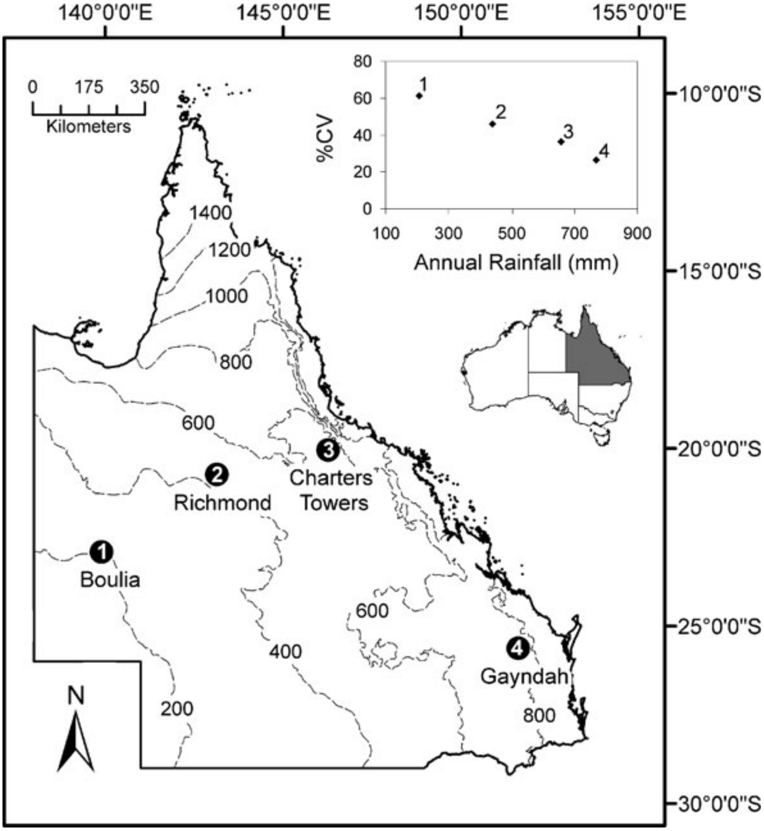

Fig. 1 Study area map showing the location of the climate stations used in the study to represent climate types, with a linear gradient of increasing mean annual rainfall and decreasing annual rainfall variability (inset)

3 Methods

3.1 Model, parameterisation and inputs

3.1.1 GRASP modelling system

The study was conducted through simulations using the GRASP (Grass Production) model (Rickert et al. 2000). The GRASP model structure, calibration and validation are described by Day et al. (1997) and Littleboy and McKeon (1997), and are summarised by McKeon et al. (2000). GRASP is an empirical point-based model that simulates a daily soil-water balance, grass growth and animal production in response to climate inputs and land management options. The climate inputs include daily rainfall (mm), maximum and minimum temperature (°C), pan evaporation (mm), solar radiation (MJ m^{-2} day^{-1}) and vapour pressure deficit (hPa).

GRASP has a number of options for representing different grazing strategies. The strategy used here was to run the model with stock consuming 20% of forage grown in each year of the simulations. This management is consistent with the strategies employed by Howden et al. (1999b) and McKeon et al. (2009).

3.1.2 Land type parameterisation

GRASP was parameterised for 14 land types representative of the Queensland rangelands, based on procedures reported by Day et al. (1997). This approach was supplemented by identifying landforms, pasture species, and soil attributes (texture, fertility and drainage characteristics) associated with each of the land types, and assigning values to corresponding model parameters based on options provided in a land resource information look-up-table (MLA 2010). The land type parameterisations are used here to represent the diversity of C_4 pasture communities rather than precisely how individual land types will function, and the results are interpreted accordingly. An additional parameterisation representing an "average" native C_4 pasture land type was also used to examine the effects of climate change without the complicating factors associated with land type differences (after Howden et al. 1999b).

Tree basal area (TBA), a model parameter that affects soil water and N availability for pasture growth, varies considerably within and between land types. Representative average values of TBA were assigned to land types on the basis of expert opinion (G. Whish pers. comm., J. Scanlan personal observation; Carter et al. 1996), and trees were given a maximum competitive advantage for soil water and N as the differential competitive effects are yet to be resolved with confidence across all of the land types. Table 1 provides a summary of the range of key functional parameters that define the productivity of each of the land types.

