RESEARCH REVIEW

Does the growth response of woody plants to elevated CO$_2$ increase with temperature? A model-oriented 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$_2$ concentration (C$_a$) will increase with increasing air temperature. Vegetation models incorporating this interaction predict that the response of net primary productivity (NPP) to elevated CO$_2$ (eC$_a$) 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$_a$ experiments by carrying out two meta-analyses. Firstly, we tested for an interaction effect on growth responses in factorial eC$_a$ × temperature experiments. This analysis showed a positive, but nonsignificant interaction effect (95% CI for above-ground biomass response = −0.8, 18.0%) between eC$_a$ and temperature. Secondly, we tested field-based eC$_a$ experiments on woody plants across the globe for a relationship between the eC$_a$ effect on plant biomass and mean annual temperature (MAT). This second analysis showed a positive but nonsignificant correlation between the eC$_a$ response and MAT. The magnitude of the interactions between CO$_2$ and temperature found in both meta-analyses were consistent with model predictions, even though both analyses gave nonsignificant results. Thus, we conclude that it is not possible to distinguish between the competing hypotheses of no interaction vs. 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.

Keywords: effect size, log response ratio, Meta-analysis, meta-regression, photosynthesis, Rubisco

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$_2$ 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), while 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$_3$ plants, eC$_a$ stimulates photosynthesis by increasing the rate of the carboxylation reaction relative

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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 model 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 μmol mol^{-1} or 330 μmol 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 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 x 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

digitized from figures, using the software 'GetData Graph digitizer' (GetData Graph Digitizer, 2008).

Criteria for categorizing 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 (i) ambient CO$_2$, low temperature; (ii) ambient CO$_2$, high temperature; (iii) high CO$_2$, low temperature; and (iv) high CO$_2$, high temperature. Ambient CO$_2$ treatments had concentrations ranging from 325 to 400 μmol mol^{-1}, while elevated CO$_2$ treatments had concentrations ranging from 530 to 800 μmol mol^{-1}. 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 treat-

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

*Denotes whether the study reported TB = total biomass, AGB = above-ground biomass or BGB = below-ground biomass.

ments. 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 eCa x temperature interaction. Under drought conditions, higher temperatures amplify the effect of drought because of higher evaporative demand. As 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; data used are given in Table S1.

Calculations. The $eC_a \times T$ interaction term was calculated from factorial experiments as described by Lajeunesse (2011). If the mean is represented as $\overline{X}$, 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:

$$r = \frac{\overline{X}_{C_eT_e}}{\overline{X}_{C_aT_e}} \bigg/ \frac{\overline{X}_{C_eT_a}}{\overline{X}_{C_aT_a}} \qquad (1)$$

To linearize this metric, r is log-transformed to give:

$$\ln(r) = \ln\left(\frac{\overline{X}_{C_eT_e}}{\overline{X}_{C_aT_e}}\right) - \ln\left(\frac{\overline{X}_{C_eT_a}}{\overline{X}_{C_aT_a}}\right) \qquad (2)$$

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:

$$v = \frac{SD^2_{C_eT_a}}{n_{C_eT_a}\overline{X}_{C_eT_a}^2} + \frac{SD^2_{C_aT_a}}{n_{C_aT_a}\overline{X}_{C_aT_a}^2} \qquad (3)$$

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

$$v = \frac{SD^2_{C_eT_e}}{n_{C_eT_e}\overline{X}_{C_eT_e}^2} + \frac{SD^2_{C_eT_a}}{n_{C_eT_a}\overline{X}_{C_eT_a}^2} + \frac{SD^2_{C_aT_e}}{n_{C_aT_e}\overline{X}_{C_aT_e}^2} + \frac{SD^2_{C_aT_a}}{n_{C_aT_a}\overline{X}_{C_aT_a}^2} \qquad (4)$$

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 ground were included (including open-top chamber, whole-tree chamber and free-air CO_2 enrichment experiments).

Criteria for categorizing studies. For studies where plants were grown from seed or seedlings, we used data on total biomass where available, or above-ground 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. Ambient CO_2 treatments had concentrations ranging from 340 to 410 μmol mol^{-1}, while elevated CO_2 treatments had concentrations ranging from 460 to 810 μmol mol^{-1}. 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, 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; data used are given in Table S2.

