



# Temperature accelerates the rate fields become forests

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Edited by Robert E. Dickinson, University of Texas at Austin, Austin, TX, and approved March 22, 2018 (received for review September 21, 2017)

**Secondary succession, the postdisturbance transition of herbaceous to woody-dominated ecosystems, occurs faster at lower latitudes with important ramifications for ecosystem processes. This pattern could be driven by the direct effect of temperature on tree growth; however, an alternative mechanism is tree–herb competition, which may be more intense in more fertile northern soils. We manipulated soil fertility and herbaceous species composition in identical experiments at six sites spanning the Eastern United States (30–43° N) and monitored the growth and survival of four early successional trees. Tree seedling mass 2 years after sowing was strongly associated with site differences in mean growing season temperature, regardless of species or soil treatment. The effect of temperature was twofold: seedlings grew faster in response to warmer site temperatures, but also due to the reduction of competitive interference from the herbaceous community, which was inhibited in warmer sites. Our results suggest that increasing temperatures will promote a faster transition of fields to forests in temperate ecosystems.**

competition | growth rate | succession | temperature | soil fertility

Ecologists have long recognized that the rate of reforestation after disturbance proceeds more slowly at higher latitudes (1–4), which impacts regional water and nutrient cycling (5–7) and global carbon budgets (8, 9). In Eastern North America, abandoned agricultural land succeeds to young forest in less than a decade across much of the southern piedmont and coastal plain, yet often persists for many decades in an herbaceous state further north (10). If the faster rate of forest regrowth at low latitudes is driven by warmer temperatures, then continued climate warming may decrease the persistence of more northern herbaceous ecosystems, with concomitant changes in ecosystem processes (11). This expectation is consistent with models of succession based on the temperature dependence of tree metabolism (12) or growing season length (13), with some tundra warming experiments exhibiting increased shrub growth at the expense of herbaceous species (14).

Resource-based plant strategy theory (15) points to an alternative explanation of biogeographic forest succession patterns based on latitudinal differences in soil fertility, due to both glacial history (16) and long-term climate effects (17). In particular, high resource-demanding herbaceous species have been shown to inhibit woody colonization in sites of high resource supply (18–20), suggesting that both the higher overall fertility of northern soils, and their dominance by fast growing, clonal forbs arrests tree recruitment and growth to a greater extent than nutrient-poor southern sites, dominated after disturbance by C4 bunchgrasses (2, 21). If the transition from an herbaceous to woody-dominated ecosystem is ultimately driven by resource availability and the traits of herbaceous dominants, then the impact of a changing climate on succession may be idiosyncratic. A third possibility is that the growth rate of pioneer trees is related to their geographic distribution (22), in that southern pioneer trees (e.g., *Pinus* spp.) grow faster as seedlings as a result of reduced allocation to cold tolerance mechanisms. In this case, climate impacts on succession occur as distributional constraints on regional species pools of early successional species, which show latitudinal turnover in Eastern North America (2, 10, 23).

We tested the relative importance of climate, soil, and biotic factors in the tree recruitment phase of secondary succession in a distributed experiment conducted at six locations in the Eastern United States spanning 13° latitude and a growing season mean temperature range of 18–25 °C (*SI Appendix, Fig. S1*). At each site, we factorially manipulated soil fertility (four levels of a topsoil–sand mix) and the composition of herbaceous species (*SI Appendix, Fig. S2*), including a “southern” composition of C4 bunchgrasses, a “northern” composition of the dominant forb *Solidago altissima*, and a no-herb control. We allowed herbaceous communities to develop over two growing seasons to maximum biomass before adding a common mixture of seeds of four pioneer tree species to all plots, including two conifers (the widely distributed *Juniperus virginiana* and the southern *Pinus taeda*) and two hardwoods (*Prunus serotina* and the southern *Liquidambar styraciflua*).

