Global Change Biology

Global Change Biology (2012) **18**, 2681–2693, doi: 10.1111/j.1365-2486.2012.02745.x

REVIEW

Simple additive effects are rare: a quantitative review of plant biomass and soil process responses to combined manipulations of CO_2 and temperature

WOUTER I. J. DIELEMAN*†[1], SARA VICCA*[1], FEIKE A. DIJKSTRA‡, FRANK HAGEDORN§, MARK J. HOVENDEN¶, KLAUS S. LARSEN‖, JACK A. MORGAN**, ASTRID VOLDER††, CLAUS BEIER‖, JEFFREY S. DUKES‡‡, JOHN KING*,§§, SEBASTIAN LEUZINGER¶¶,‖‖, SUNE LINDER***, YIQI LUO†††, RAM OREN‡‡‡,§§§, PAOLO DE ANGELIS¶¶¶, DAVID TINGEY‖‖‖, MARCEL R. HOOSBEEK**** and IVAN A. JANSSENS*

**Research Group of Plant and Vegetation Ecology, Department of Biology, University of Antwerp, Wilrijk, B-2610, Belgium, †School of Earth and Environmental Sciences, Faculty of Science and Engineering, James Cook University, Smithfield, 4878, QLD Australia, ‡Department of Environmental Sciences, Faculty of Agriculture and Environment, The University of Sydney, Sydney, 2015, NSW Australia, §Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Birmensdorf, 8903, Switzerland, ¶School of Plant Science, University of Tasmania, Locked Bag 55, Hobart, Tasmania, 7001, Australia, ‖Department of Chemical and Biochemical Engineering, Technical University of Denmark, Kgs. Lyngby, 2800, Denmark, **Rangeland Resources Research Unit, USDA-ARS, Crops Research Laboratory, 1701 Centre Ave, Fort Collins, CO, 80526, USA, ††Department. of Horticultural Sciences, Texas A&M University, TAMU 2133, College Station, TX, 77843, USA, ‡‡Department of Forestry and Natural Resources and Department of Biological Sciences, Purdue University, 715 West State Street, West Lafayette, IN, 47907-2061, USA, §§Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, NC, 27695, USA, ¶¶Forest Ecology, Department of Environmental Sciences, ETH Zurich, Universitätstrasse 16, Zurich, CH-8092, Switzerland, ‖‖The Institute of Botany, University of Basel, Schönbeinstr., Basel, 6CH-4056, Switzerland, ***Southern Swedish Forest Research Centre, SLU, P.O. Box 49, Alnarp, SE-230 53, Sweden, †††Department of Botany and Microbiology, University of Oklahoma, Norman, OK, 73069, USA, ‡‡‡Division of Environmental Science & Policy, Nicholas School of the Environment, Duke University, Durham, NC, 27708-0328, USA, §§§The Department of Forest Ecology & Management, Swedish University of Agricultural Sciences (SLU), Umeå, SE-901 83, Sweden, ¶¶¶DIBAF Department for Innovation in Biological, Agro-food and Forest systems, University of Tuscia, Via San Camillo de Lellis, Viterbo, I-01100, Italy, ‖‖‖David Tingey, 425 NW Merrie Drive, OR, Corvallis, 97330, USA, ****Department of Environmental Sciences, Earth System Science – Climate Change, Wageningen University, P. O. Box 47, Wageningen, 6700AA, The Netherlands*

Abstract

In recent years, increased awareness of the potential interactions between rising atmospheric CO_2 concentrations ($[CO_2]$) and temperature has illustrated the importance of multifactorial ecosystem manipulation experiments for validating Earth System models. To address the urgent need for increased understanding of responses in multifactorial experiments, this article synthesizes how ecosystem productivity and soil processes respond to combined warming and $[CO_2]$ manipulation, and compares it with those obtained in single factor $[CO_2]$ and temperature manipulation experiments. Across all combined elevated $[CO_2]$ and warming experiments, biomass production and soil respiration were typically enhanced. Responses to the combined treatment were more similar to those in the $[CO_2]$-only treatment than to those in the warming-only treatment. In contrast to warming-only experiments, both the combined and the $[CO_2]$-only treatments elicited larger stimulation of fine root biomass than of aboveground biomass, consistently stimulated soil respiration, and decreased foliar nitrogen (N) concentration. Nonetheless, mineral N availability declined less in the combined treatment than in the $[CO_2]$-only treatment, possibly due to the warming-induced acceleration of decomposition, implying that progressive nitrogen limitation (PNL) may not occur as commonly as anticipated from single factor $[CO_2]$ treatment studies. Responses of total plant biomass, especially of aboveground biomass, revealed antagonistic interactions between elevated $[CO_2]$ and warming, i.e. the response to the combined treatment was usually less-than-additive. This implies that productivity projections might be overestimated when models are parameterized based on single factor responses. Our results highlight the need for more (and especially more long-term) multifactor manipulation experiments. Because single factor CO_2 responses often

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Correspondence: Wouter I. J. Dieleman, tel. + 61 7 4042 1729, fax + 61 7 4042 1284, e-mail: wouter.dieleman@ua.ac.be

[1] These authors contributed equally to this manuscript

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dominated over warming responses in the combined treatments, our results also suggest that projected responses to future global warming in Earth System models should not be parameterized using single factor warming experiments.

Keywords: [CO_2] enrichment, biomass, C sequestration, elevated temperature, manipulation experiments, multifactor experiments, nitrogen availability, soil respiration

Received 19 January 2012 and accepted 25 March 2012

Introduction

Increasing concentrations of greenhouse gases in the atmosphere are expected to increase global surface temperatures in the coming decades. The latest IPCC report projects a warming of 0.2 °C per decade in the next two decades, and of 0.6–4 °C by the end of the 21st century (relative to observations in 1980–1999). At the same time increased variability and regional changes in precipitation patterns are very likely and the atmospheric CO_2 concentration [CO_2] may continue to rise, up to 490–1260 ppm by the end of this century (Ipcc, 2007). These climatic and atmospheric changes influence ecosystem functioning, whereby uptake or emission of greenhouse gases constitute an important climate-controlling feedback mechanism (Friedlingstein *et al.*, 2006; Van Groenigen *et al.*, 2011).

