

RESEARCH
PAPER



Increased water-use efficiency during the 20th century did not translate into enhanced tree growth

Josep Peñuelas^{1*}, Josep G Canadell² and Romà Ogaya¹

¹Global Ecology Unit CREAM-CEAB-CSIC, Center for Ecological Research and Forestry Applications, Facultat de Ciències, Universitat Autònoma de Barcelona, 08193 Bellaterra, Catalonia, Spain, ²Global Carbon Project, CSIRO Marine and Atmospheric Research, Canberra, Australia

ABSTRACT

Aim The goals of this study are: (1) to determine whether increasing atmospheric CO₂ concentrations and changing climate increased intrinsic water use efficiency (iWUE, as detected by changes in $\Delta^{13}\text{C}$) over the last four decades; and if it did increase iWUE, whether it led to increased tree growth (as measured by tree-ring growth); (2) to assess whether CO₂ responses are biome dependent due to different environmental conditions, including availability of nutrients and water; and (3) to discuss how the findings of this study can better inform assumptions of CO₂ fertilization and climate change effects in biospheric and climate models.

Location A global range of sites covering all major forest biome types.

Methods The analysis encompassed 47 study sites including boreal, wet temperate, mediterranean, semi-arid and tropical biomes for which measurements of tree ring $\Delta^{13}\text{C}$ and growth are available over multiple decades.

Results The iWUE inferred from the $\Delta^{13}\text{C}$ analyses of comparable mature trees increased 20.5% over the last 40 years with no significant differences between biomes. This increase in iWUE did not translate into a significant overall increase in tree growth. Half of the sites showed a positive trend in growth while the other half had a negative or no trend. There were no significant trends within biomes or among biomes.

Main conclusions These results show that despite an increase in atmospheric CO₂ concentrations of over 50 p.p.m. and a 20.5% increase in iWUE during the last 40 years, tree growth has not increased as expected, suggesting that other factors have overridden the potential growth benefits of a CO₂-rich world in many sites. Such factors could include climate change (particularly drought), nutrient limitation and/or physiological long-term acclimation to elevated CO₂. Hence, the rate of biomass carbon sequestration in tropical, arid, mediterranean, wet temperate and boreal ecosystems may not increase with increasing atmospheric CO₂ concentrations as is often implied by biospheric models and short-term elevated CO₂ experiments.

Keywords

Climate change, CO₂ fertilization, $\Delta^{13}\text{C}$, drought, forest, geographical range, tree growth, water use efficiency.

*Correspondence: Josep Peñuelas, Global Ecology Unit CREAM-CEAB-CSIC, Center for Ecological Research and Forestry Applications, Facultat de Ciències, Universitat Autònoma de Barcelona, 08193 Bellaterra, Catalonia, Spain. E-mail: josep.penuelas@uab.cat

INTRODUCTION

Changes in gas exchange and growth are among the primary responses of trees to environmental variations such as current changes in atmospheric CO₂ concentration and climate change (Hughes, 2000; Körner, 2000; Poorter & Navas, 2003; Nowak

et al., 2004). Increased atmospheric CO₂ concentration may stimulate plant growth, indirectly through reduced plant water consumption and hence slower soil moisture depletion, and directly through enhanced photosynthesis (Morgan *et al.*, 2004). Experimental results show that plants are able to increase their water-use efficiency (WUE) as CO₂ levels rise (Morison, 1993;

Overdieck & Forstreuter, 1994; Picon *et al.*, 1996; Morgan *et al.*, 2004). An analysis across multiple sites suggests that the growth response of trees to elevated CO₂ is relatively predictable across a broad range of sites, with an average increase of 23% at a median CO₂ of double the pre-industrial level (Norby *et al.*, 2005). This increased net primary productivity (NPP) in response to increasing atmospheric CO₂ is what is believed to be the dominant driver of the growing terrestrial carbon sink in the recent past and over the next decades as modelled by the state-of-the-art Earth system models (Friedlingstein *et al.*, 2006; Sitch *et al.*, 2008). Under these conditions, the terrestrial sink is expected to remove well above 150 Pg C of anthropogenic emissions over the next 50 years, significantly slowing down climate change. Failure to model a strong CO₂ fertilization effect results in the switch of the terrestrial biosphere from a CO₂ sink into a net CO₂ source because of enhanced heterotrophic respiration under the concomitant effect of warming (Sitch *et al.*, 2008). Of concern is the fact that the NPP response to raising CO₂ is the single most uncertain process in predicting the magnitude of the future carbon–climate feedback (Denman *et al.*, 2007) and therefore the fraction of anthropogenic emissions that will accumulate in the atmosphere causing climate change (Canadell *et al.*, 2007a; Le Quéré *et al.*, 2009).

At present, our state of knowledge about the long-term effects of CO₂ on NPP is largely underpinned by experimental evidence collected from CO₂ enrichment experiments and palaeorecords for which little process attribution is possible. It is acknowledged that there are shortcomings to both approaches and that other complementary techniques are necessary to further constrain the effects of increasing CO₂ on biomass accumulation. For example, most experimental studies have been conducted during short periods of time (relative to the plant's life cycle) in growth chambers or free air CO₂-enrichment (FACE) systems with seedlings or young growing plants. That is unlike the conditions experienced by mature forests growing in a natural environment with a steady-state nutrient cycle and subject to other factors that influence plant growth and therefore the response of NPP to elevated CO₂ concentrations (e.g. Karnosky, 2003; Luo *et al.*, 2004; Norby *et al.*, 2009). Likewise, short experiments (several years) do not make it possible for plants to adjust their physiological response over time to gradually increasing CO₂ concentrations (Long *et al.*, 2004; Domec *et al.*, 2009).

Results from experiments with fully coupled systems in which the natural nutrient cycling governs growth at steady-state leaf area index (LAI) yield rather moderate or no effects of elevated CO₂ on plant biomass production (Oren *et al.*, 2001; Shaw *et al.*, 2002; Körner, 2006; Norby *et al.*, 2009). Experiments with multiple CO₂ × climate/environment interactions (water, temperature, nutrient supply) yield no overall CO₂ effect in grassland systems (Shaw *et al.*, 2002), highlighting the significant influence of co-limiting environmental factors. In fact, it has been suggested that greatest CO₂ fertilization effects may be seen in savanna systems post-fire (Bond & Midgley, 2000; Bond *et al.*, 2003; Hungate *et al.*, 2006), where nutrients are less limiting because of the nutrient input from ashes. From these experi-

ments, at least four main constraints have been observed to limit the CO₂ fertilization effect: (1) element stoichiometry (nutrient imbalance through deficiency of one or more nutrients, often nitrogen and phosphorus); (2) forest tree dynamics (mature trees and closed canopy system are less responsive); (3) possible acclimation to gradually increasing CO₂ concentrations; and (4) secondary effects of CO₂ on water relations and biodiversity (often leading to structural changes less favourable for response to elevated CO₂). Given our limited knowledge of these effects globally, the magnitude of the terrestrial CO₂ fertilization effect remains uncertain.

In this paper, we explore more integrated and long-term records of the effects of elevated CO₂ on the intrinsic water use efficiency (iWUE) and tree growth through the study of tree rings over multiple decades. Variation in iWUE estimated as the ratio between photosynthesis and stomatal conductance is recorded in the variation of the carbon isotope discrimination $\Delta^{13}\text{C}$ of the annual growth rings that are laid down during each growing season (e.g. Duquesnay *et al.*, 1998). Long-term changes in the gas exchange metabolism of established trees will be recorded in the variation of this carbon isotope discrimination $\Delta^{13}\text{C}$, which will give insight into how naturally growing trees respond, or have they responded, to increasing atmospheric CO₂ concentrations. Several studies using $\Delta^{13}\text{C}$ in trees growing in natural conditions all over the world (see Table 1 and Fig. 1 for sites and references) show that trees vary in their responses to the increasing atmospheric CO₂ concentrations in an interactive way with other changing environmental factors. The apparent reason is that the carbon isotope discrimination $\Delta^{13}\text{C}$ in tree rings also responds strongly to many other environmental factors, especially climatic ones such as growing season temperature, relative humidity and precipitation (Switsur & Waterhouse, 1998, and references therein). Climate has changed in the last decades towards warmer conditions (IPCC, 2007). These warmer conditions have strongly affected plant function (Peñuelas & Filella, 2001; Peñuelas & Boada, 2003; Fischlin *et al.*, 2007) and so long-term changes in the gas exchange metabolism of established trees are expected.