3.1.3 Model performance

GRASP has been validated using a range of techniques comparing simulated and observed pasture yields from non-grazed (exclosures) and grazed pastures (e.g. Day et al. 1997;

Table 1 List of representative land types used in the study and the range of functional characteristics (model parameters) used to interpret drivers of the sensitivity of rangelands to climate change

Land type functional parameters	Range of values
Maximum Plant Available Water (MPAW)	
Total MPAW (mm)	48–260
Layer 1 MPAW (mm)	10–55
Layer 2 MPAW (mm)	30–133
Layer 3 MPAW (mm)	4–110
Maximum pasture yield (kg ha^{-1})	
(Max N uptake/%N at zero growth) x 100	1136–6857
Soil fertility	
Potential (maximum) N uptake (kg ha^{-1})	9–30
Potential daily regrowth rate per basal area (kg ha^{-1} day^{-1})	2–6
Pasture species	
%N at zero growth (minimum N)	0.35–1.2
%N at maximum growth (maximum N)	0.45–1.3
Transpiration efficiency (kg ha^{-1} mm^{-1} of transpiration at VPD=20 mb)	6–21
Trees	
Tree Basal Area (m^2 ha^{-1})	0–12

Hassett et al. 2000). For the exclosure studies, GRASP was shown to account for a high proportion (r^2=0.84 to 0.97) of both within-year and between-year variation in pasture yields over 5 years across five sites near Gayndah (Fig. 1; Day et al. 1997). For the grazed sites, GRASP was also found to explain a high proportion of peak yield variation between years (r^2=0.92).

Littleboy and McKeon (1997) describe limitations of the modelling system. These include that GRASP does not simulate: the complete nitrogen and carbon cycles; the effects of changing CO_2 concentrations on pasture or tree growth; run-on or lateral drainage; the effects of phosphorus on pasture growth and animal production; phenological development and changing leaf/stem partitioning; the contribution of browse to diet; changing species distributions in response to CO_2 or temperature changes; or the different diet selection of cattle and sheep. In the current study CO_2 effects on pasture productivity are handled by manipulating plant growth parameters (Section 3.1.6). It is the authors' opinion that the remaining limitations are unlikely to have a significant impact on the model's capacity to represent key differences in land type sensitivities to climate. These processes may affect the overall magnitude of forage production responses to changes in rainfall, temperature or CO_2, but are unlikely to change the relative size of the responses between land types, or the direction of their responses.

3.1.4 Climate types

We used data from four meteorological stations to represent the different climate types in the rangelands of north-eastern Australia. The climate types were selected to capture a gradient across the range of Köppen-Geiger climate types, rainfall seasonality and inter-annual rainfall variability in the Queensland rangelands (McBride and Nicholls 1983). The stations used were Boulia, Richmond, Charters Towers and Gayndah (Fig. 1). For each station a 100-year climate baseline of 1891–1990 was selected over which to run the model simulations. This period was chosen in order to accommodate the pasture systems' responses to the El Niño-Southern Oscillation (ENSO; 3–7 year cycle) and the Inter-decadal Pacific Oscillation (IPO; 15–30 year cycle) (Power et al. 1999; Crimp and Day 2003). Phase interactions between these teleconnections strongly influence rainfall, forage production and land condition in eastern Australia (McKeon et al. 2004). Historical daily weather data for each station were obtained from the SILO online database (www.longpaddock.qld.gov.au/silo/; Jeffrey et al. 2001).

3.1.5 Climate change scenarios

A set of climate change scenarios was used to examine the sensitivity of the land types to climate changes. The climate change scenarios capture the range of climate projections over the north-eastern Australian rangelands, produced by the 23 general circulation models (GCMs) used in CSIRO-BoM (2007) and the IPCC Fourth Assessment Report (IPCC 2007). Three scenarios were used that represent changes within the 10th, median and 90th percentiles of the GCM projections between 2050 and 2100 under the A1FI and A1B emissions scenarios. The scenarios representative of changes in the 10th and 90th percentiles include a hotter and wetter (HW) scenario of a 3°C increase in temperature and 17% increase in rainfall, and a hotter and drier (HD) scenario of a 3°C increase in temperature and 46% decrease in rainfall. A mid-range scenario consistent with the median climate change projections was selected to represent a warmer and drier (WD) scenario of an increase in temperature by 2°C and decrease in rainfall by 7%. In the simulations each climate change scenario was applied with model representations of doubled (700 ppm) atmospheric CO_2 concentrations (described in Section 3.1.6).

The climate change scenarios were used to directly scale the historical daily weather inputs for GRASP. First, following the approach of Cullen et al. (2009), monthly average temperature and rainfall over the 100-year baseline climate types were tested for linear annual trends. A warming trend of ~1°C over the 100 year time-series was evident in the minimum temperature data; however, the data were not de-trended as this change was not evident in the other variables. Changes in rainfall were applied by multiplying the rainfall scenario change factors by the historical daily values. The temperature change factors were scaled to represent proportional changes in minimum (1.05 x warming) and maximum (0.95 x warming) temperature according to projections reported by CSIRO-BoM (2007). For example, an overall change of +3°C was represented as a change of +3.15°C in minimum temperature and +2.85°C in maximum temperature. Changes in minimum and maximum daily temperature were implemented by adding the scaled temperature change factors to the historical values. Following McKeon et al. (2009) solar radiation intensity was not changed.

