



Nitrogen and water availability control plant carbon storage with warming

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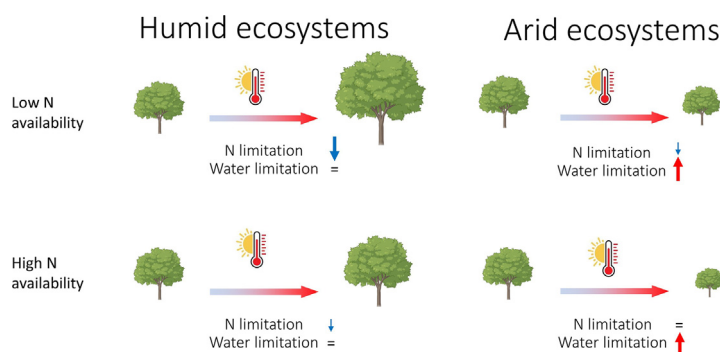
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HIGHLIGHTS

- Warming significantly increased above- and below-ground biomass.
- Warming induced change in biomass was best explained by soil C:N.
- Warming stimulated plant biomass more strongly in humid than in dry ecosystems.
- Warming increased plant growth in ecosystems where N was limiting plant growth.

GRAPHICAL ABSTRACT



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ABSTRACT

Plants may slow global warming through enhanced growth, because increased levels of photosynthesis stimulate the land carbon (C) sink. However, how climate warming affects plant C storage globally and key drivers determining the response of plant C storage to climate warming remains unclear, causing uncertainty in climate projections. We performed a comprehensive meta-analysis, compiling 393 observations from 99 warming studies to examine the global patterns of plant C storage responses to climate warming and explore the key drivers. Warming significantly increased total biomass (+8.4%), aboveground biomass (+12.6%) and belowground biomass (+10.1%). The effect of experimental warming on plant biomass was best explained by the availability of soil nitrogen (N) and water. Across the entire dataset, warming-induced changes in total, aboveground and belowground biomass all positively correlated with soil C:N ratio, an indicator of soil N availability. In addition, warming stimulated plant biomass more strongly in humid than in dry ecosystems, and warming tended to decrease root:shoot ratios at high soil C:N ratios. Together, these results suggest dual controls of warming effects on plant C storage; warming increases plant growth in ecosystems where N is limiting plant growth, but it reduces plant growth where water availability is limiting plant growth.

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1. Introduction

Terrestrial ecosystems around the world are experiencing unprecedented climate warming, with global average temperatures projected to increase between 1.1 and 6.4 °C over the next 100 years (IPCC, 2013). Rising temperatures can stimulate decomposition of soil organic matter (Chen et al., 2018), leading to a positive climate-carbon feedback (Arora et al., 2020; Nottingham et al., 2020). Counteracting this, plants may buffer the pace of global warming through enhanced photosynthesis, partly offsetting soil C losses (Lu et al., 2013).

Over the last three decades, numerous studies have aimed to quantify the response of plants to global warming by exposing them to experimental warming. Recent meta-analyses of these studies suggest that experimental warming generally stimulates plant biomass (Lin et al., 2010; Lu et al., 2013; Song et al., 2019), but individual studies also reported decreases (Lambrecht et al., 2007) and no changes in plant growth (Lim et al., 2019). Several factors have been suggested as potential drivers of the response of plant biomass to warming, including plant type (Lin et al., 2010), ecosystem type, warming method and experiment duration (Lu et al., 2013). The relative importance of these predictors remains unclear, creating uncertainty in climate projections (Bradford et al., 2016).

Warming generally increases N availability by stimulating decomposition rates, as observed across a wide range of experimental and environmental conditions (Rustad et al., 2001; Bai et al., 2013). Moreover, warming generally stimulates the production of ligninase (Chen et al., 2018), which could increase soil N availability because many N-containing molecules are physically and chemically shielded by lignified macromolecules (Moorhead and Sinsabaugh, 2006). Because N limits plant production around the world (LeBauer and Treseder, 2008; Terrer et al., 2019), these responses may stimulate plant growth, redistributing N from soils to plants and causing net ecosystem C storage (e.g. Shaver et al., 2000). Several experimental warming studies indeed suggest this is the case (e.g. Schmidt et al., 2002; Melillo et al., 2011). Other studies found that N additions reduce the positive effect or exacerbate negative effects of warming on plant growth (e.g. Chapin et al., 1995; Jonasson et al., 1999; Rasheed et al., 2020). Together, these findings suggest that soil N status is a key predictor of ecosystem responses to warming, and that warming will increase plant biomass most strongly in ecosystems where N is limiting plant growth. However, none of the aforementioned meta-analyses included soil N availability as a predictor for treatment effects across their datasets, making its role in determining the impact of warming unclear.

