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["Data Supplement"](#)

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# A global comparison of grassland biomass responses to CO<sub>2</sub> and nitrogen enrichment

Mark Lee<sup>1,†</sup>, Pete Manning<sup>2,3,\*</sup>, Janna Rist<sup>2</sup>,  
Sally A. Power<sup>1</sup> and Charles Marsh<sup>1</sup>

<sup>1</sup>*Division of Biology, and* <sup>2</sup>*NERC Centre for Population Biology, Imperial College London, Silwood Park Campus, Ascot, Berkshire SL5 7PY, UK*

<sup>3</sup>*Grantham Institute for Climate Change, Imperial College London, South Kensington Campus, London SW7 2AZ, UK*

Grassland ecosystems cover vast areas of the Earth's surface and provide many ecosystem services including carbon (C) storage, biodiversity preservation and the production of livestock forage. Predicting the future delivery of these services is difficult, because widespread changes in atmospheric CO<sub>2</sub> concentration, climate and nitrogen (N) inputs are expected. We compiled published data from global change driver manipulation experiments and combined these with climate data to assess grassland biomass responses to CO<sub>2</sub> and N enrichment across a range of climates. CO<sub>2</sub> and N enrichment generally increased aboveground biomass (AGB) but effects of CO<sub>2</sub> enrichment were weaker than those of N. The response to N was also dependent on the amount of N added and rainfall, with a greater response in high precipitation regions. No relationship between response to CO<sub>2</sub> and climate was detected within our dataset, thus suggesting that other site characteristics, e.g. soils and plant community composition, are more important regulators of grassland responses to CO<sub>2</sub>. A statistical model of AGB response to N was used in conjunction with projected N deposition data to estimate changes to future biomass stocks. This highlighted several potential hotspots (e.g. in some regions of China and India) of grassland AGB gain. Possible benefits for C sequestration and forage production in these regions may be offset by declines in plant biodiversity caused by these biomass gains, thus necessitating careful management if ecosystem service delivery is to be maximized. An approach such as ours, in which meta-analysis is combined with global scale model outputs to make large-scale predictions, may complement the results of dynamic global vegetation models, thus allowing us to form better predictions of biosphere responses to environmental change.

**Keywords:** biodiversity; carbon enrichment; ecosystem services; global change; nitrogen deposition; productivity

## 1. INTRODUCTION

Global environmental change is a multifactor phenomenon including alterations to nitrogen (N) deposition, atmospheric CO<sub>2</sub> concentration and various aspects of climate change, including increased temperatures and altered precipitation patterns (Galloway *et al.* 2004; IPCC 2007). While the relative impacts of each of these factors is currently unknown, it is widely anticipated that novel combinations of CO<sub>2</sub>, reactive N and climate will emerge over the present century, with widespread changes to ecosystems and their services occurring as a result (Millennium Ecosystem Assessment 2006). An important ecosystem service is

biological carbon (C) sequestration, which currently mitigates climate change by acting as a C sink for anthropogenic CO<sub>2</sub> emissions (Trumper *et al.* 2009). Uncertainty surrounding the potential of this mitigation is partly due to a lack of generalization regarding plant growth responses to increased CO<sub>2</sub> and N availability, and the modification of these responses by climate (Trumper *et al.* 2009). Discrepancy in observed responses to these factors may also result from differences between plant functional types (PFTs), an observation that has prompted researchers to promote a biome-based approach to understanding the global C cycle (De Deyn *et al.* 2008). This approach is echoed in recent advances in dynamic global vegetation models (Scholze *et al.* 2006; Bond-Lamberty *et al.* 2007), which are being developed to incorporate more PFTs and ecological processes. The aim of this study was to compare the magnitude of biomass responses to CO<sub>2</sub> and N enrichment, to assess climate dependency in these responses and, where possible, to construct generally applicable statistical models of grassland biomass responses to CO<sub>2</sub>

\* Author for correspondence ([pete.manning@ncl.ac.uk](mailto:pete.manning@ncl.ac.uk)).

† These authors contributed equally to this work.

‡ Present address: Agriculture Building, Newcastle University, Newcastle upon Tyne, Tyne and Wear NE1 7RU, UK.

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and N enrichment. Plant productivity in grasslands is important not only for C sequestration but also for food production and the maintenance of plant diversity. Therefore, we discuss the grassland biome, its responses to N and CO<sub>2</sub> enrichment, and how these may affect its delivery of these ecosystem services.