Pan evaporation (PE) and vapour pressure deficit (VPD) were recalculated using the approach employed by Hall et al. (1998), Rayner (2007) and McKeon et al. (2009). First, VPD was recalculated for each scenario assuming the conservation of relative humidity at minimum temperature. Daily PE (mm day^{-1}) was then calculated as a function of the adjusted VPD (hPa) and solar radiation (MJ m^{-2} day^{-1}). The method assumes that the effect of a temperature increase on PE under climate change will be consistent with the current relationship between these variables, but does not account for the effects of changing wind conditions (McKeon et al. 2009). The general equation used for calculating PE follows:

$$PE = -1.378 + 0.1647VPD + 0.2180SR \tag{1}$$

Where VPD is the adjusted vapour pressure deficit and SR is the solar radiation. Using this procedure, McKeon et al. (2009) found that the effect of recalculating PE and VPD based on temperature and solar radiation gave similar increases to those of GCM projections reported by CSIRO-BoM (2007).

3.1.6 CO_2 effects on forage production

The response of C_4 pastures to elevated CO_2 were considered following the approach of Hall et al. (1998) and McKeon et al. (2009). Five key growth parameters in GRASP were adjusted to represent the effects of doubling CO_2 concentration (from 350 to 700 ppm) on forage production. These include the radiation use efficiency (+5%), transpiration efficiency (+40%), potential daily regrowth rate (+10%), nitrogen uptake per 100 mm grass transpiration (+20%), and green yield (kg ha^{-1}) when green cover for transpiration is 50% (+40%). An important caveat of this parameterisation is that it is yet to include the effect of elevated CO_2 on plant N dilution (Nowak et al. 2004).

3.2 Model simulation and analysis

A series of simulation experiments was established to address the four research aims: to determine how the responses of rangelands to a given climate change scenario are influenced by location-specific characteristics of 1) land types, 2) trees, 3) climate type, and 4) land condition.

The first and second experiments were used to identify which functional characteristics of the land types control their forage production responses to climate change, in the absence and presence of trees. GRASP was parameterised for each of the 14 land types in good condition without trees (Section 3.1.2), then run for a 100-year simulation period using the Charters Towers climate type and adjusted for the three climate change scenarios (Section 3.1.5). The use of a single climate type eliminated climate location impacts on the forage production responses to climate change and enabled land type functional differences (Table 1) to be expressed and examined. The Charters Towers climate data was selected as the basis of this experiment because it is representative of the climate in the more productive rangelands of eastern Australia. For the second experiment in which trees were included, we assigned representative values of tree basal area (TBA) to each land type that has woody vegetation (Online Resource 1). For the open grasslands (Mitchell Grass Downs, Ashy Downs and Gibber Plains) a TBA value of 4 m^2 ha^{-1} was used to evaluate the potential effects of woody vegetation thickening or the spread of woody weeds on forage production (Noble 1997).

The sensitivity of each land type to climate change (with and without trees) was assessed by computing the percentage change in mean annual forage production under each scenario relative to the baseline production. Patterns in the land type responses to each climate change scenario were then identified by evaluating correlations between the land type functional characteristics (Table 1) and the changes in forage production. The functional characteristics were represented as individual model parameters, and two land type functional traits identified *a priori* as being important controls on forage production. The functional traits included: maximum potential pasture yield (computed as maximum N-uptake divided by percent N at zero growth, multiplied by 100); and maximum plant available water (MPAW; computed as the difference in moisture between field capacity and wilting point in each soil layer and combined for the full soil profile).

The third experiment was run as a 1×4×4 factorial of land types, climate types and climate change scenarios; designed to show to what degree climate type (e.g. rainfall levels and variability) influences forage production responses to climate change. To reduce the experimental complexity a single land type parameterisation of GRASP was used to represent an average native C_4 pasture without trees (Section 3.1.2). The four climate types described in Section 3.1.4 were used as input to GRASP as a baseline and adjusted for the three climate change scenarios. The effect of climate type on forage production was then evaluated by comparing percentage changes in mean annual forage production to the baseline simulations for each climate type.