Plant responses to warming may also depend on climatic conditions (Song et al., 2019). Indeed, several studies suggest that in water-limited ecosystems, warming may suppress plant growth by decreasing soil moisture contents (Bai et al., 2013). Warming-induced reductions in soil moisture may increase drought stress in plants (e.g. Saleska et al., 1999; Winkler et al., 2016) and may limit soil N cycling in semiarid and arid regions (Bai et al., 2013). Based on these results, we hypothesized that N availability and water availability jointly determine plant growth responses to warming. To test our hypothesis, we synthesized 393 observations from 99 warming studies conducted in the field (Fig. 1, and Supplementary Text S1), separating responses of total biomass ($n = 94$), aboveground biomass ($n = 181$) and belowground biomass ($n = 118$), to evaluate the key drivers determining warming responses of plant biomass. We trained a random-forest meta-analysis model with this dataset to identify the underlying factors that best explain variation in the plant biomass response.

2. Materials and methods

2.1. Data collection

We collected published data on total, aboveground and belowground biomass from climate warming experiments conducted in the field. We used Web of Science, Google Scholar and the China National Knowledge Infrastructure database (CNKI) to gather a total of 99 studies on manipulative warming experiments published before December 2020 (Data S1, Notes

S1). Search terms were either “experimental warming” or “elevated temperature” or “climate change” and “plant production” or “plant biomass” or “total biomass” or “aboveground biomass” or “belowground biomass”. We only included the most recent data if variables were measured multiple times within the same experiment. We excluded studies that 1) did not report information on the experimental design (e.g., warming method, warming magnitude); 2) lasted <1 growing season; 3) applied warming treatments by transplanting soils along climate gradients; 4) showed differences in initial species composition between control and warmed plots. Some studies included in our dataset included multifactor global change experiments. For these studies, we only compared control and warmed plots under equivalent experimental conditions. We excluded observations at elevated CO₂ concentrations, as we intended to study the effect of warming under environmental conditions that are existing in the world today. Mean values and standard errors were taken from tables or extracted from figures using Web PlotDigitizer (<https://apps.automeris.io/wpd/>). Our dataset is more than twice as large as those used in recent meta-analyses on the same topic (Lin et al., 2010; Lu et al., 2013; Song et al., 2019), and includes additional 61 studies that were not included in any of these previous analyses.

For each experiment in our dataset, we tabulated information on N addition, longitude, latitude, mean annual precipitation (MAP), mean annual temperature (MAT), warming magnitude (ΔT), experimental duration, plant type, ecosystem type and warming method. We also tabulated soil C:N ratio, an indicator for soil N availability (e.g. Ordoñez et al., 2009; Van Sundert et al., 2020; Terrer et al., 2019). Because plant N acquisition strategies depend on mycorrhizal association of the host plant (Terrer et al., 2016), we also tabulated information on the mycorrhizal association of the dominant species at each experimental site, using the database of Wang and Qiu (2006). Data on MAT and MAP were obtained from the WordClim database (<http://www.worldclim.org/>) if they were not reported in the reference. Soil C:N data were obtained from the reference, or from other studies conducted within the same experiment. If soil C:N data were not reported in the literature, which was the case for 25 studies in our dataset, we obtained these data (for 0–15 cm soil depth) from the SoilGrids database (<https://www.isric.org/explore/soilgrids>). Soil C:N ratios vary with depth (e.g. Marty et al., 2017), but studies in our dataset reported soil C:N ratios across a range of sampling depths. To account for this source of uncertainty, we repeated our analysis using soil C:N data derived from SoilGrids (see Materials and methods) for all observations in our dataset, thereby assuming the same sampling depth for all experiments. For each experiment in our dataset we calculated the aridity index (AI) as the ratio of annual precipitation over potential evaporation; the latter term was obtained from the WorldClim database. Based on the AI, we classified experiments as arid ($AI < 0.2$), semi-arid ($0.2 \leq AI < 0.5$), subhumid ($0.5 \leq AI < 0.65$) or humid ($0.65 \leq AI$) (Middleton and Thomas, 1997). In total, we included 12 predictors of warming effects in our analysis (Supplementary Table S1).