#### (a) *The grassland biome*

Grass dominated ecosystems cover approximately 52.5 million square kilometres of the Earth's land surface (Suttie *et al.* 2005). Grasslands are often found as early successional ecosystems and are widening their distribution as a consequence of climatic change, deforestation and other anthropogenic disturbances. However, they form the natural climax vegetation in climates where precipitation levels are inadequate to support trees but exceed those of deserts (Woodward *et al.* 2004). Plant growth in natural grasslands is thought to be co-limited by water and N (Hooper & Johnson 1999; Schenk & Jackson 2002; LeBauer & Treseder 2008; St Clair *et al.* 2009) and grasses place much of their biomass belowground to capture these resources; estimates suggest that between 24 and 87 per cent of grassland net primary production (NPP) is allocated belowground (Sims & Singh 1978). Therefore, if global change drivers alter the strength of water and nutrient limitation there may be large impacts on plant growth and biomass allocation. Such changes could have global consequences, as estimates indicate that grasslands and savannas represent a C sink of approximately 0.5 Gt C yr<sup>-1</sup> (Scurlock & Hall 1998). The future of this sink is uncertain, with predictions of grasslands' continued ability to sequester C ranging from approximately -2 Gt C yr<sup>-1</sup> to approximately 2 Gt C yr<sup>-1</sup> (Scurlock & Hall 1998).

#### (b) *CO<sub>2</sub> enrichment*

Atmospheric CO<sub>2</sub> concentrations rose from 316 ppm in 1959 to 379 in 2005 and are expected to continue to rise, possibly exceeding 600 ppm by 2100 (IPCC 2007). There is substantial evidence that elevated CO<sub>2</sub> concentrations increase plant growth (Wang 2007) and it is hypothesized that this increase is moderated by climate, with a greater response to CO<sub>2</sub> seen in drier environments because of reduced evapotranspiration through reduced stomatal opening (Owensby *et al.* 1999; Niklaus & Körner 2004). This interaction between CO<sub>2</sub> and climate is untested with regard to field data from multiple geographical locations. There is also evidence to suggest that root biomass also increases with elevated CO<sub>2</sub> (Higgins *et al.* 2002), although contrary results have also been reported (Arnone *et al.* 2000).

#### (c) *Nitrogen deposition*

Many ecosystems are now exposed to N deposition rates of more than 1 g N m<sup>-2</sup> yr<sup>-1</sup> (Dentener *et al.* 2006) and this is predicted to increase further, with N deposition rates in several regions reaching more than 5 g m<sup>-2</sup> yr<sup>-1</sup> by 2050 (Galloway *et al.* 2004). A meta-analysis of individual plant responses to N across a wide range of conditions (Xia & Wan 2008)

found a positive biomass response to N enrichment that was further stimulated in areas of high precipitation. Increases in N availability have also been shown to reduce root, relative to shoot, allocation (Wedin & Tilman 1996; Bobbink *et al.* 1998; Suding *et al.* 2005). However, the relationship between N load, climate and ecosystem level growth response has not been defined and the relative size of N and CO<sub>2</sub> enrichment effects on grassland productivity has not been examined quantitatively.

In addition to effects on biomass, N-driven reductions in plant species diversity are frequently reported (e.g. Bobbink *et al.* 1998; Stevens *et al.* 2004), and these have potentially important implications for both nature conservation and ecosystem functioning (Wamelink *et al.* 2009). A meta-analysis of N enrichment experiments found greater plant species loss in communities with cold regional temperatures and larger increases in plant biomass (Clark *et al.* 2007). The latter of these effects is thought to operate via light exclusion processes, with the shade cast by large nitrophilous dominants affecting the survival and recruitment of subordinate species (Hautier *et al.* 2009).

#### (d) *Factors modifying grassland responses to CO<sub>2</sub> and N enrichment*

Climatically, grasslands are largely defined by water limitation (Stephenson 1990; Campbell *et al.* 1997), with variations in precipitation, rather than temperature, accounting for variation in their productivity (Del Grosso *et al.* 2008). Therefore, it is possible that CO<sub>2</sub> and N will have stronger fertilizing effects on grassland ecosystems where water is less limiting. Heterogeneity in the responses of grassland ecosystems to N, CO<sub>2</sub> enrichment and climate change may also be attributed to different plant photosynthetic pathways (Ehleringer *et al.* 1997). Current evidence suggests that C4 species outperform C3 plants in N-limited conditions, perhaps due to their higher photosynthetic N use efficiency, but this relationship may not hold under elevated N (Sage & Percy 1987; Niu *et al.* 2008). It has also been hypothesized that C3 species should increase relative to C4 species under elevated CO<sub>2</sub> as a result of reduced rubisco substrate limitation. However, a previous meta-analysis of physiological responses to CO<sub>2</sub> enrichment in grasses identified no difference between C3 and C4 plants (Ward *et al.* 1999).

#### (e) *Approach*

To assess the relative size and climate dependency of grassland biomass responses to CO<sub>2</sub> and N enrichment we gathered data from published literature sources in which the effects of experimental CO<sub>2</sub> and N enrichment on field-derived grassland biomass measures were reported. Data were then combined with site level information on a range of potentially modifying variables, including temperature, precipitation and the photosynthetic pathway of the dominant species (C3/C4). These data allowed us to statistically assess grassland responses to CO<sub>2</sub> and N enrichment. Where possible, statistical models were

then combined with future projections of N deposition to form some preliminary predictions of changes in grassland biomass stocks. This approach differs from previous meta-analyses of grassland response to CO<sub>2</sub> and N enrichment (Wang 2007; LeBauer & Treseder 2008; Xia & Wan 2008) by investigating community level responses to N and CO<sub>2</sub> and their dependency on climate, and by assessing the relative impacts of two global change factors with a consistent methodology.