Other studies on naturally growing trees have focused on growth rates using tree rings to estimate tree growth over time and its response to environmental changes including increasing atmospheric CO₂ concentration and climate change (see sites and references in Table 1 and Fig. 1). Often these studies show that trees did not significantly increase growth in recent decades despite increasing atmospheric CO₂ concentration. In some cases, trees showed a decline in growth related to warming and drought, for example, at the southernmost distribution edge of temperate trees (Jump *et al.*, 2006, 2007; Peñuelas *et al.*, 2007, 2008; Piovesan *et al.*, 2008; and references and sites depicted in Table 1) and there is even a potential for amplified tree mortality due to drought and heat in forests world-wide (Allen *et al.*, 2010).

In this paper we report a survey and meta-analysis of published studies on carbon isotope composition and growth of tree rings to investigate iWUE and growth changes during a 40-year period of rapid atmospheric and climate change (from the 1960s

Table 1 Changes in $\Delta^{13}\text{C}$, intrinsic water use efficiency (iWUE) and growth (standardized tree ring width, TRW) of mature trees from the early 1960s to the early 2000s at 47 sites of arid, mediterranean, temperate and boreal biomes, as calculated from the reported data in the literature.

Articles	Biome	Species	Site	Latitude (°)	Longitude (°)	$\Delta^{13}\text{C}$ change (%)	iWUE change (%)	Growth change (%)
1	Boreal	<i>Larix cajanderi</i>	Yakutia (Siberia, Russia)	70 N	148 E	3.3	7.7	
2	Boreal	<i>Pinus sylvestris</i>	Laanila (Laponia, Finland)	68 N	27 E	4.3	5.6	
3	Boreal	<i>Picea glauca</i>	Fairbanks (Alaska, USA)	65 N	147 W	-6.8	30.6	-8.0
4	Boreal	<i>Larix cajanderi</i>	Yakutsk (Siberia, Russia)	63 N	139 E	-7.2	32.5	5.0
5	Boreal	<i>Picea glauca</i>	Kluane Lake (Alaska, USA)	61 N	156 W			9.8
6	Wet temperate	<i>Quercus robur</i> , <i>Fagus sylvatica</i> and <i>Pinus sylvestris</i>	Bedfordshire (England, UK)	60 N	0 E	-3.1	22.2	
7	Boreal	<i>Pinus sylvestris</i>	Risdalsheia (Norway)	58 N	8 E			27.8
8	Wet temperate	<i>Quercus robur</i>	Lochwood (Scotland, UK)	55 N	3 W	2.7	36.2	
9	Boreal	<i>Larix sibirica</i>	Irkutsk (Siberia, Russia)	52 N	104 E	-5.2	25.1	
10	Wet temperate	<i>Pinus ponderosa</i> and <i>Pinus sylvestris</i>	Bralitz (Germany)	52 N	14 E	-1.8	19.6	6.3
11	Boreal	<i>Pinus banksiana</i> , <i>Populus tremuloides</i> and <i>Picea mariana</i>	Winnipeg (Manitoba, Canada)	51 N	101 W			11.1
12	Boreal	<i>Picea glauca</i>	Brandon (Manitoba, Canada)	49 N	99 W			12.5
13	Wet temperate	<i>Fagus sylvatica</i>	Lorraine (France)	49 N	6 E	-2.5	20.6	
14	Wet temperate	<i>Abies alba</i>	Jura (France-Switzerland)	47 N	7 E	-3.7	25.9	
15	Wet temperate	<i>Pinus ponderosa</i>	Oregon, USA	45 N	121 W			19.1
16	Mediterranean	<i>Quercus pubescens</i>	Provence (France)	44 N	5 E			-4.2
17	Arid	<i>Juniperus occidentalis</i>	Prineville (Oregon, USA)	44 N	120 W			37.3
18	Wet temperate	<i>Pinus cembra</i>	Briançon (France)	44 N	7 E			5.3
19	Mediterranean	<i>Quercus ilex</i>	Sienna (Italy)	43 N	11 E			0.0
20	Boreal	<i>Picea schrenkiana</i>	Tianshan Mountains (Tibet, China)	43 N	87 E			29.3
21	Mediterranean	<i>Pinus halepensis</i>	Provence (France)	43 N	5 E			2.4
22	Mediterranean	<i>Arbutus unedo</i> , <i>Fraxinus ornus</i> , <i>Quercus cerris</i> , <i>Quercus ilex</i> and <i>Quercus pubescens</i>	Pisa (Italy)	43 N	11 E			-19.8
23	Mediterranean	<i>Quercus ilex</i>	Lajatico (Italy)	43 N	11 E	-2.1	22.2	
24	Wet temperate	<i>Pinus sylvestris</i> , <i>Pinus uncinata</i> and <i>Pinus nigra</i>	Iberian Peninsula	43 N	3 E	-9.7	30.4	2.6
25	Wet temperate	<i>Pinus sylvestris</i>	Catalonia (Spain)	42 N	2 E			0.0
26	Wet temperate	<i>Fagus sylvatica</i>	Apennine Mountains (Italy)	42 N	14 E			-15.8
27	Wet temperate	<i>Fagus sylvatica</i>	Apennine Mountains (Italy)	42 N	12 E			-20.8

Table 1 Continued

Articles	Biome	Species	Site	Latitude (°)	Longitude (°)	$\Delta^{13}\text{C}$ change (%)	iWUE change (%)	Growth change (%)
28 Peñuelas <i>et al.</i> (2008)	Wet temperate	<i>Fagus sylvatica</i>	Montseny Mountains (Catalonia, Spain)	41 N	2 E	-0.4	18.7	0.0
29 Liu <i>et al.</i> (2007)	Arid	<i>Sabina przewalskii</i>	MinLe (Tibet, China)	38 N	100 E	0.0	11.2	15.4
30 Koutavas (2008)	Mediterranean (alpine + seismic disturbance)	<i>Abies cephalonica</i>	Cephalonia (Greece)	38 N	21 E			137.9
31 Liu <i>et al.</i> (2007)	Arid	<i>Sabina przewalskii</i> and <i>Picea crassifolia</i>	Delingha (Tibet, China)	38 N	99 E	-1.3	18.3	
32 Biondi & Fessenden (1999)	Wet temperate	<i>Pinus contorta</i>	Mammoth Mountain (California, USA)	37 N	119 W			0.0
33 Voelker <i>et al.</i> (2006)	Wet temperate	<i>Quercus velutina</i> , <i>Quercus coccinea</i> and <i>Pinus echinata</i>	Current River (Missouri, USA)	37 N	91 W			0.0
34 Tang <i>et al.</i> (1999)	Wet temperate	<i>Pinus longaeva</i>	Sheep Mountain (California, USA)	37 N	118 W	-0.8	17.1	53.7
35 Linares <i>et al.</i> (2009)	Mediterranean	<i>Abies pinsapo</i>	Iberian Peninsula	37 N	5 E			6.2
36 Salzer <i>et al.</i> (2009)	Wet temperate	<i>Pinus longaeva</i>	Sheep Mountain (California, USA)	37 N	118 W			14.4
37 Liu <i>et al.</i> (2008)	Arid	<i>Picea crassifolia</i>	Xining (Tibet, China)	35 N	102 E	1.4		
38 Sano <i>et al.</i> (2009)	Tropical	<i>Fokienia hodginsii</i>	Mu Cang Chai (Vietnam)	22 N	104 E			5.3
39 Borgeankar <i>et al.</i> (2010)	Tropical	<i>Tectona grandis</i>	Western Ghat Mountains (India)	10 N	76 E			7.2
40 Gebrekirstos <i>et al.</i> (2008)	Arid	<i>Acacia tortilis</i> , <i>Acacia seyal</i> , <i>Acacia senegal</i> and <i>Balanites aegyptiaca</i>	Abermossa (Ethiopia)	7 N	38 E			-15.3
41 Hietz <i>et al.</i> (2005)	Tropical	<i>Cedrela odorata</i> and <i>Swietenia macrophylla</i>	Mato Grosso (Brazil)	10 S	59 W	-2.9	23.0	
42 Morales <i>et al.</i> (2001)	Arid	<i>Prosopis ferox</i>	Sapagua (Argentina-Bolivia)	23 S	65 W			-27.3
43 Silva <i>et al.</i> (2009)	Tropical	<i>Araticaria angustifolia</i>	Atlantic Forest (Brazil)	28 S	50 W	-1.5	17.3	-10
44 Heinrich <i>et al.</i> (2009)	Tropical	<i>Toona ciliata</i>	Lamington (Australia)	28 S	153 E			0.0
45 Brookhouse <i>et al.</i> (2008)	Wet temperate	<i>Eucalyptus pauciflora</i>	Mount Perisher (New South Wales, Australia)	36 S	148 E			-15.0
46 Fowler <i>et al.</i> (2008)	Wet temperate	<i>Agathis australis</i> , <i>Halocarpus biformis</i> and <i>Libocedrus bidwillii</i>	New Zealand	36 S	174 E			-3.2
47 Srur <i>et al.</i> (2008)	Boreal	<i>Nothofagus pumilio</i>	El Chaltén (Patagonia, Argentina)	49 S	73 W	1.9	9.9	-8.0