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 as follows:

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

where r is the observed response ratio, eC_a/aC_a is the fractional increase in C_a applied in the experiment, and α and β are the fitted parameters. MAT was centred on 15°C to allow better estimation of the intercept α.

Consistent mean annual temperatures for each experiment were estimated by extracting mean annual temperature for experimental site coordinates over the period 1991–2010 from a gridded monthly climatic data set (Harris *et al.*, 2014).

Table 2 List of eC_a 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	Alnus glutinosa			AG NPP	10.2	Smith et al. (2013)
2			FACE	Betula pendula			AG NPP		
3			FACE	Fagus sylvatica			AG NPP		
4	Birmensdorf	Switzerland	OTC	Fagus sylvatica	High	Acidic soil	Total biomass	9.5	Spinnler et al. (2002)
5			OTC	Fagus sylvatica	Low	Acidic soil	Total biomass		
6			OTC	Fagus sylvatica	High	Calcareous soil	Total biomass		
7			OTC	Fagus sylvatica	Low	Calcareous soil	Total biomass		
8			OTC	Picea abies	High	Acidic soil	Total biomass		
9			OTC	Picea abies	Low	Acidic soil	Total biomass		
10			OTC	Picea abies	High	Calcareous soil	Total biomass		
11			OTC	Picea abies	Low	Calcareous soil	Total biomass		
12	Bungendore	Australia	OTC	Eucalyptus pauciflora		Grown with grasses	Total biomass	12.7	Roden et al. (1999)
13			OTC*	Eucalyptus pauciflora			Total biomass		Loveys et al. (2010)
14			OTC	Eucalyptus pauciflora		Shading of chambers	Total biomass		Barker et al. (2005)
15	Darwin	Australia	CTC	Mangifera indica			Total biomass	27.2	Goodfellow et al. (1997)
16	Davos	Switzerland	FACE	Larix decidua			Shoot biomass	1.8	Dawes et al. (2011)
17			FACE	Pinus mugo			Shoot biomass	1.8	
18	Duke	NC, USA	FACE	Pinus taeda			Total NPP	15.3	McCarthy et al. (2010)
19			OTC	Pinus taeda			Total biomass		Tissue et al. (1997)
20	Flakaliden	Sweden	WTC	Picea abies		Ambient temperature	AG biomass	2	Sigurdsson et al. (2013)
21			WTC	Picea abies	High		AG biomass		
22			WTC	Picea abies	Low		AG biomass		
23	Glencorse	UK	OTC*	Betula pendula	High		Total biomass	8.3	Rey & Jarvis (1997)
24	Glendevon	UK	OTC	Alnus glutinosa	High		Total biomass	8.1	Temperton et al. (2003)
25			OTC	Alnus glutinosa	Low		Total biomass		
26			OTC	Betula pendula	High		Total biomass		Laitat et al. (1999)
27			OTC	Betula pendula	Low		Total biomass		
28			OTC	Pinus sylvestris	High		Total biomass		
29			OTC	Pinus sylvestris	Low		Total biomass		
30			OTC	Picea sitchensis	High		Total biomass		
31			OTC	Picea sitchensis	Low		Total biomass		
32	Gunnarsholt	Iceland	WTC	Populus trichocarpa	High		Total biomass	5.2	Sigurdsson et al. (2001)
33			WTC	Populus trichocarpa	Low		Total biomass		
34	Headley	UK	OTC	Quercus petraea			Total biomass	10	
35			OTC	Quercus rubra			Total biomass		

Table 2 (continued)