2.2. Meta-analysis

We quantified the effect of warming on total, aboveground and belowground biomass by calculating the natural log of the response ratio (LnR), a metric commonly used in meta-analysis (Hedges et al., 1999). We weighted LnR by the inverse of its variance and estimated missing variances using the average coefficient of variation across our data set.

We used random-forest model selection to identify the most important predictors of the warming effects on total, aboveground and belowground biomass, following the same approach as Terrer et al. (2019, 2021). In short, we conducted variable pre-selection by including the 12 predictors in the R package *metaforest* (Van Lissa, 2017) with 10,000 iterations, replicated 100 times with a recursive algorithm in the *preselect* function from the R package *metafor* (Viechtbauer, 2010). Moderators that consistently displayed negative variable importance (i.e., that showed a reduction in predictive performance) were dropped using the *preselect_vars* function. Moderators that improved predictive performance were then carried forward to optimize the model. Parameters of the *metaforest* model were optimized using the train function from the *caret* package (Kuhn, 2008). Unlike maximum likelihood

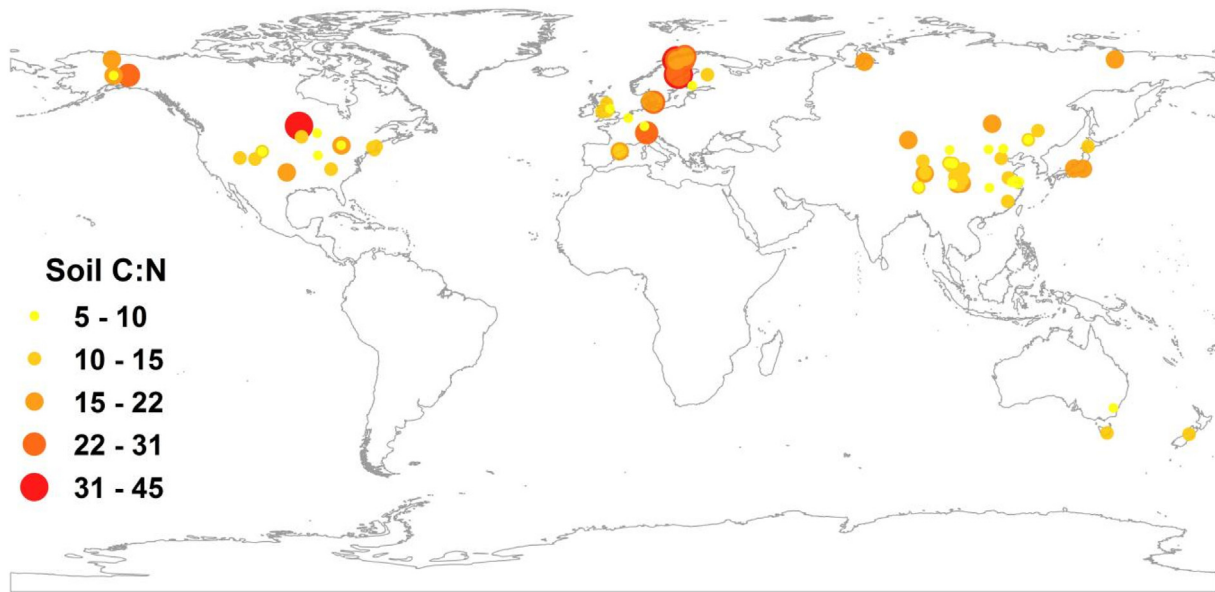


Fig. 1. Geographical distribution of experimental sites included in our dataset. The colour of each data point indicates the soil C:N value at the corresponding site.

model-selection approaches, this method can handle many potential predictors and their interactions and considers nonlinear relationships.