## Results

For all tree species, seedling growth and survival were significantly greater in southern sites (Fig. 1). Although initial seed germination was driven in part by soil fertility and herbaceous composition, and was substantially lower for hardwoods (*SI Appendix, Fig. S7 and Table S4*), variation in seedling performance was dominated by differences across sites (Fig. 1). Survivorship models fit separately by season showed that winter mortality was low overall except for the two southern trees in the three northern sites (Fig. 1 and *SI Appendix, Table S5*), suggesting lack of cold tolerance rather than soil or biotic factors as drivers of the northern range limits for these two species.

## Significance

The transition of abandoned fields into forests (secondary succession) has long informed ecologists’ understanding of community assembly and species interactions. Intriguingly, rates of secondary succession show a striking latitudinal pattern, with dominance by woody species (>50% cover) taking less than a decade in the southern United States, and up to 60 years in New England. We used a large-scale experimental network to test how multiple drivers (climate, soils, and the identity of dominant species) influence field-to-forest transitions. We found consistent evidence that climate is the strongest driver of tree establishment, suggesting that temperature limitation of succession in northern latitudes is likely to be reduced under future warming, potentially increasing rates of carbon uptake on abandoned agricultural land.

Author contributions: J.D.F. and J.P.W. designed research, performed research, analyzed data, and wrote the paper.

The authors declare no conflict of interest.

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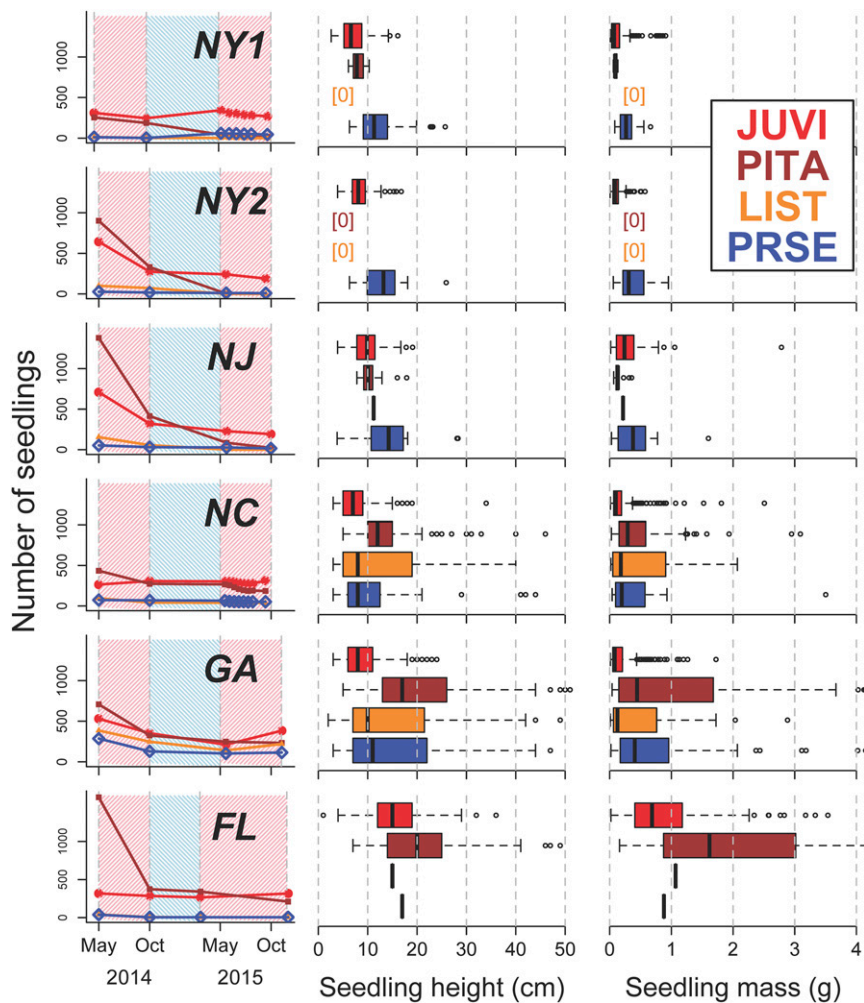
Data deposition: Data from our study are publicly available on the Knowledge Network for Biocomplexity (KNB) (archived accession no. [fridley.14.2](https://doi.org/10.1101/201803)).