An important approach to increasing our understanding of the effects of global changes on terrestrial ecosystems is manipulation of these driving variables in ecosystem experiments (e.g. Beier *et al.*, 2004; Rustad, 2008). Apart from providing enhanced understanding of ecosystem responses to global change, the data provided by these manipulation experiments can help to parameterize and evaluate Earth System models, as well as ecosystem models that predict future ecosystem functioning and ecosystem services. Because multifactor manipulation experiments test the anticipated changes in climate and [CO_2] simultaneously as opposed to single factor manipulative experiments, these can be expected to yield more relevant benchmarking data (e.g. Shaw *et al.*, 2002; Dukes *et al.*, 2005; Larsen *et al.*, 2011).

Multifactor manipulation experiments are more expensive than single factor experiments, because the number of study plots double for each additional factor involved. Therefore, these experiments are still scarce (14 sites in this analysis, see also Rustad, 2008), and most ecosystem models are therefore currently parameterized and tested with results obtained in single factor experiments. This article addresses this restriction by synthesizing the published effects of warming and elevated atmospheric CO_2 concentration, applied separately and in combination, on terrestrial ecosystem biomass production [main terrestrial carbon (C) pool taking up atmospheric CO_2], soil respiration (main flux releasing CO_2 to the atmosphere), and nitrogen (N) mineralization (main limiting factor of plant CO_2 uptake in most natural northern ecosystems).

Methods

Most of the data included in this analysis were extracted from figures and tables in published papers. Other data, not published in the peer-reviewed literature, were obtained via personal communication (Table S1–2). We collected data from 150 manipulation experiment sites across a range of different ecosystems and climates, reporting data on total biomass, aboveground biomass, root biomass, fine root biomass, soil C, heterotrophic respiration, soil respiration, and soil N availability and foliar N content, resulting in 821 entries for the meta-analysis (Table S3). When several years of data were reported in the same study, we calculated a weighted mean, using the reciprocal of the measurement variance as a weight factor. Several studies used different species in the same experiment or included other manipulations, e.g. fertilization, ozone, different soil types, different management types. Results from different treatments, plant species, soils, or measurement protocols within the same experiment were considered independent experiments and were used as different inputs in the meta-analysis. General site information, source references, and sampling methods are described in Tables S1–6. The database is freely available after contacting the corresponding author.

Data were analyzed with meta-analytical techniques using MetaWin 2.1 software (Rosenberg *et al.*, 2000). As in conventional meta-analysis, each individual observation was weighted by the reciprocal of the mixed-model variance (Hedges *et al.*, 1999). We used standard deviation (SD) values reported in the individual studies, or calculated the SD from the reported standard error and the number of replicates. Studies that did not report standard error or deviation were not included in the database. The natural log of the response ratio (r = response in treatment plots/response in untreated plots) was the metric used in the analyses, and is reported as the percentage change to elevated [CO_2] and elevated temperature. The use of the natural logarithm instead of the Hedges d-index has the advantage of linearizing the metric, thereby being less sensitive to changes in a small control group. A mixed-model was used to assess the treatment effects for the different parameters. If the number of studies used to calculate a mean and confidence interval is lower than 20, the confidence interval can be too narrow (Hedges *et al.*, 1999).

Therefore, we used the confidence interval based on resampling methods for the assessment of statistical differences (2500 iterations). As compared to standard confidence intervals, confidence intervals based on such bootstrapping tests are larger and the resulting estimates are more conservative (Adams *et al.*, 1997). If the calculated 95% confidence interval did not encompass zero, the response to the manipulation was considered significant. Significant between-group differences (i.e., categorical analyses for treatment comparisons) were identified on the basis of the within- and between-group heterogeneity. Between-group differences are reported statistically significant at $P < 0.05$. From the distribution of individual responses, we also derived median effect sizes as a comparison to the weighted effect sizes calculated in the meta-analysis.

In addition to the typical meta-analysis in which all available data were used, we also performed a more conservative comparison of the single factor and combined factor manipulation experiments by taking into account only those experiments where all three treatments were tested simultaneously: elevated [CO_2] only, warming only, and combined [CO_2]-enrichment and warming. Experiments included in this analysis are listed in Table 1.

What single factor experiments revealed

Because the effects of single factor elevated [CO_2] and elevated temperature are relatively well understood and have previously been synthesized (Ceulemans & Mousseau, 1994; Curtis & Wang, 1998; Rustad *et al.*, 2001; Nowak *et al.*, 2004; Pendall *et al.*, 2004; Ainsworth & Long, 2005; Norby *et al.*, 2005; De Graaff *et al.*, 2006; Hyvönen *et al.*, 2007; Dieleman *et al.*, 2010; Way & Oren, 2010; Wu *et al.*, 2011; Elmendorf *et al.*, 2012), we will only briefly touch upon these single factor manipulation effects.

Elevated [CO_2] increases plant photosynthesis and growth, although responses can be limited in mature tree stands and nutrient-limited systems (Körner, 2006), and tend to decline with the duration of the experiment (Leuzinger *et al.*, 2011). In many ecosystems, the indirect [CO_2] effect via reduced stomatal conductance and subsequent water savings (Volk *et al.*, 2000; Morgan *et al.*, 2004) could be much more sustainable than the direct [CO_2] effect on photosynthesis (Holtum & Winter, 2010). As a consequence of the enhanced plant production, the increased demand for nutrients stimulates belowground C allocation and fine root and mycorrhizal growth (Fig. 1a) (e.g. Rogers *et al.*, 1994; Curtis & Wang,

Table 1 Sites that applied both single factor [CO_2] and warming treatments, and a simultaneous [CO_2] and warming treatment