The final experiment was designed to elucidate the effects of land condition on the sensitivity of forage production to climate change. Land condition is known to have a significant effect on forage production and livestock performance in the rangelands (Ash et al. 1995). Declining land condition results from the heavy utilisation of pastures, and is related to a reduction in the proportion of productive, palatable and perennial grasses (Karfs et al. 2009). These changes influence pasture species composition, overall pasture productivity, forage quality and nutrition, ground cover, runoff and soil loss, and livestock carrying capacity (McIvor et al. 1995). GRASP was parameterised to represent an average native C_4 pasture in three conditions, representative of good “A” condition, poor “C” condition, and very poor “C-” condition land without trees. These land conditions were based on the pasture having on average 90%, 32% and 5% perennial grasses (after Karfs et al. 2009). Model parameters for the pasture N uptake, grass basal area, dead stem and leaf detachment rates and pasture sensitivity to water availability were adjusted to represent these different conditions (Section 3.1.1). GRASP was then run using the Charters Towers baseline climate type and three climate change scenarios. The effect of land condition on rangeland sensitivity to climate change was assessed by comparing percentage changes in mean annual forage production for each land condition under the baseline and climate change scenarios.

4 Results

4.1 Land type controls on climate sensitivity

Figure 2 summarises the responses of the 14 land types to the climate change scenarios. Forage production shows a general pattern of increasing under the hotter and wetter scenario (HW), increasing or little change under the warmer and drier scenario (WD) and decreasing under the hotter and drier scenario (HD). Table 2 presents coefficients of the correlations between changes in mean annual forage production and land type functional characteristics across the 14 land types (Table 1). In the rangelands characteristics of land types such as their soil textural properties and drainage attributes, soil fertility and plant species attributes are correlated (Friedel et al. 1993). The relationships between these soil and vegetation attributes are contained in the GRASP land type parameterisations (Online Resource 1), and can be used to inform the interpretation of forage production responses to the climate change scenarios. In Table 2, the sign of the correlations describes the direction of change in forage production associated with a change in the land type functional characteristics. Correlations with a positive sign indicate that changes in forage production are in the positive direction as the functional characteristics increase (e.g. increasing N availability). Conversely, correlations with a negative sign indicate that changes in forage production are in the negative direction as the functional characteristics increase.

Under the hotter and wetter scenario (HW), transpiration efficiency has the strongest correlation with changes in forage production ($r=-0.53$). However, this correlation is largely driven by the position of a single outlier (Yellowjacket), and other functional characteristics of the land types confound the general relationship. The weak correlations between the range of land type functional characteristics and changes in forage production (Table 2) suggest that it is the interactions between the characteristics that determine the land type responses under the HW scenario, rather than a single driving factor.

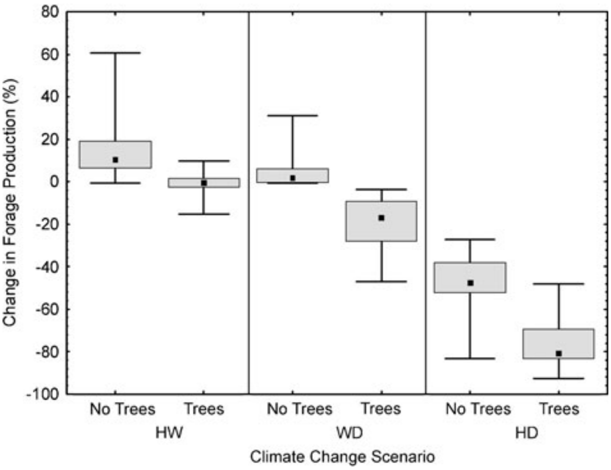

Fig. 2 Box plots showing the distribution of change in mean annual forage production without and with trees across the 14 land types for each climate change scenario: hotter and wetter (HW); warmer and drier (WD); and hotter and drier (HD). Data are based on 100-year simulations averaged for each land type. Solid squares represent the median change, boxes represent the 25th and 75th percentiles of change, and whiskers represent the maximum and minimum changes across the land types for each scenario

Table 2 Correlation coefficients (r) for the relationships between land type functional characteristics (Table 1) and changes in mean annual forage production across the 14 land types, modelled under three climate change scenarios with and without tree cover. The maximum and minimum percentage changes in forage production across the land types (corresponding with Fig. 2) provide an indication of the domain in which the changes occurred. The sign of the correlations indicates the direction of change in forage production associated with a change in the land type functional characteristics. For example, correlations with a positive sign indicate that changes in forage production are in the positive direction as the functional characteristics increase, and vice versa. Climate change scenarios are: hotter and wetter (HW); warmer and drier (WD); and hotter and drier (HD)

