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## **Does the growth response of woody plants to elevated CO<sub>2</sub> increase with temperature?**

### **A model-oriented meta-analysis**

Running head: CO<sub>2</sub> x temperature meta-analysis

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## ABSTRACT

The temperature dependence of the reaction kinetics of the Rubisco enzyme implies that, at the level of a chloroplast, the response of photosynthesis to rising atmospheric CO<sub>2</sub> concentration (C<sub>a</sub>) will increase with increasing air temperature. Vegetation models incorporating this interaction predict that the response of net primary productivity (NPP) to elevated CO<sub>2</sub> (eC<sub>a</sub>) will increase with rising temperature, and will be substantially larger in warm tropical forests than in cold boreal forests. We tested these model predictions against evidence from eC<sub>a</sub> experiments by carrying out two meta-analyses. Firstly, we tested for an interaction effect on growth responses in factorial eC<sub>a</sub> x temperature experiments. This analysis showed a positive, but non-significant interaction effect (95% CI for above-ground biomass response = -0.8, 18.0%) between eC<sub>a</sub> and temperature. Secondly, we tested field-based eC<sub>a</sub> experiments on woody plants across the globe for a relationship between the eC<sub>a</sub> effect on plant biomass and mean annual temperature (MAT). This second analysis showed a positive but non-significant correlation between the eC<sub>a</sub> response and MAT. The magnitude of the interactions between CO<sub>2</sub> and temperature found in both meta-analyses were consistent with model predictions, even though both analyses gave non-significant results. Thus, we conclude that it is not possible to distinguish between the competing hypotheses of no interaction versus an interaction based on Rubisco kinetics from the available experimental database. Experiments in a wider range of temperature zones are required. Until such experimental data are available, model predictions should aim to incorporate uncertainty about this interaction.

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## INTRODUCTION

Increasing levels of carbon dioxide in the atmosphere due to anthropogenic activities are likely to increase mean global temperatures by about 2 - 5°C during the next century, with concomitant changes in other environmental variables such as rainfall patterns and humidity (IPCC, 2013). These changes will impact on forest productivity in a number of ways. Some responses are likely to be positive, such as enhancement of photosynthetic rates by rising atmospheric CO<sub>2</sub> concentration (Ainsworth & Long, 2005; Hyvonen *et al.*, 2007; Kirschbaum, 2011), and extension of growing seasons by warmer temperatures (Norby *et al.*, 2003; Linderholm, 2006; Taylor *et al.*, 2008), whilst others may be negative, such as increasing drought impacts due to higher evaporative demand and reduced rainfall (Knapp *et al.*, 2002; Barnett *et al.*, 2005; IPCC, 2007). To predict the overall impact of climate change on tree growth, we rely on mathematical models that are based on our understanding of environmental influences on plant physiological processes (Medlyn *et al.*, 2011; Reyer *et al.*, 2014). Such models of forest response to climate change are essential for many purposes, including management of forest lands (Mäkelä *et al.*, 2000; Canadell & Raupach, 2008) and prediction of the terrestrial carbon cycle (Sitch *et al.*, 2008; Lewis *et al.*, 2013). It is important to ensure that the assumptions made by such models are strongly underpinned by scientific understanding and empirical data.

One important assumption made in many models is that there is a positive interaction between  $eC_a$  and temperature (T) on photosynthesis. At the biochemical level in C<sub>3</sub> plants,  $eC_a$  stimulates photosynthesis by increasing the rate of the carboxylation reaction relative to the oxygenation reaction in the photosynthetic carbon reduction cycle. In contrast, an increase in temperature increases the rate of oxygenation relative to carboxylation, so that the reduction of net assimilation rate due to photorespiration increases with temperature. Thus,

the suppression of oxygenation by  $eC_a$  has a larger effect at higher temperatures. Hence, at the leaf scale, an interactive effect is expected between  $eC_a$  and T, as shown by Long (1991).

Many models of the response of vegetation to climate change incorporate this  $eC_a \times T$  interaction effect on leaf photosynthesis. In the absence of any compensatory process, the interaction propagates through to larger scales. Using a forest canopy-scale model, McMurtrie & Wang (1993) showed there was a substantial rise in plant optimum growth temperature with increasing  $C_a$ , because of increased assimilation rates but similar respiration costs. Using a global-scale model, Hickler *et al.* (2008) predicted the enhancement in net primary productivity (NPP) of forest ecosystems by  $eC_a$  would increase with mean annual temperature (MAT). A positive interaction between  $eC_a$  and T is also predicted by models that take N cycling constraints into account (Medlyn *et al.*, 2000; Pepper *et al.*, 2005; Smith *et al.*, 2014). In a recent model review, Medlyn *et al.* (2011) showed that this assumption is important in determining modelled future climate impacts on productivity, because of the positive interaction between rising  $C_a$  and warming. Models that do not incorporate an  $eC_a \times T$  interaction are more likely to predict negative impacts on productivity than models that do incorporate the interaction. However, these models results assume that changes in photosynthetic rate drive changes in productivity, which is often not the case (Körner, 2013). Therefore, it is important to determine whether these predictions are supported by data.

Experimental results vary considerably in the type and magnitude of the response, meaning that it is not clear whether this assumption of an  $eC_a \times T$  interaction is supported by the available observations. For example, a study by Teskey (1997) on 22-year old loblolly pine trees, showed that a 2°C increase in air temperature had far less effect on rates of carbon assimilation than an increase in  $C_a$  by 165  $\mu\text{mol mol}^{-1}$  or 330  $\mu\text{mol mol}^{-1}$ , and the  $eC_a$  and T effects were additive rather than interactive. Similarly, Norby & Luo (2004) did not find a significant interaction of  $eC_a$  and T on tree

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growth in two different species of maple. However, Lewis *et al.* (2013) did find a significant interaction between  $eC_a$  and T on plant stem biomass accumulation in two eucalyptus species.

Meta-analysis can help to discern trends in experimental data when results from individual experiments are contradictory. There have been two recent meta-analyses examining factorial  $eC_a \times T$  experiments, but neither directly tested for the positive interaction between the two factors predicted by models. Dieleman *et al.* (2012) reviewed a number of field-based factorial experiments with forests and grasslands and found that there were more antagonistic than synergistic effects in these experiments, but did not carry out a statistical test to establish the overall effect size. Wang *et al.* (2012) carried out a meta-analysis on a wide range of factorial  $eC_a \times T$  experiments, comparing the mean  $eC_a$  response across all low temperature treatments with the mean  $eC_a$  response across all high temperature treatments. They reported that in woody plants,  $eC_a$  stimulated biomass by a similar amount in ambient and elevated temperatures. However, this approach has low power because it does not take into account the pairing of control and manipulation treatments by experiment. There is also an issue with this approach when the number of low-temperature  $eC_a$  responses does not equal the number of high-temperature  $eC_a$  responses (as in Wang *et al.*, 2012), because “low” and “high” temperatures are relative terms and therefore can only be applied to paired temperature treatments. No meta-analysis has so far directly examined the key model prediction that the  $eC_a$  response should be higher at locations with high mean annual temperature (Hickler *et al.*, 2008).

