Nitrogen availability controls plant carbon storage with warming

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Article

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Abstract

Plants may slow global warming through enhanced growth, thereby stimulating 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, suggesting that warming stimulates plant C storage most strongly in ecosystems where N limits plant growth.

Background

Terrestrial ecosystems around the world are experiencing unprecedented climate warming, with global average temperature 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 can increase N availability by stimulating decomposition rates, as observed across a wide range of experimental and environmental conditions (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 spanning the globe (Supplementary Fig. 1 and Supplementary Data 1), 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.

We found that warming significantly increased total biomass by 8.4% (95 confidence interval: 3.3 to 13.8%), aboveground biomass by 12.6% (8.1 to 17.4%) and belowground biomass by 10.1% (4.8 to 15.7%). Across a broad range of variables – including climate, experimental, vegetation and soil characteristics – the effect of warming on both above- and belowground biomass was indeed best predicted by soil C:N ratio (Fig. 1), an indicator for soil N availability (Terrer et al. 2019). 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. 1). This relation between soil C:N ratio and treatment effects held over a range of experimental (Supplementary Fig. 2) and climatic conditions (Supplementary Fig. 3). The response is 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. 1), possibly because the negative effect of warming on soil water availability (Xu et al. 2013). This interpretation is further supported by results from factorial warming × N addition experiments. In these 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. 2).

The uneven distribution of experiments around the globe limits predictions. Warming experiments are mainly clustered in North America, Europe and China (Supplementary Fig. 1), 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 (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). Incorporating the soil N status of ecosystems into future Earth system models will improve projections for ecosystem responses and feedbacks to climate change.

Materials And Methods

Data collection

We collected published and unpublished data on total, aboveground and belowground biomass from climate warming experiments conducted in the field. We used 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 1, Supplementary Notes 1). 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) combined warming with other global change treatments (e.g. elevated CO_2); 3) lasted less than 3 months; 4) applied warming treatments by transplanting soils along climate gradients.

For each experiment in our dataset, we tabulated information on N addition, soil C:N, longitude and latitude, mean annual precipitation (MAP), mean annual temperature (MAT), warming magnitude (ΔT), experimental duration, plant type, ecosystem type and warming method (see Supplementary Table 1). Because plant N acquisition strategies depend on mycorrhizal association of the host plant (Terrer et al. 2016), we tabulated information on the mycorrhizal association of the dominant species at each experimental site, using the database of Wang & Qiu (2006).

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.

Meta-analysis was conducted using the “rma.mv” function in the R package “metafor” (http://cran.r-project.org/web/packages/metafor/index.html), 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., $100 \times (e^{LnR} - 1)$) to ease interpretation.

We used random-forest model selection to identify the most important predictors of the warming effects on total, aboveground and belowground biomass (Terrer et al. 2019). This approach accounts for non-linear relations between effect size and predictors and their interactions. We included all predictors in a bootstrapped random-forest meta-analysis recursive preselection in the R package “metaforest”. We trained a random-forest meta-analysis with preselected predictors and then calculated the variable importance of the warming effects on plant biomass. 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 assessed the effect of N availability using studies that included warming × N factorial experiments, comparing plant responses to warming between high vs. low N treatments.

References

Arora, V. K., Katavouta, A., Williams, R. G., Jones, C. D., Brovkin, V., Friedlingstein, P., ... & Ziehn, T. (2020). Carbon–concentration and carbon–climate feedbacks in CMIP6 models and their comparison to CMIP5 models. *Biogeosciences*, **17(16)**, 4173-4222.

Bai, E., Li, S.L., Xu, W.H., Li, W., Dai, W.W., Jiang, P. A meta-analysis of experimental warming effects on terrestrial nitrogen pools and dynamics. *New Phytologist* **199**, 441-451 (2013).

Bradford, M. A., Wieder, W. R., Bonan, G. B., Fierer, N., Raymond, P. A., Crowther, T. W. Managing uncertainty in soil carbon feedback to climate change. *Nature Climate Change* **6**, 751-758 (2016).

Chapin, II.F.S., Matson, P.A., Mooney, H.A. Principles of Terrestrial Ecosystem Ecology. Springer, New York, NY, USA (2002).

Chen, J., Luo, Y.Q., García-Palacios, P., Cao, J., Dacal, M., Zhou, X.H., Li, J.W., Xia, J.Y., Niu, S.L., Yang, H.Y. Shelton, S., Guo, W., van Groenigen, K.J. Differential responses of carbon-degrading enzyme activities to warming: implications for soil respiration. *Global Change Biology* **24**, 4816-4826 (2018).

Cox, P. M., Betts, R. A., Jones, C. D., Spall, S. A. & Totterdell, I. J. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature* **408**, 184–187 (2000)

Davies-Barnard, T., Meyerholt, J., Zaehle, S., Friedlingstein, P., Brovkin, V., Fan, Y., ... & Wiltshire, A. J. (2020). Nitrogen cycling in CMIP6 land surface models: progress and limitations. *Biogeosciences*, 17(20), 5129-5148.