to the 2000s). The analysis includes forests in tropical, arid, mediterranean, wet temperate and boreal regions. The overall goal of this study is to determine whether there was a discernible CO₂ fertilization effect in rates of tree growth during the period from the 1960s to the 2000s as a likely result of increasing atmospheric CO₂ concentrations, or, on the contrary, whether other environmental factors override such an effect. The specific goals are: (1) to determine whether increasing atmospheric CO₂ concentrations and changing climate increased iWUE (as detected by changes in $\Delta^{13}\text{C}$), and whether that led to increased tree growth (as measured by tree-ring growth); (2) to assess whether CO₂ responses are biome dependent due to different environmental conditions including availability of nutrients and water; and (3) to discuss how the findings of this study can better inform assumptions of CO₂ fertilization effects in biospheric and climate models.

MATERIALS AND METHODS

Study sites, sampling trees and analyses

We analysed tree ring isotopic and growth data from 47 sites for which either isotopic data or growth data or both were available in the published literature. The 47 sites included tropical, arid, mediterranean, wet temperate and boreal forests distributed throughout Europe, Asia, Africa, America and Oceania (Table 1, Fig. 1). The bulk of the study sites were not disturbed sites, and the very few disturbed ones did not present any differential response, except for site number 30 (see Table 1) after a strong seismic disturbance.

Only data from control treatments were used in studies where fertilization or other treatments were applied. Preparation and analyses of tree cores is described in the surveyed studies (references in Table 1).

$\Delta^{13}\text{C}$ and calculation of water use efficiency

$\Delta^{13}\text{C}$ (carbon isotopic discrimination) was calculated as: $\Delta^{13}\text{C} = (\delta_{\text{air}} - \delta_{\text{plant}}) / (1000 - \delta_{\text{plant}}) \times 1000$ following Farquhar *et al.* (1982) and using published values for air $\Delta^{13}\text{C}$ from ice core measurements, direct atmospheric measurements and inferred from C₄ plants (McCarroll & Loader, 2004). $\Delta^{13}\text{C}$ is related to C_i (intercellular CO₂ concentration) and C_a (ambient CO₂ concentration) by the following equation:

$$\Delta^{13}\text{C}\text{‰} = a + (b - a)(C_i/C_a) \quad (1)$$

where a is the discrimination against ¹³CO₂ during diffusion of CO₂ through stomata ($a = 4.4\text{‰}$; O'Leary, 1981), b is the discrimination associated with carboxylation ($b = 27\text{‰}$; Farquhar & Richards, 1984).

Fick's law is:

$$A = g_{\text{CO}_2}(C_a - C_i) \quad (2)$$

where A is the net photosynthesis, measured as CO₂ uptake, and g_{CO_2} is the leaf conductance to CO₂. The leaf conductance to water vapour, $g_{\text{H}_2\text{O}}$, is related to g_{CO_2} by:

$$g_{\text{H}_2\text{O}} = 1.6g_{\text{CO}_2} \quad (3)$$

Given equations (1), (2) and (3), $\Delta^{13}\text{C}$ can be related to the ratio $A/g_{\text{H}_2\text{O}}$ (iWUE) (Osmond *et al.*, 1980) by the following equation:

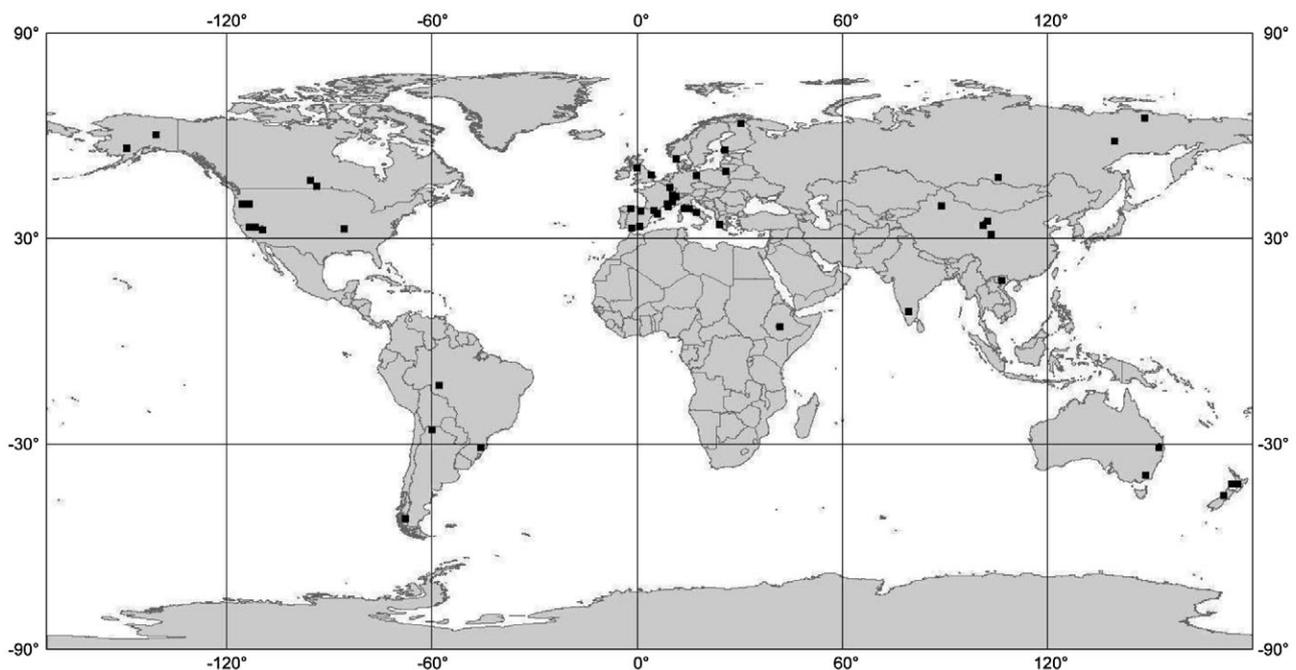


Figure 1 Map of the location of the sites studied (Mollweide projection, central meridian 0°).

$$\Delta^{13}\text{C} = a + (b - a)(1 - 1.6A/C_a g_{\text{H}_2\text{O}}).$$

Standardized tree ring width measurements

Ring width in trees changes with age. Thus, if a change in growth trend is suspected, it may be impossible to investigate it on the basis of changes in ring width alone (Phipps & Whiton, 1988). In a few studies, the conversion of radial increment (ring width) into basal area increment (BAI) overcomes this problem (Phipps & Whiton, 1988; Pedersen, 1998; see details in Jump *et al.*, 2006). We focused only on the variation between levels of growth during the mature phase of growth, marked by the abrupt change in slope (levelling off) after the release phase. We did not consider the data for the first stage in the life of a tree before reaching maturity. In most other studies, the individual tree ring width (TRW) series were standardized to remove non-climatic, tree-geometry and/or age-related trends (Cook & Kairiukstis, 1990). Standardized TRW indices for each tree were calculated as $I = R/G$, where I is the value of the index, R the measured ring width and G is the modelled ring width based on the best-fit exponential growth trend.