Meta-analysis was conducted using the *rma.mv* function in *metafor*, including the variable “study” as a random factor to account for non-independence of observations derived from the same study. The effects of warming were considered significant if the 95 % confidence interval did not overlap with zero. The results of LnR were back-transformed and reported as the percentage change under warming (i.e. $100 \times (e^{\text{LnR}} - 1)$)

to ease interpretation. We evaluated the impacts of soil C:N on warming-induced change in total, aboveground and belowground biomass using linear regression analysis in R. We also assessed the effect of N availability in the subset of studies that included warming $\times$ N factorial experiments, comparing plant responses to warming between high vs. low N treatments for total (Data S2), aboveground (Data S3) and belowground (Data S4) biomass. By keeping all other experimental factors constant, this analysis allowed us to test directly whether plant biomass responses to warming

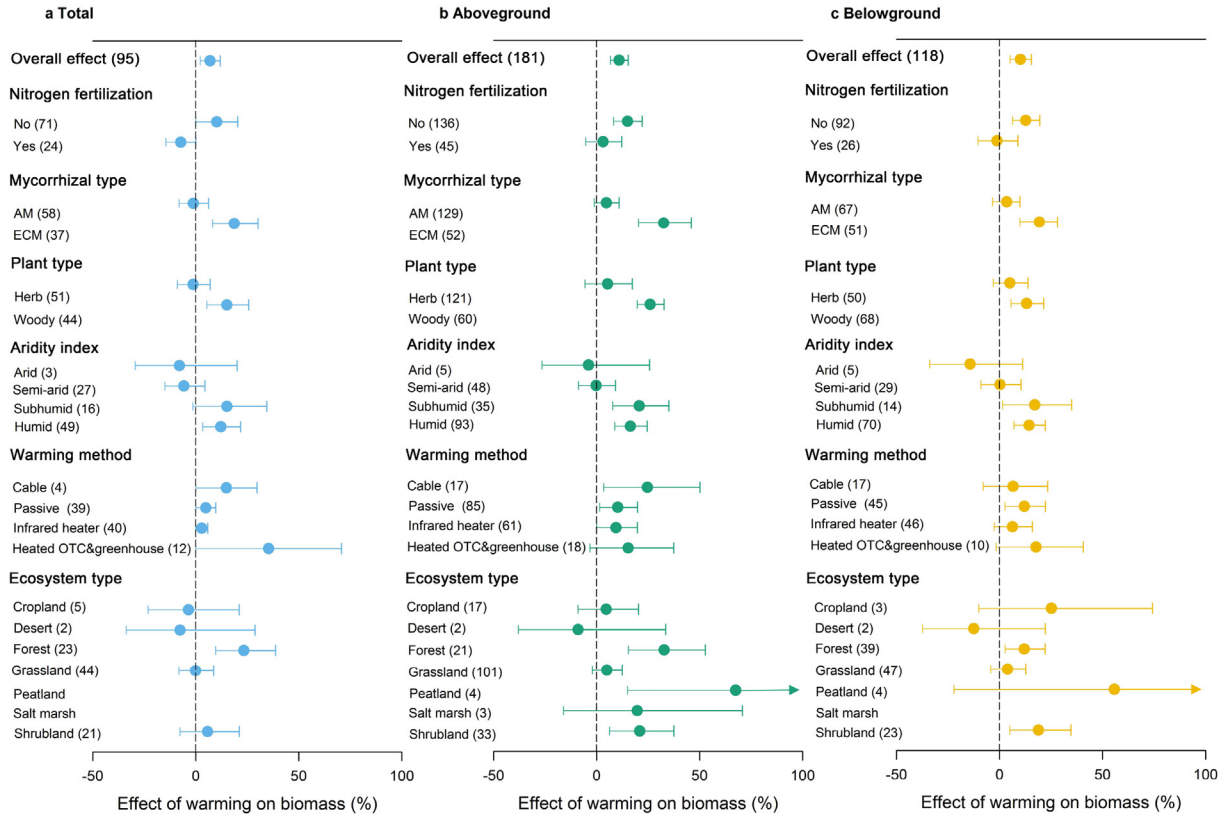


Fig. 2. Meta-analysis of the effect of experimental warming on total plant biomass (a), aboveground biomass (b) and belowground biomass (c) across different factors. Error bars represent 95 % confidence intervals; sample sizes are shown in parentheses. Arrows represent 95 % confidence intervals that extend beyond the limits of the plot. AM, arbuscular mycorrhizae; ECM, ectomycorrhizae; OTC, open top chamber.

depend on soil N availability. Due to a lack of data, the same approach could not be applied to warming $\times$ water factorial experiments.

