Nitrogen availability controls plant carbon storage with warming

Guiyao Zhou

East China Normal University

César Terrer

Stanford University <https://orcid.org/0000-0002-5479-3486>

Bruce Hungate

Northern Arizona University <https://orcid.org/0000-0002-7337-1887>

Natasja van Gestel

Texas Tech University <https://orcid.org/0000-0002-7885-9793>

Xuhui Zhou

East China Normal University <https://orcid.org/0000-0002-2038-9901>

Kees Jan van Groenigen (✉ KJ.VanGroenigen@exeter.ac.uk)

University of Exeter <https://orcid.org/0000-0002-9165-3925>

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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, the key drivers determining responses of plants to warming remain unclear, causing uncertainty in climate projections. Using meta-analysis, we show that the effect of experimental warming on plant biomass is best explained by soil nitrogen (N) availability. Warming-induced changes in total, aboveground and belowground biomass all positively correlated with soil C:N ratio, an indicator of soil N availability. In factorial N $\times$ warming experiments, warming increased plant biomass more strongly under low N than under high N availability. Together, these results suggest that warming stimulates plant C storage most strongly in ecosystems where N limits plant growth. Thus, incorporating the soil N status of ecosystems into Earth system models may improve predictions of future carbon-climate feedbacks.

1. Introduction

Terrestrial ecosystems around the world are experiencing unprecedented climate warming, with global average temperatures projected to increase between 1.1 - 6.4 °C over the next 100 years (IPCC, 2013). Rising temperatures can stimulate decomposition of soil organic matter, leading to a positive climate-carbon feedback (Arora 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).

Experimental warming generally stimulates plant biomass (Song et al. 2019), but decreases (Lambrecht et al. 2007) and no changes in plant growth (Lim et al. 2019) have also been reported. Numerous factors have been suggested as potential drivers of the response of plant biomass to warming, including climate (Song et al. 2019), plant type (Lin et al. 2011), 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).

Nitrogen regulates plant production around the world (LeBauer and Treseder 2008; Terrer et al. 2019). Warming generally increase 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 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 (Moorehead & Sinsabaugh 2007). Thus, we hypothesized that N availability is the key factor determining plant growth responses to warming, explaining more variation than any of the previously suggested determinants. In that case, warming would stimulate plant growth most strongly in ecosystems where N limits plant growth the most.

To test our hypothesis, we synthesized 350 observations from 86 warming studies conducted in the field (Supplementary Fig. S1, and Supplementary Data S1), separating responses of total biomass (n=84),

aboveground biomass (n=159) and belowground biomass (n=107), 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

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 86 studies on manipulative warming experiments published before 2021 (Supplementary Data S1, Supplementary 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 from each experimental site. We excluded studies that 1) did not report information on the experimental design (e.g., warming method, warming magnitude); 2) lasted less than 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.

For each experiment in our dataset, we tabulated information on N addition, soil C:N (an indicator for soil N availability; Terrer et al. 2019), longitude, latitude, mean annual precipitation (MAP), mean annual temperature (MAT), warming magnitude (ΔT), experimental duration, plant type, ecosystem type and warming method (see Supplementary Data S1). 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 & Qiu (2006). In total, we included 11 predictors of warming effects in our analysis (Supplementary Table S1).

Mean values and standard errors were taken from tables or extracted from figures using Web PlotDigitizer (<https://apps.automeris.io/wpd/>). Data on MAT and MAP were obtained from the WorldClim database (www.worldclim.org/) if they were not reported in the reference. Soil C:N data were obtained from the reference, from other studies conducted at the same experimental site, or from the SoilGrids database (<https://www.isric.org/explore/soilgrids>) if they were not reported.

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 11 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 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. By keeping all other experimental factors constant, this analysis allowed us to test directly whether plant biomass responses to warming depend on soil N availability.

3. Results

We found that warming significantly increased total biomass by 8.4% (Fig. 1; 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%). Given the strong variation in treatment effects across factors (Fig. 1), we used a random-forest approach to quantify the importance of the 11 potential predictors included in our analysis. Across these variables, the effects of warming on total, above- and belowground biomass were indeed best predicted by soil C:N ratio (Fig. 2). Soil C:N ratio positively correlated with warming-induced changes in total biomass ($R^2=0.19$, $P < 0.001$), aboveground biomass ($R^2=0.22$, $P < 0.001$) and belowground biomass ($R^2=0.16$, $P < 0.001$), suggesting that warming stimulates plant growth most strongly in regions where N limits plant growth (Fig. 2). This relation between soil C:N ratio and treatment effects held over a range of experimental (Supplementary Fig. S2) and climatic conditions (Supplementary Fig. S3). 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 under low N than under high N availability (Fig. 3).

4. Discussion

Our finding that warming on average increases plant biomass confirms previous meta-analyses (Lin et al. 2011; Lu et al. 2013; Song et al., 2019). However, we for the first time identify soil N availability as the key driver of plant growth responses to warming. These 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). In fact, our results suggest that climate warming slightly decreased total, aboveground and belowground biomass at low soil C:N ratios (Fig. 2), possibly because the negative effect of warming on soil water availability (Xu et al. 2013). 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.

The uneven distribution of experiments around the globe limits predictions. Warming experiments are mainly clustered in North America, Europe and China (Supplementary Fig. S1), with only a few in the Southern Hemisphere and at high latitudes in the Northern Hemisphere, and none in the tropics. This is important, because 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). Thus, 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).

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 will not happen 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, the latest generation of Earth system models now mostly include N limitations on plant growth (Davies-Barnard et al. 2020). These models therefore typically predict some stimulation of plant growth by warming, through increased soil N availability (Arora et al. 2020). 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).

5. Conclusion

This meta-analysis underlines the key role of soil N availability in driving plant growth with climate warming. Specifically, our results indicate that soil C:N ratio, an indicator of soil N availability, explained more variation in plant growth responses to warming than any of the previously suggested determinants. Thus, incorporating the soil N status of ecosystems into future Earth system models will improve projections for ecosystem responses and feedbacks to climate change.

Declarations

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Figures

Figure 1

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.

Figure 2

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). Results are based on 84 observations for total biomass, 159 observations for aboveground biomass and 107 observations for belowground biomass.

Figure 3

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.

Supplementary Files

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