Site name	Country	System	Treatments	Source references
Natural/Outdoor systems				
Brandjberg	Denmark	Temperate heathland	CO_2 x Warming x Drought	(Andresen *et al.*, 2009; Larsen *et al.*, 2011; Selsted *et al.*, 2012)
Flakaliden	Sweden	Picea abies forest	CO_2 x Warming	(Comstedt *et al.*, 2006; Kostiainen *et al.*, 2009)
Ginninderra	Australia	Phalaris aquatic swards	CO_2 x Warming	(Volder *et al.*, 2007)
Jasper ridge	USA	California annual grassland	CO_2 x Warming x Fertilization x Water	(Dukes *et al.*, 2005)
Mekrijärvi	Finland	Pinus sylvestris forest	CO_2 x Warming	(Pajari, 1995; Niinistö *et al.*, 2004)
Oak ridge grasslands	USA	Model grassland	CO_2 x Warming x Water	(Wan *et al.*, 2007; Kardol *et al.*, 2010)
Oak ridge maples	USA	Acer rubrum, Acer saccharum	CO_2 x Warming	(Edwards & Norby, 1999; Norby *et al.*, 2000; Wan *et al.*, 2004)
PHACE	USA	Northern mixed-grass prairie	CO_2 x Warming	(Dijkstra *et al.*, 2010; Morgan *et al.*, 2011)
Stillberg	Switzerland	Treeline larch and pine system	CO_2 x Warming	(Hagedorn *et al.*, 2010; Dawes *et al.*, 2011)
TasFACE	Australia	Species-rich temperate grassland	CO_2 x Warming	(Hovenden *et al.*, 2008; Pendall *et al.*, 2011)
Controlled mescocosms/ phytotrons				
Duke phytotron	USA	Pinus and Robinia seedlings	CO_2 x Warming x Fertilization	(Larigauderie *et al.*, 1994; King *et al.*, 1996; Uselman *et al.*, 2000)
NERC Ecotron	UK	Grassland model ecosystem	CO_2 x Warming	(Kandeler *et al.*, 1998)
Risø	Denmark	Pisum sativum	CO_2 x Warming	(Gavito *et al.*, 2003)
USEPA	USA	Pseudotsuga seedlings	CO_2 x Warming	(Lin *et al.*, 2001; Olszyk *et al.*, 2003; Tingey *et al.*, 2006)

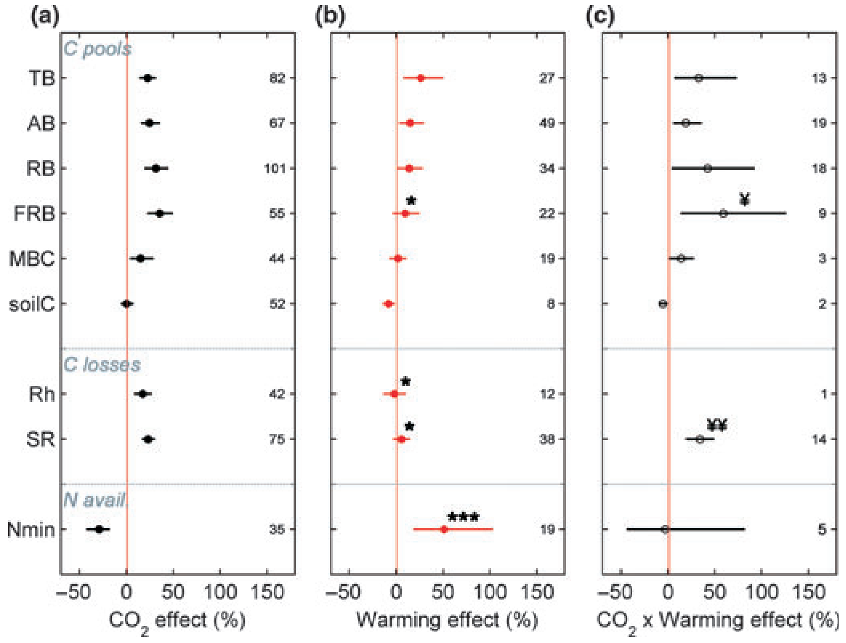

Fig. 1 Overall meta-analysis effect sizes for elevated $[CO_2]$ (a), warming (b) and the combined elevated $[CO_2]$ and warming treatment (c) reported as the percentage change relative to the control. Data listed are total biomass (TB), aboveground biomass (AB), root biomass (RB), fine root biomass (FRB), soil C content (soilC), heterotrophic respiration (Rh), soil respiration (SR), and mineral N availability (Nmin). Positive values indicate a positive treatment effect, negative values indicate a decrease. Error bars represent the 95% confidence interval. Data are the weighted means for n data points. The number of studies is given along the *Y*-axis. Significant differences in the response to $[CO_2]$ enrichment vs. the warming response are indicated (* indicates differences with the $[CO_2]$ responses, ¥ indicates differences with the warming responses. * or ¥ indicates a significant difference at $P < 0.05$; ** or ¥¥ indicates a significant difference at $P < 0.01$, *** or ¥¥¥ indicates a significant difference at $P < 0.001$). References to all individual experiments included in this meta-analysis are listed in Tables S5 and S6.

1998; Ceulemans *et al.*, 1999; De Graaff *et al.*, 2006; Litton *et al.*, 2007; Dieleman *et al.*, 2010). The associated increase in fine root turnover and rhizodeposition generally enhances substrate availability to soil organisms (Dieleman *et al.*, 2010), whose greater biomass and/or activity may stimulate the decomposition of organic material (Zak *et al.*, 2000; Heath *et al.*, 2005; Dijkstra & Cheng, 2007; Fontaine *et al.*, 2007; Hagedorn *et al.*, 2008; Kuzyakov, 2011). Results of the current meta-analysis support this pattern: heterotrophic- and total soil respiration generally increased under $[CO_2]$ enrichment (Fig. 1a). The simultaneous increase in soil C inputs and soil C losses under elevated $[CO_2]$ leaves soil C stocks largely unchanged (Schlesinger & Lichter, 2001; Dieleman *et al.*, 2010). Although other meta-analyses indicated increased soil C (Jastrow *et al.*, 2005; Luo *et al.*, 2006), especially in N-fertilized ecosystems (Hungate *et al.*, 2009), elevated $[CO_2]$ thus mainly accelerates soil C cycling in terrestrial ecosystems (Lukac *et al.*, 2009).

As a consequence of increasing plant and microbial biomass stocks in elevated $[CO_2]$, more nutrients are immobilized, which may result in progressive N limitation (PNL, for concept see Luo *et al.*, 2004) in unfertilized and infertile ecosystems. Our meta-analysis supports this hypothesis, showing a substantial reduction in mineral N availability (Nmin; NO_3^- and NH_4^+ concentration) in response to increased $[CO_2]$ (Fig. 1a), which suggests either a gradual depletion of soil N levels, or a more conservative use of N in an increasingly more closed N cycle. In general, plant biomass and soil C fluxes thus respond positively to elevated $[CO_2]$ in manipulation experiments, but nutrient availability is expected to constrain this stimulation in the long run unless total ecosystem nitrogen content increases due to CO_2-induced increases in nitrogen uptake or CO_2-induced decreases in nitrogen losses (Luo *et al.*, 2004, 2006).