3. Results

We found that warming significantly increased total biomass by 8.4 % (Fig. 2; 95 % confidence interval: 3.3 %–13.8 %), aboveground biomass by 12.6 % (8.1–17.4 %) and belowground biomass by 10.1 % (4.8–15.7 %). Across the experiments that reported both above- and belowground biomass, warming significantly increased the root:shoot ratio by 3.6 % (1.1–6.1 %). Warming significantly increased total biomass, aboveground biomass and belowground biomass of woody plants while no effect was found for herbaceous plants.

Across these variables, the effects of warming on total, above- and belowground biomass were best predicted by soil C:N ratio and AI (Fig. 3). Soil C:N ratio positively correlated with warming-induced changes in total biomass ($R^2 = 0.16$, $P < 0.001$), aboveground biomass ($R^2 = 0.26$, $P < 0.001$) and belowground biomass ($R^2 = 0.22$, $P < 0.001$) (Fig. 3). These correlations were significant within the individual subsets of studies on herbaceous and woody plants (Fig. S1). When we repeated our analysis using soil C:N ratios derived from SoilGrids for all studies in our dataset, treatment effects again increased with soil C:N for both total, aboveground and belowground biomass (Fig. S2).

The response of root:shoot ratios to warming decreased with soil C:N ratio (Fig. 4; $P < 0.05$), with positive treatment effects dominating the

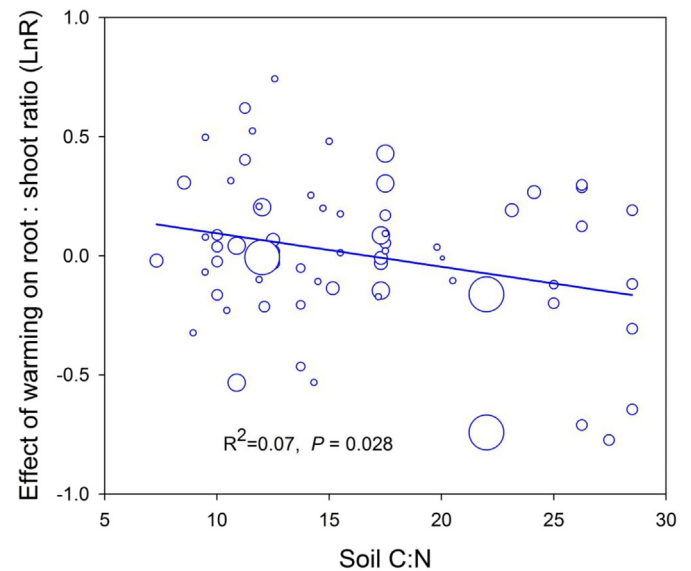


Fig. 4. The relation between root:shoot responses to warming (LnR) and soil C:N. Results are based on 67 experiments with observations for both aboveground and belowground biomass. Dots represent the individual experiments in the meta-analysis, with dot sizes proportional to the weight of the effect size.

