



Ryan, E. M., Ogle, K., Peltier, D., Walker, A. P., De Kauwe, M. G., Medlyn, B. E., Williams, D. G., Parton, W., Asao, S., Guenet, B., Harper, A. B., Lu, X., Luus, K. A., Zaehle, S., Shu, S., Werner, C., Xia, J., & Pendall, E. (2017). Gross primary production responses to warming, elevated CO₂, and irrigation: quantifying the drivers of ecosystem physiology in a semiarid grassland. *Global Change Biology*, 23(8), 3092-3106. <https://doi.org/10.1111/gcb.13602>

Peer reviewed version

Link to published version (if available):
[10.1111/gcb.13602](https://doi.org/10.1111/gcb.13602)

[Link to publication record in Explore Bristol Research](#)
PDF-document

This is the author accepted manuscript (AAM). The final published version (version of record) is available online via Wiley at <https://doi.org/10.1111/gcb.13602>. Please refer to any applicable terms of use of the publisher.

University of Bristol - Explore Bristol Research

General rights

This document is made available in accordance with publisher policies. Please cite only the published version using the reference above. Full terms of use are available: <http://www.bristol.ac.uk/red/research-policy/pure/user-guides/ebr-terms/>

**Gross primary production responses to warming, elevated CO₂, and irrigation:
quantifying the drivers of ecosystem physiology in a semiarid grassland**

Edmund M. Ryan^{1*}, Kiona Ogle^{2,3}, Drew Peltier³, Anthony P. Walker⁴, Martin G. De Kauwe⁵,
Belinda E. Medlyn⁶, David G Williams⁷, William Parton⁸, Shinichi Asao⁸, Bertrand Guenet⁹,
Anna Harper¹⁰, Xingjie Lu¹¹, Kristina A. Luus^{12,13}, Sönke Zaehle¹², Shijie Shu¹⁴, Christian
Werner¹⁵, Jianyang Xia^{16,17}, Elise Pendall^{6,7}

¹Lancaster Environment Centre, Lancaster, UK.

²School of Informatics, Computing, and Cyber Systems, Northern Arizona University, Flagstaff,
Arizona, USA

³Department of Biological Sciences, Northern Arizona University, Flagstaff, Arizona, USA

⁴Environmental Sciences Division and Climate Change Science Institute, Oak Ridge National
Laboratory, Oak Ridge, Tennessee, USA.

⁵Macquarie University, Department of Biological Sciences, New South Wales 2109, Australia

⁶Hawkesbury Institute for the Environment, Western Sydney University, Penrith, NSW,
Australia.

⁷University of Wyoming, Department of Botany, Laramie, WY, USA

⁸Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523-1499
USA.

⁹Laboratoire des Sciences du Climat et de l'Environnement, LSCE/IPSL, CEA-CNRS-UVSQ,
Université Paris-Saclay, F-91191 Gif-sur-Yvette, France.

¹⁰College of Engineering, Mathematics, and Physical Sciences, University of Exeter, Exeter, UK

¹¹CSIRO Ocean and Atmosphere, PBM #1, Aspendale, Victoria 3195, Australia.

¹²Biogeochemical Integration Department, Max Planck Institute for Biogeochemistry, Hans-
Knöll-Str. 10, 07745 Jena, Germany.

¹³Now at: Dublin Institute of Technology, Dublin, Ireland.

¹⁴Department of Atmospheric Sciences, University of Illinois, 105 South Gregory Street, Urbana, Illinois 61801-3070, USA.

¹⁵Senckenberg Biodiversity and Climate Research Centre (BiKF), Senckenberganlage 25, 60325 Frankfurt, Germany.

¹⁶Department of Microbiology & Plant Biology, University of Oklahoma, Norman, OK 73019 USA

¹⁷Research Center for Global Change and Ecological Forecasting, East China Normal University, Shanghai 200062, China.

*Corresponding author:

Lancaster Environment Centre,

Bailrigg, Lancaster.

LA1 4YW

UK

Tel: 00 44 (0) 1524 662206

Email: edmund.ryan@lancaster.ac.uk

Keywords: gross primary production, elevated CO₂, warming, multi-factor global change experiment, Bayesian modelling, carbon cycle, grasslands

For submission to: *Global Change Biology*

1 **Abstract**

2 Determining whether the terrestrial biosphere will be a source or sink of carbon (C) under a
3 future climate of elevated CO₂ (eCO₂) and warming requires accurate quantification of gross
4 primary production (GPP), the largest flux of C in the global C cycle. We evaluated six years
5 (2007-2012) of flux-derived GPP data (~2500 values) from the Prairie Heating and CO₂
6 Enrichment (PHACE) experiment, situated in a mixed prairie grassland in Wyoming, USA. The
7 GPP data were used to calibrate a light response model whose basic formulation has been
8 successfully used in a variety of ecosystems. The model, however, was extended to allow for
9 variable maximum photosynthetic rate (A_{\max}) and light-use efficiency (Q) by modeling these
10 terms as functions of time varying driving variables (soil water content, air temperature, vapor
11 pressure deficit, vegetation greenness, nitrogen) at current and antecedent (past) time scales. The
12 model fit the observed GPP well ($R^2 = 0.79$), which was confirmed by other model performance
13 checks (deviance information criterion and posterior predictive loss) that compared different
14 variants of the model (e.g., with and without antecedent effects). Stimulation of cumulative six-
15 year GPP by warming (29%, $P=0.02$) and eCO₂ (26%, $P=0.07$) was primarily driven by
16 enhanced C uptake during spring (129%, $P=0.001$) and fall (124%, $P=0.001$), respectively, which
17 were consistent across each year. Antecedent air temperature ($T_{\text{air,ant}}$) and vapor pressure deficit
18 (VPD_{ant}) effects on A_{\max} (over the past 3-4 days and 1-3 days, respectively) were the most
19 significant predictors of temporal variability in GPP among most treatments. The importance of
20 VPD_{ant} suggests that atmospheric drought plays an important role for predicting GPP under
21 current and future climate. Given the limited research supporting the role of VPD_{ant} in this
22 context, we highlight the need for experimental studies to identify the mechanisms underlying
23 such antecedent effects. The small uncertainty on the six-year GPP estimates under the control

Commented [ER1]: I've removed the speculative comment about 'mechanisms for extending the growing season', based on the first reviewer's comments. I've merged the two sentences that were here into one.

1 and eCO₂ treatments suggest that they could be used as valuable (semi-)independent data streams
2 that terrestrial biosphere (TBMs) can be compared against. We demonstrate this with 12 TBMs.

Commented [ER2]: New text, in response to the first reviewer who wanted something mentioned in the abstract about the TBMs. However, this means that the current word count for abstract is 333. The limit is 300 words. To reduce this, I could delete the previous sentence ("Given the limited research ...") which we only included in response to the review from NP. Thoughts?

4 **Introduction**

5 Gross primary production (GPP) is the largest flux in the global carbon (C) cycle, representing
6 the gross amount of C removed from the atmosphere by plants via photosynthesis at the
7 ecosystem scale (Chapin III et al., 2006). GPP represents the input of C into the terrestrial
8 biosphere, which plays an important role in determining the magnitudes of the flows and stores
9 of C within plants and soil (Beer et al., 2010, Williams et al., 2005). Despite its importance,
10 there remains large uncertainty in global model projections of future GPP – both globally and
11 regionally – under anticipated future levels of CO₂ and warming (Richardson et al., 2013, Arora
12 et al., 2013), and there is an urgent need to determine the causes of these uncertainties
13 (Friedlingstein et al., 2014). Improved accuracy of these model predictions is critical in
14 determining whether the terrestrial biosphere is likely to be a future sink or source of C.

15 While the responses of net primary production (NPP) to elevated CO₂ (eCO₂) are well-
16 studied, less work has directly evaluated GPP, partly because it is not directly measurable. The
17 few studies that exist on the singular effect of eCO₂ on GPP report a positive effect. For
18 example, Wittig *et al.* (2005) found a ~80% stimulation of GPP for *Populus* trees growing under
19 eCO₂ over a three year period. Likewise, using three years of leaf-level photosynthesis data, Luo
20 et al. (2001) found a ~40% increase in modelled GPP under eCO₂. A stimulation of NPP under
21 eCO₂ suggests a stimulation of GPP if it is assumed that NPP is proportional to GPP (Williams et
22 al., 2005, Waring et al., 1998). A ~20% increase in NPP under eCO₂ would be expected in mid-
23 latitudes (Luo et al., 2006). The expected responses, however, are highly uncertain in semi-arid

1 grasslands, which exhibit large variation in NPP responses to eCO₂ (0-100%); this variation is
2 primarily driven by spatial and temporal precipitation variability (Polley et al., 2013). The
3 stimulation of NPP by eCO₂ has been shown to be suppressed if the ecosystem is nitrogen
4 limited (Norby and Zak, 2011). GPP should also be affected by responses of leaf-level
5 photosynthesis at light saturation (A_{sat}), which increases with eCO₂ in trees (~45%), grasses
6 (~35%), shrubs (~20%) and crops (~35%) (Ainsworth and Long, 2005), but scaling from leaf-
7 level A_{sat} to ecosystem-level GPP is fraught with uncertainties (Arp, 1991, McLeod and Long,
8 1999, Morgan et al., 2001).

9 Warming affects GPP directly through the effect of temperature on leaf photosynthesis,
10 and indirectly via alterations in nitrogen mineralization and water availability (Ciais et al., 2014,
11 Cox et al., 2000). As with eCO₂, a stimulation of NPP under warming suggests a stimulation of
12 GPP if it is assumed that NPP is proportional to GPP (Williams et al., 2005, Waring et al., 1998).
13 Terrestrial biosphere models (TBMs) predict a reduction in NPP with long-term warming; if
14 warming reaches 3-5 °C by 2100 under a high CO₂ emissions scenario (Collins et al., 2013),
15 global terrestrial NPP may decrease by 15-100% (10–60 PgC/year) (Sitch et al., 2008,
16 Friedlingstein et al., 2006, Roy et al., 2001). Retrospective analyses also show a negative effect
17 of warming on NPP, such as a ~9% decrease in global NPP between 1980 and 2002, which offset
18 the CO₂ fertilization effect (Magnani et al., 2007). However, the magnitude of the GPP and NPP
19 responses to warming varies among biomes, with northern latitudes expected to exhibit the
20 largest increases (Piao et al., 2008, Rustad, 2008, Landsberg and Waring, 1997). At the site
21 level, a meta-analysis of 32 separate warming experiments found a positive effect of warming on
22 NPP for tundra sites, but no effect for temperate forest and grassland sites (Rustad et al., 2001).
23 At the regional level, a surface temperature increase of 2 °C between 1988 and 2008 in northern

1 latitudes stimulated GPP during the spring and fall (Piao et al., 2008, Rustad, 2008, Landsberg
2 and Waring, 1997).