Data treatment and statistical analysis

Latitude, longitude, altitude and distance to sea (continentality) were recorded for each studied site. Regression analyses were used to calculate the slope (annual change) in the temporal trends of $\Delta^{13}\text{C}$, iWUE and standardized TRW of mature trees in each study over the last 40 years. A meta-analysis comparing $\Delta^{13}\text{C}$, iWUE and growth in the 1960s and in the 2000s was conducted using METAWIN 2.0 (Sinauer Associates, Inc., Sunderland, MA, USA) with the data for which standard deviation (SD) of the mean was provided (only 11 sites). General linear models with $\Delta^{13}\text{C}$, iWUE and growth as dependent variables and biome, distance to the sea, altitude, latitude and forest age as explanatory variables were conducted for all sites with available data. Generalized linear models (binomial family) were also constructed with growth (increased or not) as the dependent binomial variable and the same independent variables as

explanatory variables. Dependent *t*-test comparisons between growth, $\Delta^{13}\text{C}$ and iWUE in the 1960s and 2000s were conducted, as well as ANOVA analyses by biomes. All these statistical calculations and analyses were conducted using the STATISTICA software package (StatSoft, Inc. Tulsa, OK, USA).

RESULTS

The meta-analyses conducted with the results from the 12 sites for which SD was provided showed no significant change between the 1960s and 2000s in $\Delta^{13}\text{C}$ and growth rates, both for the entire dataset and by biome. However, iWUE, significantly increased by 20% (data not shown).

When using all sites in the meta-analyses (both with and without SD), the results were similar with no significant change in the isotopic discrimination ($\Delta^{13}\text{C}$) between the 1960s and 2000s. $\Delta^{13}\text{C}$ remained at *c.* 16‰ throughout the 40-year period (Fig. 2). The iWUE significantly increased from 90 to *c.* 109 mmol mol^{-1} , i.e. 20.5% (Fig. 2). The increase in growth for the overall set of studies was not statistically significant (Fig. 2). There was an increase in growth in 18 of the 35 studies with growth data. Another 6 sites had similar growth and the other 11 sites had smaller growth in the 2000s than in the 1960s. Thus the estimated iWUE of mature trees increased with atmospheric CO_2 concentrations but it did not translate into significantly more overall growth (Fig. 2).

No significant differences were found in any of the three variables studied ($\Delta^{13}\text{C}$, iWUE and growth) among the five biomes studied (tropical, arid, mediterranean, wet temperate and boreal; Fig. 3) nor in the relationships with latitude, altitude, tree age or continentality (data not shown). There was a mediterranean site with a very large increase of growth from 1960 to 2000 (137.9%, Table 1 study number 30) that was not used for the calculation of the mean growth in mediterranean sites as *Abies cephalonica* is more of a wet mountain tree and the site experienced the influence of a strong seismic disturbance; however, even if we considered that species and site, the differences from the other biomes were still not significant.

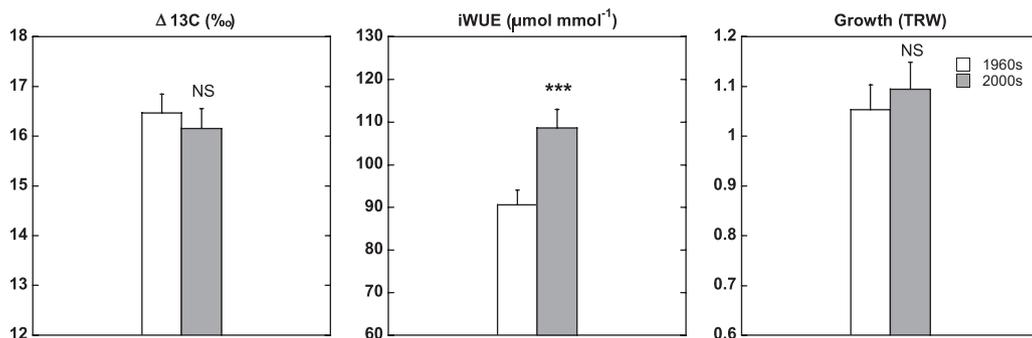


Figure 2 Mean overall values of $\Delta^{13}\text{C}$, intrinsic water use efficiency (iWUE) and growth (standardized tree ring width, TRW) of mature trees in the early 1960s and in the early 2000s. Three asterisks indicate significantly different values between sites ($P < 0.001$; dependent *t*-test analysis), and NS indicates no significant difference in values between sites. Error bars indicate SE.

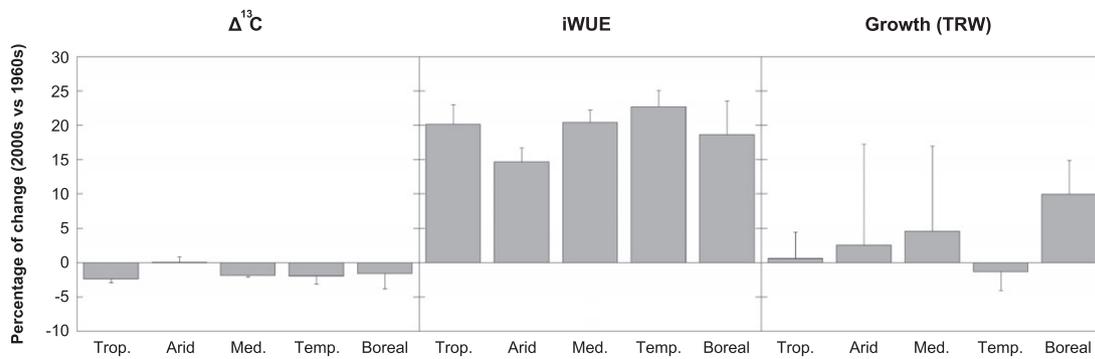


Figure 3 Mean changes in $\Delta^{13}\text{C}$, intrinsic water use efficiency (iWUE) and growth (standardized tree ring width, TRW) of mature trees from the early 1960s to the early 2000s in different biomes. No significant differences were found in any of the three variables studied ($\Delta^{13}\text{C}$, iWUE and growth) among the four biomes studied (tropical, arid, mediterranean, wet temperate and boreal). Error bars indicate SE.

DISCUSSION

The iWUE increased by an average of 20.5% over the second half of the 20th century as expected from the fast build-up of atmospheric CO_2 . The magnitude of change is in agreement with previous reports that found an increase of iWUE during the same period by using historical records in both leaves and tree rings (Peñuelas & Matamala, 1990; Peñuelas & Azcón-Bieto, 1992; Woodward, 1993; Ehleringer & Cerling, 1995; Feng & Epstein, 1995; Bert *et al.*, 1997; Duquesnay *et al.*, 1998; Feng, 1999; Peñuelas *et al.*, 2008). This increase in iWUE is linked to the sharp increase in internal CO_2 concentration because of the rise of atmospheric CO_2 concentration. However, despite higher iWUE, the expected increase in photosynthetic rates in response to rising atmospheric CO_2 (Long *et al.*, 2004) and the warming-induced lengthening of the growing season for many species (Peñuelas & Filella, 2001; Peñuelas *et al.*, 2002), there was no overall significant increase of plant growth over the study period. Thus, the CO_2 fertilization effect was either not realized or was not big enough to overcome the concomitant negative effects of climate change, e.g. drought, nutrient scarcity or photosynthetic acclimation to elevated CO_2 on plant growth.

An important part of the increase in iWUE results from the effect of the relative increase in C_a over the past 40 years (50 p.p.m./335 p.p.m.) which should increase iWUE by *c.* 15%, i.e. only a little bit less than the 20.5% average increase found here. Thus C_i/C_a would not have changed much over 40 years in trees as a whole. A near-constancy of C_i/C_a implies that if stomatal conductance decreases, then so does leaf photosynthetic capacity. The small additional increment in iWUE can result from increasing net photosynthesis (*A*), decreasing leaf conductance (g_w), or a combination of these factors. It is even possible that a decrease in g_w in response to rising atmospheric CO_2 concentration or/and increasing temperatures, and hence water stress, could cause the increase in iWUE with no associated change, or even a decline, in *A*, although smaller than the decrease in g_w . Plants growing in CO_2 -enriched atmospheres with suboptimal resources acclimate to the greater CO_2 availability by lowering photosynthetic capacity below the expected for a given CO_2 concentration (Long *et al.*, 2004). While instan-

taneous CO_2 responses can be well described by the photosynthesis model of Farquhar *et al.* (1980), photosynthetic acclimation to elevated CO_2 is much more complex to simulate and requires consideration of additional feedbacks such as water or nutrient availability (Gutschick, 2007, for a review). Increasing temperatures could also produce higher respiration rates, which would lower NPP and thus TRW and BAI, and have a negative impact on the assimilation capacity of the leaves. Most studies on trees indicate, however, that their respiration substantially acclimates to temperature changes (Atkin *et al.*, 2005), which would not explain the iWUE/growth discrepancy.