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This article contains supporting information online at [www.pnas.org/lookup/suppl/doi:10.1073/pnas.1716665115/-DCSupplemental](http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.1716665115/-DCSupplemental).

Published online April 16, 2018.



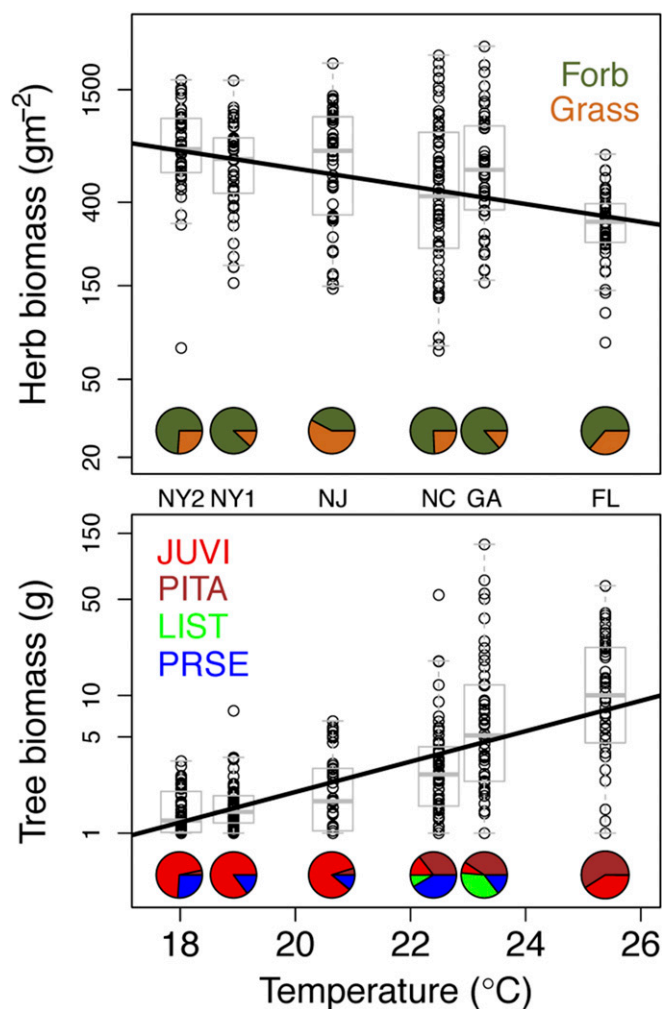
**Fig. 1.** Performance of tree seedlings across sites, from north (Top) to south (Bottom). The Left column shows the total number of seedlings alive of each species at each site in the spring and fall of 2014 and 2015; colors emphasize changes in summer (red) and winter (blue). The Middle and Right columns show quartiles and ranges of site distributions of seedling height (Middle) and biomass (Right) at harvest in fall 2015, along with medians and outliers for each species; zeros indicate no surviving seedlings. JUVI, *Juniperus virginiana*; LIST, *Liquidambar styraciflua*; PITA, *Pinus taeda*; PRSE, *Prunus serotina* (and in Fig. 2).

Surprisingly, growing season temperature also had the largest positive effect size on summer survival, although of marginal significance (*SI Appendix, Table S5*) and driven largely by the southern pine, *P. taeda* (*SI Appendix, Fig. S8*). Herbaceous composition and soil fertility were significant, but less influential, drivers of winter and summer survival, including a consistent role of higher survivorship under the more continuous forb canopy of *S. altissima*, which may have acted as a nurse plant for both cold and drought protection, as indicated by interactions with both site temperature and plot sand content (*SI Appendix, Table S5*).

Total seedling mass per plot is an integrated measure of tree recruitment that incorporates germination, seedling survival, growth rates, and differences across tree species, and was several-fold higher in southern sites after 2 y (Fig. 2). About half (45%) of the variation in seedling mass was attributed to site differences; of this variation, nearly all (>90%) was explained by growing season temperature (*SI Appendix, Table S6*). Within-site variation in seedling biomass was related to herbaceous biomass (*SI Appendix, Fig. S9*), which also decreased with site temperature (Fig. 2). Overall, the effect size of temperature on seedling biomass was about three times that of herbaceous biomass (*SI Appendix, Table S6*).