3 TBM s assume that the interactive effect of eCO₂ and warming is positive (Luo et al.,
4 2008, Norby and Luo, 2004). Field data from climate change experiments support this for
5 certain years (Dukes et al., 2005), but over multiple years there is growing evidence that the
6 positive interactive response does not exist or is not as strong as models suggest (Dieleman et al.,
7 2012, Shaw et al., 2002). The effects of eCO₂ and warming – whether singular or combined –
8 may be dependent upon precipitation inputs in water-limited ecosystems (Fay et al., 2003,
9 Huxman et al., 2004, Knapp and Smith, 2001, Schwinning et al., 2004). For example, an
10 experiment in a mixed C3/C4 semi-arid grassland found that aboveground NPP was increased by
11 ~80% when annual precipitation was delivered in a few, large rain events compared to more
12 frequent, smaller events (Heisler-White et al., 2008). Recent work has generalized this by
13 considering the effect of past or antecedent conditions on primary production. For example,
14 Ogle et al. (2015) found that event size and antecedent precipitation explained 75% of the
15 variation in aboveground NPP (ANPP) in the same semi-arid grassland. Likewise, antecedent
16 soil water content was a significant predictor of ANPP in a tall grass prairie (Sherry et al., 2008).

17 We identified three major knowledge gaps with regard to the response of GPP to climate
18 change. First, few climate change experiments have investigated the combined effects of eCO₂
19 and warming on primary production (Luo et al., 2008). Second, most of the literature on the
20 ecosystem responses of primary productivity to eCO₂ and warming are based on measurements
21 of NPP (as highlighted above); very few evaluate GPP, yet this is critical for constraining
22 predictions of C cycle responses to climate change (Norby and Luo, 2004). Third, while
23 analyses of climate change experiments often report that treatment effects are contingent upon

1 background climate conditions (e.g., Morgan et al. 2011), the effects of antecedent climate
2 conditions are often not evaluated.

3 To address these knowledge gaps, we measured and analyzed GPP for six years as part of
4 the Prairie Heating and CO₂ Enrichment Experiment (PHACE). The experiment consisted of six
5 treatments, four of which were applied in a full factorial design with CO₂ (ambient vs. elevated)
6 and temperature (ambient vs. warming), and two others involved deep and shallow irrigation
7 applied under ambient CO₂ and temperature. We drew upon this six-year dataset to address three
8 questions: (1) How does GPP respond to the main and interactive effects of eCO₂ and warming
9 in the context of variable precipitation? (2) What environmental and meteorological factors (e.g.,
10 soil water content, antecedent conditions) govern potential responses of GPP to climate change?
11 Finally, we illustrate how our modeling approach can be applied to generate more realistic data
12 products for informing TBMs, and we ask: (3) How does the inclusion of antecedent conditions
13 affect the magnitude and uncertainty in such GPP data products? Accurate estimation of
14 uncertainty is essential in model evaluation exercises, and we provide a full accounting of
15 uncertainty in our analyses.

16

17 **Materials and methods**

18 *Site description*

19 The PHACE site is situated near Cheyenne, Wyoming at an elevation of 1930 m, with a semi-
20 arid, temperate climate. Thirty-year mean annual temperature is 8.3°C and precipitation is 378
21 mm, with ~75% falling during the growing season (Zelikova et al., 2015). The vegetation is a
22 mixed grass prairie, dominated by two C₃ grasses, western wheatgrass (*Pascopyrum smithii*
23 (*Rydb.*) *A. Löve*) and needle-and-thread grass (*Hesperostipa comata Trin and Rupr.*), and the C₄

1 perennial grass blue grama (*Bouteloua gracilis* (H.B.K.) Lag). Live plant cover ranges up to 70%
2 of ground area (Zelikova et al., 2015), and roots extend to 40 cm with 75% of root biomass
3 occurring above 15-cm depth (Carrillo et al., 2014). The soil is a fine-loamy, mixed, mesic
4 Aridic Argiustoll, and biological crusts are not present (Bachman et al., 2010).

5 *Experimental design*

6 The PHACE experiment was set up as an incomplete factorial design consisting of six treatments
7 and five replicate plots (3.4 m in diameter) per treatments (Morgan et al., 2011). Four of the six
8 treatments – abbreviated as ct, cT, Ct, CT – are a full factorial design of atmospheric CO₂
9 (ambient at 380-400 ppm [abbreviated as ‘c’] versus elevated at 600 ppm [‘C’]) and warming (no
10 warming [‘t’] versus heated by 1.5 °C in the daytime and 3.0 °C in the nighttime [‘T’]). The
11 increase in atmospheric CO₂ (600 ppm) for the elevated CO₂ plots (Ct and CT) was achieved
12 using Free Air CO₂ Enrichment (FACE) technology (Miglietta et al., 2001). Warming was
13 simulated (cT and CT) by applying a ceramic heater system using a proportional-integral
14 derivative (PID) feed-back loop (Kimball, 2005).

15 The final two treatments (cts and ctd) involve irrigation applied to ambient CO₂ and no
16 warming plots (shallow [‘s’] or deep [‘d’] irrigation). In the context of the PHACE study, the
17 main aim of the irrigation treatments was to test the hypothesis that responses to eCO₂ are
18 indirectly due to increases in soil water. As such, water was applied to the cts and ctd plots in an
19 effort to increase their soil water contents to match that of the Ct treatment. In the cts treatment,
20 irrigation was applied when soil moisture fell below 85% of Ct at the 5-25 cm depth: in 2007,
21 five, 18-mm precipitation events were applied (totaling 90 mm); during 2008-2011, three 21-mm
22 events per year (totaling 63 mm each year), and 2012, four 65-mm events (totaling 260 mm)

1 were applied. The total amount of water applied to the ctd plots was the same as the cts plots,
2 but water was only added twice per year (spring and fall), in approximately equal amounts.

3 *Data description*

4 All data were measured in the field from 2007-2012, and consisted of GPP ($\mu\text{mol C m}^{-2} \text{ s}^{-1}$),
5 associated air temperature (T_{air} ; $^{\circ}\text{C}$), volumetric soil water content (SWC; m^3/m^3), ecosystem
6 phenology (“greenness”; %), photosynthetically active radiation (PAR; $\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$),
7 aboveground plant nitrogen content (N; g m^{-2}), and relative humidity (RH; %); vapor pressure
8 deficit (VPD; kPa) was computed from T_{air} and RH. GPP data were obtained indirectly as the
9 difference between measurements of net ecosystem exchange (NEE; $\mu\text{mol C m}^{-2} \text{ s}^{-1}$) and
10 ecosystem respiration (R_{eco} ; $\mu\text{mol C m}^{-2} \text{ s}^{-1}$) that were made within two minutes of each other.
11 NEE was measured using a 0.1 m^3 canopy gas exchange chamber by measuring the rate of
12 change of CO_2 concentration for 1 minute (Bachman et al., 2010, Jasoni et al., 2005). R_{eco} was
13 measured immediately afterwards and in exactly the same way as the NEE one, except that an
14 opaque cover was placed over the chamber to eliminate light. Midday measurements were made
15 on a total of 88 days over six growing seasons (May through September), and measurement days
16 were typically separated by 2 to 4 weeks. Additional measurements of NEE and R_{eco} , and thus
17 GPP, were made every 6 weeks at five measurement times per day in each plot (nominal times =
18 04:00, 09:00, 12:00, 16:00 and 21:00). More details on the methods can be found in Bachman *et*
19 *al.* (2010) and Pendall et al. (2013). See Ryan et al. (2015) for descriptions of the environmental
20 data and the gap-filling employed to estimate missing covariate data on certain days and hours.

21

22

23 *Data synthesis and modeling*

1 We fit a non-linear mixed effects model to the GPP data to quantify how GPP varied among the
 2 experimental treatments at the season, annual, and multi-annual scales. The goal of this analysis
 3 is two-fold: (1) to quantify the combined effects of the categorical treatment effects and the time-
 4 varying concurrent and antecedent environmental effects (addressing questions 1 and 2), and (2)
 5 to estimate GPP on non-measurements times, while accounting for different sources of
 6 uncertainty, thus allowing us to gap-fill the GPP dataset and produce estimates of cumulative
 7 GPP fluxes (addressing question 3).

8 Given the distributional properties of the observed GPP data (GPP^{obs}), we assumed that
 9 GPP^{obs} followed a normal distribution. Thus, observation i ($i = 1, \dots, 2456$):

$$GPP_i^{obs} \sim Normal(\mu_i, \sigma_{t(i)}^2) \quad (1)$$

10 μ is the mean or predicted GPP value, σ^2 represents the observation variance, and $t(i)$ indicates
 11 treatment t ($t = 1, 2, \dots, 6$ treatment levels) associated with observation i . We employ a semi-
 12 empirical model for the mean GPP, μ , based on the rectangular hyperbola light-response model
 13 (Desai et al., 2008, Falge et al., 2001, Thornley, 1976, Landsberg and Waring, 1997), which we
 14 adapted to include the effect of atmospheric CO_2 concentration (Acock et al., 1976). We lack
 15 sufficient data to parameterize more complex or mechanistic models (E.g. Farquhar et al., 1980).
 16 However, the light-response or radiation-use efficiency type model has been frequently applied,
 17 in various formulations, to ecosystem level GPP and NPP flux data (see above references), and
 18 thus there is good precedence for using it here. The model for μ is:

$$\mu_i = \frac{Q_i PAR_i A_{max_i} C_i}{Q_i PAR_i + A_{max_i} C_i} \quad (2)$$

19 PAR_i is the measured PAR ($\mu mol m^{-2} s^{-1}$); Q_i ($\mu mol CO_2 \mu mol^{-1}$ quanta) is the quantum yield or
 20 canopy light-use efficiency (i.e., the slope of the light response curve at $PAR=0$); A_{max_i} ($\mu mol C$

1 $\text{m}^2 \text{s}^{-1}$) is the maximum CO_2 uptake rate of the canopy (maximum GPP) at light saturation. $C_i =$
2 $c_j \exp\left(\text{CO}_{2i} - \overline{\text{CO}_{2j}}\right)$ accounts for variation in atmospheric CO_2 relative to the mean observed
3 atmospheric $[\text{CO}_2]$ ($\overline{\text{CO}_{2j}}$) in the ambient ($j = 1$; ct, cT, ctd, cts) and elevated ($j = 2$; Ct, CT) CO_2
4 plots, where CO_{2i} is the measured atmospheric $[\text{CO}_2]$, and the parameter c_j describes the effect of
5 deviations from the mean concentration ($\overline{\text{CO}_{2j}} = 376$ ppm and 572 ppm for $j = 1$ and $j = 2$,
6 respectively). An exponential function is applied to the deviations to ensure $C_i > 0$.