Regardless of the ultimate causation of the observed response, the data show that an increase in iWUE does not necessarily translate into increased plant growth. Thus, we show that a number of forests in diverse biomes have already saturated in response to further increases in atmospheric CO_2 given other concurrent growth-limiting factors. This finding is consistent and supported by many experimental studies (see reviews by Körner *et al.*, 2007, and Oren *et al.*, 2001; see also Canadell *et al.*, 2007b; Norby *et al.*, 2009). Nutrient limitations (mostly N and P) prevent the full expression of the CO_2 fertilization effect on plant growth and seem to drive the saturation of the plant CO_2 response (Luo *et al.*, 2004; Edwards *et al.*, 2005; Reich *et al.*, 2006; Norby *et al.*, 2009), and may thus explain the lack of growth responses to increased CO_2 at some of the sites.

The increased iWUE often results in a slower rate of depletion of soil moisture, favouring plants in arid ecosystems. CO_2 -induced changes in soil moisture are suggested to account for a significant component of the CO_2 fertilization effect such as that found in woody plants in a steppe grassland (Morgan *et al.*, 2007). However, in our study we found no significant differences in responses between arid and wet ecosystems. Other factors limiting plant growth, such as nutrient limitations or acclimation, may have precluded such responses.

Whichever mechanism or mechanisms underlying this response, the lack of expected growth does not support some of the assumptions and model outputs which predict a continuing rise in terrestrial carbon storage as a result of a strong CO_2 effect alone over the next half a century (Melillo *et al.*, 1996; Cao & Woodward, 1998; Friedlingstein *et al.*, 2006; Leuzinger &

Körner, 2007; Sitch *et al.*, 2008). This lack of growth does not support either the expected growth response following the increase of biologically reactive nitrogen in the atmosphere over the past century, and especially in recent decades as a consequence of the use of fossil fuels and fertilizers (Magnani *et al.*, 2007; Janssens *et al.*, 2010), and is not easily reconciled with results reporting recent biomass accumulation greatly exceeded the expected growth caused by natural recovery from disturbance (McMahon *et al.*, 2010). These uncertain and apparently contradictory results warrant further study to get a better understanding of the changes in growth rates in forest systems, which influence current and future states of the atmosphere and biosphere.

If the expectation of a significant CO₂ fertilization effect is not realized, future terrestrial carbon storage will be overestimated, leading to faster accumulation of atmospheric CO₂ and associated climate change. It is thus critical that models are able to reproduce past long-term trends in ecosystem dynamics in addition to gain knowledge from short-term experiments.

Lack of a detectable net effect of the CO₂ fertilization effect on tree growth in our analysis does not negate the existence of a terrestrial net carbon sink and its possible growth in the future. In fact, there are now multiple lines of independent evidence that confirm the existence of a terrestrial net sink and its growth over the last decades (Canadell *et al.*, 2007a; Le Quéré *et al.*, 2009). Our findings suggest that the drivers of the net extratropical terrestrial sink (largely in the Northern Hemisphere) may be dominated by processes other than the CO₂ fertilization effect such as forest regrowth after land abandonment, woody encroachment and thickening. A key consequence of this set of drivers is that they are the legacy of past land-use changes and that their effects on carbon sequestration will diminish as forest regrowth reaches maturity and no additional land is abandoned. Our results also point out the lack of knowledge of the CO₂ fertilization effect in tropical systems thought to play an equal or even larger role in terrestrial CO₂ uptake (Stephens *et al.*, 2007). To date, no elevated CO₂ experiments have been undertaken in tropical forest ecosystems.

CONCLUSIONS

Changes in carbon isotope composition of tree rings show increasing iWUE in the last decades, implying that the ratio between assimilation rates and stomatal conductance has increased. The results emphasize that the global rise of atmospheric CO₂ and changing climate are already influencing the gas exchange of forests and might be decreasing plant water use. However, an increase in iWUE alone is not sufficient to produce increased plant growth. Other factors such as increasing temperature, drought, nutrient limitation and/or plant acclimation may preclude such growth increase. The lack of an increase in tree growth with increasing atmospheric CO₂ suggests that most current terrestrial vegetation models could be overestimating the magnitude of plausible C sequestration in a future CO₂-rich world. The trends of the dendroecological data reviewed here suggest the importance of multiple interactive effects in deter-

mining the net effect on plant growth and that caution is necessary when drawing conclusions from single-factorial experiments, particularly when estimating the future potential of terrestrial carbon sequestration.

ACKNOWLEDGEMENTS

This research was supported by Spanish Government CGL2006-04025/BOS and Consolider-Ingenio Montes CSD2008-00040 grants, and a Catalan Government SGR2009-458 grant. The work is a contribution to the research agenda of the Global Carbon Project of the Earth System Science Partnership. J.G.C. acknowledges the support of the Australian Climate Change Science Program.

REFERENCES

- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., González, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A. & Cobb, N. (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, **259**, 660–684.
- Andreu, L., Planells, O., Gutiérrez, E., Helle, G. & Schleser, G.H. (2008) Climatic significance of tree-ring width and $\delta^{13}\text{C}$ in a Spanish pine forest network. *Tellus*, **60**, 771–781.
- Atkin, O.K., Bruhn, D., Hurry, V.M. & Tjoelker, M.G. (2005) The hot and the cold: unravelling the variable response of plant respiration to temperature. *Functional Plant Biology*, **32**, 87–105.
- Barber, V.A., Juday, G.P. & Finney, B.P. (2000) Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. *Nature*, **405**, 668–673.
- Bert, G.D., Leavitt, S.W. & Dupouey, J.L. (1997) Variations of wood $\delta^{13}\text{C}$ and water-use efficiency of *Abies alba* (Mill.) during the last century. *Ecology*, **78**, 1588–1596.
- Biondi, F. & Fessenden, J.E. (1999) Response of lodgepole pine growth to CO₂ degassing at Mammoth Mountain, California. *Ecology*, **80**, 2420–2426.
- Bond, W.J. & Midgley, G.F. (2000) A proposed CO₂-controlled mechanism of woody plant invasion in grasslands and savannas. *Global Change Biology*, **6**, 865–869.
- Bond, W.J., Midgley, G.F. & Woodward, F.I. (2003) The importance of low atmospheric CO₂ and fire in promoting the spread of grasslands and savannas. *Global Change Biology*, **9**, 973–982.
- Boonstra, R., Desantis, L., Krebs, C.J. & Hik, D.S. (2008) Climate and nutrient influences on the growth of white spruce trees in the boreal forests of the Yukon. *Climate Research*, **36**, 123–130.
- Borgaonkar, H.P., Sikder, A.B., Ram, S. & Pant, G.B. (2010) El Niño and related monsoon drought signals in 523-year-long ring width records of teak (*Tectona grandis* L.f.) trees from south India. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **285**, 74–84.