Change in forage production	Without trees			With trees		
	HW	WD	HD	HW	WD	HD
Maximum (%)	22.7	10.3	−27.1	9.7	−2.7	−23.2
Minimum (%)	−0.7	−1.4	−78.6	−14.5	−46.7	−92.6
GRASP functional parameter	Correlation with Forage Production Response					
Maximum potential pasture yield	0.07	−0.00	−0.77	−0.19	−0.34	−0.43
Potential (maximum) N uptake (kg ha^{-1})	−0.31	−0.23	−0.47	0.07	0.06	−0.30
%N at zero growth (minimum N)	−0.40	−0.08	0.55	0.25	0.37	0.19
Potential daily regrowth rate (kg ha^{-1} day^{-1})	−0.28	−0.29	0.15	0.16	0.27	0.15
Transpiration efficiency	−0.53	−0.23	0.02	−0.02	0.21	0.06
Total maximum plant available water	−0.05	−0.58	−0.17	0.18	0.46	0.39
MPAW layer 1	−0.19	−0.36	−0.62	0.08	0.06	−0.18
MPAW layer 2	−0.35	−0.36	−0.23	−0.07	0.12	0.03
MPAW layer 3	0.27	−0.56	0.10	0.33	0.63	0.65
Tree basal area (m^2 ha^{-1})	–	–	–	−0.43	−0.62	−0.38

Under the warmer and drier scenario (WD), the MPAW in the full soil profile has the strongest influence on the magnitude of changes in forage production (Online Resource 2). Within the soil profile, the MPAW in the third soil layer has the strongest effect on the forage production response ($r=-0.56$). The results show that land types with a greater capacity for storing plant available water are less responsive to a net decline in water availability (i.e. rainfall) than land types with a low capacity for storing plant available water. These latter types appear to benefit more from improved water-use efficiency under elevated CO_2 concentrations, and show a greater (positive) growth response to a small degree of warming than land types with more plant available water. Land types with higher fertility (Basalt and Coolabah) and MPAW in the third soil layer (Hard Gidyea) show larger forage production responses (increases) than other land types with similar MPAW in the full soil profile (Online Resource 2).

Land types with high maximum potential pasture yield and high MPAW in the first soil layer are most responsive to the hotter and drier (HD) climate change scenario, showing larger declines in forage production (Table 2). There is a negative correlation between change in forage production and maximum potential pasture yield ($r=-0.77$), a positive correlation with %N at zero growth ($r=0.55$), and a negative correlation with MPAW in the first soil layer ($r=-0.62$). This response, illustrated in Online Resource 2, shows that land types that have low N availability (and experience N-limited growth under the baseline climate) may not experience large reductions in growth under the hotter and drier (HD) scenario. Underpinning this response is that the rainfall under the hotter and drier (HD) scenario is high enough to keep the soil water profile near its maximum capacity. Pasture growth in these land types therefore remains N-limited under the changed climate and is less affected by water availability. Growth in these land types will not be affected by their low MPAW until rainfall decreases below the amount that makes growth limited by N availability. That is, the stage at which growth becomes water-limited. Conversely, pastures that have high N availability for growth and have a greater capacity for storing plant available soil water (Online Resource 1) will in fact be most responsive to rising temperatures and extreme declines in rainfall (Table 2). The potential daily regrowth rate of the land types has a very weak positive correlation (r=0.15) with the simulated change in forage production, and does not appear to have a significant effect on the land type responses to the hotter and drier scenario (Table 2).

4.2 Tree effects on climate sensitivity

The addition of trees in the simulations reduced the magnitude of the forage production responses to climate change under the hotter and wetter (HW) scenario and increased the magnitude of its response to the warmer and drier (WD) and hotter and drier (HD) scenarios (Fig. 2). Table 2 shows that TBA has the strongest effect on the forage production responses to the warmer and drier scenario (r=−0.62), and that this effect is apparently weaker under the hotter and wetter (r=−0.43) and hotter and drier (r=−0.38) scenarios. Importantly, the presence of trees alters the strength of other land type functional characteristics in controlling the sensitivity of forage production to climate change.

Under the hotter and wetter (HW) scenario, the effects of grass transpiration efficiency and potential N uptake on forage production decrease considerably in comparison with the simulations without trees (Table 2). Under this scenario there is sufficient rainfall (+17%) to reduce the effects of tree-grass competition for soil water and N, and the effect of trees is to offset any increases in forage production that may result from the improved growing conditions (Fig. 2).

Under the warmer and drier (WD) and hotter and drier (HD) scenarios, the effect of MPAW in the third soil layer increases when trees are present (Table 2). Under both scenarios there is a positive correlation between this land type functional characteristic and the percentage change in forage production (WD r=0.63; HD r=0.65). This suggests that when trees are present, forage production in land types with greater plant available soil water will in fact be less responsive to a warmer or hotter and drier climate. Interestingly, this effect is the reverse of that found for MPAW in the absence of trees.