Obs.	Site name	Location	Type of Experiment	Species	Nutrients	Other treatment	Parameter	Mean Annual Temperature °C	Reference
36			OTC	*Fraxinus excelsior*			Total biomass		Broadmeadow & Jackson (2000)
37			OTC	*Quercus petraea*			Total biomass		
38			OTC	*Pinus sylvestris*			Total biomass		
39	Hyderabad	India	OTC	*Gmelina arborea*			Total biomass	27	Reddy *et al.* (2010)
40	Merritt	FA, USA	OTC	*Quercus myrtifolia/ Quercus geminata*			AG NPP	22.4	Day *et al.* (2013)
41	Mekrijärvi	Finland	CTC	*Pinus sylvestris*			Biomass	2.5	Peltola *et al.* (2002)
42	Oak Ridge	TN, USA	OTC	*Acer rubrum*			Total biomass	14.6	Norby *et al.* (2000)
43			OTC	*Acer saccharum*			Total biomass		
44			FACE	*Liquidambar styraciflua*			Total NPP		Norby *et al.* (2010)
45			OTC	*Quercus alba*		eC_a 500 $\mu mol\ mol^{-1}$	Total biomass		Norby *et al.* (1995)
46			OTC	*Quercus alba*		eC_a 650 $\mu mol\ mol^{-1}$	Total biomass		
47			OTC	*Liriodendron tulipifera*		eC_a Ambient + 150 $\mu mol\ mol^{-1}$	Total biomass		Norby *et al.* (1992)
48			OTC	*Liriodendron tulipifera*		eC_a Ambient + 300 $\mu mol\ mol^{-1}$	Total biomass		
49	Parque Natural Metropolitano	Panama	OTC	Tree communities			Biomass	26.3	Lovelock *et al.* (1998)
50	Phoenix	AR, USA	OTC*	*Pinus eldarica*		eC_a 554 $\mu mol\ mol^{-1}$	Total biomass	21.9	Idso & Kimball (1994)
51			OTC*	*Pinus eldarica*		eC_a 680 $\mu mol\ mol^{-1}$	Total biomass		
52			OTC*	*Pinus eldarica*		eC_a 812 $\mu mol\ mol^{-1}$	Total biomass		
53			OTC	*Citrus aurantium*			Total biomass		Kimball *et al.* (2007)
54	Placerville	NV, USA	OTC	*Pinus ponderosa*	High	eC_a 525 $\mu mol\ mol^{-1}$	Total biomass	14.1	Johnson *et al.* (1997)
55			OTC	*Pinus ponderosa*	Low	eC_a 525 $\mu mol\ mol^{-1}$	Total biomass		
56			OTC	*Pinus ponderosa*	High	eC_a 700 $\mu mol\ mol^{-1}$	Total biomass		
57			OTC	*Pinus ponderosa*	Low	eC_a 700 $\mu mol\ mol^{-1}$	Total biomass		
58			OTC	*Pinus ponderosa*	Medium		Total biomass		
59	Rhinelander	WI, USA	FACE	*Populus tremuloides*			Total NPP	4.3	King *et al.* (2005)
60			FACE	*Populus tremuloides/ Betula papyrifera*			Total NPP		
61	Richmond	Australia	WTC	*Eucalyptus saligna*			Total biomass	17	Barton *et al.* (2012)
62	Sapporo	Japan	FACE	*Larix gmelinii*		Brown forest soil	Total biomass	7.6	Watanabe *et al.* (2013)
63			FACE	*Larix gmelinii*		Volcanic ash soil	Total biomass		
64	Suonenjoki	Finland	OTC	*Betula pendula*		O3 tolerant (Clone 4)	Total biomass	3.8	Riikonen *et al.* (2004)

Table 2 (continued)

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

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 that had single tree in treatment chambers.

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 fertilized vs. unfertilized 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 & 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 (Γ^*) 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 optimized 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 maximize net canopy photosynthesis, resulting in an 'acclimation' of V_{cmax} to growth conditions including temperature and eC_a. This model was parameterized 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 μmol mol^{-1} and 690 μmol mol^{-1}) and two temperatures (16 and 20.5°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, 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), at 0.5 degree spatial resolution and a 3-h 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_2 record, reconstructed land-use change and an estimate of N deposition, as described in Le Quéré *et al.* (2013). The simulations were then continued for the period 1996–2002 (with interannual climate variation but static land cover and N deposition from 1996) either holding C_a constant at the 1996 value or with a step increase to 550 μmol mol^{-1}.

For the analyses of this paper, nonforest 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 savannah. Grid cells with very low NPP (<100 g m^{-2} yr^{-1}) 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 that had predicted NPP <100 g m^{-2} yr^{-1}; 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^{-2} yr^{-1} or where forest cover <25% (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