## 2. MATERIAL AND METHODS

### (a) Data collection

Data were obtained from peer-reviewed journal articles describing field experiments in which CO<sub>2</sub> and/or N availability were manipulated and community level biomass measures were taken. We endeavoured to collect data without bias by taking an objective, consistent and methodical approach to searching the ISI Web of Knowledge (WoK) ([www.isiknowledge.com](http://www.isiknowledge.com)) for suitable studies. In total 100 searches were made, and more than 2500 abstracts were screened (see the electronic supplementary material, appendix S1 for search details). Articles cited in studies which matched our criteria and were added to our dataset were also searched to see if additional data could be obtained. Only experiments performed on natural or semi-natural grassland systems with low intensity management and no species introductions were included. Greenhouse experiments, experiments involving species addition or removal, and planted grasslands were excluded but studies were included if monoliths were taken from nearby grasslands. This decision was made on the basis that responses to CO<sub>2</sub> enrichment in artificial systems may differ significantly to those in natural and semi-natural systems (Wang 2007). We also excluded plots in which the natural climate of the region was manipulated e.g. temperature, precipitation or photoperiod. These strict search criteria limited the size of our dataset, but did allow us to be confident that sites were genuinely comparable, and that our conclusions are as robust and relevant to natural ecosystems as possible.

Grasslands were defined as ecosystems where grasses comprise more than 50 per cent of above-ground biomass (AGB), and with woody plants absent, as their presence may generate unrepresentative biomass values. Several PFTs were represented in the dataset, with approximately 50 per cent of sites dominated by typical tall grasses. Sites dominated by short bunch grasses, short sward grasses, tall tussock grasses and short tussock grasses were also represented (for definitions see Box 1981).

Data were collected at two levels—experimental location (site) and treatment, i.e. the mean values taken from several plots in which the same treatment had been applied. At the site level we recorded the following characteristics: (i) mean annual precipitation (mm) (MAP), (ii) mean annual temperature (°C) (MAT), (iii) level of environmental management (natural, semi-natural or intensively managed), (iv) photosynthetic pathway of the dominant species

(C3/C4), (v) experimental plot size (m<sup>-2</sup>) and (vi) the duration of manipulation (months). Two treatment level variables were also recorded: mean biomass and the magnitude of manipulation.

Where site characteristics were not published in the original article, information was obtained from alternative sources, including other publications from the same location and publically available databases. Latitudinal and longitudinal data were obtained using Google Earth ([www.earth.google.com](http://www.earth.google.com)) and MAP, MAT and altitude were obtained by linking site co-ordinates to the closest measurement on a high resolution (0'10" × 0'10") global climatology dataset (New *et al.* 2002). This dataset was interpolated from weather station means of the 1961–1990 period. MAP and MAT values were also used to assign sites to bioclimatic zones, according to Whittaker (1975).

For treatment-level measures biomass was recorded as mean biomass per area (g m<sup>-2</sup>) in both control plots and at each level of experimental manipulation. Total AGB and total belowground biomass (BGB) were recorded from text or tables. When this was not possible data were obtained from graphs using the digitizing software, DATATHIEF ([www.datathief.org](http://www.datathief.org)). To maximize data comparability we aimed to collect data gathered after three years of experimental manipulation. Where data were not available for this period, the nearest time was taken. As a result 86 per cent of the data were obtained from measurements taken between 18 and 48 months of experimental manipulation, with a mean duration of 36 months (s.e. ± 2). The intensity of manipulation was measured as the total amount of N added in g m<sup>-2</sup> yr<sup>-1</sup> and as the final CO<sub>2</sub> concentration in parts per million (ppm). Where only relative values were given, data were included only if there was sufficient information within the article to allow conversion into the stated units. To minimize error, data were not taken from plots where CO<sub>2</sub> or N enrichment was applied simultaneously with other experimental treatments (e.g. P, K or water addition).

Throughout data collection, we ensured that data independence was properly defined. Where a single published source described experiments conducted at several sites, each was assumed to be independent. Studies published separately but performed at the same site at different time periods were not deemed independent and were selected on the basis of experimental duration. In some cases multiple data points were taken from the same site where multiple treatment levels were applied (e.g. several levels of N addition). This within-site nesting was dealt with by the random effects of our statistical models (see §2b). The high degree of world coverage, range of climatic conditions and the large number of studies with multiple treatments in the dataset ensured minimal sampling bias.