7 To capture potential temporal changes in the GPP response, we modeled Q and A_{\max} as
8 functions of various biotic (greenness and N) and abiotic (SWC, T_{air} , and VPD) factors at both
9 current and antecedent (described in detail in the section below) time-scales. It is well known
10 that plant photosynthesis is partly governed by leaf N content (Williams et al., 1996, Landsberg
11 and Waring, 1997, Magnani et al., 2007) and temperature (Farquhar et al., 1980, Bernacchi et al.,
12 2001) via their effects on enzyme-mediated reactions. VPD also plays an important role via its
13 effect on stomatal conductance, which in turn controls photosynthetic rates (Collatz et al., 1991,
14 Medlyn et al., 2011). Furthermore, vegetation greenness is expected to correspond to GPP; for
15 example, satellite estimates of GPP are inferred from the light reflectance of the vegetation,
16 which describes greenness of the vegetation. To ensure that A_{\max} is positive, we modeled A_{\max}
17 on the log scale, and to constrain Q between 0 and 1, we modeled Q on the logit scale. For
18 example, we modeled $\log(A_{\max})$ as a linear function of the aforementioned current and
19 antecedent (subscript = ant) biotic and abiotic drivers, with parameters that vary by treatment t (t
20 = 1, 2, ..., 6) associated with observation i :

$$21 \log(A_{\max,i}) = \alpha_{0,t(i)} + \alpha_{1,t(i)} \text{SWC}_i + \alpha_{2,t(i)} \text{VPD}_i + \alpha_{3,t(i)} T_{\text{air}_i} + \alpha_{4,t(i)} \text{SWC}_{\text{ant},i} + \alpha_{5,t(i)} \text{VPD}_{\text{ant},i} \quad (3)$$

$$+ \alpha_{6,t(i)} T_{\text{air}_{\text{ant},i}} + \alpha_{7,t(i)} N_i + \alpha_{8,t(i)} \text{Greenness}_i + \alpha_{9,t(i)} \Delta \text{Greenness}_{\text{ant},i} + \text{interactions} + \varepsilon_{t(i),p(t(i))}$$

1 $\varepsilon_{t,p}$ represents a plot (nested in treatment) random effect, and $p(t(i))$ indicates plot p associated
2 with treatment t and observation i ($p = 1, 2, 3, 4, 5$ for each treatment). $\Delta\text{Greenness}_{\text{Sant}}$ represents
3 the antecedent rate of change of greenness; when greenness is increasing, $\Delta\text{Greenness}_{\text{Sant}} > 0$, and
4 when leaves are senescing $\Delta\text{Greenness}_{\text{Sant}} < 0$. We define ‘interactions’ in Eqn (3) to potentially
5 include all 2-way interactions between the covariates indicated in Eqn (3). Preliminary analysis
6 identified five two-way interactions (of 36 possible) that were most important for understanding
7 GPP (see appendix S1 for details of preliminary analysis), including $\text{Tair} \times \text{Tair}$, $\text{SWC}_{\text{ant}} \times \text{Tair}_{\text{ant}}$,
8 $\text{SWC}_{\text{ant}} \times \text{VPD}_{\text{ant}}$, $\text{SWC} \times \text{SWC}_{\text{ant}}$ $\text{Tair} \times \text{Tair}_{\text{ant}}$ and $\text{VPD} \times \text{Tair}$; these five interactions represent the
9 “interactions” term and are assigned interaction effects parameters $\alpha_{10,t} - \alpha_{15,t}$, respectively.
10 Including these interactions is further justified because: (1) $\text{Tair} \times \text{Tair}$ accounts for a potential
11 peaked temperature response; (2) $\text{SWC}_{\text{ant}} \times \text{Tair}_{\text{ant}}$ indicates the seasonality of moisture
12 availability; (3) $\text{SWC}_{\text{ant}} \times \text{VPD}_{\text{ant}}$ indicates differential below- versus aboveground water stress
13 effects; and, (4) previous studies have reported important interactions between current and
14 antecedent factors. Regarding the last point, C fluxes are likely to respond differently to a rain
15 event (increase in current SWC) that occurs during a dry period (low SWC_{ant}) compared to
16 during a wet period (high SWC_{ant}) (Arp, 1991, Barron-Gafford et al., 2014, Cable et al., 2013,
17 Ryan et al., 2015), thus reflecting potential hysteresis patterns (Oikawa et al., 2014, Barron-
18 Gafford et al., 2011).

19 The function for $\text{logit}(Q)$ is the same as for $\text{log}(A_{\text{max}})$ except that: (1) there is no N term
20 because N is primarily expected to affect the amount of RuBisCO in the photosynthetic tissues,
21 which in turn primarily limits A_{max} (Reich et al., 2009); and (2) it has its own nested plot random
22 effects and treatment-specific effects parameters ($\beta_0, \dots, \beta_{13}$) (see Table 3 for a summary of model
23 parameters).

1 *Quantification of antecedent drivers*

2 We characterized and quantified antecedent covariates following the stochastic antecedent
3 modeling (SAM) framework described by Ogle *et al.* (2015); examples of practical
4 implementation are given by Ryan *et al.* (2015), Cable *et al.* (2013), and Barron-Gafford *et al.*
5 (2014). Traditional methods of defining antecedent variables often compute a deterministic
6 average of the variable over a fixed past time period. SAM is different in that it allocates
7 parameters (“importance weights”) to specific periods in the past, thus enabling quantification of
8 the relative importance of the variable at those different past times. Following Cable *et al.* (2013)
9 and Ryan *et al.* (2015), we allowed GPP to be influenced by Tair and VPD over daily time-
10 scales, and by SWC and greenness over weekly time-scales. In general, we describe the
11 antecedent variable (X_{ant}) associated with observation i as:

$$X_{ant,i} = \sum_{k=1}^{Nperiods} W_{X_{k,t(i)}} \bar{X}_{tp(i)-k+1,p(t(i))} \quad (4)$$

12 where $X = VPD$ or Tair, \bar{X} is the 24-hour mean for a particular day or time period, k is the time
13 lag into the past (for Nperiod = 7 time steps) such that when $k = 1$, \bar{X} is the observed 24-hour
14 mean that occurred during $tp(i)$, the time period associated with observation i ; again, $t(i)$ and
15 $p(t(i))$ are the treatment ($t = 1, \dots, 6$) and plot ($p = 1, \dots, 5$ per treatment) associated with observation
16 i . W_X are the weight parameters to be estimated. The expression for SWC_{ant} is similar to equation
17 (4) except that \bar{X} is the 7-day mean for a particular week such that tp denote the week associated
18 with each observation and k denotes the time (week scale) lag (Nperiods = 6); as done in Ryan *et*
19 *al.* (2015), we allocated a separate weight for each of the first few weeks in the past ($k = 1, 2, 3,$
20 4), the fifth ($k = 5$) weight to past weeks 5-6, and the sixth ($k = 6$) weight to past weeks 7-10. We
21 made a slight modification to calculate $\Delta Greenness_{ant}$:

$$\Delta Greenness_{ant,i} = \sum_{k=1}^{Nperiods} W_{X_k,t(i)} \left(\bar{X}_{tp(i)-k+1,p(t(i))} - \bar{X}_{tp(i)-k,p(t(i))} \right) \quad (5)$$

1 where \bar{X} , i , k , t , tp , and p are as defined previously for the weekly scale covariates. Like SWC_{ant} ,
 2 the time periods are on a weekly scale, but $k = 1, 2, 3$, and 4 correspond to the past week, two
 3 weeks ago, three weeks ago, and four weeks ago ($Nperiods = 4$), respectively.

4 We refer to the model described above as the ‘main’ model. We also implemented an
 5 ‘alternative’ model that excludes all antecedent covariates from the Q and A_{max} functions, as
 6 defined in Eqn (3), to evaluate the importance of including antecedent effects. The alternative
 7 model (no antecedent effects) is more similar to the types of models that are often applied for
 8 partitioning eddy-covariance NEE data into its GPP and ecosystem respiration components, such
 9 as those described in the review paper by Desai et al. (2008).

10 *Model implementation and assessment*

11 We implemented the model within a hierarchical Bayesian framework (see Appendix S2 for
 12 details) using the software package JAGS (Plummer, 2003), which uses Markov chain Monte
 13 Carlo (MCMC) to sample from the joint posterior of the model parameters. Depending on the
 14 model (main or alternative model), we ran three parallel chains for 100,000-200,000 iterations
 15 each. After discarding the first 50% of iterations as ‘burn in’, we thinned the chains by 100 to
 16 reduce within-chain autocorrelation and to reduce storage requirements; convergence was
 17 assessed using the Brooks-Gelman-Rubin diagnostic tool (Gelman et al., 2013). This produced
 18 roughly 3000 independent samples from the posterior distribution for each parameter, which
 19 were summarized by their posterior means, central 95% credible intervals (CIs) defined by the
 20 2.5th and 97.5th percentiles, and Bayesian p-values (Gelman et al., 2013).

1 We assessed the performance of the model by comparing predicted GPP versus observed
2 GPP. We used the coefficient of determination (R^2) as an informal measure of model accuracy.
3 A limitation with solely using R^2 is that it does not detect when over-fitting occurs, the
4 phenomenon by which R^2 can increase with greater model complexity (more parameters). To
5 overcome this, we also calculated two other commonly used model assessment diagnostics: the
6 deviance information criterion (DIC) and the posterior predictive loss (PPL). Each of these
7 statistics are the sum of a goodness of fit term and a model complexity (penalty) term that
8 describes the effective number of parameters (Spiegelhalter et al., 2002, Gelfand and Ghosh,
9 1998). One model is more desirable over another if it has a lower DIC and lower PPL. Using
10 these two indices, we compared our main model with the alternative model.

11 *Estimates of seasonal, annual and six-year GPP*

12 Our Bayesian approach to analyzing the GPP data also provides a framework for predicting GPP
13 for time periods for which it was not measured. Each of the fitted models (main and alternative)
14 was subsequently applied on an hourly time-step during the March-October period (we assumed
15 $GPP = 0$ during other months due to the lack of vegetation during these winter months) for 2007-
16 2012, and for every plot using each of the 3000 parameter sets sampled from the posterior
17 distribution. The model simulations were implemented using equations (2)-(5) as well as all
18 measurements of plot-level data (daily SWC, daily greenness, hourly T_{air} , hourly VPD, and
19 annual N). The resulting hourly GPP predictions were summed within each season, each year,
20 and across all years for each of the 3000 model executions, yielding posterior predictive
21 distributions of seasonal (spring [March-May], summer [June-August], fall [Sept-Oct]), annual
22 (March-October), and six-year GPP estimates. These distributions account for both model
23 uncertainty (e.g., lack of fit) and parameter uncertainty.