In this paper, we used meta-analysis to test specifically whether empirical data support the assumption of a positive interaction between  $eC_a$  and T that is embedded in many vegetation models. We carried out two meta-analyses, and

compared their results with model predictions. In the first meta-analysis, we examined factorial  $eC_a \times T$  experiments to test for an interaction-term between the  $eC_a$  and  $T$  treatments. In the second meta-analysis, we examined field-based experiments across the globe to test the hypothesis that the  $eC_a$  effect on plant biomass increases with mean annual temperature.

## **MATERIALS AND METHODS**

### **Meta-analysis of Factorial $CO_2 \times$ Temperature Experiments**

#### *Data collection*

Data were gathered by searching the ISI 'Web of Science' database for peer reviewed papers until December 2013 for elevated  $CO_2$  concentration  $\times$  temperature factorial studies on woody species. These studies were located by searching the database using the search terms "elevated  $CO_2$  and temperature effect on plants", "high  $CO_2$  and high temperature effect on trees" and "elevated  $CO_2$  and warming effects on plant biomass". Data were taken from tables or digitised from figures, using the software "GetData Graph digitizer" (GetData Graph Digitizer, 2008).

#### *Criteria for categorising studies*

We constructed our database with plant biomass responses to the respective treatments with means, standard deviations and number of replicates. Factorial experiments had four treatments a) ambient  $CO_2$ , low temperature b) ambient  $CO_2$ , high temperature c) high  $CO_2$ , low temperature and d) high  $CO_2$ , high temperature. Studies were categorised with  $CO_2$  treatment range between 325-400  $\mu\text{mol mol}^{-1}$  for ambient levels, and 530-800  $\mu\text{mol mol}^{-1}$  for elevated levels. Factorial experiments had at least two temperature treatments in addition to

two  $C_a$  treatments. Most experiments used two temperature levels, where the ‘high’ temperature treatments were in the range 2°-5° C above ‘low’ or ‘ambient’ temperature treatments. There were four studies with more than two temperature treatments. For these studies we divided treatments into two independent pairs. Two of the studies had five temperature treatments; for these, we disregarded the lowest temperature treatment (4°C below ambient). For some studies, root biomass and shoot biomass were calculated from root to shoot ratio and total biomass. To weight these studies in the meta-analysis, we took standard deviations from the total biomass data. Some studies involved additional manipulations such as nutrient levels and different plant species. Results from these treatments within the same experiment were considered independent and were treated as independent responses in the database. For experiments including watering treatments, only well-watered treatments were included. We omitted treatments where there was an explicit attempt to drought plants, as low water availability may alter the  $eC_a \times$  temperature interaction. Under drought conditions, higher temperatures amplify the effect of drought because of higher evaporative demand. Since this effect is not explicitly included in our model baseline, we ignored these treatments when comparing against the baseline.

Several in-ground studies had to be omitted because there were no published estimates of above-ground or below-ground biomass increment. Studies used in this meta-analysis are listed in Table 1.

### *Calculations*

The  $eC_a \times$  temperature interaction term was calculated from factorial experiments as described by Lajeunesse (2011). If the mean is represented as  $\bar{X}$ ,  $C_e$  and  $C_a$  represent elevated and ambient  $C_a$ , and  $T_e$  and  $T_a$  represent high and low temperature, then the interaction term in a factorial experiment can be written as the following response ratio:

$$r = \frac{\bar{X}_{C_e T_e} / \bar{X}_{C_e T_a}}{\bar{X}_{C_a T_e} / \bar{X}_{C_a T_a}} \quad (1)$$

To linearise this metric,  $r$  is log transformed to give:

$$\ln(r) = \ln\left(\frac{\bar{X}_{C_e T_e}}{\bar{X}_{C_a T_e}}\right) - \ln\left(\frac{\bar{X}_{C_e T_a}}{\bar{X}_{C_a T_a}}\right) \quad (2)$$

That is, the log of the  $eC_a \times T$  interaction term is equal to the difference between the log of the  $C_a$  response ratio at elevated temperature, and the log of the  $C_a$  response ratio at ambient temperature. Hedges *et al.* (1999) showed that the variance  $v$  of a log response ratio at ambient temperature is given by:

$$v = \frac{SD_{C_e T_a}^2}{n_{C_e T_a} \bar{X}_{C_e T_a}^2} + \frac{SD_{C_a T_a}^2}{n_{C_a T_a} \bar{X}_{C_a T_a}^2} \quad (3)$$

Using the additive property of variances, the variance of the log of the  $eC_a \times T$  interaction term is equal to

$$v = \frac{SD_{C_e T_e}^2}{n_{C_e T_e} \bar{X}_{C_e T_e}^2} + \frac{SD_{C_e T_a}^2}{n_{C_e T_a} \bar{X}_{C_e T_a}^2} + \frac{SD_{C_a T_e}^2}{n_{C_a T_e} \bar{X}_{C_a T_e}^2} + \frac{SD_{C_a T_a}^2}{n_{C_a T_a} \bar{X}_{C_a T_a}^2} \quad (4)$$

To estimate an overall interaction term, weighted means were used, where greater weights were given to experiments whose estimates had greater precision (i.e., smaller variance). We used a random effects model because between-study variance was found to be statistically significant. The meta-analysis calculations were done using software R (R Development Core Team, 2010) with package 'metafor' (Viechtbauer, 2010).

### **Meta-regression against Mean Annual Temperature**

#### *Data collection*

The second type of study was field-based manipulative  $C_a$  enrichment experiments with woody species. These studies were also located by searching the ISI 'Web of Science' database for peer reviewed papers, with the terms used "elevated  $CO_2$  effect on plants", "high  $CO_2$  effect on trees" and "elevated  $CO_2$  effects on plant biomass". Experiments had treatments with ambient  $C_a$  and elevated  $C_a$ . Only studies where trees were planted directly into the field were included (including open-top chamber, whole-tree chamber and free-air  $CO_2$  enrichment experiments).

#### *Criteria for categorising studies*

For studies where plants were grown from seed or seedlings, we used data on total biomass where available, or aboveground plant biomass where total plant biomass was not reported.

In studies where plants were established prior to the experiment, the response variable was biomass increment or Net Primary Production or, in cases where neither variable was available, basal area increment. All Free-Air  $CO_2$  Enrichment (FACE) studies had Net Primary Production data available except for the Sapporo, Japan FACE study. Studies were categorised with  $C_a$  treatment range between 325-400  $\mu\text{mol mol}^{-1}$  for ambient levels, and

530-800  $\mu\text{mol mol}^{-1}$  for elevated levels. Results from different plant species were considered to be independent and were treated as independent responses in the database. Three studies had more than one  $eC_a$  treatment; for these studies we compared each  $eC_a$  treatment with the control treatment. As in the first meta-analysis, we omitted drought treatments because low water availability may affect the  $eC_a$  response. Studies used in this meta-analysis are listed in Table 2.