Land types in Queensland with a lower MPAW tend to have higher TBA (Online Resource 1) and experience larger declines in forage production under scenarios of increased water stress, and smaller increases in forage production under the hotter and wetter (HW) scenario, than land types with low TBA and greater MPAW. This produces the positive correlations between MPAW and the changes in forage production with trees (Table 2). Conversely, in the simulations without trees, land types with low MPAW benefit most (increases in forage production) under the hotter and wetter (HW) scenario, and experience relatively smaller declines in forage production under scenarios of increased water stress as pasture growth tends to be in a N-limited condition; giving negative correlations between MPAW and the changes in forage production (Table 2).

4.3 Climate type and climate sensitivity

Figure 3 illustrates the response of an average native C_4 pasture to climate changes under four climate types (Fig. 1). Forage production shows a positive change in response

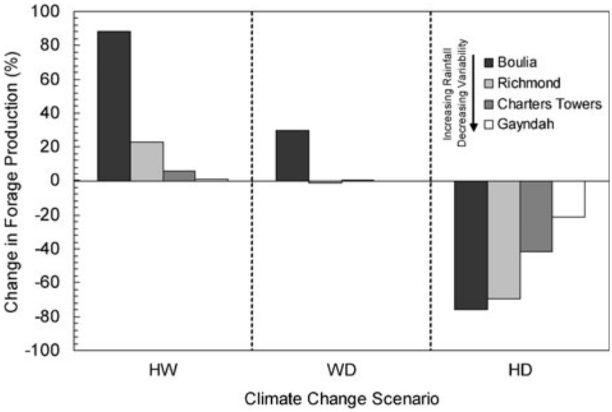

Fig. 3 Changes in mean annual forage production for an average native pasture modelled for four climate types under hotter and wetter (HW), warmer and drier (WD) and hotter and drier (HD) climate change scenarios. Climate types follow a gradient from Boulia (mean annual rainfall 262 mm) to Richmond (467 mm), Charters Towers (658 mm) and Gayndah (770 mm) (see Fig. 1)

to the hotter and wetter (HW) scenario, being most responsive to this change under the Boulia (driest) climate, increasing by 88%, and least responsive under the Gayndah (most productive) climate, increasing by only 1%. The changes in forage production exceed the percentage change in rainfall (17%) under the Boulia and Richmond (drier) climates, but not under the Gayndah and Charters Towers (wetter) climates. A large increase in rainfall can therefore outweigh the potentially negative effects of a rise in temperature on forage production under an arid climate, and could result in more growth where forage production was previously water-limited (e.g. Boulia) than under a sub-tropical climate in which growth is N-limited and has little capacity to increase (e.g. Gayndah). This is despite the rise in temperature extending the length of the growing season under the cooler sub-tropical climate (Gayndah).

Under the warmer and drier climate change scenario (WD), mean annual forage production shows little change under the Gayndah and Charters Towers climates. Under the Boulia climate forage production increases by 30%. This increase in growth is consistent with an increased plant water-use efficiency under elevated CO_2 concentrations, which appears to have the greatest effect on forage production under a climate characterised by consistent water stress (e.g. Boulia).

Under the hotter and drier (HD) scenario the magnitude of change in forage production under the Boulia and Richmond climates exceeds the percentage change in rainfall (−46%). The changes in forage production are lower under the Gayndah and Charters Towers climates (Fig. 3). Under the Boulia climate, forage production shows the greatest sensitivity, decreasing by 76%. Overall, pasture growth under the Gayndah (−21%) climate type is least responsive to the climate change, and shows only small change relative to the change in rainfall (−46%).

4.4 Land condition effects on climate sensitivity

Table 3 summarises the effect of land condition on the sensitivity of an average native C_4 pasture to the three climate change scenarios. Under all scenarios land in good “A” condition responds better under climate change than land in poor “C” or very poor “C-” condition.

An average native C_4 pasture in “A” condition shows the greatest positive forage production response to a hotter and wetter climate change scenario and the least negative response to drier conditions (Table 3). Land condition has the greatest percentage effect on forage production under the hotter and drier (HD) climate change scenario. Land in “A”

Table 3 Percentage changes in mean annual forage production under three climate change scenarios for an average native pasture modelled in three land conditions: "A" good condition (90% perennial grasses); "C" poor condition (32% perennial grasses); and "C-" very poor condition (5% perennial grasses)

Land condition	A condition	C condition	C- condition
Baseline growth (kg/ha)	2692	1827	1437
Scenario	Change in forage production (%)		
Hotter-Wetter	4.35	0.77	1.46
Warmer-Drier	0.19	−6.35	−8.28
Hotter-Drier	−29.42	−46.91	−60.68

condition shows a 29% decline in forage production, whereas land in "C" and "C-" condition experiences forage declines of 47% and 61% respectively.