To isolate the direct and indirect effects of climate, soil, and biotic variables on tree seedling growth, we created a Bayesian

hierarchical model (Fig. 3 and *SI Appendix, Appendix S1*) that distinguished: (i) the effects of climate and experimental treatments on herbaceous communities; (ii) the effects of climate and herbs on available resources [light, soil moisture, and soil nutrients nitrogen (N) and phosphorus (P)]; and (iii) the effects of climate and resources on seedling height increment, which is a strong indicator of the rate of woody dominance. Seedling growth was driven primarily by warmer growing season temperatures and light, and secondarily by soil moisture and, marginally, N availability (Fig. 3 and *SI Appendix, Fig. S10*). Seedling light levels, in turn, were significantly lower in plots of high herbaceous biomass, which was reduced in warmer sites but also influenced by herbaceous composition, soil treatments, and interactions between herbaceous composition and climate (*SI Appendix, Fig. S10*). We found other effects of experimental treatments on resource availability, including strong effects of soil treatments on moisture and both N and P availability, but plot- and site-level variation in these resources were minor contributions to seedling growth. Although the light response was common to all species when assessed in species-specific growth models, the temperature effect was driven by the response of the two conifer species that accounted for a large proportion of total seedlings (*J. virginiana* and *P. taeda*; *SI Appendix, Fig. S11*).



**Fig. 2.** Relationships of plot herbaceous biomass (*Top*) and total tree seedling biomass (*Bottom*) to site mean growing season temperature. Boxplots show data median, range, and quantiles; site  $n = 48$  (no-herb controls excluded). Pie charts at *Top* show the relative site biomass representation of forbs vs. grasses; those at *Bottom* show the relative contributions of four sown tree species to site tree biomass. Regression lines are from ordinary least squares ( $R^2 = 11\%$  herbs and  $36\%$  trees, both  $P < 0.001$ ).

### Discussion

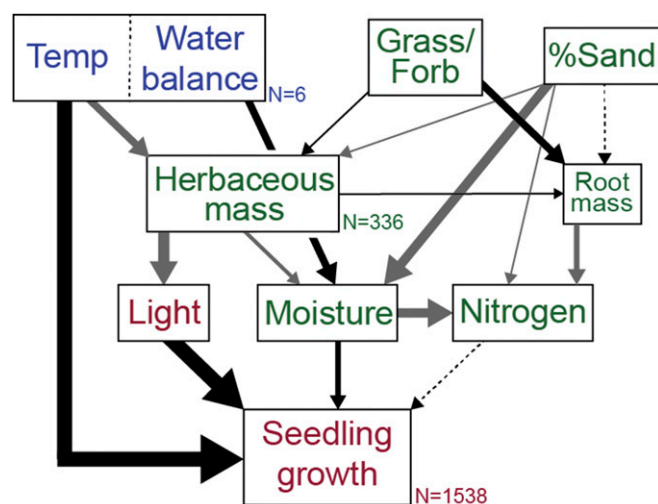
Our hypothesis that tree recruitment during early succession is driven by the composition of herbaceous communities was not supported. The fast spreading, clonal forb *S. altissima* did not outperform the more stress tolerant bunchgrasses in fertile plots, nor did it prefer northern sites (Fig. 2). Although herbaceous root mass was greater in *S. altissima* plots compared with bunchgrasses, the lower nutrient levels associated with high herbaceous biomass did not have a strong effect on tree seedling growth in comparison with temperature and light (Fig. 3 and *SI Appendix*, Fig. S10). The decline of herbaceous biomass in warmer sites is consistent with the greater predominance of productive herbaceous meadows in northern landscapes (10), but its stronger response to site climate variables than soil fertility or herb composition (*SI Appendix*, Fig. S10) suggests herbs experienced stress or disturbance unrelated to nutrients, such as water availability or herbivory (24). However, our model does suggest that herbaceous abundance plays a strong role in limiting tree establishment, and that this effect, combined with temperature-related constraints on tree seedling growth, is a primary driver of the persistence of northern old fields. What remains unresolved

is whether herbaceous communities will respond predictably to climate warming, or whether additional factors, and particularly increased atmospheric  $CO_2$ , preclude simple predictions of old field compositional change (25).