In contrast to elevated $[CO_2]$, which affects different terrestrial ecosystems quite uniformly at the leaf level, resulting in increased photosynthesis, biomass production, and resource demands, warming is a more complex driver that affects multiple processes (e.g. photosynthesis, respiration, evapotranspiration, N mineralization) in various direct as well as indirect ways (Luo, 2007). Plant productivity, for example, can be influenced by warming directly through accelerated reaction rates, cell division and elongation, but is also affected indirectly through altered water (De Boeck *et al.*, 2008) and nutrient availabilities or a lengthening of the growing season (Jarvis & Linder, 2000; Saxe *et al.*, 2001). In addition, optimal growth temperatures differ between biomes at different latitudes, which will largely determine the responsiveness of different ecosystems to different degrees of warming (Way & Oren, 2010).

This greater complexity of the warming response results in average response patterns that differ strongly from those to [CO_2]-enrichment, not only in size and statistical significance, but especially in the direction of the responses. First, N availability declines substantially under elevated [CO_2], while warming typically stimulates nutrient availability via enhanced net N mineralization rates (Rustad *et al.*, 2001; Pendall *et al.*, 2004; Hyvönen *et al.*, 2007; but Niu *et al.*, 2010) (Fig. 1a and b). Second, in contrast to elevated [CO_2] experiments, higher temperatures enhance aboveground biomass, but do not stimulate (fine) root biomass (Fig. 1b) (Way & Oren, 2010). This apparent difference in the impact on biomass distribution patterns may be partly due to the increased N availability in warming experiments (Fig. 1b), as higher nutrient availability reduces the need to develop an elaborate belowground nutrient acquisition system (Melillo *et al.*, 2011). A third striking difference is the lack of stimulation of soil respiration in the warming experiments (Fig. 1b). Whereas elevated [CO_2] typically increases soil respiration (Zak *et al.*, 2000; Dieleman & Janssens, 2011; Selsted *et al.*, 2012) (Fig. 1a), soil respiration does not show a consistent long-term response to warming (Fig. 1b). Although soil respiration generally increases when temperature rises on a short time scale (±5 years, Rustad *et al.*, 2001; Melillo *et al.*, 2002), several mechanisms can prevent a persistent positive warming effect on microbial and soil respiration (Davidson & Janssens, 2006). Particularly important in this regard are depletion of labile soil organic matter pools following extended stimulation of microbial decomposition during earlier phases in the warming experiments (Kirschbaum, 2004; Eliasson *et al.*, 2005; Knorr *et al.*, 2005; Hartley *et al.*, 2007; Bradford *et al.*, 2008), warming-induced water limitation of microbial activity (Suseela *et al.*, 2012), and thermal acclimatization of root and/or microbial respiration (Atkin & Tjoelker, 2003; Vicca *et al.*, 2010).

Elevated [CO_2] and warming thus elicit very different ecosystem responses, but *in situ* these two global change factors are changing concurrently. Therefore, combined [CO_2] enrichment and warming experiments are crucial to test whether ecosystem processes in a warmer, [CO_2]-enriched world will mirror those observed in warming, those in elevated [CO_2], or whether their responses will be additive, antagonistic or even synergistic.

Average responses to combined [CO_2] and warming

To date, combined warming and [CO_2] enrichment studies have been rare and only few C-cycle related variables were reported for at least five manipulation experiments (Fig. 1c). Because of this we performed a more extensive analysis on response variables: a first analysis based on conventional meta-analysis with weighted effect estimates, and a second analysis based on histograms and median effect estimates to study the distribution of effect sizes in our dataset (see Method section).

For total, aboveground and belowground biomass, the weighted meta-analysis estimates of the responses to elevated [CO_2] and warming were considerably higher compared to the median effect estimates (Fig. 2). As meta-analysis gives

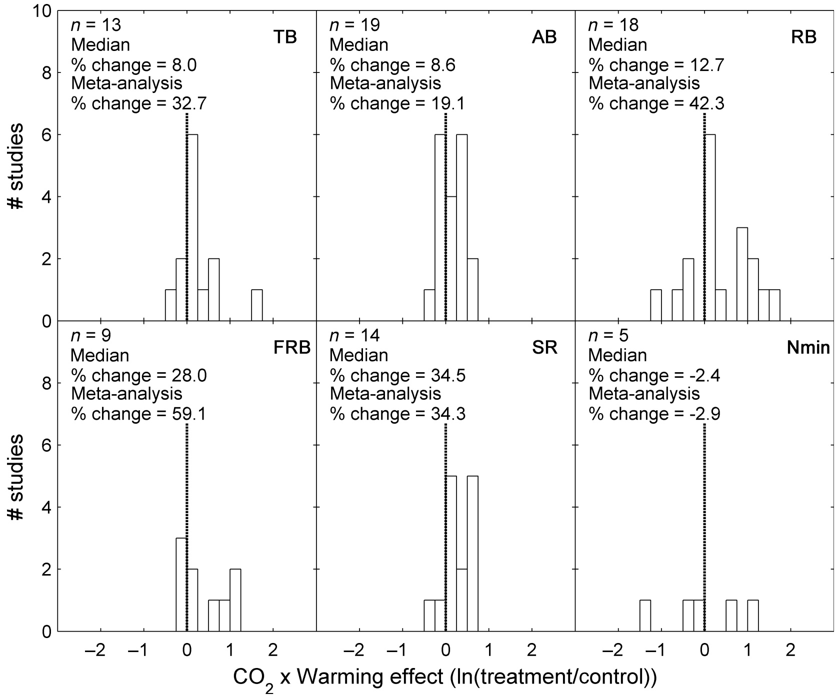

Fig. 2 Histograms for the combined elevated [CO_2] and warming treatment effect on total biomass (TB), aboveground biomass (AB), root biomass (RB), fine root biomass (FRB), soil respiration (SR), and mineral N availability (Nmin). The number of studies, the median effect estimates and the meta-analysis effect estimates are given for each dataset.

more weight to larger studies (i.e. studies with more treatment replicates), this indicates that larger studies tended to report larger responses. However, while the median effect estimates were smaller, the number of studies reporting positive responses was consistently larger than the number of studies reporting negative responses (Fig. 2). Hence, a positive effect of a combined warming and elevated [CO_2] treatment on biomass production was supported by both analyses. In addition, the trend for a larger belowground biomass response compared to the aboveground biomass response was also apparent in both analyses. The increased allocation to belowground biomass translated into a strong positive fine root biomass response in both analyses (Fig. 2).

Both the median effect estimate and the meta-analysis estimate (Figs 1c and 2) indicated a stimulated soil respiration in response to combined warming and elevated [CO_2] treatment. Indeed, of 14 studies, only two reported a negative response to the combined treatment, adding confidence to the observation of a consistently higher soil respiration rate in a warmer climate and higher [CO_2]. Effects on mineral N availability, on the other hand, were very variable (Fig. 2), from very negative to very positive, suggesting a large dependence on site-specific circumstances.