1 *Comparisons to GPP simulated from 12 terrestrial biosphere models*
2 The data-driven predicted GPP values could serve as important ‘data-products’ for informing and
3 evaluating terrestrial biosphere models (TBMs). Importantly, the Bayesian procedure explicitly
4 quantifies uncertainty in such data products. To exemplify the importance of quantification of
5 data product uncertainty, we considered two different types of data products: (1) six-year
6 cumulative GPP from the main and alternative models as described in the previous subsection,
7 and (2) the percent change in the six-year GPP under warming (cT) and eCO₂ (Ct) relative to the
8 control (ct). As with the first, the second data product was computed using Monte Carlo
9 simulations based on the 3000 posterior estimates of the six-year GPP (see Appendix S3 for
10 description of how both data products were computed). The six-year GPP and GPP responses
11 predicted from 12 TBMs were compared against the corresponding data products. The TBMs
12 included: six land surface models (CABLE, CLM4.0, CLM4.5, ISAM, OCN, and ORCHIDEE);
13 three global dynamic vegetation models (JULES, LPJ-GUESS and SDGVM); and three
14 ecosystem models (DAYCENT, GDAY, and TECO); see Table S1 in the supplementary material
15 for a description of the TBMs. The TBMs were not calibrated to the site using response data, but
16 they were provided optional data or parameter values (e.g., V_{cmax}, specific leaf area, rooting
17 depth, soil texture) representative of the site. Models were also forced with site meteorological
18 data covering the six years of the experiment (see Appendix S4 for details).

19 As a result of the TBMs not being rigorously calibrated against the PHACE data, there
20 was no expectation that the TBM responses would match or be close to the expected PHACE
21 responses. The purpose of comparing our “GPP data product” against the TBM output was to
22 illustrate how our data product could be used to inform the TBMs. Our analysis represents a
23 more flexible and potentially more rigorous method for “gap-filling” missing data – compared to

1 algorithms that are currently used to gap fill, for example, fill eddy flux data – and we show how
2 it can be used to generate GPP estimates (data products) over the course of the experiment.

3 **Results**

4 *Assessment of model performance*

5 Our main model was able to explain a large portion of the variation in the hourly GPP
6 observations (overall R^2 of 0.79). However, the accuracy of the GPP predictions varied among
7 the treatments (Fig. 1), with treatment-specific fits: cT ($R^2=0.86$), ctd ($R^2=0.81$), ct ($R^2=0.80$), cts
8 ($R^2=0.77$), CT ($R^2=0.77$), and Ct ($R^2=0.67$). The alternative model, which excluded all of the
9 antecedent covariates, resulted in a poorer fit (Fig. S1, $R^2 = 0.58$ overall, R^2 ranged from 0.40 to
10 0.67 among treatments). The more robust DIC and PPL measures also strongly indicated much
11 better model performance for the main model compared to the alternative model (DIC=12,690
12 and PPL=45,852 for the main model, with DIC=13,903 and PPL=80,067 for the alternative
13 model).

14 The deviation away from the 1:1 line of the points (i.e. the bias) in figure 1 is minimal,
15 except for the Ct treatment which is slightly more pronounced. However, we note that amongst a
16 number of treatments there are a handful of measurements which are significantly higher than the
17 modelled values. These seem to mainly be concentrated on one or two days during fall (Fig. S5).

18 *Phenology of grassland carbon uptake and its relation to precipitation*

19 The time series of predicted GPP revealed high interannual variability (Fig. 2). For example, for
20 the control treatment (ct), predicted daily GPP reached a maximum around $10 \text{ g C m}^{-2} \text{ day}^{-1}$ for
21 2009 and 2010, which was double the predicted maximum in 2012 ($\sim 5 \text{ g C m}^{-2} \text{ day}^{-1}$; Fig. 2a).

Commented [E3]: New comment addressing the final comment from the first reviewer.

1 Within years, bimodal peaks in GPP were predicted in 2007, 2008, 2011, and 2012 in response to
2 spring and late-summer precipitation inputs.

3 *Treatment effects on GPP*

4 Over the entire experimental period (2007-2012), the largest and most statistically significant
5 increases in GPP relative to the control treatment (ct) occurred under warming (29% increase;
6 Table 1 and Fig. 3b; $P=0.02$ for ct vs cT), eCO₂ (26%; Table 1 and Fig. 3b; $P=0.07$ for ct vs Ct),
7 and deep irrigation (28%; Table 1 and Fig. 3b; $P<0.01$ for ct vs ctd).

8 At the annual time scale, relative to ct, annual GPP increased under eCO₂ (Ct) in 2007,
9 2008, 2011, and 2012 (Fig. 3a and Table 1; ct vs Ct, $P=0.007$, 0.09, 0.02 and 0.009, respectively).
10 Warming (cT) also stimulated annual GPP in 2007, 2008, 2010, and 2011 (Fig. 3a and Table 1; ct
11 vs cT, $P=0.006$, 0.04, 0.09, and 0.005 respectively). There is some evidence that the combination
12 of eCO₂ and warming (CT) enhanced GPP in 2007 and 2011 (Fig. 3a and Table 1; ct vs CT,
13 $P=0.09$ and 0.08, respectively). The large increase in GPP under deep irrigation (ctd) was
14 reflected across individual years, with four showing statistically significant increases of 28-61%.
15 In the absence of warming, annual GPP under eCO₂ (Ct) was similar to annual GPP under
16 shallow irrigation (cts) for all years (Table 1; Ct vs cts, $P>0.18$ for any individual year).

17 Seasonal differences in the treatment effects emerged. The 29% overall increase in GPP
18 under warming (cT) relative to the control (ct) during all six years was primarily driven by
19 enhanced spring productivity (Fig. 3b, black-filled portion of cT bars; Table 1, ct vs cT: 129%
20 increase, $P=0.001$). During the summer, there was on average an 11% decline in GPP under cT
21 (Table 1, ct vs cT, $P=0.15$), which is consistent with Pendall *et al.* (2013) who used linear
22 regression and linear interpolation to estimate April-September GPP sums from data. Although
23 the CO₂ effect was only statistically significant ($P<0.09$) for four out of the six years, GPP

1 increased by 124% under eCO₂ (Ct) during fall. The spring cT and fall Ct GPP estimates were
2 the only treatment by season combinations that were always significantly different (P<0.03) from
3 the corresponding season-level ct estimates, for all years (Table 2, rows 1 and 3). Compared to
4 spring and summer, GPP also increased the most during fall under eCO₂ and warming (ct vs CT:
5 42% increase, P=0.03), deep irrigation (ct vs ctd: 68% increase, P=0.002), and shallow irrigation
6 (ct vs cts: 66% increase, P=0.008) (Table 1).

7 *Importance of current and antecedent conditions for understanding treatment effects on GPP*

8 Including antecedent terms in the submodels for A_{max} and Q (see Eqn (3)) resulted in decreases
9 in the predicted six-year GPP relative to the alternative model, with the greatest reductions
10 occurring for the control treatment (by 12%, P=0.14), the eCO₂ × warming treatment (by 20%,
11 P=0.04), and the deep irrigation treatment (by 14%, P=0.05). Furthermore, 34 out of the 36
12 treatment × year combinations corresponded to a decrease in annual GPP of between 1% and
13 42% for the main model versus the alternative model (Tables S3a, S3b, S3c). Both A_{max} and Q
14 were not significantly affected by concurrent covariates (SWC, VPD, Tair, greenness, and N), for
15 most or all treatments, depending on the covariate (Table 3). Conversely, the main effect of two
16 of the three antecedent covariates (VPD_{ant} and Tair_{ant}) on A_{max} was significant for the majority of
17 treatments (Fig. 4a,b; Table 3). The most important predictors for Q involved the SWC_{ant}×Tair_{ant}
18 and SWC_{ant}×VPD_{ant} interactions, which were significant for four and three of the treatments,
19 respectively (Fig. 4c,d; Table 3). Although the direction of the VPD_{ant} (for A_{max}), Tair_{ant} (A_{max}),
20 SWC_{ant}×Tair_{ant} (Q), and SWC_{ant}×VPD_{ant} (Q) effects were consistent for the vast majority of
21 treatments (Table 3), the magnitude of the antecedent effects differed among certain pairs of
22 treatments (Fig. 4a,c,d).

1 Given that antecedent conditions are important for understanding GPP, we can evaluate
2 the time-scales over which each variable influences GPP. For SWC_{ant}, the first two weeks prior
3 to the GPP measurement were generally the most important for predicting GPP (Fig. S2a). For
4 the majority of treatments, Tair experienced 3-4 days prior and VPD from 1-3 days prior tended
5 to be the most important for predicting GPP (Fig. S2b,c).

6 *Comparison of predicted six-year GPP with TBMs*

7 When comparing the GPP predictions from our data-driven analysis with those of 12 terrestrial
8 biosphere models (TBMs), the 95% credible intervals (CIs) of our six-year GPP "data product"
9 (whether generated from the main or alternative model) under the control (ct) and eCO₂ (Ct)
10 treatments are fairly narrow compared to the range of TBM predictions (Fig. 5a,b). Under the
11 control treatment, only one of the twelve TBM predictions fell within the 95% CI of the data
12 product if antecedent conditions were included in the calculation of the data product (Fig. 5a,
13 black cross and error bar). The number of TBM predictions consistent, or almost so, with the
14 data product increased to five if antecedent conditions were not included when computing the
15 data product (Fig. 5a, grey cross and error bar). Under the eCO₂ scenario, there was greater
16 similarity in the number of TBM predictions agreeing with the data product if antecedent versus
17 no antecedent conditions were included for determining the data product (Fig. 5b).

18 The TBMs also need to accurately predict the relative change in GPP under scenarios of
19 environmental change (e.g., eCO₂, warming, or some combination). We used our GPP analysis
20 framework to produce a data product of the percent difference in GPP under treatment conditions
21 relative to control conditions. In contrast to the cumulative GPP estimates, these percent
22 differences were associated with high uncertainty, sometimes spanning both decreases and
23 increases (e.g., Fig. 5c,d). This resulted in the majority of TBM simulations are consistent with

1 this data product (i.e., the TBM predictions lie within the CIs; Fig. 5c,d), despite the wide range
2 of TBM predictions. Thus, the data product associated with GPP on the absolute scale (Figs.
3 3a,b) is more useful for evaluating and informing TBMs than the data product on the percent
4 change scale (e.g. Figs. 3c,d).