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 seven 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
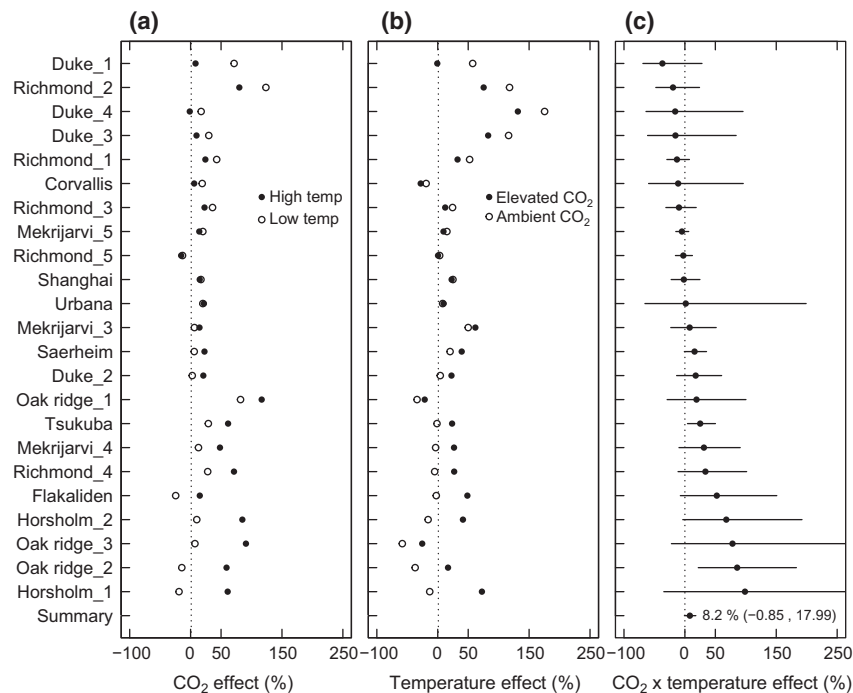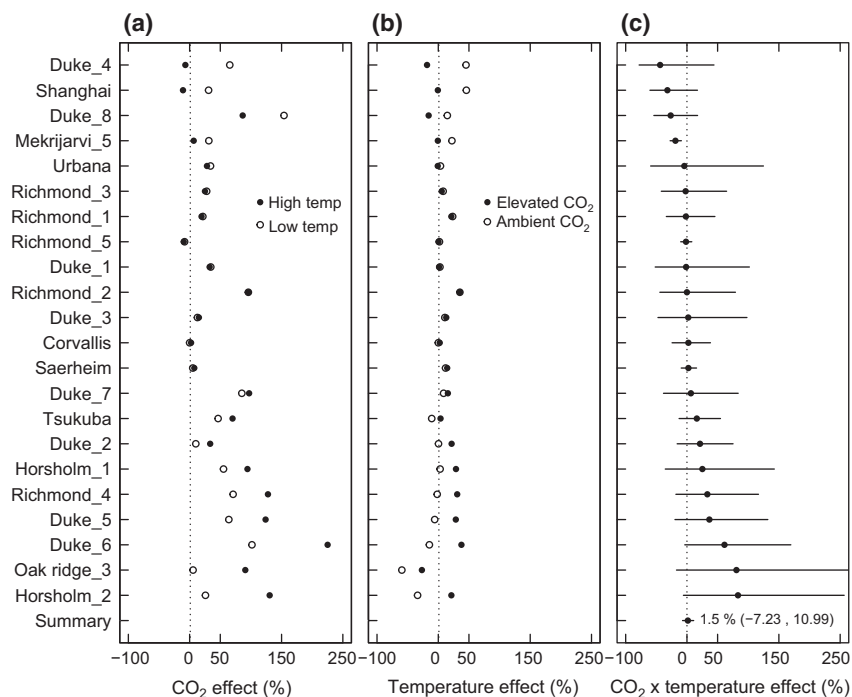
Fig. 1 Forest plots of standardized effect sizes for (a) the eC_a effect at low and high temperature; (b) the temperature effect at aC_a and eC_a; and (c) the $eC_a \times$ temperature interaction term for above-ground plant biomass in $eC_a \times T$ factorial experiments. Each point represents the 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.

(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

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 & 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	% $eC_a \times T$
Meta-analysis			
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)
Models			
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%

Fig. 2 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 below-ground plant biomass in $eC_a \times T$ factorial experiments. Layout as for Fig. 1.