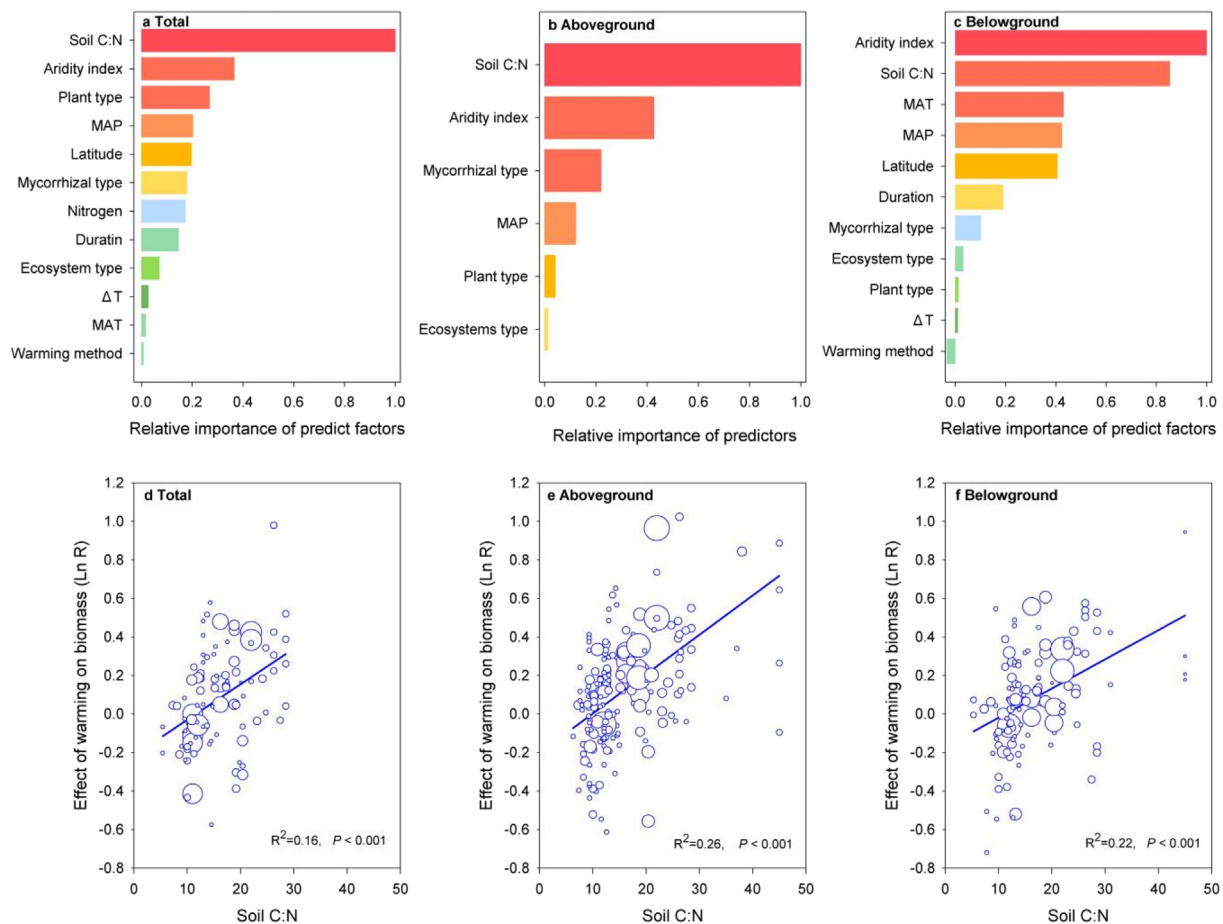


Fig. 3. The relative importance of predictors for the effect of warming on total biomass (a), aboveground biomass (b) and belowground biomass (c), and the relation between soil C:N and the effect of warming on total biomass (d), aboveground biomass (e) and belowground biomass (f). One LnR value for aboveground biomass fell outside the upper limit of the plot e; this data point was included in all statistical analyses. Results are based on 94 observations for total biomass, 181 observations for aboveground biomass and 118 observations for belowground biomass. Dots in panels (d)–(f) represent the individual experiments in the meta-analysis, with dot sizes proportional to the weight of the effect size.