Hedges LV, Gurevitch J, Curtis PS (1999) The meta-analysis of response ratios in experimental ecology. *Ecology* **80**, 1150-1156

IPCC (ed.) (2013). Climate change 2013: The physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK/New York, NY, USA.

Lambrecht, S.C., Loik, M.E., Inouye, D.W, Harte, J. Reproductive and physiological responses to simulated climate warming for four subalpine species. *New Phytologist* **173**, 121-134 (2007).

LeBauer, D. S., & Treseder, K. K. (2008). Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. *Ecology*, **89(2)**, 371-379.

Lin, D.L., Xia, J.Y., Wan. S.Q. Climate warming and biomass accumulation of terrestrial plants: a meta-analysis. *New Phytologist* **188**, 187-198 (2010).

Lu M., Zhou, X.H., Yang, Q., Li, H., Luo, Y.Q., Fang, C.M., Chen, J., Yang, X, Li, B. Responses of ecosystem carbon cycle to experimental warming: a meta-analysis. *Ecology* **94**, 726-738 (2013).

Moorhead, D. L., & Sinsabaugh, R. L. (2006). A theoretical model of litter decay and microbial interaction. *Ecological Monographs*, 76(2), 151-174.

Song, J., Wan, S., Piao, S., Knapp, A. K., Classen, A. T., Vicca, S., ... & Zheng, M. (2019). A meta-analysis of 1,119 manipulative experiments on terrestrial carbon-cycling responses to global change. *Nature ecology & evolution* **3(9)**, 1309-1320.

Terrer, C., Vicca, S., Hungate, B. A., Phillips, R. P., & Prentice, I. C. (2016). Mycorrhizal association as a primary control of the CO_2 fertilization effect. *Science*, **353(6294)**, 72-74.

Terrer, C., Jackson, R.B., Prentice, C., Keenan, T.F., Kaiser, C., Vicca, S., Fisher, J.B., Reich, P.B., Stocker, B.D., Hungate, B.A., Peñuelas, J., McCallum. I., Soudzilovskaia, N.A., Cernusak, L.A., Talhelm, A.F., Sundert, K.V., Piao, S.L., Newton, P,C.D., Hovenden, M.J., Blumenthal, D.M., Liu, Y.Y., Müller, C.,Winter, K., Field, C.B.,Viechtbauer, W.,Van Lissa,C.J., Hoosbeek, M.R.,Watanabe, M., Koike, T., Leshyk, V.O., Wayne Polley, H., Franklin O. Nitrogen and phosphorus constrain the CO_2 fertilization of global plant biomass. *Nature Climate Change* **9**, 684-689 (2019).

Wang, B. Qiu, Y.L. Phylogenetic distribution and evolution of mycorrhizas in land plants. *Mycorrhiza* **16**, 299-363 (2006).

Wang, X. et al. A two-fold increase of carbon cycle sensitivity to tropical temperature variations. *Nature* 506, 212–215 (2014).

Xu, W., Yuan, W., Dong, W., Xia, J., Liu, D., & Chen, Y. (2013). A meta-analysis of the response of soil moisture to experimental warming. *Environmental Research Letters*, 8(4), 044027.