### (b) Analysis

The response ratio (RR) is a single unitless response metric that is frequently used in meta-analyses to control for variations between sites and

Table 1. Summary of optimal mixed effects model output across all experimental sites for N and CO<sub>2</sub> manipulation experiments. RR, response ratio = biomass<sub>t</sub>/biomass<sub>c</sub>; ΔB, log *e* absolute biomass; MAP, mean annual precipitation; MAT, mean annual temperature. Intercept fitted as 1 in null model.

variable	optimal model terms	<i>n</i>	<i>t</i>	<i>p</i>	terms deleted from full model
RR NAGB	intercept	26	-2.02	0.06	MAT, MAP × MAT, N added × MAT, N added × MAP, N added × MAP × MAT
	N added		2.90	0.03	
	MAP		2.29	0.03	
RR NBGB	intercept	9	-1.11	0.30	MAP, MAT, N added <sup>a</sup>
RR CO <sub>2</sub> AGB	intercept	13	0.78	0.45	MAP, MAT, CO <sub>2</sub> concentration
RR CO <sub>2</sub> BGB	intercept	9	0.40	0.71	MAP, MAT, CO <sub>2</sub> concentration <sup>a</sup>
ΔB (NAGB)	intercept	46	10.1	<0.001	MAT, MAP × MAT, N added × MAT, N added × MAP, N added × MAP × MAT
	N added		-1.29	0.21	
	MAP		-1.52	0.15	
	N added × MAP		2.15	0.04	

<sup>a</sup>Variables placed singly in multiple full models as data insufficient to support multiple variables.

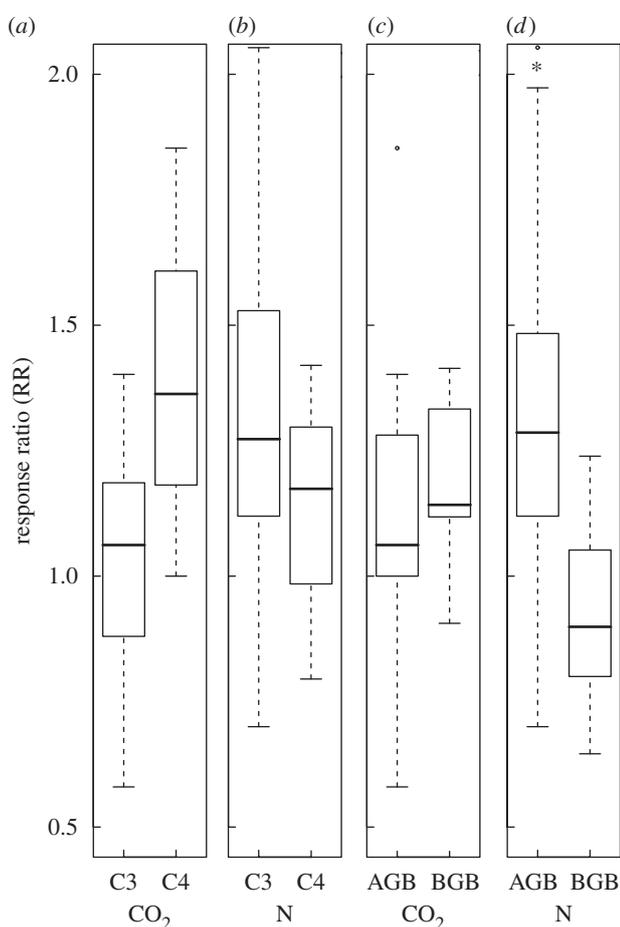


Figure 1. Box and whisker plot to show response ratio (RR) for (a) CO<sub>2</sub> enrichment and (b) N enrichment for C3 and C3-dominated grasslands, (c) CO<sub>2</sub> enrichment and (d) N enrichment above- (AGB) and below-ground biomass (BGB). Asterisk indicates significance at *p* < 0.05. An RR of 1 indicates no difference between control and treated plots.

methodologies. In this study, RR is the ratio between mean biomass in treated plots (*t*) and the mean in control plots (*c*),  $RR = \text{biomass}_t / \text{biomass}_c$ . A separate RR was calculated for each treatment level where there were several levels of N or CO<sub>2</sub> enrichment at a site.

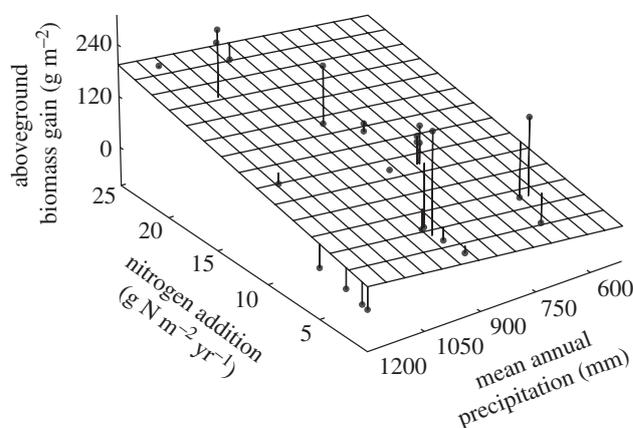


Figure 2. The relationship between mean annual precipitation and N manipulation on the change in aboveground biomass. This plane represents a fitted relationship with linear regression, with each point representing the mean of a treatment level within an experiment. Random effects and weighting used in the model of table 1 were not applied to the relationship shown here, which is for illustrative purposes only.