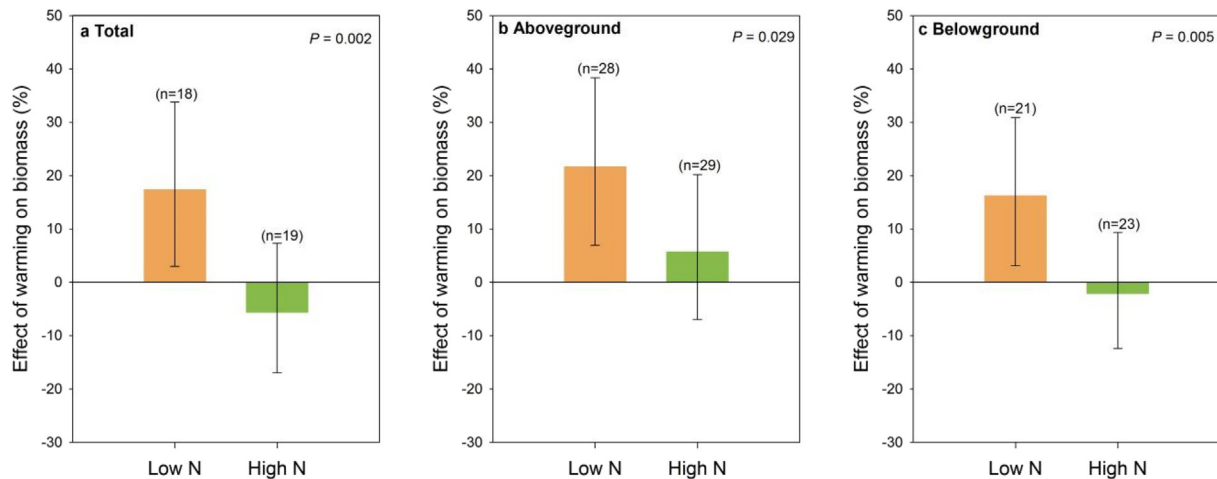


Fig. 5. Effect of warming on plant biomass for low and high N additions in warming $\times$ N factorial experiments. Results are shown for total biomass (a), aboveground biomass (b) and belowground biomass (c). The total number of observations included in each category is displayed in parentheses. Error bars indicate 95 % confidence intervals.

lower half of the soil C:N range, and negative treatment effects dominating the upper half.

Within the subset of data from factorial warming $\times$ N addition experiments, the positive effects of warming on total, aboveground and belowground biomass were all significantly higher in the low N treatments than in the high N treatments (Fig. 5). In addition to soil C:N, AI was also an important predictor for plant growth responses to warming, with plants in humid climates responding more strongly to warming than in dry climates (Figs. 2, S3). Across our dataset, soil C:N ratios increased with AI ($P < 0.05$; Fig. S4).

4. Discussion

Our finding that warming on average increases plant biomass confirms previous meta-analyses (Lin et al., 2010; Lu et al., 2013; Song et al., 2019), and our analysis identified N as a key driver of plant growth responses to warming. Warming responses are diminished in low soil C:N regions, because plant growth is less limited by the amount of available N (Chapin et al., 2002). Soil C:N is a stronger predictor for total and aboveground biomass responses to warming than root biomass responses, consistent with previous meta-analyses showing that increases in N availability stimulate aboveground biomass more strongly than root biomass (e.g. Lu et al., 2011).

The key role of soil N availability is further supported by our analysis of factorial warming $\times$ N addition experiments; our finding that N additions negated the positive effect of warming on plant biomass confirms that warming stimulates plant growth most strongly at low soil N availability and suggests that warming enhances plant growth by increasing N availability. These results partly confirm Song et al. (2019), who found a significant interaction between warming and N addition in their analysis of factorial warming $\times$ N experiments for aboveground biomass, but not for total and belowground plant biomass. This difference between our study and Song et al. (2019) possibly reflects the larger size of our dataset, increasing statistical power to detect differences between experimental categories.

In the temperate zone, soils under herbaceous vegetation typically have lower C:N ratios than soils under woody vegetation (e.g. Cotrufo et al., 2019). Thus, the correlation between soil C:N and treatment effects on plant biomass could in theory be driven by differences between plant functional types rather than by soil C:N per se. However, the same correlations outlined above were also significant within the individual subsets of studies on herbaceous and woody plants (Fig. S1). Together, these findings provide further support for our interpretation that the response of plant biomass to warming is largely determined by soil N availability.