5

6 **Discussion**

7 *Implications of treatment effects on annual GPP*

8 Annual GPP was predicted to be most stimulated by elevated CO₂ (eCO₂, Ct treatment) during
9 the three driest years of our study (2007, 2011, and 2012), suggesting that increased GPP under
10 eCO₂ could have resulted from enhanced water-use efficiency (Kelly et al., 2015). The shallow
11 irrigation (cts) treatment confirmed the role of SWC in mediating the GPP responses to eCO₂,
12 consistent with findings in a similar grassland system (Parton et al., 2012). Moreover, deep
13 irrigation led to a greater percentage increase in GPP compared with eCO₂ or surface irrigation
14 (Table 1; Fig. 3). This may reflect the frequency and magnitude in which irrigation was applied
15 under ctd (twice, large events) compared to cts (three-five smaller events). Larger, less frequent
16 precipitation events are expected to stimulate GPP to a greater extent than smaller, more frequent
17 events, especially early in the growing season (Heisler-White et al., 2008, Lauenroth and Sala,
18 1992, Ogle et al., 2015). A prior, linear interpolation estimate of annual GPP for this same site,
19 but not including 2011-2012 data, suggested a reduction in GPP by eCO₂ in 2009 (Pendall et al.,
20 2013), but our analysis revealed that a significant difference existed only during summer of that
21 year (P=0.06). We also found that 2009 had the highest annual GPP under the control treatment
22 compared to all other study years, and 2009 was also the wettest year (Fig. 3, Table S2, Table

1 S3a). Other grassland studies have found no response or a reduction in primary production under
2 eCO₂ during wet years (Hovenden et al., 2014, Polley et al., 2013)

3 Climate change treatments altered the seasonality of GPP, particularly in spring and fall,
4 as observed for species and community-level measurements at the same site (Reyes-Fox et al.,
5 2014, Zelikova et al., 2015). Across all years, warming (cT) consistently increased annual GPP
6 by 12-50%, and this was predominantly driven by enhanced production during the spring (Fig.
7 3a; Tables 1,2), when temperature limits constrained productivity in this high elevation system.
8 Increased annual GPP for all treatments, except cT, relative to the control (ct) was dominated by
9 increases in GPP during the fall (Table 1, furthest right column). The consistency of the
10 statistical significance of this fall enhancement across all or most years, as well as the spring
11 warming enhancement in spring (Table 2), may be due to two potential co-occurring

12 mechanisms: (i) Spring warming directly stimulates snow melt, photosynthesis, and plant growth
13 (Figs. S4, Luo, 2007, Richardson et al., 2010, Sherry et al., 2008); and/or (ii) the SWC in fall is

14 sustained for longer as a result of the water-saving effects of eCO₂ but only in water limited
15 systems like at PHACE (Webb et al., 2012, Morgan et al., 2004, Morgan et al., 2011, Nowak et
16 al., 2004). Our results indicate that these GPP enhancements in spring and fall may extend the

17 growing season, for example for 2008 (an average year in terms of meteorology) GPP increases
18 under warming consistently between DOY 80-100 from ~0.01 gCm⁻² to ~0.05 gCm⁻² and
19 separately between DOY 100-120 (Fig S5a,b). Similarly in fall, modelled GPP drops to ~0.01
20 gCm⁻² around DOY 280, but under warming GPP levels off at ~ 0.05 gCm⁻² (Fig S5c,d). Hourly
21 observations for this year and other years are consistent with the modelled GPP during spring
22 and fall, with the exception of observations made around DOY 270 which are significantly
23 higher than what the model predicts.

Commented [ER4]: This used to say 'suggests an extension of the growing season by two potential co-occurring mechanisms:', but I changed this because based on fig. S5 in the supplemental I couldn't see any good evidence for this. All that I can see is that there is an overall consistent enhancement across most days in the spring and fall.

Commented [ER5]: Replaced 'the growing season begins earlier because' with this.

Commented [ER6]: Replaced 'the growing season ends later because SWC' with this.

Commented [ER7]: Deleted: "and/or the direct effects of adding water via irrigation (ctd and cts)" because we're just talking about eCO₂ here so want to keep it focused.

Commented [ER8]: New text. Please amend / expand if required.

1 *Importance of antecedent conditions for predicting GPP and evaluating treatment differences*

2 An increasing number of studies recognize the importance of antecedent conditions in
3 understanding the terrestrial C cycle (Barron-Gafford et al., 2014, Cable et al., 2013, Ryan et al.,
4 2015, Gamnitzer et al., 2011). Our main model (with antecedent effects) explained 67-86% of
5 the variation in the GPP data, but the alternative model (without antecedent effects) only
6 explained 40-67% of the variation. This difference in the explanatory power of models that
7 include antecedent conditions has also been demonstrated for other C flux components, including
8 soil respiration (Ogle et al., 2015, Barron-Gafford et al., 2014), annual aboveground NPP, and
9 annual tree growth (Ogle et al., 2015). The increased explanatory power of the “antecedent
10 models” cannot not be solely explained by the additional parameters that they introduce given
11 the support conveyed by model selection indices that penalize for the number of parameters or
12 model complexity. In particular, our results suggest that antecedent vapor pressure deficit
13 (VPD_{ant}) and antecedent air temperature ($T_{air_{ant}}$) were the most important predictors of GPP,
14 primarily via their effects on maximum potential GPP (A_{max}). Antecedent SWC (SWC_{ant})
15 interacted with these two factors to affect light-use efficiency (Q).

16 The importance of $T_{air_{ant}}$ suggests that accounting for seasonal changes in air temperature
17 is critical for obtaining good estimations of A_{max} in this temperate grassland, especially in spring
18 when moisture is less limiting (Lauenroth and Sala, 1992). The importance of antecedent
19 temperature has been implicated as depicting a temperature acclimation response (Ogle et al.,
20 2015). However, the general positive effect of $T_{air_{ant}}$ on A_{max} actually indicates that warmer past
21 temperatures tend to enhance A_{max} and GPP, regardless of the current air temperature which
22 appears to have little impact on GPP once antecedent temperature is accounted for (see Table 3).
23 It appears that GPP is more likely to respond to concurrent changes in soil water (SWC), and to

1 some extent VPD, compared to temperature. The importance of concurrent SWC and VPD on
2 GPP likely reflects stomatal regulation of plant water status, which in turn is expected to affect
3 photosynthesis, and thus GPP.

4 While we would expect GPP to be partly regulated by short-term (sub-daily) changes in
5 VPD (e.g., via stomatal control; Oren et al. 1999), we also found that VPD experienced over the
6 past few days (VPD_{ant}) affects GPP, especially through its influence on A_{max} . In particular, high
7 VPD for about 1-3 days prior, is predicted to reduce A_{max} , across all treatments (Fig. 4a). While
8 the effect of VPD on stomatal closure and photosynthesis is usually treated as being
9 instantaneous due to tight coupling of stomatal conductance to VPD (Collatz et al., 1991), this
10 study suggests that plants may adjust to VPD over longer time scales. VPD conditions occurring
11 over the past 1-7 days represent a proxy for past atmospheric drought conditions (Haddad et al.,
12 2002), and GPP is likely to be negatively impacted by cumulative atmospheric drought.
13 Furthermore, the VPD_{ant} effect was more negative under eCO_2 (Fig. 4a), indicating greater
14 sensitivity of stomata (and hence, photosynthesis) to atmospheric drought, potentially leading to
15 higher integrated water-use efficiency under eCO_2 .

16 The use of VPD as a predictor of GPP is not new (Groenendijk et al., 2011), but the
17 proposition that antecedent VPD is an important driver of GPP has not been previously
18 considered. One possibility is that this effect is just an artifact of our model because VPD
19 depends upon T_{air} , and the VPD_{ant} effect could reflect a non-linear $T_{air,ant}$ effect. However, this is
20 unlikely because although current VPD is highly correlated with current T_{air} ($r = 0.85$), the
21 correlation between the antecedent covariates (VPD_{ant} versus $T_{air,ant}$) is weaker ($r = 0.68$).
22 Furthermore, our model contains quadratic T_{air} (T_{air}^2) terms in both the A_{max} and Q functions,
23 thus the shape of the expected response of GPP to T_{air} (peaked) should already be accounted for.

1 A more plausible explanation for the VPD_{ant} effect is that stomatal conductance or
2 photosynthesis acclimate to VPD. For example, Kutsch et al. (2001) found that a decrease in
3 stomatal aperture in beech trees – implying a decrease in GPP – was negatively correlated with
4 the previous month’s mean VPD. The importance of past VPD, rather than past SWC, prompted
5 the authors to suggest that plants possess a biochemical memory of past climatic. Buckley
6 (2005) also suggests that when VPD exceeds some threshold, water potential can reach a
7 cavitation threshold, leading to cavitation and reducing transpiration at any given VPD. If VPD
8 is further reduced, then there is a lag between the recovery of water potential and embolism
9 repair; the time scale of this recovering is not well understood but could contribute to a GPP
10 versus VPD lag. Various mechanisms have been proposed to explain the stomatal behavior
11 versus VPD lag including the hydroactive feedback hypothesis (Buckley 2016) or delays
12 associated with abscisic-acid (ABA) signaling (Aliniaieifard and van Meeteren, 2014). Clearly,
13 additional research is required to establish the generality of a GPP versus VPD lag (antecedent
14 effect) and to identify underlying mechanisms related to stomatal behavior, biochemical
15 acclimation, or other explanations.

16 Terrestrial biosphere models (TBMs) indirectly incorporate the effect of past
17 meteorological conditions (e.g., VPD) when simulating photosynthesis through the evolving
18 state of the soil water pool. Nevertheless, models commonly do not account for the potential
19 direct effects of antecedent VPD on the physiological components, for example, through
20 acclimation of photosynthesis (Kattge and Knorr, 2007, Smith et al., 2015). Our results highlight
21 accounting for such an acclimation process, which directly considers the effect of antecedent
22 conditions, could improve modelled estimates of photosynthesis.