- Brookhouse, M., Lindsay, J. & Brack, C. (2008) The potential of tree rings in *Eucalyptus pauciflora* for climatological and hydrological reconstruction. *Geophysical Research*, **46**, 421–434.
- Canadell, J.G., Le Quéré, C., Raupach, M.R., Field, C.B., Buitenhuis, E.T., Ciais, P., Conway, T.J., Gillet, N.P., Houghton, R.A. & Marland, G. (2007a) Contributions to accelerating atmospheric CO₂ growth from economic activity, carbon intensity, and efficiency of natural sinks. *Proceedings of the National Academy of Sciences USA*, **104**, 18866–18870.
- Canadell, J.G., Pataki, D., Gifford, R., Houghton, R.A., Luo, Y., Raupach, M.R., Smith, P. & Steffen, W. (2007b) Saturation of the terrestrial carbon sink. *Terrestrial ecosystems in a changing world* (ed. by J.G. Canadell, D. Pataki and L. Pitelka), pp. 59–78. Springer-Verlag, Berlin Heidelberg.
- Cao, M. & Woodward, F.I. (1998) Dynamic responses of terrestrial ecosystem carbon cycling to global climate change. *Nature*, **393**, 249–252.
- Cook, E.R. & Kairiukstis, L.A. (1990) *Methods of dendrochronology applications in the environmental sciences*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Denman, K.L., Chidthaisong, G.B.A., Ciais, P. *et al.* (2007) Couplings between changes in the climate system and biogeochemistry. *Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (ed. by S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor, H.L. Miller *et al.*), pp. 499–587. Cambridge University Press, Cambridge.
- Domec, J.C., Palmroth, S., Ward, E., Maier, C.A., Thérézien, M. & Oren, R. (2009) Acclimation of leaf hydraulic conductance and stomatal conductance of *Pinus taeda* (loblolly pine) to long-term growth in elevated CO₂ (free-air CO₂ enrichment) and N-fertilization. *Plant Cell and Environment*, **32**, 1500–1512.
- Duquesnay, A., Breda, N., Stievenard, M. & Dupouey, J.L. (1998) Changes of tree-ring delta C-13 and water use efficiency of beech (*Fagus sylvatica* L.) in north-eastern France during the past century. *Plant Cell and Environment*, **21**, 565–572.
- Edwards, E.J., McCaffery, S. & Evans, J.R. (2005) Phosphorus status determines biomass response to elevated CO₂ in a legume: C₄ grass community. *Global Change Biology*, **11**, 1968–1981.
- Ehleringer, J.R. & Cerling, T.E. (1995) Atmospheric CO₂ and the ratio of intercellular to ambient CO₂ concentrations in plants. *Tree Physiology*, **15**, 105–111.
- Farquhar, G.D. & Richards, R.A. (1984) Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes. *Australian Journal of Plant Physiology*, **11**, 539–552.
- Farquhar, G.D., Caemmerer, S. & Berry, J.A. (1980) A biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ species. *Planta*, **149**, 78–90.
- Farquhar, G.D., O'Leary, M.H. & Berry, J.A. (1982) On the relationship between carbon isotope discrimination and intercellular carbon dioxide concentration in leaves. *Australian Journal of Plant Physiology*, **9**, 121–137.
- Feng, X. (1999) Trends in intrinsic water-use efficiency of natural trees for the past 100–200 years: a response to atmospheric CO₂ concentrations. *Geochimica et Cosmochimica Acta*, **63**, 1891–1903.
- Feng, X. & Epstein, S. (1995) Carbon isotopes of trees from arid environments and implications for reconstructing atmospheric CO₂ concentration. *Geochimica et Cosmochimica Acta*, **59**, 2599–2608.
- Fischlin, A., Midgley, G.F., Price, J.T., Leemans, R., Gopal, B., Turley, C., Rounsevell, M.D.A., Dube, O.P., Tarazona, J. & Velichko, A.A. (2007) Ecosystems, their properties, goods, and services. *Climate change 2007: impacts, adaptation and vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (ed. by M.L. Parry, O.F. Canziani, J.P. Palutikof, P.J. van der Linden and C.E. Hanson), pp. 211–272. Cambridge University Press, Cambridge.
- Fowler, A.M., Palmer, J. & Fenwick, P. (2008) An assessment of the potential for centennial-scale reconstruction of atmospheric circulation from selected New Zealand tree-ring chronologies. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **265**, 238–254.
- Friedlingstein, P., Cox, P., Betts, R. *et al.* (2006) Climate–carbon cycle feedback analysis. Results from the C4MIP model intercomparison. *Journal of Climate*, **19**, 3337–3353.
- Gagen, M., McCarroll, D., Robertson, I., Loader, N.J. & Jalkanen, R. (2008) Do tree ring δ¹³C series from *Pinus sylvestris* in northern Fennoscandia contain long-term non-climatic trends? *Chemical Geology*, **252**, 42–51.
- Gebrekirstos, A., Mitlöhner, R., Teketay, D. & Worbes, M. (2008) Climate-growth relationships of the dominant tree species from semi-arid savanna woodland in Ethiopia. *Trees*, **22**, 631–641.
- Girardin, M.P., Raulier, F., Bernier, P.Y. & Tardif, J.C. (2008) Response of tree growth to a changing climate in boreal central Canada: a comparison of empirical, process-based, and hybrid modelling approaches. *Ecological Modelling*, **213**, 209–228.
- Gutschick, V.P. (2007) Plant acclimation to elevated CO₂ – from simple regularities to biogeographic chaos. *Ecological Modelling*, **200**, 433–451.
- Hättenschwiler, S., Miglietta, F., Raschi, A. & Körner, C. (1997) Thirty years of *in situ* tree growth under elevated CO₂: a model for future forest responses? *Global Change Biology*, **3**, 463–471.
- Heinrich, I., Weidner, K., Helle, G., Vos, H., Lindsay, J. & Banks, J.C.G. (2009) Interdecadal modulation of the relationship between ENSO, IPO and precipitation: insights from tree rings in Australia. *Climate Dynamics*, **33**, 63–73.
- Hietz, P., Wanek, W. & Dünisch, O. (2005) Long-term trends in cellulose δ¹³C and water-use efficiency of tropical *Cedrela* and *Swietenia* from Brazil. *Tree Physiology*, **25**, 745–752.
- Hughes, L. (2000) Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution*, **15**, 56–61.