### *Calculations*

For the second analysis, we carried out a meta-regression using the effect estimate of log response ratio of biomass as the outcome variable and mean annual temperature as the explanatory variable. To allow for the fact that the  $eC_a$  concentration applied differed among experiments, which would interact with mean annual temperature, the meta-regression equation fitted was:

$$\ln(r) = \ln\left(\frac{eC_a}{aC_a}\right) \times (\alpha + \beta(\text{MAT} - 15)) \quad (5)$$

where  $r$  is the observed response ratio,  $eC_a / aC_a$  is the fractional increase in  $C_a$  applied in the experiment, and  $\alpha$  and  $\beta$  are the fitted parameters. MAT was centred on  $15^\circ\text{C}$  to allow better estimation of the intercept  $\alpha$ .

Consistent mean annual temperatures for each experiment were estimated by extracting mean annual temperature for experimental site co-ordinates over the period 1991-2010 from a gridded monthly climatic data set (Harris *et al.*, 2014). Individual studies were weighted by the inverse of variance of their respective effect size. Random-effects meta-regression was

carried out using statistical programming software R (R Development Core Team, 2010) with package ‘metafor’ (Viechtbauer, 2010).

In the random-effects model, at least part of the heterogeneity may be due to the influence of moderators. For example, the response to  $eC_a$  may depend on whether the studies are FACE or chamber-based; whether or not nutrients are added; and whether NPP or total plant biomass is used as the response variable. We examined the influence of these variables by fitting a mixed-effects model including FACE vs chamber, NPP vs Biomass and fertilised vs unfertilised as moderators.

#### **Baseline Model Predictions**

We used model simulations to predict the magnitude of effect sizes as a baseline against which to compare the meta-analysis results. For the first meta-analysis, we used leaf and canopy photosynthesis models to estimate the expected effect sizes of an increase in  $C_a$ , an increase in temperature, and the interaction between the two effects. At leaf scale, we used the standard biochemical leaf photosynthesis model of Farquhar & von Caemmerer (1982). Calculations were made for both the Rubisco limited reaction ( $A_c$ ) and the RuBP-regeneration limited reaction ( $A_j$ ). We took temperature dependences for the Michaelis-Menten coefficient of Rubisco ( $K_m$ ) and the  $CO_2$  compensation point in the absence of mitochondrial respiration ( $\Gamma^*$ ) from Bernacchi *et al.* (2001). The activation energies of maximum Rubisco activity,  $V_{cmax}$ , and potential electron transport,  $J_{max}$ , were taken to be 58.52 and 37.87  $KJ\ mol^{-1}$  respectively, following Medlyn *et al.* (2002), while leaf day respiration was assumed to have a Q10 of 2.

At canopy scale we used the optimised net canopy photosynthesis model of Haxeltine & Prentice (1996), which is embedded in the LPJ family of Dynamic Global Vegetation Models (Sitch *et al.*, 2003). This model is based on the Collatz *et al.* (1991) simplification of the Farquhar model and assumes that leaf N content varies to maximise net canopy photosynthesis, resulting in an “acclimation” of  $V_{\text{cmax}}$  to growth conditions including temperature and  $eC_a$ . This model was parameterised with values from Haxeltine & Prentice (1996). We also used the canopy photosynthesis scheme of the O-CN model (Friend 2010).

Using these three models, we calculated photosynthesis at two levels of  $C_a$  ( $370 \mu\text{mol mol}^{-1}$  and  $690 \mu\text{mol mol}^{-1}$ ) and two temperatures (16 and  $20.5^\circ\text{C}$ ) where these levels of  $C_a$  and temperature represent the mean values of  $C_a$  and temperature used in the factorial experiments. From these outputs we calculated the expected size of the  $eC_a$  and T effects, and the  $eC_a \times T$  interaction.

To obtain baseline predictions of the NPP enhancement at varying mean annual temperatures across the globe for the second meta-analysis, we ran global simulations using two Dynamic Global Vegetation Models (DGVMs), the JULES model (Best *et al.*, 2011; Clark *et al.*, 2011), and the O-CN model (Zaehle *et al.*, 2010; Zaehle *et al.*, 2011) following as far as possible the simulation protocol of Hickler *et al.* (2008). We also took baseline predictions from simulations with the LPJ DGVM by Hickler *et al.* (2008) (their Fig. A1). The JULES simulations were driven with the WATCH-forcing data based on the ERA interim climatology ([http://www.eu-watch.org/data\\_availability](http://www.eu-watch.org/data_availability)), at 0.5 degree spatial resolution and a 3 hourly time step and observed atmospheric  $C_a$ , for the period 1986-1996. For the period 1996-2002, two simulations were performed, one with constant  $C_a$  at the 1996 levels and one with  $C_a$  constant at 550 ppm. The JULES model was run with fixed land cover, calculated for

the JULES plant functional types based on the MODIS in IGBP land cover map, and time invariant LAI for each plant functional type.

The O-CN simulations at 1 degree spatial resolution and a half-hourly time step were based on simulations from 1860 until 1995 driven with the daily CRU-NCEP climate data set, the observed atmospheric CO<sub>2</sub> record, reconstructed land-use change, and an estimate of N deposition, as described in Le Quéré *et al.* (2013). The simulation were then continued for the period 1996-2002 (with interannual climate variation but static land-cover and N deposition from 1996) either holding C<sub>a</sub> constant at the 1996 value or with a step increase to 550 μmol mol<sup>-1</sup>.

For the analyses of this paper, non-forest pixels were excluded for all three models. Hickler *et al.* (2008) ran the LPJ-model with potential natural vegetation and included only grid cells that carry natural forests other than savanna. Grid cells with very low NPP (< 100 g m<sup>-2</sup> yr<sup>-1</sup>) or woody LAI of <0.5 for boreal forests, or <2.5 for other forests, were also excluded.

Following the same protocol, for the O-CN model, we excluded pixels which had predicted NPP <100 g m<sup>-2</sup> yr<sup>-1</sup>; pixels with less than 25% forest cover in total; and pixels with LAI < 2.5 where latitude < 60°N or LAI < 1 where latitude > 60°N. Similarly, for the JULES model, pixels were excluded where NPP < 100 g m<sup>-2</sup> yr<sup>-1</sup> or where forest cover < 25% ([http://daac.ornl.gov/NPP/guides/NPP\\_BOREAL.html#HDataDescrAccess](http://daac.ornl.gov/NPP/guides/NPP_BOREAL.html#HDataDescrAccess)). Subsequently, savannahs were also removed by using the dominant vegetation type map from Ramankutty & Foley (1999). As there are default LAI fields used in the JULES model which are specific for broad-leaf or needle-leaf, no LAI filtering was done. Also, this implies there is no NPP-LAI feedback in these simulations.