To summarize, effects of combined elevated [CO_2] and warming on plant biomass compartments tended to be variable, but nevertheless positive, with a tendency for greater increase in C allocation to belowground biomass. Feedbacks related to availability of nutrients might be part of the explanation, but we could not conclusively test this mechanism. Most convincing, however, is the consistent increase in soil respiration in the vast majority of experiments. While our results thus suggest a consistent increase of C release to the atmosphere, we reported relative changes here, precluding inferences on the actual C balance. Our results are consistent with a study comparing four ecosystem models that found that combined [CO_2] and warming treatment stimulated net primary production (NPP) and decomposition (Rh) (Luo *et al.*, 2008). However, these authors found that combined [CO_2] and warming generally resulted in a net increase of C storage in a range of different terrestrial ecosystems, suggesting that effects on plant net primary production and soil C inputs are proportionally larger than effects on decomposition of soil organic matter. The currently available data from combined [CO_2] and warming experiments are, however, too small to test this model outcome.

Which factor dominates the response to combined [CO_2] and warming?

Direct comparison of the average meta-analytical effect estimates for combined warming and CO_2-fumigation (as shown in Fig. 1c) with those for single factor manipulation (Fig. 1a and b) was hampered by the low number of experiments combining elevated [CO_2] and warming treatments as opposed to a multitude of single factor experiments (14 vs. 130 experimental sites). Therefore, we performed the meta-analysis taking into account only those ecosystem manipulation experiments that tested all three treatments (i.e. [CO_2] only,

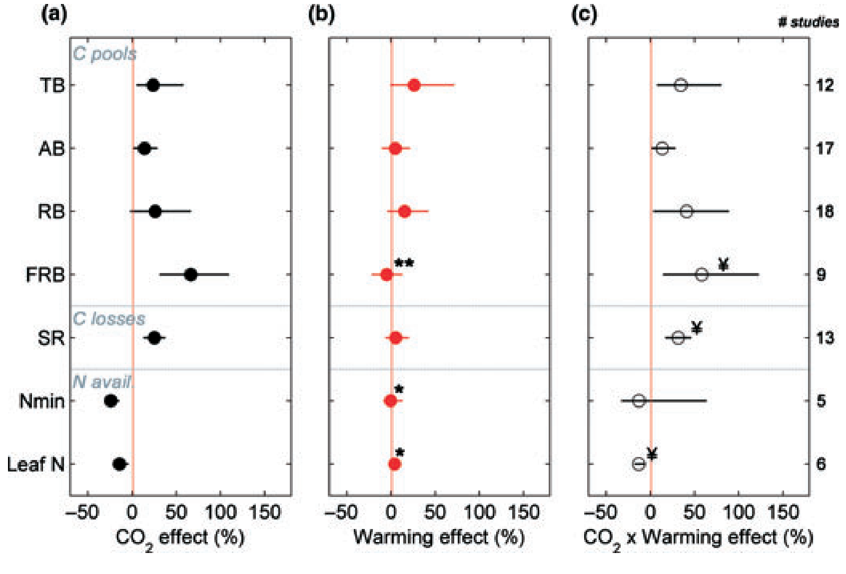

Fig. 3 Meta-analysis effect sizes for experiments where all three treatments were tested simultaneously: elevated [CO_2] (a), warming (b) and the combined elevated [CO_2] and warming treatment (c), reported as the percentage change relative to the control. Data listed are total biomass (TB), aboveground biomass (AB), root biomass (RB), fine root biomass (FRB), soil respiration (SR), mineral N availability (Nmin) and foliar N concentration (Leaf N). Positive values indicate a positive treatment effect, negative values indicate a decrease. Error bars represent the 95% confidence interval. Data are the weighted means for *n* data points. The number of studies is given along the *Y*-axis. Significant differences in the response to [CO_2] enrichment vs. the warming response are indicated (*indicates differences with the [CO_2] responses, ¥ indicates differences with the warming responses. *or ¥ indicates a significant difference at $P < 0.05$; ** or ¥ ¥ indicates a significant difference at $P < 0.01$). References to all individual experiments included in this meta-analysis are listed in Tables S5 and 6.

warming only and the combined treatment, hereafter 'paired meta-analysis') (Fig. 3, Table 1). Responses to warming-only and [CO$_2$]-only treatments (Fig. 3a and b) were very similar to those in the much larger, comprehensive dataset (Fig. 1a and b), indicating that the experiments used in this more robust, but restricted paired meta-analysis provided a representative sample.

A first observation in the paired meta-analysis is that the uncertainties in the combined treatment, tended to be larger than those in the single factor experiments (error bars in Fig. 3c vs. those in 3a and b). In other words: responses to the combined treatment were much less consistent across experiments. Second, across all tested variables, the response pattern in the combined treatment appeared to be more similar to that of the [CO$_2$]-only treatment than to the warming-only treatment: root biomass (+41% in the combined treatment) and especially fine root biomass (+58%) were stimulated more than aboveground biomass (only +15%), and soil respiration increased substantially (+32%) (Fig. 3). This suggests that, averaged over all multifactor manipulation experiments, [CO$_2$] manipulation affected ecosystem carbon cycling more strongly than warming. The impact of CO$_2$ enrichment may have been greater because the degree of CO$_2$ alteration in the experiments was typically larger in relative terms than the imposed temperature change (i.e. [CO$_2$] is often (nearly) doubled (Fig. S1), while temperature treatments generally remain within the temperature range plants experience in the current climate (Fig. S2)). This is, however, not a drawback or artifact, because the much larger relative increase in [CO$_2$] than in temperature is consistent with the projected future scenarios. As mentioned before, the effect of a warming treatment will depend on optimal growth temperature and the magnitude of the treatment relative to the prevailing temperatures at a particular site (Way & Oren, 2010). For this reason, future warming in high latitude/altitude ecosystems could still be proportionally more important than [CO$_2$] increases, although our meta-analysis indicates otherwise.