5 Discussion

5.1 Underpinning controls on rangeland sensitivity to climate change

Rangeland land types show great diversity in their sensitivity to climate change, with both potential opportunities from increases in forage production and challenges from reduced forage availability. The controls on this sensitivity are complex, with functional characteristics of land types interacting to determine the magnitude and direction of their responses (Table 2; Fuhrer 2003). More than half of the land types evaluated in this study show an increase in forage production in the order of 5% to 20% in response to an extreme hotter and wetter climate change scenario, and change of −38% to −52% in response to a hotter and drier (−46% rainfall) scenario (Fig. 2). For the two extreme scenarios the effects of changing rainfall appear to outweigh the influence of rising temperature. However, in both cases the elevated temperature effects on vapour pressure deficit (VPD) are likely to result in some reduction in pasture growth. This reduced the magnitude of increases in forage production under the hotter and wetter scenario, and enhanced reductions in forage production under the hotter and drier scenario. While some land types show considerably amplified responses to the climate change scenarios, the ranges are consistent with the magnitude of responses of native pasture communities elsewhere in Australia (Cullen et al. 2009; Perring et al. 2010). The directions of the changes in forage production are in agreement with those identified in analyses of climate change impacts on grasslands around the world (Baker et al. 1993; Xiao et al. 1995; Riedo et al. 1997), and field-scale experiments on the effects of elevated CO_2 and rainfall change on C_4 plant growth (Ainsworth and Long 2005; Tubiello et al. 2007).

The results indicate that the degree to which forage production will respond to climate change is dependent on whether pasture growth in a particular land type is water or N-limited under the present (baseline) climate, and if and by how much these limitations change under climate change (Table 2). To illustrate, if forage production in a land type is water-limited under the current climate, it is likely to show large changes (increase or decrease) in response to changing moisture availability. Furthermore, forage production reduced by the smallest percentage under the hotter and drier (HD) scenario in land types that are N-limited and have low soil water storage capacity (Total MPAW;

Online Resource 2). This is perhaps counterintuitive, as we might expect land types that have low N availability and low soil water storage capacity to be most affected by the large (64%) reduction in rainfall. However, the response can be explained by the fact that when forage production is N-limited, implying that water availability is not a constraint on growth, declining rainfall will not affect growth as much as in land types where it readily becomes water-limited under reduced rainfall conditions. This latter case occurs in land types with high N availability, which happen to also have higher MPAW (Online Resource 1). Under scenarios of declining rainfall, changes in forage production in N-limited land types will increase in magnitude once growth becomes water-limited. These responses are also climate sensitive, as the climate at a location prior to climate changes occurring (here the simulation baseline climate) will determine whether forage production in a land type is water or N-limited, and therefore the size of its forage production responses to climate change. This is demonstrated in Fig. 3 which shows that, for the hotter and drier (HD) scenario, forage production will decline more in arid climates in which growth is water-limited (hence not N-limited) than in humid climates in which growth is N-limited and less affected by water availability. Under the hotter and wetter (HW) scenario this pattern is not clear, with the forage production responses being moderated by the combination of land type attributes of MPAW in the second soil layer, and the transpiration efficiency, potential N uptake and ability of the pastures to dilute N before growth ceases (Table 2). On a seasonal basis under conditions of above-average rainfall forage production in land types with low fertility frequently reaches the maximum potential pasture yield (Table 1), determined by the availability of N for growth and the degree to which plants can internally dilute N before growth ceases (Day et al. 1997). Such a response currently occurs in the northern Australian rangelands during the Australian summer monsoon (Cobiac 2007).

The range of forage production responses due to climatic factors (Fig. 3) is similar in magnitude to the forage production responses due to location-specific land type characteristics (Fig. 2; Crimp et al. 2002; McKeon et al. 2009). In arid climates where water is limited (e.g. Boulia), a large increase in rainfall is shown to result in a larger forage production response (increase) than in wet climates where growth is not water-limited, or is N limited (Fig. 3). The same applies under the scenario of extreme drying, which has a greater effect on forage production under an arid climate than under a wetter tropical climate. Thus, forage production is most responsive to climate change under a drier climate, which magnifies both positive and negative impacts, and is less responsive to change under a wetter climate where growth is not restricted by water availability. The effects of rising temperature on growing season length are difficult to elucidate under these climate types, with temperature effects being confounded by the magnitude of rainfall changes. However, preceding climate change impacts studies of Hall et al. (1998) and McKeon et al. (2009) have specifically evaluated the role of temperature changes on native pasture growth, demonstrating that a 3°C rise in temperature alone (as applied here within the climate change scenarios) can reduce forage production by 10% to 30% across the Queensland rangelands.