## RESULTS

### Meta-analysis of Factorial Experiments

Out of 42 experiments, we could obtain above-ground biomass for 23 experiments, either directly from data reported or by calculating it from root: shoot ratio and total biomass. Of these 23 experiments, 16 observations were total above-ground biomass and 7 were stem biomass. We also obtained 22 observations for plant below-ground biomass and 32 for total biomass responses (Table 1). For plant above-ground biomass there were significant positive mean effects of both  $eC_a$  (mean effect size +21.4%) and temperature (mean effect size +18.1%) (Fig. 1a, b, Table 3). Most studies showed a positive effect of  $eC_a$  (Fig. 1a) whereas there was more variation among studies in the temperature effect (Fig. 1b). Rising temperature may have positive or negative effects depending on whether plants are above or below their temperature optimum. For the interaction term, the mean effect size was +8.2% (95% CI = -0.85, 18.0). This effect was not significantly different from zero ( $p = 0.08$ ), but neither was it significantly different from the effect sizes predicted by the leaf and canopy models, which were in the range 3.5 – 8.3% (Table 3).

Similar results were found for below-ground and total biomass plant responses. For below-ground biomass, a slightly larger mean  $eC_a$  effect (+35.2%) was observed, while the mean temperature effect was rather lower (+6.6%, Fig. 2a). The mean  $eC_a \times T$  interaction was positive, but not significantly different from zero (+1.5%, Fig. 2c). For total biomass,  $eC_a$  had a positive effect (+22.3%), as did increased temperature (+7.7%) while the mean  $eC_a \times T$  interaction was +0.5%, with a 95% CI of (-8.0, 9.8). Large confidence intervals were observed for individual studies in plant total biomass responses (Fig. 3c) due to within-study and between-study variation (Between-group heterogeneity  $Q (df = 31) = 84.8, p\text{-value} < 0.0001$ ).

Although the interaction term was not significantly different from zero for any response variable, the 95% confidence intervals also included the interaction sizes predicted by the leaf-scale and canopy-scale models (Table 3). Using the Farquhar & von Caemmerer (1982) photosynthesis model, we predicted that under RuBP-regeneration limitation, the percentage increases of photosynthesis in response to  $eC_a$ , temperature and their interaction would be +16%, +16.5% and +3.5%, respectively, indicating that the size of the  $eC_a \times T$  interaction is relatively small. The 95% confidence intervals found in the meta-analysis for the effect sizes include these effect sizes. However, when Rubisco activity ( $A_c$ ) is assumed to limit photosynthesis, the predicted  $eC_a$  effect (+44.6%) is above the observed CIs for above-ground and total biomass (Table 3). The  $eC_a$  effect and  $eC_a \times T$  interaction effect predicted by the LPJ canopy model are comparable to the RuBP-regeneration limited response ( $A_j$ ), and also fall within the observed confidence intervals, but the model predicts a reduction (-7.3%) in photosynthesis with an increase in temperature, which disagrees with observations (Table 3). The OCN canopy model also predicts T effect and  $eC_a \times T$  effect similar to  $A_j$ , but the  $eC_a$  effect was closer to that predicted with  $A_c$ , and was at the upper end of the 95% CI of the experimental responses (Table 3).

### **Meta-regression against Mean Annual Temperature**

For our second analysis, data were obtained from 82 studies around the globe in which trees were planted directly into the ground and exposed to  $aC_a$  or  $eC_a$  concentrations (Table 2). The response ratio for these studies was calculated from measures of total biomass, above-ground biomass, net primary production, or basal area increment, depending on the information available for each experiment. We carried out a meta-regression of the log response ratio in these studies against mean annual temperature of the site, using a random effects model, in which larger weight (indicated by larger circles in Fig. 4) is given to studies with lower variance.

When all studies were included, there was a statistically significant relationship between the response ratio and mean annual temperature. However, it appeared that this relationship was being driven by a single experiment on young *Pinus eldarica* trees (Idso & Kimball 1994). The response ratios found in this experiment were clear outliers and may have been caused by the fact that, in contrast to most other experiments, trees were grown singly in treatment chambers, with no competition from other trees. We therefore excluded all studies (see Table 2) that had single trees in treatment chambers (five studies; grey points in Fig. 4). When these studies were excluded, the slope of the meta-regression remained positive ( $0.0087\text{ }^{\circ}\text{C}^{-1}$ , CI= -0.007, 0.0249), but was no longer significantly different from zero (Fig. 4). Coefficients for this regression are given in Table 4.

The fitted intercept term,  $\alpha$ , can be used in equation (5) to estimate the average  $C_a$  effect size at MAT of  $15^{\circ}\text{C}$ . For an increase in  $C_a$  from  $360$  to  $550\text{ }\mu\text{mol mol}^{-1}$ , the estimated average effect size across the whole dataset at MAT of  $15^{\circ}\text{C}$  is +22.2%, with a 95% CI of (16.1, 28.6%).

We tested whether the relationship was affected by experimental factors by including additional factors in the meta-regression. Dummy variables were used to test whether the relationship differed between FACE and chamber studies, fertilised vs non-fertilised studies or whether the relationship differed for NPP vs total plant biomass. None of the three factors had a significant effect on the slope.

### **Comparison with baseline model predictions**

To investigate how the response obtained from meta-analysis compares to model predictions, we compared the meta-regression relationship with outcomes from the photosynthesis models (Fig. 5) and the three DGVMs (Fig. 6). The comparison to the leaf/canopy level models in Figure 5 is indicative only, since it compares the modelled  $eC_a$  response of photosynthesis at a given

instantaneous temperature, against measured biomass responses integrating the seasonal course of temperatures, at the reference mean annual temperature. The response obtained with the Haxeltine & Prentice (1996) model is very close to the response obtained for RuBP-regeneration-limited photosynthesis, while the O-CN canopy model lies in between the RuBP-regeneration limited and Rubisco-limited responses, reflecting the fact that this multi-layer canopy model explicitly separates sunny and shaded layers throughout the canopy (see also Table 3). Of the modelled relationships, the response of Rubisco-limited photosynthesis is the most sensitive to temperature, due to the high temperature sensitivity of the  $K_m$  of Rubisco. All model-based response curves are steeper than the meta-regression relationship.

In Figure 6, we compare the meta-regression relationship with GPP enhancements predicted by the JULES and O-CN model. We also compared NPP enhancements predicted by these models plus LPJ, which relies on the Haxeltine & Prentice (1996) model to simulate photosynthesis. The GPP enhancement is lower at all mean annual temperatures in the O-CN model than in the JULES model (Fig. 6a, c), possibly due to a higher fraction of photosynthesis that is light limited (i.e.  $A_l$ -limited photosynthesis) as well as gradual acclimation of foliar N due to limited N supply under  $eC_a$  in the O-CN model. Both models show an increasing  $eC_a$  response with mean annual temperatures above  $0^\circ\text{C}$ . We fitted linear regressions for the model output for pixels with  $\text{MAT} > 0^\circ\text{C}$  (Fig. 6). The slope of the response in JULES is very similar to the slope of the meta-regression, but the slope of the response is less steep in O-CN. Interestingly, both models appear to show that the predicted  $eC_a$  response of GPP increases as MAT decreases below  $0^\circ\text{C}$ . However, when plotted against growing season temperature rather than MAT, the relationship is monotonically positive (not shown), suggesting that locations with extremely low MAT may still have comparatively high growing season temperature, possibly due to a continentality effect. There have been no experiments in locations

with MAT below the 0°C threshold to date, so there are no data against which to compare this response.