Although our study concerns only the initial stages of secondary succession, it captures the critical period during which tree seedling growth and survival is most likely to be affected by competition with the herbaceous layer, as at the southern locations multiple seedlings had already exceeded the height of the herbaceous canopy after 2 y. The faster growth of early successional tree species in warmer sites, even when in competition with potentially fast growing herbaceous perennials, is consistent with a metaanalysis documenting a larger impact of warming experiments on woody species compared with herbs (26), and suggests that even relatively small increases in growing season temperature and duration will accelerate the transition of old fields to forested stands. In the absence of further resource limitation from warming (e.g., drought), both longer growing seasons (27, 28) and the temperature dependency of assimilation rate in trees (12) suggest later stages of forest succession in the temperate zone will also accelerate. Moreover, the results of this and a prior study (23) confirm the widely held view that the northern range limits of many southern trees is determined by cold temperatures (29); to the extent that these species are inherently faster growing (23), further increases in the rate of secondary succession will occur as southern species move northward (30). As warm-temperate, early successional conifers, including many species of *Pinus*, are increasingly dominant in postdisturbance landscapes of the Northern Hemisphere and widely invasive in the Southern (31), it is likely that the temperature-based acceleration of forest development we report here applies globally.

### Materials and Methods

**Experimental Design and Construction.** In 2012, we established identical experiments at six locations (*SI Appendix*, Fig. S1). Each site contained 72 experimental units consisting of circular, freely draining plastic pools 1.52-m



**Fig. 3.** Effects of experimental treatments (*Top* row) on seedling growth, as mediated by climate (growing season temperature and site water balance) and the effects of herbaceous competitors on light and soil resources. Seedling growth is the height increment in 2015. Sample sizes refer to factors varying between sites (blue), between plots (green), and within plots (red). Width and color of arrows describe relative effect sizes in mixed models (*SI Appendix*, Fig. S6) for each factor (black, positive; gray, negative; and dashed, marginal;  $P < 0.1$ ). The water balance effect on moisture includes an interaction with %sand; other interactions and the soil phosphorus model are not shown.



inner diameter and 28-cm soil depth separated by 1-m walkways, placed on top of landscape fabric in full sun and fenced to exclude deer herbivory. In a randomized block design, we established six replicates each of 12 treatments, consisting of four soil types crossed with three levels of herbaceous composition. The four soil types included 100% topsoil and three homogenized mixtures of topsoil and coarse sand (3:1, 1:1, and 1:3 topsoil:sand, respectively). Transport limitations required the use of locally sourced commercial topsoil and sand for each site, with the result that mean soil pH varied by site, although not with respect to latitude (*SI Appendix, Fig. S6 and Table S3*). Chemical analyses are described in *SI Appendix*. The three types of herbaceous composition included: (i) a “grass” community of a 1:1 mixture of the bunchgrasses *Andropogon virginicus* L. and *Schizachyrium scoparium* (Michx.) Nash; (ii) a “forb” community planted with rhizomes of the common goldenrod *S. altissima* L. ssp. *altissima*; and (iii) bare “control” plots. We added the same mixture of tree seeds to all plots in the experiment, once in October 2013 and once in May 2014. The mix included 2 g dry mass of *J. virginiana* (approximately 300 seeds), 2 g *L. styraciflua* (300 seeds), 5 g *P. taeda* (200 seeds), and 12 g *P. serotina* (175 seeds).

To account for the potential for local adaptation to climatic or edaphic factors in widespread species, we included both northern and southern seed sources for all tree and herbaceous species except the southern endemic *P. taeda* (Georgia). *S. altissima* and *S. scoparium* plants were collected in New York and North Carolina, and *A. virginicus* from Missouri and North Carolina. Tree seeds for *J. virginiana* were collected from Nebraska and Louisiana; *L. styraciflua* from Missouri and Louisiana; and *P. serotina* from Pennsylvania and Florida. Climates of seed sources were similar to average temperature regimes of our northern and southern experimental locations. We found no significant effects of tree population provenance in a related previous study (23), using the same provenances and five of the same sites.