23 *Implications for the terrestrial carbon cycle*

1 Estimates of global GPP used in the last IPCC report were calculated from site-level GPP
2 estimates that were derived by fitting a light response curve to flux tower NEE data (Beer et al.,
3 2010, Lasslop et al., 2010). The site-level A_{\max} terms in these analyses were also represented as
4 exponential functions of environmental covariates, but only current conditions (Lasslop et al.,
5 2010). If antecedent conditions (such as VPD_{ant} , SWC_{ant} , and $T_{\text{air}_{\text{ant}}}$) had been included, our
6 analysis suggests that annual estimates of GPP at semi-arid grasslands could have been improved
7 (Fig. 1 vs. Fig. S1). For other ecosystems or plant functional types that are less sensitive to
8 drought, the effect of antecedent meteorological conditions may be less pronounced. Moreover,
9 our results show that including antecedent conditions could result in lower estimates of
10 cumulative GPP in temperate grasslands under current climate (by 12%), and especially under a
11 future, warmer climate and $e\text{CO}_2$ (by 20%; see Table S3c).

12 Since the early 1990s, global change experiments, such as Free Air CO_2 Enrichment
13 (FACE) studies, have generated data on responses of key biogeochemical processes to future
14 environmental conditions. Such experiments have become invaluable for informing model
15 forecasts (Piao et al., 2013, Zaehle et al., 2014, De Kauwe et al., 2014, Walker et al., 2014). One
16 of the challenges associated with applying terrestrial biosphere models (TBMs) to understand
17 climate change impacts on GPP and the C cycle is limited access to accurate data products for
18 informing and evaluating the models. Since many data products are derived from simpler models
19 that are fit to observational data, it is prudent to account for uncertainty in such data products
20 since they are not perfect representations of the real system. Our hierarchical Bayesian approach
21 to analyzing the GPP data in the context of a fairly simple light-response model provides a
22 mechanism for predicting GPP at non-measurement time-periods, while accounting for
23 uncertainty in these predictions. However, we wish to emphasize that the purpose of the TBM

Commented [E9]: Next text, based on last comment by second reviewer.

1 versus our “data product” comparison (Fig. 5) was not to validate the TBMs in any way; rather,
2 we wish to evaluate the utility of the data products.

3 We are confident in our seasonal, annual, and six-year cumulative GPP predictions given
4 their relatively narrow 95% CIs (e.g., Fig. 5a and 3b). The width of the intervals, however, did
5 vary among global change treatments, with the widest intervals (and weakest model fits [lowest
6 R^2 s]) occurring for treatments involving eCO_2 (Ct and CT). This suggests that additional
7 information or improved model structure is required to obtain more accurate GPP estimates
8 under eCO_2 . In general, the tight estimates for cumulative GPP at different time scales suggest
9 that this would be a valuable (semi-)independent data stream that TBMs can be compared
10 against.

11 The importance of antecedent environmental conditions on grassland GPP has been
12 highlighted by the Bayesian model selection procedure used in this study. Antecedent conditions
13 were key predictors of GPP, in particular air temperature and vapor pressure deficit of the past
14 week, and research into the mechanism by which antecedent T_{air} and VPD affect GPP would be
15 an interesting and useful contribution to understanding the carbon cycle in these grassland
16 ecosystems. Including antecedent conditions substantially improved the fit of the Bayesian
17 model and led to a consistent reduction in the computed multi-year GPP in this grassland
18 ecosystem, across the vast majority of treatments and years. Given the global coverage of
19 grassland ecosystems, understanding the effect of antecedent environmental conditions more
20 broadly is likely to have implications for our understanding of the global carbon cycle.

21

22 **Data availability**

23 Ryan EM Data from: Gross primary production responses to warming, elevated CO_2 , and
24 irrigation: quantifying the drivers of ecosystem physiology in a semiarid grassland. *Global*
25 *Change Biology* <http://dx.doi.org/10.5061/dryad.71h30>

1 **Acknowledgements**

This material is based upon work supported by the US Department of Agriculture, Agricultural Research Service Climate Change, Soils & Emissions Program, USDA-CSREES Soil Processes Program (#2008-35107-18655), US Department of Energy Office of Science (BER), through the Terrestrial Ecosystem Science program (#DE-SC0006973) and the Western Regional Center of the National Institute for Climatic Change Research, and by the National Science Foundation (DEB#1021559). Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation. We thank D. LeCain, J.A. Morgan, J. Heisler-White, A. Brennan, S. Bachman, Y. Sorokin, T.J. Zelikova, D. Blumenthal, K. Mueller and numerous others for assistance in data collection and operation of PHACE facilities, and B. Yang for use of his gap-filled meteorological data at the site. We also thank D. Kinsman for his helpful comments on the discussion section.

2 **Author contributions**

ER, KO, and EP designed the study; ER conducted the analysis and wrote the paper, with contributions from KO, EP, AW, MDK, and BM. The Bayesian analysis was directed by KO; DP assisted with implements. The remaining authors provided GPP model output from eight of the TBMs in order to construct Figure 5.

3

4 **References**

5

- 6 ACOCK, B., HAND, D., THORNLEY, J. & WILSON, J. W. 1976. Photosynthesis in stands of
7 green peppers. An application of empirical and mechanistic models to controlled-
8 environment data. *Annals of Botany*, 40, 1293-1307.
- 9 AINSWORTH, E. A. & LONG, S. P. 2005. What have we learned from 15 years of free-air CO₂
10 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy
11 properties and plant production to rising CO₂. *New Phytologist*, 165, 351-372.
- 12 ALINIAEIFARD, S. & VAN MEETEREN, U. 2014. Natural variation in stomatal response to
13 closing stimuli among *Arabidopsis thaliana* accessions after exposure to low VPD as a
14 tool to recognize the mechanism of disturbed stomatal functioning. *Journal of*
15 *experimental botany*, 65, 6529-6542.
- 16 ARORA, V. K., BOER, G. J., FRIEDLINGSTEIN, P., EBY, M., JONES, C. D., CHRISTIAN, J.
17 R., BONAN, G., BOPP, L., BROVKIN, V. & CADULE, P. 2013. Carbon-concentration
18 and carbon-climate feedbacks in CMIP5 Earth system models. *Journal of Climate*, 26,
19 5289-5314.
- 20 ARP, W. 1991. Effects of source-sink relations on photosynthetic acclimation to elevated CO₂.
21 *Plant, Cell & Environment*, 14, 869-875.
- 22 BACHMAN, S., HEISLER-WHITE, J. L., PENDALL, E., WILLIAMS, D. G., MORGAN, J. A.
23 & NEWCOMB, J. 2010. Elevated carbon dioxide alters impacts of precipitation pulses
24 on ecosystem photosynthesis and respiration in a semi-arid grassland. *Oecologia*, 162,
25 791-802.
- 26 BARRON-GAFFORD, G. A., CABLE, J. M., BENTLEY, L. P., SCOTT, R. L., HUXMAN, T.
27 E., JENERETTE, G. D. & OGLE, K. 2014. Quantifying the timescales over which
28 exogenous and endogenous conditions affect soil respiration. *New Phytologist*, 202, 442-
29 454.

- 1 BARRON-GAFFORD, G. A., SCOTT, R. L., JENERETTE, G. D. & HUXMAN, T. E. 2011. The
2 relative controls of temperature, soil moisture, and plant functional group on soil CO₂
3 efflux at diel, seasonal, and annual scales. *Journal of Geophysical Research:*
4 *Biogeosciences (2005–2012)*, 116.
- 5 BEER, C., REICHSTEIN, M., TOMELLERI, E., CIAIS, P., JUNG, M., CARVALHAIS, N.,
6 RÖDENBECK, C., ARAIN, M. A., BALDOCCHI, D. & BONAN, G. B. 2010.
7 Terrestrial gross carbon dioxide uptake: global distribution and covariation with climate.
8 *Science*, 329, 834-838.
- 9 BERNACCHI, C., SINGSAAS, E., PIMENTEL, C., PORTIS JR, A. & LONG, S. 2001.
10 Improved temperature response functions for models of Rubisco-limited photosynthesis.
11 *Plant, Cell & Environment*, 24, 253-259.
- 12 BUCKLEY, T. N. 2005. The control of stomata by water balance. *New Phytologist*, 168, 275-
13 291.
- 14 CABLE, J. M., OGLE, K., BARRON-GAFFORD, G. A., BENTLEY, L. P., CABLE, W. L.,
15 SCOTT, R. L., WILLIAMS, D. G. & HUXMAN, T. E. 2013. Antecedent conditions
16 influence soil respiration differences in shrub and grass patches. *Ecosystems*, 16, 1230-
17 1247.
- 18 CARRILLO, Y., DIJKSTRA, F. A., LECAIN, D., MORGAN, J. A., BLUMENTHAL, D.,
19 WALDRON, S. & PENDALL, E. 2014. Disentangling root responses to climate change
20 in a semiarid grassland. *Oecologia*, 1-13.
- 21 CHAPIN III, F. S., WOODWELL, G. M., RANDERSON, J. T., RASTETTER, E. B., LOVETT,
22 G. M., BALDOCCHI, D. D., CLARK, D. A., HARMON, M. E., SCHIMEL, D. S. &
23 VALENTINI, R. 2006. Reconciling carbon-cycle concepts, terminology, and methods.
24 *Ecosystems*, 9, 1041-1050.
- 25 CIAIS, P., SABINE, C., BALA, G., BOPP, L., BROVKIN, V., CANADELL, J., CHHABRA, A.,
26 DEFRIES, R., GALLOWAY, J. & HEIMANN, M. 2014. Carbon and other
27 biogeochemical cycles. *Climate Change 2013: The Physical Science Basis. Contribution*
28 *of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on*
29 *Climate Change*. Cambridge University Press.
- 30 COLLATZ, G. J., BALL, J. T., GRIVET, C. & BERRY, J. A. 1991. Physiological and
31 environmental regulation of stomatal conductance, photosynthesis and transpiration: a
32 model that includes a laminar boundary layer. *agricultural and forest meteorology*, 54,
33 107-136.
- 34 COLLINS, M., KNUTTI, R., ARBLASTER, J., DUFRESNE, J.-L., FICHEFET, T.,
35 FRIEDLINGSTEIN, P., GAO, X., GUTOWSKI, W., JOHNS, T. & KRINNER, G. 2013.
36 Long-term climate change: projections, commitments and irreversibility.
- 37 COX, P. M., BETTS, R. A., JONES, C. D., SPALL, S. A. & TOTTERDELL, I. J. 2000.
38 Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate
39 model. *Nature*, 408, 184-187.
- 40 DE KAUWE, M. G., MEDLYN, B. E., ZAEHLE, S., WALKER, A. P., DIETZE, M. C., WANG,
41 Y. P., LUO, Y., JAIN, A. K., EL-MASRI, B. & HICKLER, T. 2014. Where does the
42 carbon go? A model–data intercomparison of vegetation carbon allocation and turnover
43 processes at two temperate forest free-air CO₂ enrichment sites. *New Phytologist*, 203,
44 883-899.
- 45 DESAI, A. R., RICHARDSON, A. D., MOFFAT, A. M., KATTGE, J., HOLLINGER, D. Y.,
46 BARR, A., FALGE, E., NOORMETS, A., PAPAIE, D. & REICHSTEIN, M. 2008.