The NPP response of both models is larger, and more strongly related to temperature, than the GPP response (Fig. 6b, d). The response is steepest in the JULES model, less steep in O-CN, and least steep in LPJ. Of the three models, the relationship predicted by the LPJ model is closest to the meta-regression. However, outputs from all three models lie largely within the 95% CI of the meta-regression, indicating that the modelled  $eC_a \times T$  interaction of all three models is consistent with experimental observations.

## DISCUSSION

In this study we asked the question, “Are responses of plants to  $eC_a$  higher at high temperatures?”.

We used two meta-analyses to address this question. Firstly, we looked at factorial  $eC_a \times T$  experiments and analysed whether there is an interaction; and secondly, we analysed whether there is a trend in  $eC_a$  response across experiments with different mean annual temperatures. In both analyses, variability among and within experiments was sufficiently large that confidence intervals included both zero and the modelled effect size. The experimental data available to date therefore do not allow us to distinguish between the competing hypotheses of a positive interaction of  $eC_a$  and temperature on growth, and no interaction.

Applying meta-analysis to the factorial experiments, we found an overall positive, but non-significant  $eC_a \times$  temperature interaction for plant above-ground, below-ground and total biomass (Table 3).

However, the confidence intervals also included the predicted interaction size for light-limited and

canopy-scale photosynthesis, meaning that we cannot statistically reject the possibility that an interaction exists. For the size of the temperature increase typically applied in factorial experiments, the predicted interaction term is small (+3.5 to +8.3%, Table 3). Very few individual experiments have sufficient power to detect an effect of this size. Combining experiments in meta-analysis often increases power, enabling small effects to be detected, but high variability among experiments may counteract this increase in power.

Variability amongst the factorial  $eC_a \times T$  experiments in this meta-analysis was high, likely caused by a range of experimental design factors. In some experiments, temperature levels were held constant, while in others, temperatures varied with the ambient temperature. Plant material varied widely, from boreal to subtropical species, with some species grown at below-optimal temperatures and others grown at or above their optimal temperatures. In some studies, additional nutrients were provided to reduce nutrient stress, while others did not add nutrients. Experiments also varied in the length of time that plants were exposed to  $eC_a$  (60 days to 4 years), the age at which treatment started (0-8 years old) and whether plants were freely rooted or grown in pots. With a limited number of experimental datasets, and such a wide range of experimental conditions, it was not possible to conclusively identify the factors responsible for variation among experiments.

Previous meta-analyses did not find evidence for a significant interaction between  $eC_a$  and temperature (Dieleman *et al.*, 2012; Wang *et al.*, 2012), but these analyses did not test whether the interaction term was significantly different from that predicted by models. By determining confidence intervals for the interaction effect size, we show that it is not possible to reject the hypothesis of a positive  $eC_a \times T$  interaction as predicted by models based on these experiments. The chief reason for the small, observation-based interaction term is that the temperature increments

applied in the factorial experiments were relatively small (typically +2 to +5°C). To increase the chance of detecting an interactive effect, it may be appropriate to consider factorial experiments with larger temperature increments. For a 10°C increase in temperature from 20°C to 30°C, for example, the predicted interaction effect size rises to 10% for  $A_j$  and 20% for  $A_c$ . However, such experiments would need to be conducted with caution, as there is a high potential for experimental artifacts with larger changes in temperature.

In the second meta-analysis we compared  $eC_a$  responses from experiments with trees around the globe, giving a much larger range in growth temperature. We attempted to include all published experiments, but some high-profile experiments had to be omitted from this analysis because there was no estimate of  $eC_a$  effect on biomass increment or NPP that was comparable with other studies.

The Swiss webFACE experiment (Bader *et al.*, 2013) on a mature deciduous forest is one such experiment; however, the uncertainty bounds on stem growth for that experiment were sufficiently large (Fatichi & Leuzinger, 2013) that inclusion of that experiment, had it been possible, would not have affected the outcome of the regression.

The second meta-analysis was also inconclusive. We did not find a statistically significant relationship between the  $eC_a$  response of plant biomass production and mean annual temperature. However, there was high variability among experiments and the 95% CI for the meta-regression included the relationships predicted by three DGVMs, meaning it was not possible to reject the interaction effect sizes embedded in the models.

Comparison of the meta-regression with model outputs does need to be interpreted with caution because the model outputs do not exactly coincide with the experiments. The experiments were conducted on a range of experimental material, but principally on young, rapidly expanding trees,

whereas the DGVMs simulated the effects of a step change in  $C_a$  on established forests. In young, rapidly growing plants, leaf area feedbacks amplify the response of photosynthesis, and these feedbacks may be more pronounced at high temperatures. This effect will not be captured in the DGVMs. On the other hand, in the DGVMs, the slope of the NPP response vs MAT is much steeper than the GPP response vs MAT (Fig. 6) because respiration is estimated from plant biomass, and in established forests the  $eC_a$  effect on plant biomass lags behind the effect on GPP. This effect is amplified at high temperatures. Following a step change in atmospheric  $CO_2$  concentration, therefore, the slope of the NPP response vs MAT relationship predicted by DGVMs is steep, but the slope diminishes over time. The latter effect will not be present in experiments on young trees.

Despite this incompatibility between the experiments and model outputs, we can nonetheless draw some useful observations from the comparison. Firstly, the comparison helps to understand causes for the differences among the models. The LPJ model predicts lower  $eC_a$  responses than the JULES model, as has been observed previously (Sitch *et al.*, 2008). At a MAT of  $15^\circ C$ , the JULES model predicts an average 33.6% increase in NPP whereas the LPJ-model predicts only 25.8% increase in NPP (Hickler *et al.*, 2008). This difference likely arises because of the use of the Haxeltine & Prentice (1996) photosynthesis model in LPJ, in which  $V_{cmax}$  acclimates to  $eC_a$ , reducing the  $eC_a$  effect compared to JULES which uses the Farquhar photosynthesis model without acclimation (Fig. 5).

Secondly, the comparison highlights the need for experiments in a wider range of growing temperatures. Although the  $eC_a$  experiments included in the second meta-analysis cover a much wider range of temperature than the factorial  $eC_a \times T$  experiments, they are nonetheless largely restricted to zones with MAT between  $5^\circ C$  and  $15^\circ C$  (Fig. 4). Very few data are available for the

largest forested regions – the boreal zone and the tropics – underscoring the need for further experiments investigating  $C_a$  responses in these regions.