Figures

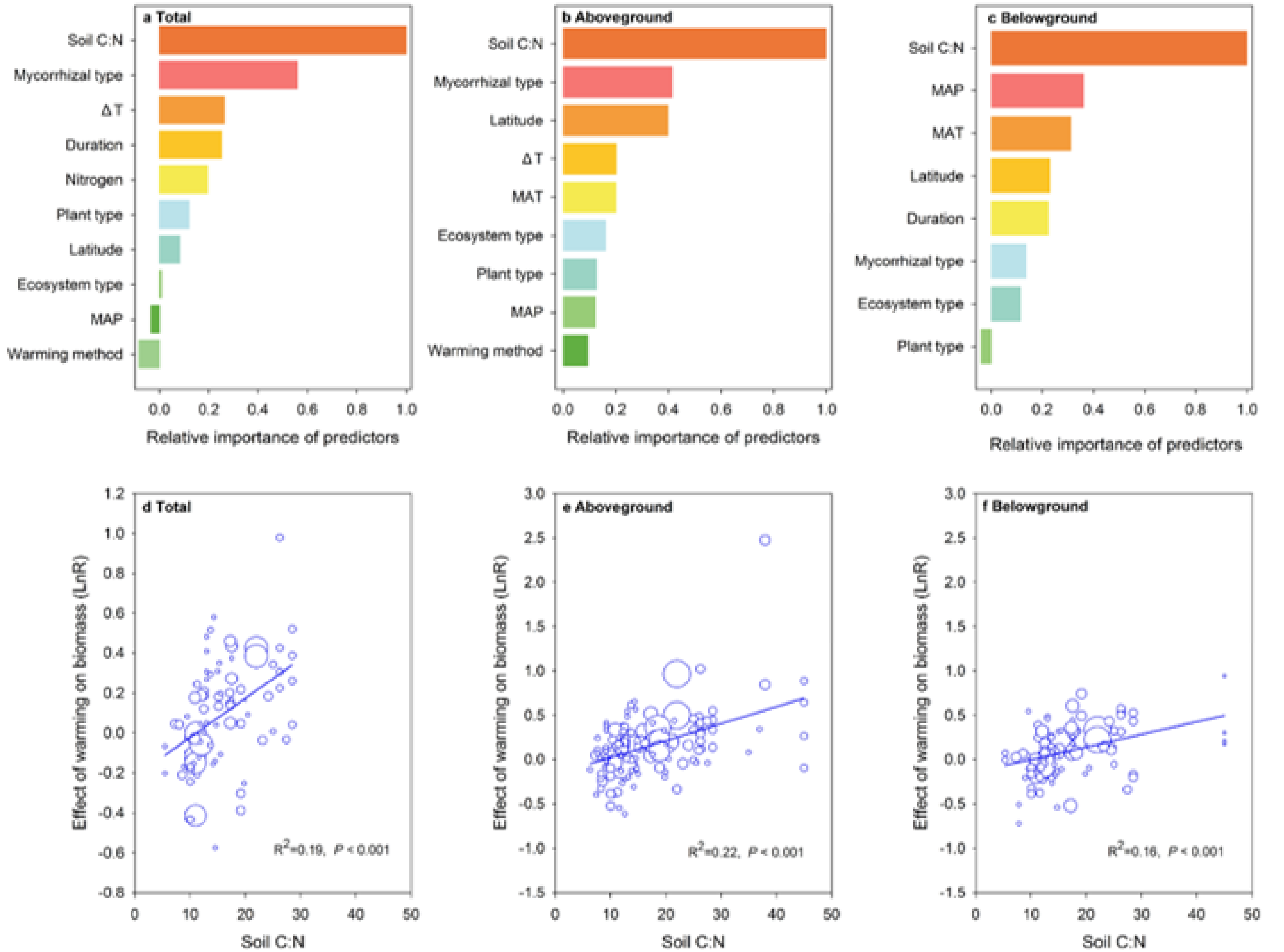

Figure 1

Potential predictors of the response of plant biomass to warming a-f. 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.

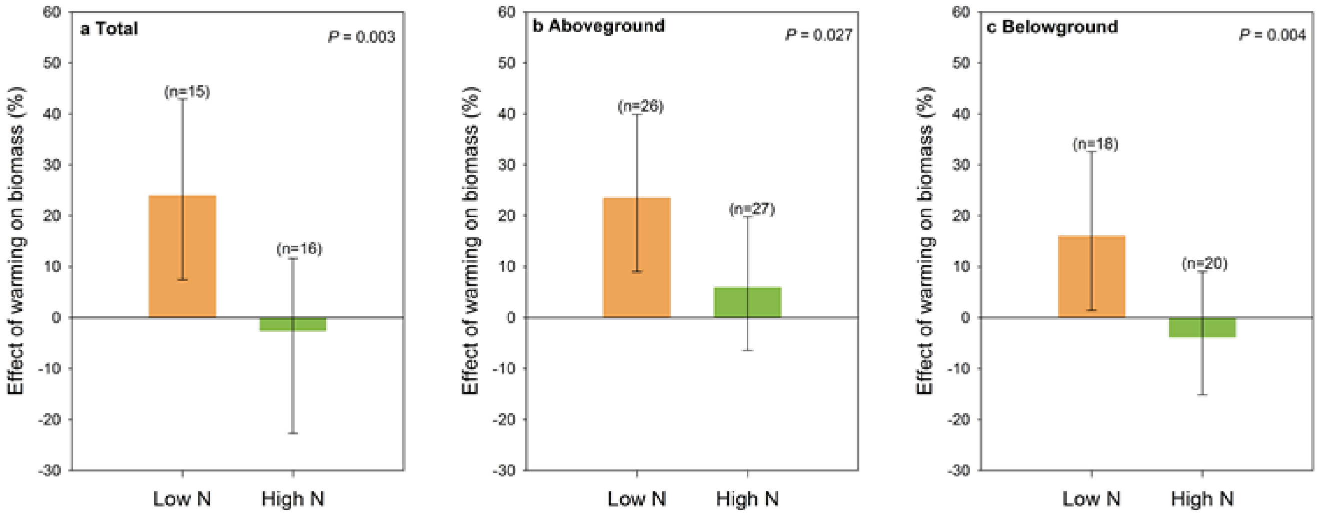

Figure 2

Effect of warming on plant biomass for low and high N additions in warming × N factorial experiments. Results 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

This is a list of supplementary files associated with this preprint. Click to download.

- Supplementarymaterial.docx
- DataS1.xlsx