1 Cross-site evaluation of eddy covariance GPP and RE decomposition techniques.
2 *Agricultural and forest meteorology*, 148, 821-838.

3 DIELEMAN, W. I., VICCA, S., DIJKSTRA, F. A., HAGEDORN, F., HOVENDEN, M. J.,
4 LARSEN, K. S., MORGAN, J. A., VOLDER, A., BEIER, C. & DUKES, J. S. 2012.
5 Simple additive effects are rare: a quantitative review of plant biomass and soil process
6 responses to combined manipulations of CO₂ and temperature. *Global Change Biology*,
7 18, 2681-2693.

8 DUKES, J. S., CHIARIELLO, N. R., CLELAND, E. E., MOORE, L. A., SHAW, M. R.,
9 THAYER, S., TOBECK, T., MOONEY, H. A. & FIELD, C. B. 2005. Responses of
10 grassland production to single and multiple global environmental changes. *PLoS biology*,
11 3, e319.

12 FALGE, E., BALDOCCHI, D., OLSON, R., ANTHONI, P., AUBINET, M., BERNHOFER, C.,
13 BURBA, G., CEULEMANS, R., CLEMENT, R. & DOLMAN, H. 2001. Gap filling
14 strategies for defensible annual sums of net ecosystem exchange. *Agricultural and forest*
15 *meteorology*, 107, 43-69.

16 FARQUHAR, G., VON CAEMMERER, S. V. & BERRY, J. 1980. A biochemical model of
17 photosynthetic CO₂ assimilation in leaves of C₃ species. *Planta*, 149, 78-90.

18 FAY, P. A., CARLISLE, J. D., KNAPP, A. K., BLAIR, J. M. & COLLINS, S. L. 2003.
19 Productivity responses to altered rainfall patterns in a C₄-dominated grassland.
20 *Oecologia*, 137, 245-251.

21 FRIEDLINGSTEIN, P., COX, P., BETTS, R., BOPP, L., VON BLOH, W., BROVKIN, V.,
22 CADULE, P., DONEY, S., EBY, M. & FUNG, I. 2006. Climate-carbon cycle feedback
23 analysis: Results from the C4MIP model intercomparison. *Journal of Climate*, 19, 3337-
24 3353.

25 FRIEDLINGSTEIN, P., MEINSHAUSEN, M., ARORA, V. K., JONES, C. D., ANAV, A.,
26 LIDDICOAT, S. K. & KNUTTI, R. 2014. Uncertainties in CMIP5 climate projections
27 due to carbon cycle feedbacks. *Journal of Climate*, 27, 511-526.

28 GAMNITZER, U., MOYES, A., BOWLING, D. & SCHNYDER, H. 2011. Measuring and
29 modelling the isotopic composition of soil respiration: insights from a grassland tracer
30 experiment. *Biogeosciences*, 8, 1333-1350.

31 GELFAND, A. E. & GHOSH, S. K. 1998. Model choice: A minimum posterior predictive loss
32 approach. *Biometrika*, 85, 1-11.

33 GELMAN, A., CARLIN, J. B., STERN, H. S., DUNSON, D. B., VEHTARI, A. & RUBIN, D. B.
34 2013. *Bayesian data analysis*, CRC press.

35 GROENENDIJK, M., DOLMAN, A., AMMANN, C., ARNETH, A., CESCATTI, A.,
36 DRAGONI, D., GASH, J., GIANELLE, D., GIOLI, B. & KIELY, G. 2011. Seasonal
37 variation of photosynthetic model parameters and leaf area index from global Fluxnet
38 eddy covariance data. *Journal of Geophysical Research: Biogeosciences (2005–2012)*,
39 116.

40 HADDAD, N. M., TILMAN, D. & KNOPS, J. M. 2002. Long-term oscillations in grassland
41 productivity induced by drought. *Ecology letters*, 5, 110-120.

42 HEISLER-WHITE, J. L., KNAPP, A. K. & KELLY, E. F. 2008. Increasing precipitation event
43 size increases aboveground net primary productivity in a semi-arid grassland. *Oecologia*,
44 158, 129-140.

45 HOVENDEN, M. J., NEWTON, P. C. & WILLS, K. E. 2014. Seasonal not annual rainfall
46 determines grassland biomass response to carbon dioxide. *Nature*, 511, 583-586.

- 1 HUXMAN, T. E., SNYDER, K. A., TISSUE, D., LEFFLER, A. J., OGLE, K., POCKMAN, W.
2 T., SANDQUIST, D. R., POTTS, D. L. & SCHWINNING, S. 2004. Precipitation pulses
3 and carbon fluxes in semiarid and arid ecosystems. *Oecologia*, 141, 254-268.
- 4 JASONI, R. L., SMITH, S. D. & ARNONE, J. A. 2005. Net ecosystem CO₂ exchange in Mojave
5 Desert shrublands during the eighth year of exposure to elevated CO₂. *Global Change
6 Biology*, 11, 749-756.
- 7 KATTGE, J. & KNORR, W. 2007. Temperature acclimation in a biochemical model of
8 photosynthesis: a reanalysis of data from 36 species. *Plant, Cell & Environment*, 30,
9 1176-1190.
- 10 KELLY, J. W., DUURSMA, R. A., ATWELL, B. J., TISSUE, D. T. & MEDLYN, B. E. 2015.
11 Drought× CO₂ interactions in trees: a test of the low-intercellular CO₂ concentration (C_i)
12 mechanism. *New Phytologist*.
- 13 KIMBALL, B. 2005. Theory and performance of an infrared heater for ecosystem warming.
14 *Global Change Biology*, 11, 2041-2056.
- 15 KNAPP, A. K. & SMITH, M. D. 2001. Variation among biomes in temporal dynamics of
16 aboveground primary production. *Science*, 291, 481-484.
- 17 KUTSCH, W. L., HERBST, M., VANSELOW, R., HUMMELSHOJ, P., JENSEN, N. O. &
18 KAPPEN, L. 2001. Stomatal acclimation influences water and carbon fluxes of a beech
19 canopy in northern Germany. *Basic and Applied Ecology*, 2, 265-281.
- 20 LANDSBERG, J. & WARING, R. 1997. A generalised model of forest productivity using
21 simplified concepts of radiation-use efficiency, carbon balance and partitioning. *Forest
22 Ecology and Management*, 95, 209-228.
- 23 LASSLOP, G., REICHSTEIN, M., PAPALE, D., RICHARDSON, A. D., ARNETH, A., BARR,
24 A., STOY, P. & WOHLFAHRT, G. 2010. Separation of net ecosystem exchange into
25 assimilation and respiration using a light response curve approach: critical issues and
26 global evaluation. *Global Change Biology*, 16, 187-208.
- 27 LAUENROTH, W. & SALA, O. E. 1992. Long-term forage production of North American
28 shortgrass steppe. *Ecological Applications*, 2, 397-403.
- 29 LUO, Y. 2007. Terrestrial carbon-cycle feedback to climate warming. *Annu. Rev. Ecol. Evol.
30 Syst.*, 38, 683-712.
- 31 LUO, Y., GERTEN, D., LE MAIRE, G., PARTON, W. J., WENG, E., ZHOU, X., KEOUGH, C.,
32 BEIER, C., CIAIS, P. & CRAMER, W. 2008. Modeled interactive effects of
33 precipitation, temperature, and [CO₂] on ecosystem carbon and water dynamics in
34 different climatic zones. *Global Change Biology*, 14, 1986-1999.
- 35 LUO, Y., HUI, D. & ZHANG, D. 2006. Elevated CO₂ stimulates net accumulations of carbon
36 and nitrogen in land ecosystems: a meta-analysis. *Ecology*, 87, 53-63.
- 37 MAGNANI, F., MENCUCCINI, M., BORGHETTI, M., BERBIGIER, P., BERNINGER, F.,
38 DELZON, S., GRELLA, A., HARI, P., JARVIS, P. G. & KOLARI, P. 2007. The human
39 footprint in the carbon cycle of temperate and boreal forests. *Nature*, 447, 849-851.
- 40 MCLEOD, A. & LONG, S. 1999. Free-air carbon dioxide enrichment (FACE) in global change
41 research: a review. *Advances in ecological research*, 28, 1-56.
- 42 MEDLYN, B. E., DUURSMA, R. A., EAMUS, D., ELLSWORTH, D. S., PRENTICE, I. C.,
43 BARTON, C. V., CROUS, K. Y., DE ANGELIS, P., FREEMAN, M. & WINGATE, L.
44 2011. Reconciling the optimal and empirical approaches to modelling stomatal
45 conductance. *Global Change Biology*, 17, 2134-2144.