New experiments are needed not only to investigate whether the interaction between  $eC_a$  and T on plant biomass production exists, but also to explore the potential mechanisms that might cause the interaction not to occur. Such mechanisms could include acclimation of photosynthesis and/or respiration to growth temperature, or feedbacks via water or nutrient availability. If, with further experiments, we are able to statistically reject the  $eC_a \times T$  interaction currently predicted by models, it will be important to modify the models accordingly. To do so, we will need to identify the most important mechanisms causing the leaf-level interaction to be over-ridden at whole-plant scale.

Comparison of experimental data against model predictions, as done here, will be key for identifying such mechanisms.

In conclusion, neither of the meta-analyses that we performed allowed us to distinguish between the two competing hypotheses of a positive  $eC_a \times T$  interaction, and no interaction. Until further data become available, it would be useful for modelling studies to indicate how this uncertainty affects projected responses to climate change by evaluating the consequences of both hypotheses.

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#### **SUPPLEMENTARY MATERIAL**

S1. Database of factorial eC<sub>a</sub> x T experiments used in first meta-analysis

S2. Database of field-based eC<sub>a</sub> experiments used in second meta-analysis

**Table 1:** List of factorial eC<sub>a</sub> x temperature experiments used in the first meta-analysis, with study sites and location. Study codes were used to identify each study in meta-analysis forest plots.

Site	Location	Study code	Treatment	Species	TB	AGB	BGB	Source Paper
Athens	GA, USA	Athens		<i>Quercus rubra</i>	*			Bauweraerts <i>et al.</i> , 2013
Corvallis	OR, USA	Corvallis		<i>Pseudotsuga menziesii</i>	*	*	*	Olszyk <i>et al.</i> , 2003
Dahlem	Germany	Dahlem-1	-2 to 2° C	<i>Fagus sylvatica</i>	*			Overdieck <i>et al.</i> , 2007
		Dahlem-2	0 to 4° C		*			"
Duke	NC, USA	Duke-1		<i>Pinus ponderosa</i>	*	*	*	Delucia <i>et al.</i> , 1997
		Duke-2		<i>Pinus ponderosa</i>	*	*	*	Callaway <i>et al.</i> , 1994
		Duke-3	High Nutrient	<i>Robinia pseudoacacia</i>	*	*	*	Uselman <i>et al.</i> , 2000
		Duke-4	Low Nutrient		*	*	*	"
		Duke-5	High Nutrient	<i>Pinus taeda</i>			*	King <i>et al.</i> , 1996
		Duke-6	Low Nutrient				*	"
		Duke-7	High Nutrient	<i>Pinus ponderosa</i>			*	"
		Duke-8	Low Nutrient				*	"
Flakaliden	Sweden	Flakaliden		<i>Picea abies</i>		*		Kostiainen <i>et al.</i> , 2009
Harvard	MA, USA	Harvard		<i>Betula alleghaniensis</i>	*			Wayne <i>et al.</i> , 1998
Horsholm	Denmark	Horsholm-1	-2 to 2.3° C	<i>Fagus sylvatica</i>	*	*	*	Bruhn <i>et al.</i> , 2000
		Horsholm-2	0 to 4.8° C		*	*	*	
Mekrijarvi	Finland	Mekrijarvi-1		<i>Betula pendula</i>	*			Kuokkanen <i>et al.</i> , 2001
		Mekrijarvi-2		<i>Betula pendula</i>	*			Kellomaki & Wang 2001
		Mekrijarvi-3		<i>Pinus sylvestris</i>		*		Sallas <i>et al.</i> , 2003
		Mekrijarvi-4		<i>Salix myrsinifolia</i>		*		Veteli <i>et al.</i> , 2002
		Mekrijarvi-5		<i>Betula pendula</i>	*	*	*	Lavola <i>et al.</i> , 2013)
Oak ridge	TN, USA	Oak ridge-1		<i>Acer rubrum</i>	*	*		Norby & Luo 2004
		Oak ridge-2		<i>Acer saccharum</i>	*	*		"
		Oak ridge-3		<i>Acer rubrum/saccharum</i>		*	*	Wan <i>et al.</i> , 2004
Richmond	Australia	Richmond-1		<i>Eucalyptus saligna</i>	*	*	*	Ghannoum <i>et al.</i> , 2010
		Richmond-2		<i>Eucalyptus sideroxylon</i>	*	*	*	"
		Richmond-3		<i>Eucalyptus saligna</i>	*	*	*	Lewis <i>et al.</i> , 2013
		Richmond-4		<i>Eucalyptus sideroxylon</i>	*	*	*	"
		Richmond-5		<i>Eucalyptus globulus</i>	*	*	*	Duan <i>et al.</i> , 2013
Saerheim	Norway	Saerheim		<i>Betula pubescens</i>	*	*	*	Mortensen, 1995
Shanghai	China	Shanghai		<i>Abies faxoniana</i>	*	*	*	Hou <i>et al.</i> , 2010)
Taichung	Taiwan	Taichung		<i>Shima superba</i>	*			Sheu & Lin, 1999
Tsukuba	Japan	Tsukuba		<i>Quercus myrsinaefolia</i>	*	*	*	Usami <i>et al.</i> , 2001
Urbana	IL, USA	Urbana		<i>Pinus ponderosa</i>	*	*	*	Maherali & DeLucia, 2000
St. Paul	MN, USA	St. Paul_1	21° C - 24° C	<i>Picea mariana</i>	*			Tjoelker <i>et al.</i> , 1998
		St. Paul_2	27° C - 30° C	<i>Picea mariana</i>	*			"
		St. Paul_3	21° C - 24° C	<i>Pinus banksina</i>	*			"
		St. Paul_4	27° C - 30° C	<i>Pinus banksina</i>	*			"
		St. Paul_5	21° C - 24° C	<i>Larix laricina</i>	*			"
		St. Paul_6	27° C - 30° C	<i>Larix laricina</i>	*			"
		St. Paul_7	21° C - 24° C	<i>Betula papyrifera</i>	*			"
		St. Paul_8	27° C - 30° C	<i>Betula papyrifera</i>	*			"

\* denotes whether the study reported TB = Total Biomass, AGB = Above Ground Biomass and/or BGB = Below Ground Biomass.

**Table 2:** List of eC<sub>a</sub> experiments with woody species rooted in the ground used in the second meta-analysis.