Once data were collected and RR was calculated they were used to fit statistical models describing the relationship between the RR of AGB and BGB to N or CO<sub>2</sub> enrichment and climate. In modelling all four response variables (NAGB, NBGB, CO<sub>2</sub>AGB, CO<sub>2</sub>BGB) RR was log *e* transformed and we used a weighted, restricted maximum-likelihood linear mixed-effects model (LME; Pinheiro & Bates 2001). In these models, site was treated as a random effect and all other variables were treated as fixed effects. This random effect structure allowed us to account for the nested structure of our data, in which several RRs could be taken from a single site if there were multiple levels of N or CO<sub>2</sub> enrichment. To account for variations in the sample sizes used to generate treatment means, and subsequently RRs, analyses were weighted by within-site replication using the formula:  $(n_t \times n_c) / (n_t + n_c)$ , when *n<sub>t</sub>* is the number of treated plots and *n<sub>c</sub>* is the number of control plots (Adams *et al.* 1997). This made the influence of a study

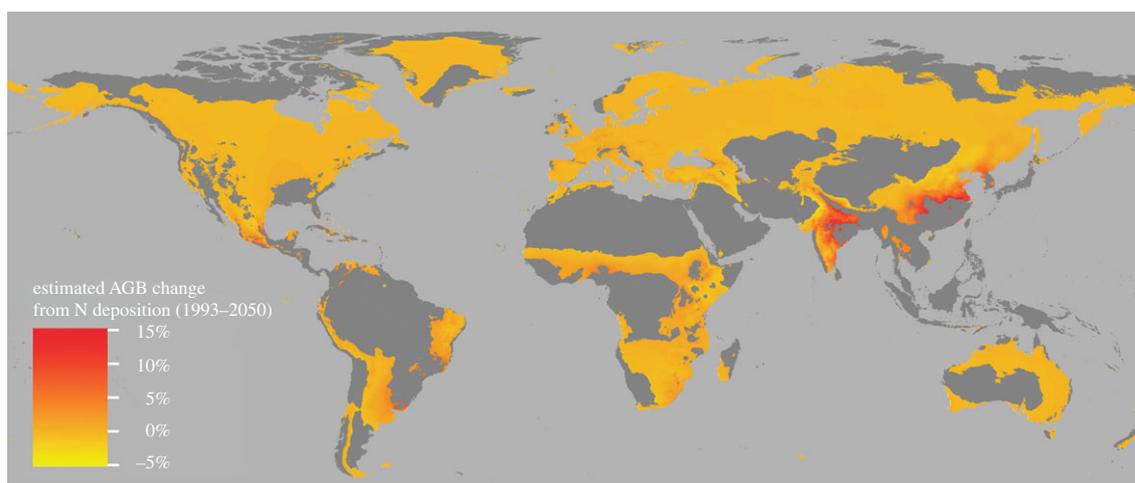


Figure 3. Geographical distribution of predicted aboveground biomass changes ( $\text{g m}^{-2}$ ) in grassland ecosystems under 2050 predicted N. Regions with a MAP outside of 300–1200 are represented as dark grey as they were not covered in the dataset from which the model was constructed.

in the model fitting proportional to its degree of replication. All analyses were computed using R ([www.r-project.org](http://www.r-project.org)).

For each variable an initial ‘full’ model was constructed, containing the most complex possible combination of MAP, MAT, and N/CO<sub>2</sub> concentration, given the data available (for details see §3). From this full model we then sequentially deleted the terms with the least influence on model likelihood, starting with interaction terms, to achieve an optimal model (Crawley 2007). As standard measures of explained deviance (e.g.  $r^2$ ) are not possible with LMEs, the influence of terms on model likelihood was assessed by comparing the Akaike’s information criterion (AIC) of the current model with that of a simplified model, with terms deleted until the AIC ceased to decline (Richards 2005). Before conducting this modelling process we checked that two potentially confounding variables, plot size and experimental duration, were not significantly related to RR by testing them individually against each biomass response variable in an LME model with the stated structure. They were not significant in all cases ( $p > 0.05$  in all fitted models). Using this approach we also tested for effects of the photosynthetic pathway of the dominant species, and compared the RR of AGB and BGB to CO<sub>2</sub> enrichment and N addition.

### (c) Predicted changes in absolute biomass

As NAGB demonstrated climate dependency in its response (see §3 and table 1) we sought to use this knowledge to produce some basic predictions of future biomass change in response to N deposition. The first stage in doing this was to re-fit the NAGB optimal model using the same initial terms and model simplification procedure as in the full RR model, but with  $\log e$  absolute biomass ( $\Delta B$ ) as the response variable (table 1). Model predictions for future N deposition (Dentener 2006) were then fed into the optimal model to generate a map of estimated biomass change in grasslands. The data used in the model were annual precipitation (mm) for 2000 (New *et al.* 2002) and N deposition rate. The latter was estimated

from the data of Dentener (2006) which contains estimates for N deposition rates in 1993 and 2050. Predictions in the 2050 dataset are based on the ‘business as usual’ IS92a scenario, which is broadly similar to the medium-high emissions’ A2a climate scenario of the HadC3M model (IPCC 2008), but from the earlier generation of global change modelling. Data for alternative scenarios were not available for N deposition. Percentage change in AGB was then calculated by calculating biomass estimates for 1993 and relating these to those for 2050 and from these estimates maps were drawn in ARCGIS ([www.esri.com](http://www.esri.com)). An assumption underlying these projections is that grasslands from climatically similar but geographically distinct regions are functionally similar. Predictions were not made for climates that were absent from our dataset (see figure 3).