- 1 MIGLIETTA, F., HOOSBEEK, M., FOOT, J., GIGON, F., HASSINEN, A., HEIJMANS, M.,
2 PERESSOTTI, A., SAARINEN, T., VAN BREEMEN, N. & WALLEN, B. 2001. Spatial
3 and temporal performance of the MiniFACE (Free Air CO₂ Enrichment) system on bog
4 ecosystems in northern and central Europe. *Environmental Monitoring and Assessment*,
5 66, 107-127.
- 6 MORGAN, J., PATAKI, D. E., KÖRNER, C., CLARK, H., DEL GROSSO, S., GRÜNZWEIG,
7 J., KNAPP, A., MOSIER, A., NEWTON, P. & NIKLAUS, P. A. 2004. Water relations in
8 grassland and desert ecosystems exposed to elevated atmospheric CO₂. *Oecologia*, 140,
9 11-25.
- 10 MORGAN, J. A., LECAIN, D. R., MOSIER, A. R. & MILCHUNAS, D. G. 2001. Elevated CO₂
11 enhances water relations and productivity and affects gas exchange in C₃ and C₄ grasses
12 of the Colorado shortgrass steppe. *Global Change Biology*, 7, 451-466.
- 13 MORGAN, J. A., LECAIN, D. R., PENDALL, E., BLUMENTHAL, D. M., KIMBALL, B. A.,
14 CARRILLO, Y., WILLIAMS, D. G., HEISLER-WHITE, J., DIJKSTRA, F. A. & WEST,
15 M. 2011. C₄ grasses prosper as carbon dioxide eliminates desiccation in warmed semi-
16 arid grassland. *Nature*, 476, 202-205.
- 17 NORBY, R. J. & LUO, Y. 2004. Evaluating ecosystem responses to rising atmospheric CO₂ and
18 global warming in a multi-factor world. *New Phytologist*, 162, 281-293.
- 19 NORBY, R. J. & ZAK, D. R. 2011. Ecological lessons from free-air CO₂ enrichment (FACE)
20 experiments. *Annual review of ecology, evolution, and systematics*, 42, 181.
- 21 NOWAK, R. S., ELLSWORTH, D. S. & SMITH, S. D. 2004. Functional responses of plants to
22 elevated atmospheric CO₂—do photosynthetic and productivity data from FACE
23 experiments support early predictions? *New phytologist*, 162, 253-280.
- 24 OGLE, K., BARBER, J. J., BARRON-GAFFORD, G. A., BENTLEY, L. P., YOUNG, J. M.,
25 HUXMAN, T. E., LOIK, M. E. & TISSUE, D. T. 2015. Quantifying ecological memory
26 in plant and ecosystem processes. *Ecology letters*, 18, 221-235.
- 27 OIKAWA, P., GRANTZ, D., CHATTERJEE, A., EBERWEIN, J., ALLSMAN, L. &
28 JENERETTE, G. 2014. Unifying soil respiration pulses, inhibition, and temperature
29 hysteresis through dynamics of labile soil carbon and O₂. *Journal of Geophysical*
30 *Research: Biogeosciences*, 119, 521-536.
- 31 PARTON, W., MORGAN, J., SMITH, D., DEL GROSSO, S., PRIHODKO, L., LECAIN, D.,
32 KELLY, R. & LUTZ, S. 2012. Impact of precipitation dynamics on net ecosystem
33 productivity. *Global Change Biology*, 18, 915-927.
- 34 PENDALL, E., HEISLER-WHITE, J. L., WILLIAMS, D. G., DIJKSTRA, F. A., CARRILLO,
35 Y., MORGAN, J. A. & LECAIN, D. R. 2013. Warming reduces carbon losses from
36 grassland exposed to elevated atmospheric carbon dioxide. *PloS one*, 8, e71921.
- 37 PIAO, S., CIAIS, P., FRIEDLINGSTEIN, P., PEYLIN, P., REICHSTEIN, M., LUYSSAERT, S.,
38 MARGOLIS, H., FANG, J., BARR, A. & CHEN, A. 2008. Net carbon dioxide losses of
39 northern ecosystems in response to autumn warming. *Nature*, 451, 49-52.
- 40 PIAO, S., SITCH, S., CIAIS, P., FRIEDLINGSTEIN, P., PEYLIN, P., WANG, X., AHLSTRÖM,
41 A., ANAV, A., CANADELL, J. G. & CONG, N. 2013. Evaluation of terrestrial carbon
42 cycle models for their response to climate variability and to CO₂ trends. *Global Change*
43 *Biology*, 19, 2117-2132.
- 44 PLUMMER, M. Year. JAGS: A program for analysis of Bayesian graphical models using Gibbs
45 sampling. *In: Proceedings of the 3rd international workshop on distributed statistical*
46 *computing*, 2003. Technische Universit at Wien, 125.

- 1 POLLEY, H. W., BRISKE, D. D., MORGAN, J. A., WOLTER, K., BAILEY, D. W. & BROWN,
2 J. R. 2013. Climate Change and North American Rangelands: Trends, Projections, and
3 Implications. *Rangeland Ecology and Management*, 66, 493-511.
- 4 REICH, P. B., OLEKSYN, J. & WRIGHT, I. J. 2009. Leaf phosphorus influences the
5 photosynthesis–nitrogen relation: a cross-biome analysis of 314 species. *Oecologia*, 160,
6 207-212.
- 7 REYES-FOX, M., STELTZER, H., TRLICA, M., MCMASTER, G. S., ANDALES, A. A.,
8 LECAIN, D. R. & MORGAN, J. A. 2014. Elevated CO₂ further lengthens growing
9 season under warming conditions. *Nature*, 510, 259-262.
- 10 RICHARDSON, A. D., BLACK, T. A., CIAIS, P., DELBART, N., FRIEDL, M. A., GOBRON,
11 N., HOLLINGER, D. Y., KUTSCH, W. L., LONGDOZ, B. & LUYSSAERT, S. 2010.
12 Influence of spring and autumn phenological transitions on forest ecosystem productivity.
13 *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 3227-3246.
- 14 RICHARDSON, A. D., KEENAN, T. F., MIGLIAVACCA, M., RYU, Y., SONNENTAG, O. &
15 TOOMEY, M. 2013. Climate change, phenology, and phenological control of vegetation
16 feedbacks to the climate system. *Agricultural and forest meteorology*, 169, 156-173.
- 17 ROY, J., MOONEY, H. A. & SAUGIER, B. 2001. *Terrestrial global productivity*, Academic
18 Press.
- 19 RUSTAD, L., CAMPBELL, J., MARION, G., NORBY, R., MITCHELL, M., HARTLEY, A.,
20 CORNELISSEN, J. & GUREVITCH, J. 2001. A meta-analysis of the response of soil
21 respiration, net nitrogen mineralization, and aboveground plant growth to experimental
22 ecosystem warming. *Oecologia*, 126, 543-562.
- 23 RUSTAD, L. E. 2008. The response of terrestrial ecosystems to global climate change: towards
24 an integrated approach. *Science of the Total Environment*, 404, 222-235.
- 25 RYAN, E. M., OGLE, K., ZELIKOVA, T. J., LECAIN, D. R., WILLIAMS, D. G., MORGAN, J.
26 A. & PENDALL, E. 2015. Antecedent moisture and temperature conditions modulate the
27 response of ecosystem respiration to elevated CO₂ and warming. *Global Change
28 Biology*.
- 29 SCHWINNING, S., SALA, O. E., LOIK, M. E. & EHLERINGER, J. R. 2004. Thresholds,
30 memory, and seasonality: understanding pulse dynamics in arid/semi-arid ecosystems.
31 *Oecologia*, 141, 191-193.
- 32 SHAW, M. R., ZAVALA, E. S., CHIARIELLO, N. R., CLELAND, E. E., MOONEY, H. A. &
33 FIELD, C. B. 2002. Grassland responses to global environmental changes suppressed by
34 elevated CO₂. *Science*, 298, 1987-1990.
- 35 SHERRY, R. A., WENG, E., ARNONE III, J. A., JOHNSON, D. W., SCHIMEL, D. S.,
36 VERBURG, P. S., WALLACE, L. L. & LUO, Y. 2008. Lagged effects of experimental
37 warming and doubled precipitation on annual and seasonal aboveground biomass
38 production in a tallgrass prairie. *Global Change Biology*, 14, 2923-2936.
- 39 SITCH, S., HUNTINGFORD, C., GEDNEY, N., LEVY, P., LOMAS, M., PIAO, S., BETTS, R.,
40 CIAIS, P., COX, P. & FRIEDLINGSTEIN, P. 2008. Evaluation of the terrestrial carbon
41 cycle, future plant geography and climate-carbon cycle feedbacks using five Dynamic
42 Global Vegetation Models (DGVMs). *Global Change Biology*, 14, 2015-2039.
- 43 SMITH, N. G., MALYSHEV, S. L., SHEVLIAKOVA, E., KATTGE, J. & DUKES, J. S. 2015.
44 Foliar temperature acclimation reduces simulated carbon sensitivity to climate. *Nature
45 Climate Change*.

- 1 SPIEGELHALTER, D. J., BEST, N. G., CARLIN, B. P. & VAN DER LINDE, A. 2002. Bayesian
2 measures of model complexity and fit. *Journal of the Royal Statistical Society: Series B*
3 (*Statistical Methodology*), 64, 583-639.
- 4 THORNLEY, J. H. 1976. *Mathematical models in plant physiology*, Academic Press (Inc.)
5 London, Ltd.
- 6 WALKER, A. P., HANSON, P. J., DE KAUWE, M. G., MEDLYN, B. E., ZAEHLE, S., ASAO,
7 S., DIETZE, M., HICKLER, T., HUNTINGFORD, C. & IVERSEN, C. M. 2014.
8 Comprehensive ecosystem model-data synthesis using multiple data sets at two temperate
9 forest free-air CO₂ enrichment experiments: Model performance at ambient CO₂
10 concentration. *Journal of Geophysical Research: Biogeosciences*, 119, 937-964.
- 11 WARING, R., LANDSBERG, J. & WILLIAMS, M. 1998. Net primary production of forests: a
12 constant fraction of gross primary production? *Tree Physiology*, 18, 129-134.
- 13 WEBB, N. P., STOKES, C. J. & SCANLAN, J. C. 2012. Interacting effects of vegetation, soils
14 and management on the sensitivity of Australian savanna rangelands to climate change.
15 *Climatic Change*, 112, 925-943.
- 16 WILLIAMS, M., RASTETTER, E., FERNANDES, D., GOULDEN, M., WOFSY, S., SHAVER,
17 G., MELILLO, J., MUNGER, J., FAN, S. & NADELHOFFER, K. 1996. Modelling the
18 soil-plant-atmosphere continuum in a Quercus-Acer stand at Harvard Forest: the
19 regulation of stomatal conductance by light, nitrogen and soil/plant hydraulic properties.
20 *Plant, Cell & Environment*, 19, 911-927.
- 21 WILLIAMS, M., SCHWARZ, P. A., LAW, B. E., IRVINE, J. & KURPIUS, M. R. 2005. An
22 improved analysis of forest carbon dynamics using data assimilation. *Global Change*
23 *Biology*, 11, 89-105.
- 24 WITTIG, V. E., BERNACCHI, C. J., ZHU, X. G., CALFAPIETRA, C., CEULEMANS, R.,
25 DEANGELIS, P., GIELEN, B., MIGLIETTA, F., MORGAN, P. B. & LONG, S. P. 2005.
26 Gross primary production is stimulated for three Populus species grown under free-air
27 CO₂ enrichment from planting through canopy closure. *Global Change Biology*, 11, 644-
28 656.
- 29 ZAEHLE, S., MEDLYN, B. E., DE KAUWE, M. G., WALKER, A. P., DIETZE, M. C.,
30 HICKLER, T., LUO, Y., WANG, Y. P., EL-MASRI, B. & THORNTON, P. 2014.
31 Evaluation of 11 terrestrial carbon-nitrogen cycle models against observations from two
32 temperate Free-Air CO₂ Enrichment studies. *New Phytologist*, 202, 803-822.
- 33 ZELIKOVA, T. J., WILLIAMS, D. G., HOENIGMAN, R., BLUMENTHAL, D. M., MORGAN,
34 J. A. & PENDALL, E. 2015. Seasonality of soil moisture mediates responses of
35 ecosystem phenology to elevated CO₂ and warming in a semi-arid grassland. *Journal of*
36 *Ecology*, 103, 1119-1130.

37
38