Obs.	Site name	Location	Type of Experiment	Species	Nutrients	Other treatment	Parameter	Mean Annual Temperature °C	Reference
1	Bangor	UK	FACE	<i>Alnus glutinosa</i>			AG NPP	10.2	Smith <i>et al.</i> , 2013
2			FACE	<i>Betula pendula</i>			AG NPP		
3			FACE	<i>Fagus sylvatica</i>			AG NPP		
4	Birmendorf	Switzerland	OTC	<i>Fagus sylvatica</i>	High	Acidic soil	Total Biomass	9.5	Spinnler <i>et al.</i> , 2002
5			OTC	<i>Fagus sylvatica</i>	Low	Acidic soil	Total Biomass		
6			OTC	<i>Fagus sylvatica</i>	High	Calcareous soil	Total Biomass		
7			OTC	<i>Fagus sylvatica</i>	Low	Calcareous soil	Total Biomass		
8			OTC	<i>Picea abies</i>	High	Acidic soil	Total Biomass		
9			OTC	<i>Picea abies</i>	Low	Acidic soil	Total Biomass		
10			OTC	<i>Picea abies</i>	High	Calcareous soil	Total Biomass		
11			OTC	<i>Picea abies</i>	Low	Calcareous soil	Total Biomass		
12	Bungendore	Australia	OTC	<i>Eucalyptus pauciflora</i>			Total Biomass	12.7	Roden <i>et al.</i> , 1999
13			OTC*	<i>Eucalyptus pauciflora</i>		Grown with grasses	Total Biomass		Loveys <i>et al.</i> , 2010
14			OTC	<i>Eucalyptus pauciflora</i>		Shading of chambers	Total Biomass		Barker <i>et al.</i> , 2005
15	Darwin	Australia	CTC	<i>Mangifera indica</i>			Total Biomass	27.2	Goodfellow <i>et al.</i> , 1997
16	Davos	Switzerland	FACE	<i>Larix decidua</i>			Shoot Biomass	1.8	Dawes <i>et al.</i> , 2011
17			FACE	<i>Pinus mugo</i>			Shoot Biomass	1.8	
18	Duke	NC, USA	FACE	<i>Pinus taeda</i>			Total NPP	15.3	McCarthy <i>et al.</i> , 2010
19			OTC	<i>Pinus taeda</i>			Total Biomass		Tissue <i>et al.</i> , 1997
20	Flakaliden	Sweden	WTC	<i>Picea abies</i>			AG Biomass	2	Sigurdsson <i>et al.</i> , 2013
21			WTC	<i>Picea abies</i>	High		AG Biomass		
22			WTC	<i>Picea abies</i>	Low		AG Biomass		
23	Glencorse	UK	OTC*	<i>Betula pendula</i>			Total Biomass	8.3	Rey & Jarvis, 1997
24	Glendevon	UK	OTC	<i>Alnus glutinosa</i>	High		Total Biomass	8.1	Temperton <i>et al.</i> , 2003
25			OTC	<i>Alnus glutinosa</i>	Low		Total Biomass		
26			OTC	<i>Betula pendula</i>	High		Total Biomass		
27			OTC	<i>Betula pendula</i>	Low		Total Biomass		
28			OTC	<i>Pinus sylvestris</i>	High		Total Biomass		
29			OTC	<i>Pinus sylvestris</i>	Low		Total Biomass		
30			OTC	<i>Picea sitchensis</i>	High		Total Biomass		

Obs.	Site name	Location	Type of Experiment	Species	Nutrients	Other treatment	Parameter	Mean Annual Temperature °C	Reference
31			OTC	<i>Picea sitchensis</i>	Low		Total Biomass		
32	Gunnesholt	Iceland	WTC	<i>Populus trichocarpa</i>	High		Total Biomass	5.2	Sigurdsson <i>et al.</i> , 2001
33			WTC	<i>Populus trichocarpa</i>	Low		Total Biomass		
34	Headley	UK	OTC	<i>Quercus petraea</i>			Total Biomass	10	
35			OTC	<i>Quercus rubra</i>			Total Biomass		
36			OTC	<i>Fraxinus excelsior</i>			Total Biomass		Broadmeadow & Jackson, 2000
37			OTC	<i>Quercus petraea</i>			Total Biomass		
38			OTC	<i>Pinus sylvestris</i>			Total Biomass		
39	Hyderabad	India	OTC	<i>Gmelina arborea</i>			Total Biomass	27	Reddy <i>et al.</i> , 2010
40	Merritt	FA, USA	OTC	<i>Quercus myrtifolia</i> / <i>Quercus geminata</i>			AG NPP	22.4	Day <i>et al.</i> , 2013
41	Mekrijarvi	Finland	CTC	<i>Pinus sylvestris</i>			Biomass	2.5	Peltola <i>et al.</i> , 2002
42	Oak ridge	TN, USA	OTC	<i>Acer rubrum</i>			Total Biomass	14.6	Norby <i>et al.</i> , 2000
43			OTC	<i>Acer saccharum</i>			Total Biomass		
44			FACE	<i>Liquidambar styraciflua</i>			Total NPP		Norby <i>et al.</i> , 2010
45			OTC	<i>Quercus alba</i>		eC <sub>a</sub> 500 μmol mol <sup>-1</sup>	Total Biomass		Norby <i>et al.</i> , 1995
46			OTC	<i>Quercus alba</i>		eC <sub>a</sub> 650 μmol mol <sup>-1</sup>	Total Biomass		
47			OTC	<i>Liriodendron tulipifera</i>		eC <sub>a</sub> Ambient + 150 μmol mol <sup>-1</sup>	Total Biomass		Norby <i>et al.</i> , 1992
48			OTC	<i>Liriodendron tulipifera</i>		eC <sub>a</sub> Ambient + 300 μmol mol <sup>-1</sup>	Total Biomass		
49	Parque	Panama	OTC	Tree communities			Biomass	26.3	Lovelock <i>et al.</i> , 1998
50	Phoenix	AR, USA	OTC*	<i>Pinus elliottii</i>		eC <sub>a</sub> 554 μmol mol <sup>-1</sup>	Total Biomass	21.9	Idso & Kimball, 1994
51			OTC*	<i>Pinus elliottii</i>		eC <sub>a</sub> 680 μmol mol <sup>-1</sup>	Total Biomass		
52			OTC*	<i>Pinus elliottii</i>		eC <sub>a</sub> 812 μmol mol <sup>-1</sup>	Total Biomass		
53			OTC	<i>Citrus aurantium</i>			Total Biomass		Kimball <i>et al.</i> , 2007
54	Placerville	NV, USA	OTC	<i>Pinus ponderosa</i>	High		Total Biomass	14.1	Johnson <i>et al.</i> , 1997
55			OTC	<i>Pinus ponderosa</i>	Low		Total Biomass		
56			OTC	<i>Pinus ponderosa</i>	High		Total Biomass		
57			OTC	<i>Pinus ponderosa</i>	Low		Total Biomass		
58			OTC	<i>Pinus ponderosa</i>	Medium		Total Biomass		
59	Rhineland	WI, USA	FACE	<i>Populus tremuloides</i>			Total NPP	4.3	King <i>et al.</i> , 2005
60			FACE	<i>Populus tremuloides</i> / <i>Populus deltoides</i>			Total NPP		
61	Richmond	Australia	WTC	<i>Eucalyptus saligna</i>			Total Biomass	17	Barton <i>et al.</i> , 2012