## 3. RESULTS

The data covered a wide range of climatic conditions and geographical regions (see the electronic supplementary material, tables S1–S4). Almost 75 per cent of data points were from areas that support grasslands as their climax vegetation, based upon their MAT and MAP values (Whittaker 1975; Woodward *et al.* 2004), but grass-dominated experimental sites were also found in the boreal forest and temperate forest zones. Over 80 per cent of sites were managed, usually at a low intensity, with the remainder not subject to direct human intervention. Experimental N addition ranged from 0.5 to 25  $\text{g m}^{-2} \text{yr}^{-1}$ . CO<sub>2</sub> enrichment ranged from 439 to 720 ppm. These CO<sub>2</sub> manipulations are not outside the ranges expected by 2050 (IPCC 2007), and the N additions, while sometimes high compared to N deposition loads (considered high at 5  $\text{g N m}^{-2} \text{yr}^{-1}$ ), are not uncommon in agricultural systems, where N enrichment is expected to continue rising, especially in the developing world.

### (a) AGB response to N

The NAGB data were drawn from 26 treatment levels (46 including controls) from 20 experimental sites

(200 plots), in which MAP ranged from 1200 to 513 mm around a mean of 841 mm, and MAT ranged from 18°C to -3°C around a mean of 10°C (see the electronic supplementary material, table S1). On average, N addition caused a 31.7 per cent increase in AGB ( $\pm$ s.d. 33.9), though this response depended on climate and N load. The full model contained terms for the rate of N addition, MAT, MAP and all first-order interactions between these. This was reduced to an optimal model containing a significant, positive relationship between RR and the amount of N added (table 1). Grassland RR also showed a significant relationship with MAP (table 1). Under drier conditions RR was lower, with greater relative responses to N seen in high precipitation regions. MAT did not influence model likelihood ( $p > 0.05$ ).

#### (b) BGB response to N

The NBGB data were from nine studies (96 plots), in which MAP ranged from 1063 to 311 mm around a mean of 740 mm, and MAT ranged from 18°C to -3°C around a mean of 10°C (see the electronic supplementary material, table S2). On average, N addition caused a 6 per cent decrease in BGB, though there was much variability around this value (s.d.  $\pm$ 21.0). This response was not significantly modified by MAP, MAT or the amount of N added; none of these variables increased model likelihood ( $p > 0.05$ ) and the optimal model was a null model, containing only a non-significant intercept (table 1).

#### (c) AGB response to CO<sub>2</sub>

The CO<sub>2</sub>AGB data were derived from 13 studies (156 plots), in which MAP ranged from 1782 to 321 mm around a mean of 818 mm, and MAT ranged from 14°C to -1°C around a mean of 10°C (see the electronic supplementary material, table S2). RR showed a mean 11.5 per cent increase in AGB ( $\pm$ s.d. 32.5) in response to CO<sub>2</sub> enrichment. The full model contained main effects for CO<sub>2</sub> concentration, MAT and MAP. However, none of these potentially modifying variables increased model likelihood ( $p > 0.05$ ) and the selected model was a null model containing a non-significant intercept (table 1).

#### (d) BGB response to CO<sub>2</sub>

The CO<sub>2</sub>BGB data were obtained from nine studies (118 plots), in which MAP ranged from 1782 to 321 mm around a mean of 770 mm, and MAT ranged from 14°C to -1°C around a mean of 10°C (see the electronic supplementary material, table S4). On average CO<sub>2</sub> enrichment caused a 10.6 per cent increase in BGB, a similar overall response to AGB, though there was considerable variation in this response ( $\pm$ s.d. 30.5). This response was not significantly modified by MAP, MAT or CO<sub>2</sub> concentration; none of these variables increased model likelihood ( $p > 0.05$ ) and the optimal model was a null model (table 1), containing only a non-significant intercept.

#### (e) Comparative responses of grasslands

C3- and C4-dominated grasslands did not differ in their biomass responses to CO<sub>2</sub> ( $t = 1.87$ ,  $p = 0.09$ )

or N enrichment ( $t = -1.1$ ,  $p = 0.28$ ; figure 1), although there was a trend for C4 grasslands to show stronger responses to CO<sub>2</sub> (figure 1). There was no significant difference between aboveground (mean RR = 1.11, s.e.  $\pm$ 0.36) and belowground (mean RR = 1.11, s.e.  $\pm$ 0.40) responses to CO<sub>2</sub> enrichment ( $t = 0$   $p = 0.99$ ; figure 1). This contrasted strongly with highly significant differences between above- and below-ground responses to N addition ( $t = -3.33$ ,  $p = 0.006$ ; figure 1).