The similarity between the response to the combined treatment and that to the [CO$_2$]-only treatment, as suggested by the general mean response pattern in Fig. 3, is not that clear when looking across individual experiments (Fig. 4). While for aboveground and fine root biomass, the response to the combined treatment was clearly more similar to the [CO$_2$]-only treatment rather than to the warming-only treatment, this is not the case for total below-ground biomass or N mineralization (Fig. 4). Assessing which factor dominates the response to combined [CO$_2$] and warming requires acknowledging the processes that underlie the response of interest and understanding which factors control their responses. For example, the dominance of the [CO$_2$] impact in the response of soil respiration to the combined treatment is very likely due to the dominant effect of elevated [CO$_2$] on fine root biomass, both across experiments (Fig. 4) and when averaged over all experiments (Fig. 3). Very often, however, understanding which factor dominates the response to combined warming and [CO$_2$] enrichment is not straightforward. In one of the few [CO$_2$] x warming studies on mature trees, for example, warming enhanced shoot-scale net photosynthesis early in the season only, while elevated [CO$_2$] increased maximum net photosynthesis only late in the season (Slaney *et al.*, 2007; Hall *et al.*, 2009). Both climate change factors thus contributed to the increase in the combined treatment, but this would not have become apparent without detailed process measurements. Observations limited to only part of the season would have attributed increased carbon assimilation by new shoots in the combined treatment to either warming or elevated [CO$_2$], when in fact it should be attributed to their combined effect. Thus, for process responses that are monitored only infrequently, (seasonal) variation in the relative contribution of individual treatment effects to the response in the combined treatment may have contributed to the large variation in process responses within and between individual experiments.

Is there evidence for progressive nitrogen limitation in combined elevated [CO$_2$] and warming?

Although the stimulation of plant productivity in elevated [CO$_2$] is known to gradually decline due to progressive nitrogen limitation (Oren *et al.*, 2001; Hungate *et al.*, 2003; Luo *et al.*, 2004), warming is known to accelerate organic matter mineralization and thus to enhance nutrient availability. The combined warming and elevated [CO$_2$] experiments provide the opportunity to test whether or not PNL occurs when these contrasting determinants of soil N availability are combined.

As expected, our meta-analysis reveals that elevated [CO$_2$] decreased soil N availability (Figs 1a and 3a), but that it increased (or tended to increase) under warming (Figs 1b and 3b). On average, these opposite responses counterbalanced each other in the combined elevated [CO$_2$] and warming experiments, resulting in little change in N availability relative to the control treatments (Figs 1c and 3c). Furthermore, across individual experiments, responses of soil N availability in the combined [CO$_2$] and warming experiments were positively correlated with responses in the warming-only experiments, but were not significantly correlated with the responses in the [CO$_2$]-only experiments (Fig. 4). These two observations are highly relevant, because they imply that results of [CO$_2$]-only experiments overstate the likelihood that PNL will occur in future.

However, we also assembled a dataset for foliar N concentrations as an indirect indication of PNL [Figs 2c and 4 (inset)]. Plant nutrient concentrations are not only influenced by the soil nutrient availability, but also by the dilution effects of the enlarged biomass and by the competitive immobilization by soil microbes. Interestingly, our meta-analysis indicated that foliar N concentration did decline significantly in combined elevated [CO$_2$] and warming (Fig. 3c). Moreover, across the individual experiments, foliar N concentration responses showed a contrasting pattern compared to the response of soil nutrient availability: a positive correlation between the combined treatment effects and the single factor [CO$_2$] effects (thus also in line with the responses of soil respiration and biomass production), compared to a marginally significant negative correlation for single factor warming effects [Figs 3 and 4 (inset)]. While it is important to express the foliar N concentration

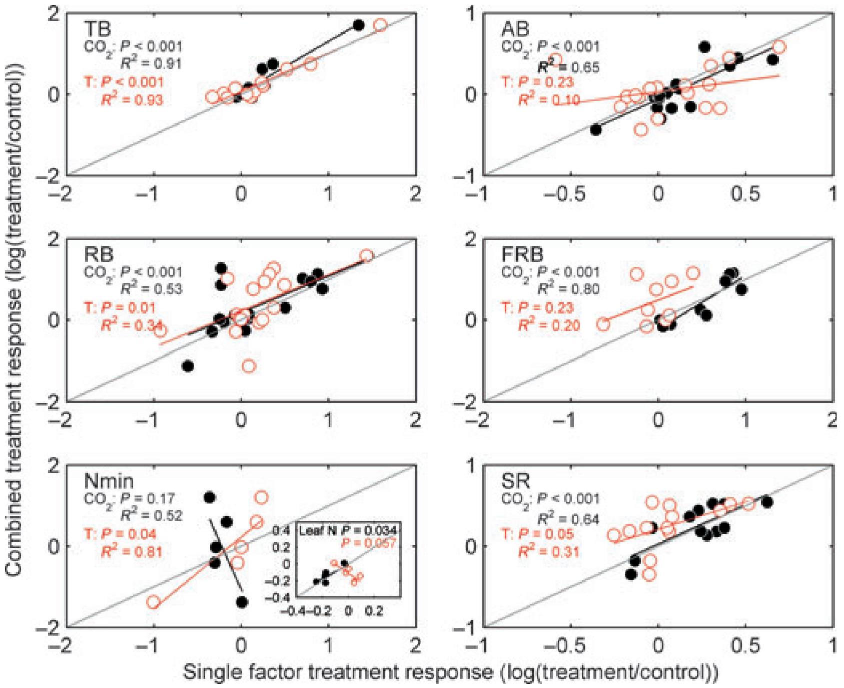

Fig. 4 Meta-analysis effect sizes for single factor [CO_2] effects (black filled circles) and single factor warming effects (red open circles) plotted against the combined [CO_2] x warming effect sizes. Data are reported as log (Treatment/Control). Data listed are total biomass (TB), aboveground biomass (AB), root biomass (RB), fine root biomass (FRB), mineral N availability (Nmin), foliar N concentration (Leaf N, inset), and soil respiration (SR). *P*-values and R^2 values for linear regressions between single factor and combined treatment effects are given. Correlations were considered statistically significant at $P < 0.05$.

on structural dry mass since there are major seasonal variations in foliar starch concentration that are also affected by the treatments (Jarvis & Linder, 2000), these analyses of the response of foliar N concentration to the combined treatments both suggest that PNL can be expected to occur also when [CO_2] and temperature increase together. In addition, many soil warming studies revealed only short-lived stimulation of organic matter decomposition (Luo *et al.*, 2001; Melillo *et al.*, 2002; but see Vicca *et al.*, 2009), implying that also the stimulatory effect of warming on net N mineralization might not be sustainable in the long term and therefore that warming can only postpone the occurrence of PNL. Our dataset for mineral N availability is, however, dominated by short-term experiments (2–5 years) and at this stage there clearly are insufficient long-term data available to support a robust conclusion on the occurrence of PNL in a future warmer and [CO_2]-enriched world.