Obs.	Site name	Location	Type of Experiment	Species	Nutrients	Other treatment	Parameter	Mean Annual Temperature °C	Reference
62	Sapporo	Japan	FACE	<i>Larix gmelinii</i>			Total Biomass	7.6	Watanabe <i>et al.</i> , 2013
63			FACE	<i>Larix gmelinii</i>			Total Biomass		
64	Suonenjoki	Finland	OTC	<i>Betula pendula</i>		O3-tolerant (Clone 4)	Total Biomass	3.8	Riikonen <i>et al.</i> , 2004
65			OTC	<i>Betula pendula</i>		O3-sensitive (Clone 80)	Total Biomass		
66	TUB	Germany	ME	<i>Fagus sylvatica</i>			Biomass	13.8	Forstreuter, 1995
67	UIA	Belgium	OTC	<i>Pinus sylvestris</i>			Total Biomass	10.8	Janssens <i>et al.</i> , 2005
68			OTC	<i>Poplar Beaupre</i>			Biomass	10.8	Ceulemans <i>et al.</i> , 1996
69			OTC	<i>Poplar Robusta</i>			Biomass	10.8	
70	UMBS	MI, USA	OTC	<i>Populus tremuloides</i>			Total Biomass	5.9	Zak <i>et al.</i> , 2000
71			OTC	<i>Populus tremuloides</i>			Total Biomass		
72			OTC	<i>Populus tremuloides</i>	High		Total Biomass		Mikan <i>et al.</i> , 2000
73			OTC	<i>Populus tremuloides</i>	Low		Total Biomass		
74			OTC	<i>Alnus glutinosa</i>			Total Biomass		Vogel <i>et al.</i> , 1997
75			OTC	<i>Populus euramericana</i>	High		Total Biomass		Pregitzer <i>et al.</i> , 1995
76			OTC	<i>Populus euramericana</i>	Low		Total Biomass		
77			OTC	<i>Populus grandidentata</i>			Total Biomass		Zak <i>et al.</i> , 1993
78	UPS	France	ME	<i>Fagus sylvatica</i>			Biomass	15	Badeck <i>et al.</i> , 1997
79	Vielsalm	Belgium	OTC	<i>Picea abies</i>			Biomass	7.5	Laitat <i>et al.</i> , 1994
80	Viterbo	Italy	FACE	<i>Populus euramericana</i>			Total NPP	16	Calfapietra <i>et al.</i> , 2003
81			FACE	<i>Populus alba</i>			Total NPP		
82			FACE	<i>Populus nigra</i>			Total NPP		

Abbreviations: FACE=free air carbon dioxide enrichment, OTC=open top chamber, CTC= closed top chambers, WTC= whole tree chambers, ME = mini-ecosystem. AG = above-ground, NPP= net primary productivity. \* indicates studies which had single tree in treatment chambers.

**Table 3:** Comparison between meta-analytic and modelled estimates of percentage effects of  $eC_a$ , T and their interaction in factorial experiments. Meta-analysis values are mean effect sizes with 95% CIs. The Farquhar & von Caemmerer (1982) model was used to estimate effects on net leaf photosynthesis when Rubisco activity is limiting ( $A_c$ ) or when RuBP regeneration is limiting ( $A_j$ ). The models of Haxeltine & Prentice (1996) and Friend (2010) were used to estimate effects on canopy net photosynthesis (Canopy LPJ and Canopy OCN, respectively).

	% $eC_a$ effect	% T effect	% $eC_a \times T$
<b>Meta-analysis:</b>			
Above-ground biomass	21.4% (11.0, 32.8)	18.1% (9.3, 27.7)	8.2% (-0.8, 18.0)
Below-ground biomass	35.2% (18.8, 53.9)	6.6% (1.0, 12.5)	1.5% (-7.2, 10.9)
Total biomass	22.3% (13.9, 31.4)	7.7% (-1.4, 17.7)	0.5% (-8.0, 9.8)
<b>Models:</b>			
Leaf $A_c$	44.6%	15.9%	8.3%
Leaf $A_j$	16.0%	16.5%	3.5%
Canopy LPJ	19.5%	-7.3%	4.7%
Canopy OCN	32.4%	12.1%	3.9%

**Table 4:** Results of meta-regression. Equation (5) was fitted to data from experiments listed in Table 2. Statistics given are Coefficient (estimate), standard error (SE), 95% confidence interval (CI) and p-value.

	<b>Coefficient</b>	<b>SE</b>	<b>CI</b>	<b>p</b>
Intercept $\alpha$	0.4735	0.0615	0.3529 0.5941	<.0001
Slope $\beta$	0.0087	0.0082	-0.0074 0.0249	0.289

### Figure Captions

Figure 1: Forest plots of standardized effect sizes for (a) the  $eC_a$  effect at low and high temperature; (b) the temperature effect at  $aC_a$  and  $eC_a$ ; and (c) the  $eC_a \times$  temperature interaction term for above ground plant biomass in  $eC_a \times T$  factorial experiments. Each point represents the mean effect size of an individual study, apart from the last point in (c) which shows the mean (summary) effect size of all studies. Lines in (c) indicate 95% confidence intervals. The dashed vertical line shows zero effect. Studies are ordered by the  $eC_a \times T$  interaction effect size.

Figure 2: As for Figure 1, but for below-ground plant biomass.

Figure 3: As for Figure 1, but for total plant biomass.

Figure 4: Meta-regression of the  $eC_a$  response ratio in field-based experiments with woody species, against mean annual temperature. The area of each circle is inversely proportional to the variance of the log response ratio estimate and indicates the weighting assigned to each study. The dotted line

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shows zero or no effect, the solid black line represents the fitted regression line (equation 5, slope=0.0034,  $p>0.05$ ) for studies in which trees were grown in groups and dashed black lines show the 95% confidence interval. Grey circles represent single tree studies (refer to Table 2). Red circles denote data from FACE (Free-Air CO<sub>2</sub> Enrichment) experiments. Note that y-axis is log transformed.

Figure 5: Meta-regression relationship with  $C_a$  increment = 190  $\mu\text{mol mol}^{-1}$ , compared to modelled percentage response of net photosynthesis to the same increase in  $C_a$  as a function of mean leaf temperature. Solid red line: meta-regression. Dotted line: modelled response of Rubisco-limiting leaf net photosynthetic rate ( $A_c$ ). Dashed line: modelled response of RuBP-regeneration-limited leaf net photosynthetic rate ( $A_j$ ). Both  $A_c$  and  $A_j$  were calculated according to the Farquhar & von Caemmerer (1982) model. Solid green line: modelled response of net daily canopy photosynthesis according to the Haxeltine & Prentice (1996) model. Solid blue line: modelled response of net daily canopy photosynthesis according to the canopy model (Friend, 2010) of the OCN model (Zaehle & Friend, 2010).

Figure 6: Comparison of meta-regression relationship with DGVM predictions of CO<sub>2</sub> enhancement of GPP (a, c) and NPP (b, d). Data points are output from the JULES model (a, b) and O-CN model (c, d). Blue lines represent best linear fits to these model outputs for MAT > 0. Solid red line: Meta-regression relationship with  $C_a$  increment of +190  $\mu\text{mol mol}^{-1}$ . Dashed red lines: 95% CI for meta-regression. Solid green line: Linear relationship fitted to output from LPJ model by Hickler et al. (2008). Grey line: mean  $eC_a$  effect from the observations, estimated by fitting equation (5) to data whilst holding slope  $\beta = 0$ .