#### (f) Predicted change in absolute biomass increase in response to N

The optimal model for log *e* AGB ( $\Delta$ B) included a significant interaction between MAP and the amount of N enrichment ( $t = 2.15$ ,  $p = 0.04$ ), although individually these variables were marginally/non-significant ( $t = -1.52$ ,  $p = 0.15$  and  $t = -1.21$ ,  $p = 0.21$ , respectively). The positive value of the interaction term indicates a greater increase in biomass following N addition in regions of higher MAP (illustrated with linear regression in figure 2).

When this model was used with N deposition projections a map was generated which indicates that widespread increases in grassland AGB could be observed by 2050 (figure 3), including the Earth's largest grassland regions in Asia, central Africa and North America. This highlighted potential hotspots of AGB gain in several regions, where N deposition is expected to increase and precipitation is high, including parts of China and India (figure 3).

## 4. DISCUSSION

### (a) Impacts of N enrichment on grassland biomass stocks

Despite large increases in N availability throughout the globe (Galloway *et al.* 2004), most systems continue to be classified as N limited (LeBauer & Treseder 2008). The current study supports this conclusion for grassland systems, with N addition being found to generally increase aboveground plant biomass accumulation. Such an increase may be exaggerated if only aboveground stocks are considered, as BGB constitutes a large proportion of grassland plant biomass (e.g. 50–95%, Fan *et al.* 2009) and it showed a much weaker response to N. The difference between above- and below-ground responses to N enrichment may represent an allocation shift from belowground competition for N towards light competition (Wilson & Tilman 1993). While the greater increase in biomass production aboveground than decline belowground indicates a positive effect of N on overall C sequestration, the net effect may depend on the relative initial sizes of above- and below-ground stocks. Based on the averages presented here a grassland with a root : shoot ratio more than 5.28 would show an overall decrease in biomass in response to N enrichment. Clearly, better characterization of belowground responses to N are required if accurate ecosystem level responses are to be defined.

Our results suggest that sites with high precipitation showed greater AGB increases in response to N addition. This may reflect the fact that grasslands in

these regions are more N, and less water, limited than those of dry regions and that low water availability in these regions may also prevent added N from becoming available, as nutrients are not in solution. Precipitation is predicted to increase at high latitudes and in parts of the tropics while decreasing in subtropical regions and some mid-latitude regions (IPCC 2008), potentially modifying the response to ecosystems to the future changes in N deposition shown in figure 3.

The significant interaction with precipitation, but not temperature, in the response of AGB to N in this analysis is also in line with results of a recent model, which identified the importance of precipitation, but not temperature, when estimating NPP in grass- and shrub-dominated systems (Del Grosso *et al.* 2008). In contrast, temperature appears to be an important determinant of NPP in tree-dominated ecosystems, highlighting the importance of using a biome-specific approach to modelling the effects of global change. The relationship between biomass response and precipitation we present contrasts with the recent meta-analysis of LeBauer & Treseder (2008), who found no significant relationship between biomass response and precipitation in grasslands, but not with that of Xia & Wan (2008), who showed that the N responses of terrestrial plants generally increased with annual precipitation. The cause of discrepancy with LeBauer and Treseder may arise from methodological differences; they measured response over the longest time possible and also defined grasslands as sites belonging climatically to the grassland biome. This would probably exclude the successional temperate grasslands that would have given our data a wider precipitation gradient over which to detect differences in response to N.

### (b) Impacts of CO<sub>2</sub> enrichment on grassland biomass

Grassland biomass responses to CO<sub>2</sub> enrichment were highly variable but the overall trend was for CO<sub>2</sub> to increase grassland biomass above- and below-ground, most probably via increased rates of photosynthesis and greater water use efficiency (Ward *et al.* 1999). Despite this overall increase there was no significant relationship between RR and the magnitude of CO<sub>2</sub> manipulation. The lack of any detectable effect of CO<sub>2</sub> concentration on response size may result from the reasonably narrow range of CO<sub>2</sub> manipulations but could also be a property of the downregulation of photosynthesis, or CO<sub>2</sub> saturation. The latter explanation is consistent with the typically small response, both above- and below-ground, to CO<sub>2</sub>, which indicates that other resources, e.g. nutrients and water, are the primary limitations of plant growth in grasslands. These low responses contrast with those of forests, which show strong responses of NPP to CO<sub>2</sub> enrichment, with a median increase of  $23 \pm 2$  per cent, to CO<sub>2</sub> across a wide range of conditions (Norby *et al.* 2005). Although Norby *et al.*'s study looked at NPP and ours at biomass, these are reasonably comparable measures, especially in the case of grassland AGB, which in seasonal systems dies back

to low levels in the dormant season and is usually sampled at its peak.