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-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 & 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.
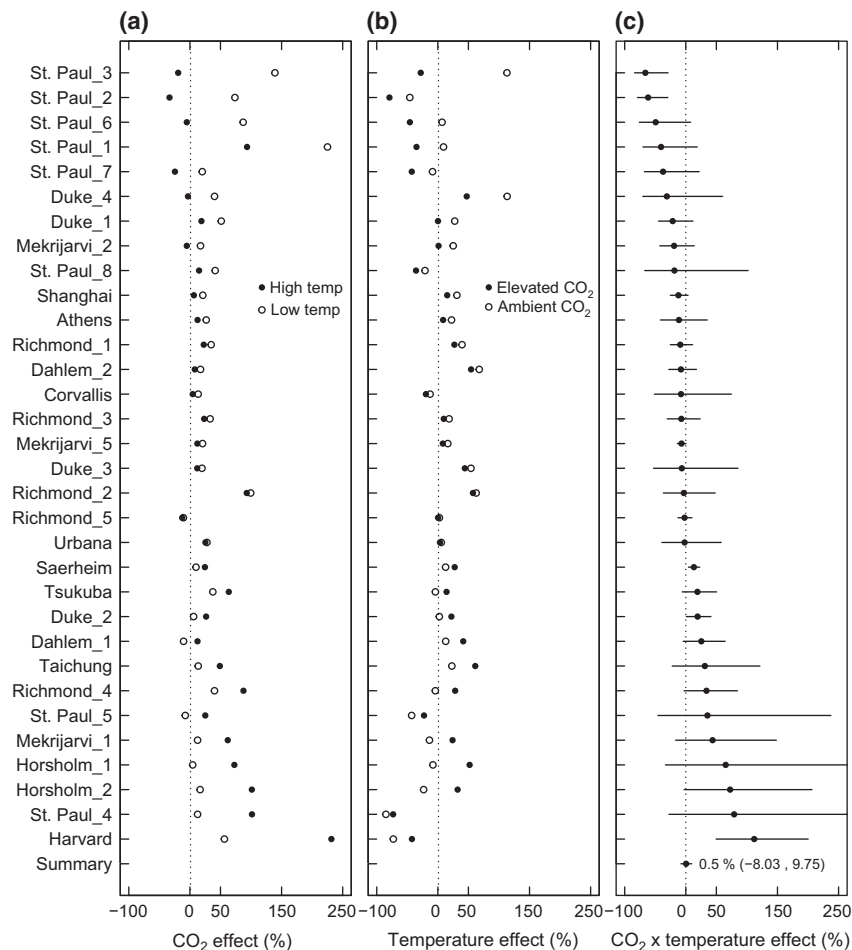
Fig. 3 Forest plots of standardized effect sizes for (a) the eC$_a$ effect at low and high temperature; (b) the temperature effect at aC$_a$ and eC$_a$; and (c) the eC$_a$ × temperature interaction term for total plant biomass in eC$_a$ × T factorial experiments. Layout as for Fig. 1.

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°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, α, can be used in eqn (5) to estimate the average C$_a$ effect size at MAT of 15°C. For an increase in C$_a$ from 360 to 550 μmol mol^{-1}, the esti-

mated average effect size across the whole data set at MAT of 15°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, fertilized and nonfertilized studies or NPP and 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 Fig. 5 is indicative only, as it compares the modelled eC$_a$ response of photosynthesis at a given instantaneous temperature, against measured biomass
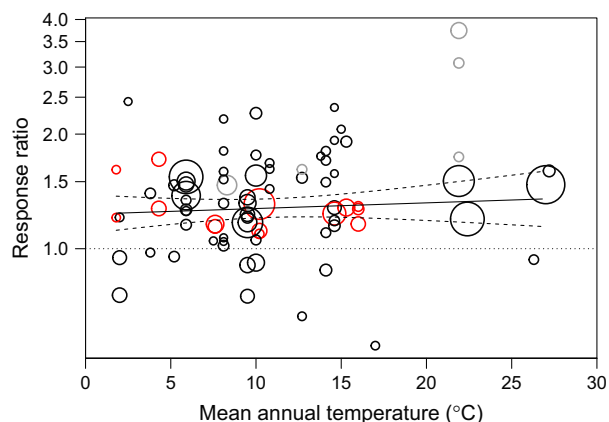
Fig. 4 Meta-regression of the eC_a response ratio in field-based experiments with woody species, against mean annual temperature. The area of each circle is inversely proportional to the variance of the log response ratio estimate and indicates the weighting assigned to each study. The dotted line shows zero or no effect, the solid black line represents the fitted regression line (eqn 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_2 enrichment) experiments. Note that y-axis is log-transformed.
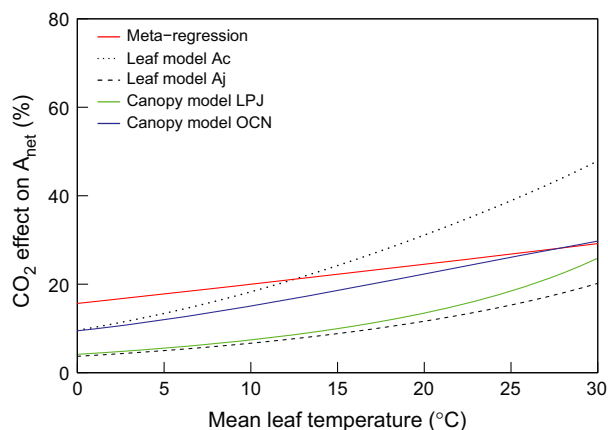