The fact that the current set of manipulation experiments does not provide a conclusive indication about the occurrence of PNL in a future warmer and [CO_2]-enriched world is not only related to the limited size and duration of the data set, but probably more to the fact that local conditions determine the likelihood that PNL will occur. In theory, PNL is most likely to occur in northern and temperate-zone ecosystems in which biomass production is typically N-limited than in tropical ecosystems where N is typically not the limiting nutrient (Aerts & Chapin, 2000). Due to the growing intensity and global distribution of atmospheric deposition of reactive N compounds (Galloway *et al.*, 2004), however, more and more extra-tropical ecosystems are shifting from a state of N (co-)limitation to a state of N-saturation (Aber *et al.*, 1998). Both PNL and N-saturation are plant-centered concepts that are often used to explain plant responses to elevated [CO_2] and to N deposition, but these concepts are not independent from one another. Ecosystems where N inputs exceed N demands will simultaneously evolve in the direction of N-saturation and be less prone to exhibit PNL with rising atmospheric [CO_2]. In other words, PNL is highly unlikely to occur in ecosystems with a very open and leaky N cycle (high N input rates combined with high rates of N leaching and N volatilization), characterized by excess plant available N and high temporal variability in ecosystem N content at annual or decadal timescale (Luo *et al.*, 2006; Liao *et al.*, 2008; Lu *et al.*, 2011). In the long term, PNL can thus be expected under elevated [CO_2], but only where the N cycle is closed (Rastetter *et al.*, 1997) and where warming-induced increases in net N mineralization are unlikely to cope with the increasing N immobilization in plant biomass, litter, and soil organic matter.

Are responses synergistic, antagonistic, or additive?

When applied in combination, interactive effects of elevated [CO_2] and warming may not simply result in additive responses, but might elicit synergistic or antagonistic responses. For example, accelerated nutrient mineralization caused by warming could counterbalance [CO_2]-induced nutrient limitations and allow the full [CO$_2$] fertilization effect to be expressed. In this case, the [CO$_2$] effect could be larger in the combined treatment than in the [CO$_2$]-only treatment. Similarly, increased water use efficiency (WUE), caused by elevated [CO$_2$], could overcome warming-induced water limitation and thereby allow the full warming effect on biomass production (Morgan *et al*., 2011). Hence, synergistic responses of biomass production to warming and elevated [CO$_2$] are not unrealistic (Norby & Luo, 2004).

The responses of plant biomass in combined treatment experiments relative to the sum of the single factor treatment responses are shown in Fig. 5. In the case of synergistic responses, individual experiments should be situated above the 1 : 1 line, which is clearly the exception rather than the rule. However, this is not that surprising *per se*, since warming will only tend to enhance the [CO$_2$] response if the response is actually suppressed by nutrient limitations. Similarly, elevated [CO$_2$] will only tend to increase the warming response if it helps to overcome a warming-induced water limitation. Therefore, synergistic responses should only be expected where nutrient limitation is currently suppressing the [CO$_2$] response and where water constraints are currently limiting the growth stimulation by warming. The general absence of a synergistic response therefore suggests that either current experiments rarely involve nutrient- or water-limited ecosystems, or that warming does not sufficiently mitigate nutrient limitation and/or elevated [CO$_2$] does not sufficiently mitigate drought.

In combination, warming and elevated [CO$_2$] clearly increase total and belowground biomass (Fig. 3c), but this effect is less than synergistic (Fig. 5), especially for aboveground biomass. This suggests the possible occurrence of antagonistic mechanisms. One such potential antagonistic mechanism is that both elevated [CO$_2$] and warming typically increase leaf area (Wullschleger *et al*., 2002; McCarthy *et al*., 2007; Way & Oren, 2010). Consequently, the evapotranspiration in the combined treatment might be increased in response to the higher vapor pressure deficit and higher leaf area, despite the improved WUE as a consequence of elevated [CO$_2$] alone. In this case, the combined [CO$_2$] and warming treatment would deplete soil water reserves more rapidly than warming alone (but see Morgan *et al*., 2011). Similarly, a reduction of root biomass (relative to the increased leaf area) as a consequence of higher nutrient availability due to the warming treatment might make plants more susceptible to periodic droughts (Way & Oren, 2010), possibly limiting the balancing effect of the increasing WUE in elevated [CO$_2$].

Differences in plant growth strategies might also affect the capacity of ecosystems to respond to a combined treatment. For example, Medlyn *et al.* (2001) have shown that stomatal conductance in evergreen trees is less responsive to elevated [CO$_2$], and therefore water savings might be lower, increasing their susceptibility to warming-induced droughts. If other biogeochemical processes (e.g. root exudation) differ in similar ways between species and ecosystems types, this might affect responses in a combined treatment as well. Furthermore,

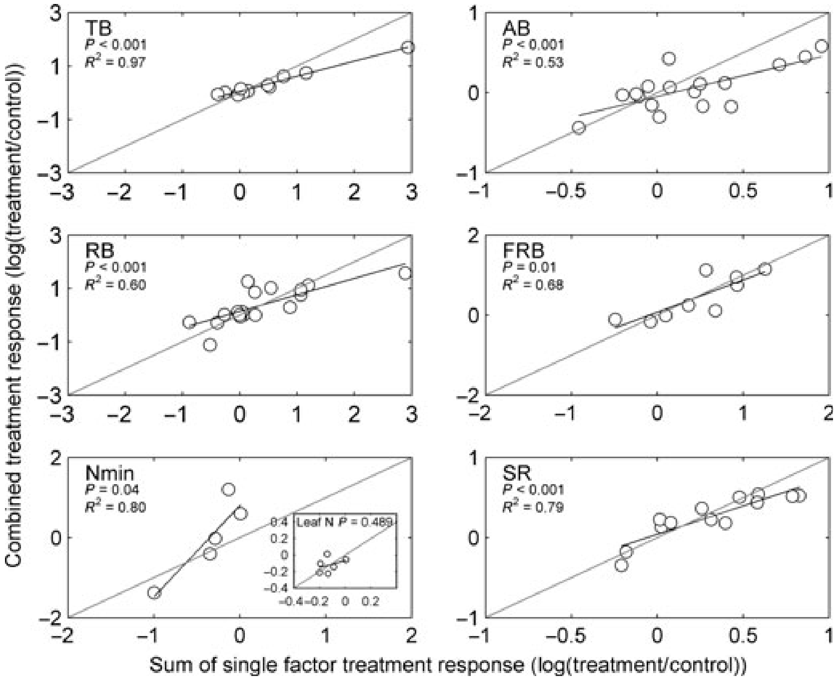

Fig. 5 Meta-analysis effect sizes for the calculated sum of single factor [CO$_2$] effects and single factor warming effects, plotted against the combined [CO$_2$] x warming effect sizes. Data are reported as log (Treatment/Control). Data listed are total biomass (TB), aboveground biomass (AB), root biomass (RB), fine root biomass (FRB), mineral N availability (Nmin), foliar N concentration (Leaf N), and soil respiration (SR). *P*-values and R^2 values for linear regressions between single factor and combined treatment effects are given. Correlations were considered statistically significant at $P < 0.05$.