We did not detect any effect of climate in altering the strength of response to CO<sub>2</sub> enrichment within our dataset and so this study does not support the hypothesis that rising atmospheric CO<sub>2</sub> concentrations have a greater effect on plant growth in low rainfall regions, despite a limited number of studies indicating this interaction (Owensby *et al.* 1999; Niklaus & Körner 2004). The lack of climate effects in modifying the effects of CO<sub>2</sub> enrichment may be because variability in grassland response to CO<sub>2</sub> is primarily controlled by other factors such as local hydrology and soil factors (e.g. N and P availability), variation in plant community composition, or other more complex climate factors such as the length of the growing season.

### (c) Implications for grassland carbon storage

It has been suggested that rising atmospheric CO<sub>2</sub> concentrations may be buffered by increased C sequestration at high CO<sub>2</sub> concentrations (Koch & Mooney 1996; Fu & Ferris 2006; Körner 2006). While our results indicate widespread increases in C storage in grasslands as a result of N-, and to a lesser extent, C-enrichment, these results should be treated with caution. CO<sub>2</sub> and N influence not just the amount of plant material produced but also tissue quality (Niklaus & Körner 2004), and in the case of N, soil chemistry (Manning *et al.* 2008). As a result of these changes they may subsequently influence decomposition and soil respiration. N, for example, is known to influence decomposition directly via altered soil chemistry and the alteration of microbial metabolism but also via changes to species composition and litter quality (Manning *et al.* 2008), and so the responses reported here should not be seen as indicative of whole-system C storage. Further complexity emerges from the probable interaction between concurrent increases in N and CO<sub>2</sub>. The few studies that have looked at combined effects of CO<sub>2</sub> and N enrichment reveal interactions between these factors that significantly affect soil soluble C, leaf chemistry, soil microbial biomass and above- and below-ground biomass production (Maestre *et al.* 2005; Fu & Ferris 2006; Reich *et al.* 2006).

An additional caveat of the approach taken in our study is that compositional dynamics, including potential biome shifts (e.g. to woody plant-dominated systems) are not incorporated into our predictions. This limits our conclusions to sites which will remain grasslands in the future and stresses the great importance of developing the tools to incorporate compositional change into our predictions of ecosystem response to environmental change (e.g. Klumpp & Soussana 2009). Long-term responses may also be poorly represented by our analyses and predictions, which, being drawn from studies of 36 months duration, may either under or overestimate ecosystem responses depending on whether dampened or accelerated responses occur over time. This however, is a fundamental problem of almost all experimental global change driver manipulation

experiments, in which new regimes are imposed suddenly and over short-time periods. Overcoming all these difficulties requires a new generation of studies with wider geographical coverage in which climate and N changes are looked at simultaneously, and combined with other global change factors in more holistic studies of ecosystem C cycling. Future developments in experimental design, statistics and data assimilation and availability should also provide researchers with the means to advance models of this type further and provide more reliable predictions of ecosystem responses to future environmental change.

#### (d) *Impacts of CO<sub>2</sub> and N enrichment on biodiversity and forage production*

Changes to grassland biomass stocks have major implications for the conservation of plant biodiversity in grasslands, as productivity gains can result in plant species loss (Clark *et al.* 2007; Hautier *et al.* 2009). According to our projections (figure 3), many regions will experience gains in grassland biomass production of approximately 15 per cent, a similar magnitude of increase that has been seen to be responsible for species loss in experimental systems (Hautier *et al.* 2009). Several of these regions are also biodiversity hotspots (e.g. Indo-Burma, Phoenix *et al.* 2006), and so the threat to biodiversity as the result of grassland biomass gains may be greatest here. Biomass production is also vital for agricultural systems, and plant responses to N and CO<sub>2</sub> fertilization may have important impacts on local, regional and national economies. The results here suggest substantial increases in total forage production (AGB) in response to future increases in N availability, in many parts of the world. The issue of forage quality remains unresolved but it is probable that forage nutrient content will see decreased or stable C:N with possible declines in P concentration, relative to other elements, as it becomes more limiting (Güsewell 2004; Menge & Field 2007).

## 5. CONCLUSION

The findings of our study suggest that spatially variable increases in grassland AGB are probable over the course of the present century and that these increases are likely to represent a trade off between beneficial increases in C sequestration and forage production and associated declines in plant species richness. By using a consistent methodology to assess the relative impact of two drivers we were also able to demonstrate that the effects of N enrichment are likely to be just as strong, and possibly stronger, than the more widely publicized effects of CO<sub>2</sub> enrichment. Our analysis also shows that the effects of N enrichment depend upon precipitation, with the largest gains being seen in wetter regions. An approach such as ours, in which meta-analysis is combined with statistical modelling and spatial data to make large-scale predictions, is not without its limitations. However, it may possess the capacity to reveal general patterns and inform and complement dynamic global vegetation models (e.g. by allowing for better parameterization of vegetation responses),

allowing us to form better predictions of biosphere responses to environmental change.

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