Climate warming slightly decreased total, aboveground and belowground biomass at low soil C:N ratios (Fig. 3). These results likely reflect the negative effect of warming exacerbating drought stress in dry

ecosystems (Xu et al., 2013), which are characterized by low C:N ratios (Fig. S4; Miller et al., 2004). This explanation is supported by the overall importance of AI as a predictor (Fig. 2; Song et al., 2019), and by individual studies indicating that water addition negates negative effects of warming on plant growth in dry climates (e.g. Zhao et al., 2019; Yu et al., 2019). On the other hand, N addition stimulates plant growth more strongly in humid climates than in dry climates (Xia and Wan, 2008). Together, these findings suggest that plant growth responses to warming are dictated by Liebig's law of the minimum; warming increases plant growth in ecosystems where N is limiting plant growth by increasing N availability, but it reduces plant growth where water availability is limiting plant growth by increasing drought stress (Figs. 2, S3). This interpretation is consistent with the negative correlation we found between soil C:N and the effect of warming on root:shoot ratios. Plants typically shift carbon allocation aboveground following an increase in N availability (e.g. Lu et al., 2011), especially in systems where N is limiting, i.e. in soils with high C:N ratios, thereby decreasing root:shoot ratios. In contrast, N is less likely to be limiting plant growth in soils with low C:N ratios. Because ecosystems with low soil C:N ratios tend to be relatively dry, warming-induced drought stress increases carbon allocation to roots (e.g. Zhou et al., 2016; Song et al., 2019), thereby increasing root:shoot ratios.

The uneven distribution of experiments around the globe limits predictions. Warming experiments are mainly clustered in North America, Europe and China, with only a few in the Southern Hemisphere and at high latitudes in the Northern Hemisphere. Our dataset also does not include any studies conducted in the tropics. This spatial bias is important, because the largely unstudied tropical forests contain the largest reservoir of biomass C, and some models suggest that warming will decrease the tropical land C sink (e.g. Cox et al., 2000). Indeed, a study published after our literature search had finished suggests that experimental warming decreases root growth in a humid tropical forest with relatively low soil C:N ratios (Yaffar et al., 2021). This warming experiment was affected by two hurricane events and may therefore not be representative for large areas of tropical forests. Nonetheless, these findings suggest that the results of our meta-analysis possibly cannot be extrapolated to the tropics and emphasize the need for more experimental warming studies in this climate zone. Clearly, to improve predictions of carbon-climate feedbacks we need a better understanding of the processes driving the response of tropical ecosystems to warming (Wang et al., 2014; Cavaleri et al., 2015).

Warming-induced increases in plant growth may decrease over time, as mineralizable N pools will eventually deplete following increases in decomposition rates and plant N uptake (Lim et al., 2019). Our finding that warming responses did not depend on experiment duration suggests that this may not happen globally within the time frame of the studies in our dataset (that is, 1–14 years). Predicting dynamics of warming-induced

increases in N availability beyond this range requires longer-term experiments and modelling efforts. Indeed, early terrestrial ecosystem models already predicted that warming stimulates plant growth by stimulating N mineralization, and that warming stimulates plant growth most strongly in N limited ecosystems (e.g. Melillo et al., 1993). The latest generation of Earth system models now mostly include N limitations on plant growth as well (Davies-Barnard et al., 2020). Most of these models predict a decrease in global NPP with warming (Arora et al., 2020), largely because projected temperatures exceed the optimal temperature for photosynthesis in the tropics (Ziehn et al., 2021). However, some stimulation of plant growth occurs by warming through increased soil N availability (Arora et al., 2020), causing smaller warming-induced decreases in global NPP in the ESMs that include the N cycle relative to those that do not (Ziehn et al., 2021). Our findings may inform these models by identifying quantitative relationships between the plant growth response to warming and empirical indicators of N availability that are spatially explicit at the global scale (Terrer et al., 2019). Similarly, droughts will increase with future climate warming (Lehner et al., 2017; Park et al., 2018), causing drylands to expand (Huang et al., 2016). Therefore, in addition to soil N availability, water limitation of plant growth and plant traits associated with drought stress resistance (e.g. Rowland et al., 2021) will be key to predicting future plant C storage.

CRedit authorship contribution statement

KJvG conceived the study. GZ, NvT and KJvG compiled the dataset. GZ, AH, KJvG and CT conducted the statistical analyses. GZ, XZ and KJvG wrote the first draft of the manuscript, with substantial input from all authors.

Data availability

The datasets used in this study are available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.wm37pvmqv>.

Declaration of competing interest

The authors declared no conflict of interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2022.158243>.

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