- Hungate, B.A., Johnson, D.W., Dijkstra, P., Hymus, G., Stilling, P., Megonigal, J.P., Pagel, A.L., Moan, J.L., Day, F., Li, J.H., Hinkle, C.R. & Drake, B.G. (2006) Nitrogen cycling during seven years of atmospheric CO₂ enrichment in a scrub oak woodland. *Ecology*, **87**, 26–40.
- IPCC (2007) *Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor, H.L. Miller *et al.* (eds) Cambridge University Press, Cambridge, UK.
- Ivlev, A.A. & Voronin, V.I. (2007) The mechanism of carbon isotope fractionation in photosynthesis and carbon dioxide component of the greenhouse effect. *Biology Bulletin*, **34**, 603–609.
- Janssens, I.A., Dieleman, W., Luysaert, S. *et al.* (2010) Reduction of forest soil respiration in response to nitrogen deposition. *Nature Geoscience*, **3**, 315–322.
- Jump, A., Hunt, J. & Peñuelas, J. (2006) Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. *Global Change Biology*, **12**, 2163–2174.
- Jump, A., Hunt, J. & Peñuelas, J. (2007) Climate relationships of growth and establishment across the altitudinal range of *Fagus sylvatica* in the Montseny Mountains, NE Spain. *Ecoscience*, **14**, 507–518.
- Karnosky, D.F. (2003) Impacts of elevated CO₂ on forest trees and forest ecosystems: knowledge gaps. *Environmental International*, **29**, 161–169.
- Kirilyanov, A.V., Treydte, K.S., Nikolaev, A., Helle, G. & Schleser, G.H. (2008) Climate signals in tree-ring width, density and δ¹³C from larches in eastern Siberia (Russia). *Chemical Geology*, **252**, 31–41.
- Knapp, P.A., Soule, P.T. & Grissino-Mayer, H.D. (2001) Detecting potential regional effects of increased atmospheric CO₂ on growth rates of western juniper. *Global Change Biology*, **7**, 903–917.
- Körner, C. (2000) Biosphere responses to CO₂ enrichment. *Ecological Applications*, **10**, 1590–1619.
- Körner, C. (2006) Plant CO₂ responses: an issue of definition, time and resource supply. *New Phytologist*, **172**, 393–411.
- Körner, C., Morgan, J. & Norby, R. (2007) CO₂ fertilization: when, where, how much? *Terrestrial ecosystems in a changing world*, (ed. by J. Canadell, D. Pataki and L. Pitelka), pp. 9–21. Springer-Verlag, Berlin.
- Koutavas, A. (2008) Late 20th century growth acceleration in Greek firs (*Abies cephalonica*) from Cephalonia Island, Greece: a CO₂ fertilization effect? *Dendrochronologia*, **26**, 13–19.
- Le Quéré, C., Raupach, M.R., Canadell, J.G. *et al.* (2009) Trends in the sources and sinks of carbon dioxide. *Nature Geoscience*, **2**, 831–836.
- Leuzinger, S. & Körner, C. (2007) Water savings in mature deciduous forest trees under elevated CO₂. *Global Change Biology*, **13**, 2498–2508.
- Linares, J.C., Delgado-Huertas, A., Camarero, J.J., Merino, J. & Carreira, J.A. (2009) Competition and drought limit the response of water-use efficiency to rising atmospheric carbon dioxide in the Mediterranean fir *Abies pinsapo*. *Oecologia*, **161**, 611–624.
- Liu, X., Shao, X., Liang, E., Zhao, L., Chen, T., Qin, D. & Ren, J. (2007) Species-dependent responses of juniper and spruce to increasing CO₂ concentration and to climate in semi-arid and arid areas of northwestern China. *Plant Ecology*, **193**, 195–209.
- Liu, X., Shao, X., Wang, L., Liang, E., Qin, D. & Ren, J. (2008) Response and dendroclimatic implications of δ¹³C in tree rings to increasing drought on the northeastern Tibetan Plateau. *Journal of Geophysical Research*, **113**, G03015, doi: 10.1029/2007JG000610.
- Loader, N.J., Santillo, P.M., Woodman-Ralph, J.P., Rolfe, J.E., Hall, M.A., Gagen, M., Robertson, I., Wilson, R., Froyd, R. & McCarroll, D. (2008) Multiple stable isotopes from oak trees in southwestern Scotland and the potential for stable isotope dendroclimatology in maritime climatic regions. *Chemical Geology*, **252**, 62–71.
- Long, S.P., Ainsworth, E.A., Rogers, A. & Ort, D.R. (2004) Rising atmospheric carbon dioxide: plants FACE the future. *Annual Review of Plant Biology*, **55**, 591–628.
- Luo, Y., Currie, W.S., Dukes, J.S., Finzi, A., Hartwig, U., Hungate, B., McMurtrie, R.E., Oren, R., Parton, W.J., Pataki, D.E., Shaw, M.R., Zak, D.R. & Field, C.B. (2004) Progressive nitrogen limitation of ecosystem responses to rising atmospheric carbon dioxide. *Bioscience*, **54**, 731–739.
- McCarroll, D. & Loader, N.J. (2004) Stable isotopes in tree rings. *Quaternary Science Reviews*, **23**, 771–801.
- McMahon, S.M., Parker, G.G. & Miller, D.R. (2010) Evidence for a recent increase in forest growth. *Proceedings of the National Academy of Sciences USA*, doi: 10.1073/pnas.0912376107.
- Magnani, F., Mencuccini, M., Borghetti, M. *et al.* (2007) The human footprint in the carbon cycle of temperate and boreal forests. *Nature*, **447**, 848–850.
- Martínez-Vilalta, J., López, B.C., Adell, N., Badiella, L. & Ninyerola, M. (2008) Twentieth century increase of Scots pine radial growth in NE Spain shows strong climate interactions. *Global Change Biology*, **14**, 2868–2881.
- Melillo, J.M., Prentice, I.C., Farquhar, G.D., Schulze, E.D. & Sala, O.E. (1996) Terrestrial biotic responses to environmental change and feedbacks to climate. *Climate change 1995* (ed. by J.T. Houghton, L.G. Meira Filho, B.A. Callander, N. Harris, A. Kattengerg and K. Maskell), pp. 445–481. Cambridge University Press, Cambridge.
- Morales, M.S., Villalba, R., Grau, H.R., Villagra, P.E., Boninseña, J.A., Ripalta, A. & Paolini, L. (2001) Potencialidad de *Prosopis ferox* Griseb (Leguminosae, subfamilia: Mimosoidae) para estudios dendrocronológicos en desiertos subtropicales de alta montaña. *Revista Chilena de Historia Natural*, **74**, 889.
- Morgan, J.A., Pataki, D.E., Körner, C., Clark, H., Del Grosso, S.J., Grünzweig, J.M., Knapp, A.K., Mosier, A.R., Newton, P.C.D., Niklaus, P.A., Nippert, J.B., Nowak, R.S., Parton, W.J., Polley, H.W. & Shaw, M.R. (2004) Water relations in grassland and desert ecosystems exposed to elevated atmospheric CO₂. *Oecologia*, **140**, 11–25.

- Morgan, J.A., Milchunas, D.G., Lecaïn, D.R., West, M. & Mosier, A.R. (2007) Carbon dioxide enrichment alters plant community structure and accelerates shrub growth in the shortgrass steppe. *Proceedings of the National Academy of Sciences USA*, **104**, 14724–14729.
- Morison, J.I.L. (1993) Response of plants to CO₂ under water limited conditions. *Vegetatio*, **104**, 193–209.
- Norby, R.J., DeLucia, E.H., Gielen, B., Calfapietra, C., Giardina, C.P., King, J.S., Ledford, J., McCarthy, H.R., Moore, D.J.P., Ceulemans, R., De Angelis, P., Finzi, A.C., Karnosky, D.F., Kubiske, M.E., Lukac, M., Pregitzer, K.S., Scarascia-Mugnozza, G.E., Schlesinger, W.H. & Oren, O. (2005) Forest response to elevated CO₂ is conserved across a broad range of productivity. *Proceedings of the National Academy of Sciences USA*, **102**, 18052–18056.
- Norby, R.J., Warren, J.M., Iversen, C.M., Garten, C.T. Jr, Medlyn, B.E. & McMurtrie, R.E. (2009) CO₂ enhancement of forest productivity constrained by limited nitrogen availability. *Nature Precedings*. Available at: <http://precedings.nature.com/documents/3747/version/1/files/npre20093747-1.pdf> (accessed 20 April 2010).
- Nowak, R.S., Ellsworth, D.S. & Smith, S.D. (2004) Functional responses of plants to elevated atmospheric CO₂ – do photosynthetic and productivity data from FACE experiments support early predictions? *New Phytologist*, **162**, 253–280.
- O’Leary, M.H. (1981) Theoretical basis of carbon isotope fractionation in plants. *Phytochemistry*, **20**, 553–567.
- Oren, R., Ellsworth, D.S., Johnsen, K.H., Phillips, N., Ewers, B.E., Maier, C., Schafer, K.V.R., McCarthy, H., Hendrey, G., McNulty, S.G. & Katul, G.G. (2001) Soil fertility limits carbon sequestration by forest ecosystems in a CO₂-enriched atmosphere. *Nature*, **411**, 469–472.
- Osmond, C.B., Björkman, O. & Anderson, D.J. (1980) *Physiological processes in plant ecology. Toward a synthesis with Atriplex*. Springer-Verlag, New York.
- Overdieck, D. & Forstreuter, M. (1994) Evapotranspiration of beech stands and transpiration of beech leaves subject to atmospheric CO₂ enrichment. *Tree Physiology*, **14**, 997–1003.
- Pedersen, B.S. (1998) The role of stress in the mortality of mid-western oaks as indicated by growth prior to death. *Ecology*, **79**, 79–93.
- Peñuelas, J. & Azcón-Bieto, J. (1992) Changes in leaf $\Delta^{13}\text{C}$ of herbarium plant species during the last 3 centuries of CO₂ increase. *Plant Cell and Environment*, **15**, 485–489.
- Peñuelas, J. & Boada, M. (2003) A global change-induced biome shift in the Montseny Mountains (NE Spain). *Global Change Biology*, **9**, 131–140.
- Peñuelas, J. & Filella, I. (2001) Phenology: responses to a warming world. *Science*, **294**, 793–795.
- Peñuelas, J. & Matamala, R. (1990) Changes in N and S leaf content, stomatal density and specific leaf area of 14 plant species during the last three centuries of CO₂ increase. *Journal of Experimental Botany*, **41**, 1119–1124.
- Peñuelas, J., Filella, I. & Comas, P. (2002) Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. *Global Change Biology*, **8**, 531–544.
- Peñuelas, J., Ogaya, R., Boada, M. & Jump, A. (2007) Migration, invasion and decline: changes in recruitment and forest structure in a warming-linked biome shift in Catalonia (NE Spain). *Ecography*, **30**, 830–838.
- Peñuelas, J., Hunt, J.M., Ogaya, R. & Jump, A. (2008) Twentieth century changes of tree-ring $\delta^{13}\text{C}$ at the southern range-edge of *Fagus sylvatica*: increasing water-use efficiency does not avoid the growth decline induced by warming at low altitudes. *Global Change Biology*, **14**, 1076–1088.
- Phipps, R.L. & Whiton, J.C. (1988) Decline in long-term growth trends of white oak. *Canadian Journal of Forest Research*, **18**, 24–32.
- Picon, C., Guehl, J.M. & Aussenac, G. (1996) Growth dynamics, transpiration and water-use efficiency in *Quercus robur* plants submitted to elevated CO₂ and drought. *Annales des Sciences Forestières*, **53**, 431–446.
- Piovesan, G., Di Filippo, A., Alessandrini, A., Biondi, F. & Schirone, B. (2005) Structure, dynamics and dendroecology of an old-growth *Fagus* forest in the Apennines. *Journal of Vegetation Science*, **16**, 13–28.
- Piovesan, G., Biondi, F., Di Filippo, A., Alessandrini, A. & Maugeri, M. (2008) Drought-driven growth reduction in old beech (*Fagus sylvatica* L.) forests of the central Apennines, Italy. *Global Change Biology*, **14**, 1265–1281.
- Poorter, H. & Navas, M.-L. (2003) Plant growth and competition at elevated CO₂: on winners, losers and functional groups. *New Phytologist*, **157**, 175–198.
- Rasmussen, L., Beier, C. & Bergstedt, A. (2002) Experimental manipulations of old pine forest ecosystems to predict the potential tree growth effects of increased CO₂ and temperature in a future climate. *Forest Ecology and Management*, **158**, 179–188.
- Rathgeber, C., Guiot, J., Roche, P. & Tessier, L. (1999) Augmentation de productivité du chêne pubescent en région méditerranéenne Française. *Annals of Forest Science*, **56**, 211–219.
- Rathgeber, C., Nicault, A., Guiot, J., Keller, T., Guibal, F. & Roche, P. (2000) Simulated responses of *Pinus halepensis* forest productivity to climatic change and CO₂ increase using a statistical model. *Global and Planetary Change*, **26**, 405–421.
- Reich, P.B., Hobbie, S.E., Lee, T., Ellsworth, D.S., West, J.B., Tilman, D., Knops, J.M.H., Naeem, S. & Trost, J. (2006) Nitrogen limitation constrains sustainability of ecosystem response to CO₂. *Nature*, **440**, 922–925.
- Salzer, M.W., Hughes, M.K., Bunn, A.G. & Kipfmüller, K.F. (2009) Recent unprecedented tree-ring growth in bristlecone pine at the highest elevations and possible causes. *Proceedings of the National Academy of Sciences USA*, **106**, 20348–20353.
- Sano, M., Buckley, B.M. & Sweda, T. (2009) Tree-ring based hydroclimate reconstruction over northern Vietnam from *Fokienia hodginsii*: eighteenth century mega-drought and tropical Pacific influence. *Climate Dynamics*, **33**, 331–340.
- Saurer, M., Cherubini, P., Bonani, G. & Siegwolf, R. (2003) Tracing carbon uptake from a natural CO₂ spring into tree rings: an isotope approach. *Tree Physiology*, **23**, 997–1004.