In spring and fall 2014, we counted the number of all germinated seedlings in all plots, and randomly tagged up to 10 seedlings per species per plot for subsequent survival and height measurements. In fall 2014, spring 2015, and fall 2015, we measured the status and height of tagged seedlings and randomly added new living seedlings as needed to maintain a sample size of 10 per species per plot. All seedlings were harvested in fall 2015, separated into above- and belowground components, and dried for 48 h at 70 °C.

**Covariate Measurement.** At the start of the experiment in 2012, 25 g of soil was collected from each soil mixture from each site ( $n = 24$ ). These samples were analyzed for organic matter content, pH, and concentrations of P, K, Ca, and Mg. We measured plant-available nutrients in all plots in June/July 2014 with plant root simulator (PRS) ion exchange probes (Western Ag Innovations). Herbaceous biomass was sampled at the same time as tree seedling harvest in fall 2015. We calculated site water balance as the difference between water supply (rainfall) and climatic demand (potential

evapotranspiration, PET), assuming a negligible soil storage component (32), using daily temperature and rainfall data from 2013 to 2015 obtained from the US National Oceanic and Atmospheric Administration’s National Climatic Data Center weather stations in close proximity to each site.

**Statistical Analyses of Tree Recruitment.** We analyzed tree seed germination at the plot level in response to experimental treatments (percent sand and herbaceous composition: forbs = 1, grasses = 0) and 2014 climate summaries across sites (mean May–October monthly temperature and water balance). We analyzed seedling survival at the plot level in two models distinguishing winter (2014–15) and summer (2015) climate drivers, along with plot-level treatment effects of herbaceous composition (forbs = 1, grasses = 0) and soil fertility (%sand). We used two models to examine patterns of total harvested seedling biomass per plot, involving a 336-plot dataset that excluded 96 control plots from four sites (NY2, NJ, GA, and FL) that were not monitored in 2015. A first model examined effects of only the experimental treatments (soil fertility, represented by a percent sand gradient of 0%, 25%, 50%, and 75%; and a three-category herb composition factor of grass/forb/control) and two climate factors (mean May–October daily temperature, and site water balance). A second model retained the climate variables but replaced experimental treatments with realized herbaceous biomass (continuous). To better understand the influence of climate, soil, and vegetation variables on resource availability (light, moisture, and nutrients), and the subsequent response of tree seedling growth to variation in these resources, we created a hierarchical model of relationships in a Bayesian framework using JAGS (33) and the “R2jags” package (34) in R. The model had a three-level structure (Fig. 3), including (i) the response of seedling height increment in 2015 to seedling-level photosynthetically active radiation, plot-level soil moisture and nutrients (N and P), and site-level temperature; (ii) the response of light, soil moisture, and nutrients to the herbaceous community, soil treatments, and climate; and (iii) the response of herbaceous community performance (above- and belowground mass) to climate and experimental treatments.

**ACKNOWLEDGMENTS.** We acknowledge the generous support of faculty and staff at the Cary Institute of Ecosystem Studies (C. Canham, M. Fargione, and R. Winchcombe); Hutcheson Memorial Forest (S. Handel, J. Lockwood, and P. Morin); Whitehall Forest (D. Markewitz); and Tall Timbers Research Station (W. Palmer and E. Staller). For field and laboratory assistance, we thank S. Anderson, J. Chieppa, A. Craddock, A. Fox, E. Hinman, I. Jo, M. Lesser, J. Lynn, B. McGill, M. McPartland, L. Negroita, D. Nwaeze, E. Pipher, A. Reese, E. Unger, and J. Wiley; and for valuable manuscript comments, S. Meiners. This study was supported by US National Science Foundation Grants DEB 1119743 (to J.D.F.) and DEB 1119715 (to J.P.W.). The authors declare no competing interests.

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