While the effects of CO_2 were not evaluated independently here, our results suggest that the simulated pastures expressed more benefit from elevated CO_2 under the warmer and drier climate change scenario and under the drier climate type (Boulia) than under the extreme hotter and wetter or hotter and drier scenarios and wetter climates (Figs. 2 and 3). This outcome is consistent with our current understanding of how elevated CO_2 benefits native pastures. That is, through improved water-use efficiency and fertilisation effects on photosynthesis, which may offset small (<10%) declines in water availability brought about by reduced rainfall and increased evaporative demands associated with rising temperatures (Ainsworth and Long 2005; Tubiello et al. 2007). These positive effects of CO_2 are likely to have a greater impact on land types that have low soil water storage capacity (implying less water available for growth), than land types that have higher soil water storage capacities and by implication more water available for growth (as shown in Online Resource 2). This simulated response is in agreement with previous studies that have evaluated the effects of doubling CO_2 (with and without other climate changes) on forage production in Australia (e.g. Crimp et al. 2002; Cullen et al. 2009; McKeon et al. 2009).

5.2 Tree effects on climate sensitivity

Trees reduced the sensitivity of pastures to the hotter and wetter climate change scenario, and increased their sensitivity to climate change under the warmer and drier and hotter and drier scenarios. These changes in sensitivity are due to the competitive effects of trees with grasses for soil water, and the results are consistent with the findings of Scanlan (2002), and the analysis of global change impacts on a woodland ecosystem by Howden et al. (2001). Had a dynamic tree model been available to capture the effects of CO_2 on tree-grass competition, the system could have shown even greater changes (increases) in its sensitivity to climate change (Howden et al. 2001). The non-linear effect of increasing TBA on forage production (Scanlan 2002) indicates that the initial establishment of trees in open grasslands will have a greater effect on rangelands than tree thickening in existing wooded land types, as found by Howden et al. (2001). If tree densities were to increase in the rangelands, irrespective of land type functional characteristics, our results suggest that it will largely be the level at which woody vegetation stabilises (i.e. the resulting tree density and leaf biomass) that determines the competitive effects of trees with grasses and the sensitivity of rangelands to future climate change. Best-practice grazing and woody plant management (e.g. using fire) in savanna rangelands will therefore become more critical in the future, and must be handled in the context of ongoing environmental and legislative considerations (Howden et al. 2001; McAlpine et al. 2009).

5.3 Land condition effects on climate sensitivity

Improving land condition has been shown to maximise potential gains in forage production under favourable climate changes (Table 3). These results indicate that maintaining land in a good condition will reduce potential declines in forage production by 20% to 30% under a warmer and drier or hotter and drier future climate. Land managers who overstock and run land in a poor condition are also likely to experience the greatest negative impacts of climate change on forage production. The impacts will flow through to animal liveweight gains and the profitability of enterprises that are dependent on rangeland resources (MacLeod et al. 2004). These results are consistent with the well-documented response of forage production in rangelands to climate variability (Ash et al. 1995; McIvor et al. 1995). In some regions (e.g. tropical) C_4 pastures may experience declines in forage quality under elevated atmospheric CO_2 concentrations, further exacerbating the impacts of declining pasture growth on livestock production in the rangelands (Roumet et al. 1996; Barbehenn et al. 2004; Taub and Wang 2008). The implications of these findings are that maintaining land in good condition or improving land condition today will allow land managers to pre-adapt and be responsive to both climate variability and future climate change (Hunt 2008).

6 Conclusions

The research presented here provides new and useful insights into the underpinning controls on the sensitivity of savanna rangelands to climate change, as influenced by location-specific characteristics of land types, trees, climate types, and land condition.

Rangelands show great diversity in their responses to climate change. Results show that the responses of land types to climate change are complex and influenced by interactions between their functional characteristics of fertility, soil-water storage capacities and plant water-use efficiencies. The role these factors play also depends on atmospheric CO_2 concentrations and local climate characteristics such as temperature and rainfall amounts and variability. These results suggest that there must be an emphasis on developing flexible adaptation strategies, as a range of responses will be required to manage the evolving directions of both future climate change and its effects on different land types. Despite the range of possible changes, rangelands do display some clear responses to climate change. The modelling results indicate that rising tree densities and declining land condition reduce potential opportunities from increases in forage production and raise the sensitivity of pastures to the impacts of climate-induced water stress. Thus, managing tree densities and the spread of woody weeds and maintaining pastures in good condition will likely have co-benefits in reducing the level of impact that climate change will have on savanna rangelands. Additional responses will be required to deal with the diversity of as yet unseen challenges and opportunities that could emerge across the rangelands.

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