- Shaw, M.R., Zavaleta, E.S., Chiariello, N.R., Cleland, E.E., Mooney, H.A. & Field, C.B. (2002) Grassland responses to global environmental changes suppressed by elevated CO₂. *Science*, **298**, 1987–1990.
- Sidorova, O., Siegwolf, R.T.W., Saurer, M., Naurzbaev, M.M. & Vaganov, E.A. (2008) Isotopic composition ($\delta^{13}\text{C}$, $\delta^{18}\text{O}$) in wood and cellulose of Siberian larch trees for early Medieval and recent periods. *Journal of Geophysical Research*, **113**, G02019; doi: 10.1029/2007JG000473.
- Silva, L.C.R., Anand, M., Oliveira, J.M. & Pillar, V. (2009) Past century changes in *Araucaria angustifolia* (Bertol.) Kuntze water use efficiency and growth in forest and grassland ecosystems of southern Brazil: implications for forest expansion. *Global Change Biology*, **15**, 2387–2396.
- Sitch, S., Huntingford, C., Gedney, N., Levy, P.E., Lomas, M., Piao, S.L., Betts, R., Ciais, P., Cox, P., Friedlingstein, P., Jones, C.D., Prentice, I.C. & Woodward, F.I. (2008) Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five dynamic global vegetation models (DGVMs). *Global Change Biology*, **14**, 2015–2039.
- Soulé, P.T. & Knapp, P.A. (2006) Radial growth rate increases in naturally occurring ponderosa pine trees: a late-20th Century CO₂ fertilization effect? *New Phytologist*, **171**, 379–390.
- Srur, A.M., Villalba, R., Villagra, P.E. & Hertel, D. (2008) Influencias de las variaciones en el clima y en la concentración de CO₂ sobre el crecimiento de *Nothofagus pumilio* en la Patagonia. *Revista Chilena de Historia Natural*, **81**, 239–256.
- Stephens, B.B., Gurney, K.R., Tans, P.P., Sweeney, C., Peters, W., Brawler, L., Ciais, P., Nakazawa, T., Aoki, S., Machida, T., Inoue, G., Vinnichenko, N., Lloyd, J.J., Langfields, R., Jordon, A., Heimann, M., Shibistova, O., Francey, R. & Denning, S. (2007) Weak northern and strong tropical land carbon uptake from vertical profiles of atmospheric CO₂. *Science*, **316**, 1732–1735.
- Su, H., Sang, W., Wang, Y. & Ma, K. (2007) Simulating *Picea schrenkiana* forest productivity under climatic changes and atmospheric CO₂ increase in Tianshan Mountains, Xinjiang Autonomous Region, China. *Forest Ecology and Management*, **246**, 273–284.
- Switsur, R. & Waterhouse, J. (1998) Stable isotopes in tree ring cellulose. *Stable isotopes: integration of biological, ecological and geochemical processes* (ed. by H. Griffiths), pp. 303–321. BIOS Scientific Publishers Ltd, Oxford.
- Tang, K., Feng, X. & Funkhouser, G. (1999) The $\delta^{13}\text{C}$ of tree rings in full-bark and strip-bark bristlecone pine trees in the White Mountains of California. *Global Change Biology*, **5**, 33–40.
- Tognetti, R., Cherubini, P. & Innes, J.L. (2000) Comparative stem-growth rates of Mediterranean trees under background and naturally enhanced ambient CO₂ concentrations. *New Phytologist*, **146**, 59–74.
- Voelker, S.L., Muzika, R.M., Guyette, R.P. & Stambaugh, M.C. (2006) Historical CO₂ growth enhancement declines with age in *Quercus* and *Pinus*. *Ecological Monographs*, **76**, 549–564.
- Wagner, R., Insinna, P.A., Götz, B., Junge, S. & Boetger, T. (2007) ¹³C discriminations of *Pinus sylvestris* vs. *Pinus ponderosa* at a dry site in Brandenburg (eastern Germany): 100-year growth comparison. *Isotopes in Environmental and Health Studies*, **43**, 117–128.
- Wang, G.G., Chhin, S. & Bauerle, W.L. (2006) Effect of natural atmospheric CO₂ fertilization suggested by open-grown white spruce in a dry environment. *Global Change Biology*, **12**, 601–610.
- Waterhouse, J.S., Switsur, V.R., Barker, A.C., Carter, A.H.C., Hemming, D.L., Loader, N.J. & Robertson, I. (2004) Northern European trees show a progressively diminishing response to increasing atmospheric carbon dioxide concentrations. *Quaternary Science Reviews*, **23**, 803–810.
- Woodward, F.I. (1993) Plant responses to past concentrations of CO₂. *Vegetatio*, **104/105**, 145–155.

BIOSKETCHES

Josep Peñuelas and Romà Ogaya are ecologists at the Global Ecology Unit CREAM-CEAB-CSIC in Bellaterra (Barcelona, Spain). Their work is focused on the study of the global change interactions with terrestrial ecosystems.

Josep G. Canadell is an ecologist at CSIRO Marine and Atmospheric Research Center in Canberra, Australia. His work is focused on the global carbon cycle.

J.P. and J.C. conceived the ideas; all three authors gathered the databases, analysed the data and prepared the paper.

Editor: Brad Murray