increased competition in a mixed C_3 (favored by elevated [CO_2]) and C_4 (favored by warming) plant community might increase competition for resources and limit the full effect of both drivers (see Morgan *et al.*, 2011; for shift toward more C_4). Last, co-limitation of primary productivity by N and phosphorus (P) (Harpole *et al.*, 2011) may constrain combined effects of [CO_2] and warming when reduced N availability with [CO_2] is counteracted by reduced P availability with warming (Dijkstra *et al.*, in prep.). Such antagonistic responses appear to be the rule rather than the exception in the response of aboveground biomass, where the response to combined [CO_2] and warming is smaller than the response to [CO_2] alone in the vast majority of experiments (Fig. 3). Fine root biomass responded much less to warming than to [CO_2] enrichment, whether analyses encompassed all studies (Figs 1b and 2b), or when only studies that included both the single and combined treatments were evaluated (Fig. 3). Small responses of root biomass to warming are consistent with increased nutrient availability, which typically affects fine root biomass very little, but induces a substantial allocation shift in favor of aboveground biomass (Litton *et al.*, 2007; Brassard *et al.*, 2009).

Limitations and recommendations

Although the current set of experiments indicated a significant increase in biomass and soil respiration in response to elevated [CO_2] and warming, this may not be robust because the current set of experiments may not be large enough to equally represent the range of different ecosystem types. The amount of available data did not allow us to test for treatment duration effects, for differences among manipulation types or intensities, for differences among vegetation types, etc. This further highlights the urgent need for more multifactorial experiments. Nevertheless, with the currently available data, we have shown that the combined treatments elicited responses that were more similar to [CO_2]-only than to warming-only experiments. Therefore, model testing with data from [CO_2] enrichment-only experiments is to be preferred over testing with data from warming-only experiments.

Secondary effects of warming and [CO_2] enrichment (i.e. changes in water and nutrient availability) determine the ultimate response of terrestrial ecosystems. We were not able to test their influence due to a lack of data, or differences in reported parameters. Therefore, more attention should be given to standardized protocols for experimental design and measurements, not only for biomass production and ecosystem C fluxes, but especially for water availability/stress, as well as for nutrient availability.

We did not include precipitation changes in this analysis although they form an essential part of the changing climate and have been shown to affect responses in combined elevated [CO_2] and warming (e.g. N mineralization response at Brandbjerg, DK, Larsen *et al.*, 2011). Similarly, increasing amounts of reactive N deposition could strongly affect the responses observed here. The replication of combined [CO_2] and warming experiments on dry vs. wet, and nutrient-poor vs. –rich sites could be an alternative approach where both water and nutrient effects can be incorporated in analyses like ours.

Conclusions

Elevated [CO_2] and warming exert fundamentally different effects on C storage and C and nutrient cycling in terrestrial ecosystems. In a combined treatment, effects of elevated [CO_2] often dominated the response, suggesting a larger sensitivity of terrestrial ecosystems to rising [CO_2] compared to rising temperatures. This dominance of [CO_2] in the combined treatments is probably attributable to the larger imposed relative changes in [CO_2] than in temperature, as is consistent with projected changes. Responses to single factor treatments were rarely additive, and interactions may lead to overestimation of effects based on the single factor results. Our results suggest that ecosystem models should ideally be tested against results from multifactor experiments to optimize their model structures.

Acknowledgements

The authors acknowledge the support of the ESF-network CLIMMANI (Climate Change – Manipulation Experiments in Terrestrial Ecosystems). This research was partly funded by the UA-Research Centre of Excellence ECO. IAJ holds a Flemish National Science Foundation grant (FWO). WIJD held a James Cook University International Research Scholarship at the time of writing. SV is a postdoctoral research associate of the Fund for Scientific Research – Flanders. Funding for SL came from FP7 project ACQWA. CB and KL were supported by the Villum Kann Rasmussen Foundation through the CLIMAITE project. JSK received sabbatical support from the U.S. State Department Fulbright Program and the Belgian Francqui Foundation during the writing of this manuscript. RO was supported by the US Department of Energy, Office of Science, Biological and Environmental Research, and the Swedish Governmental Agency for Innovation Systems (VINNOVA). FAD acknowledges support from the Australian Research Council (Future Fellowship). The authors acknowledge Yolima Carrillo, Elise Pendall, and Dan LeCain for their work related to the PHACE site data.

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Supporting Information

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

Figure S1. Histograms presenting the frequency distribution of [CO_2] treatments in combined warming and elevated [CO_2] studies for total biomass (TB), aboveground biomass (AB), root biomass (RB), fine root biomass (FRB), soil respiration (SR), and mineral N availability (Nmin). Mean treatment intensity and standard deviations (SD) are given.
Figure S2. Histograms presenting the frequency distribution of temperature treatments in combined warming and elevated [CO_2] studies for total biomass (TB), aboveground biomass (AB), root biomass (RB), fine root biomass (FRB), soil respiration (SR), and mineral N availability (Nmin). Mean treatment intensity and standard deviations (SD) are given.
Table S1. General information about the sites included in the database. The experiments performed at these sites can include one of the treatments or species listed in the columns below. Site location, annual precipitation and temperature are given where available.
Table S2. All experiments included in the database are listed, fumigation and warming techniques used in the experiments, and the amount of [CO_2] or T increment are indicated.
Table S3. All experiments included in the database are listed, and stars indicate which experiment provided what kind of data.
Table S4. All experiments included in the database are listed, with the methodology used to obtain the respective datapoints. For more detailed methodologies, we refer to the source references (to be found in the supplementary Table S5).
Table S5. All experiments included in the database are listed. Source references used for the respective sites are given (Full references are given in supplementary Table S6).
Table S6. Full source references used in the database.

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