Fig. 5 Meta-regression relationship with C_a increment = 190 μmol mol^{-1}, compared to modelled percentage response of net photosynthesis to the same increase in C_a as a function of mean leaf temperature. Solid red line: meta-regression. Dotted line: modelled response of Rubisco-limiting leaf net photosynthetic 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 & 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).

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 sunlit 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 Fig. 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

Table 4 Results of meta-regression. Eqn (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.

	Coefficient	SE	CI		P
Intercept α	0.4735	0.0615	0.3529	0.5941	<0.0001
Slope β	0.0087	0.0082	−0.0074	0.0249	0.289

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_j-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°C. We fitted linear regressions for the model output for pixels with MAT >0°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°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
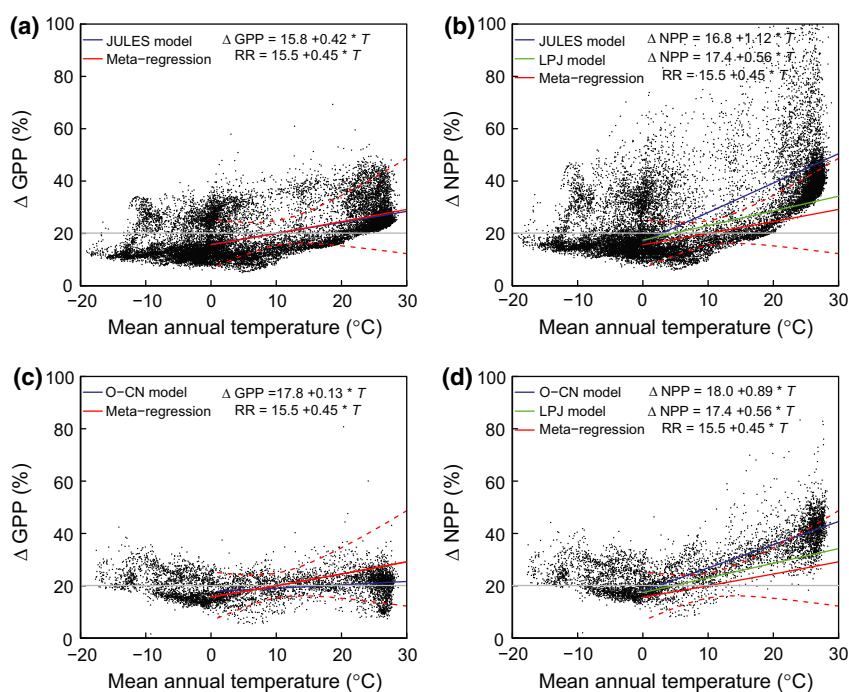
Fig. 6 Comparison of meta-regression relationship with DGVM predictions of CO_2 enhancement of GPP (a, c) and NPP (b, d). Data points are output from the JULES model (a, b) and O-CN model (c, d). Blue lines represent best linear fits to these model outputs for MAT > 0. Solid red line: meta-regression relationship with C_a increment of +190 μmol 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 eqn (5) to data while holding slope $\beta = 0$.

(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$_a$ × 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$_a$ × 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 nonsignificant eC$_a$ × 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 among the factorial eC$_a$ × 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 data sets, 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 artefacts 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 web-FACE 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°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°C and 15°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$_a$ × 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 overridden 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$_a$ × 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.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Data used in meta-analysis of factorial CO₂ × temperature experiments.
Table S2. Data used in meta-regression against mean annual temperature.