



TEXAS TECH UNIVERSITY
Libraries™

**WARMING INCREASES THE SENSITIVITY OF SEEDLING GROWTH CAPACITY
TO RAINFALL IN SIX TEMPERATE DECIDUOUS TREE SPECIES**

The Texas Tech community has made this publication openly available. [Please share](#) how this access benefits you. Your story matters to us.

Citation	Rodgers, VL, NG Smith, SS Hoepfner, and JS Dukes (2018). Warming increases the sensitivity of seedling growth capacity to rainfall in six temperate deciduous species. <i>Annals of Botany – Plants</i> 10(1): ply003. https://doi.org/10.1093/aobpla/ply003
Citable Link	https://hdl.handle.net/2346/86917
Terms of Use	CC-BY 4.0

Research Article

Warming increases the sensitivity of seedling growth capacity to rainfall in six temperate deciduous tree species

Vikki L. Rodgers^{1*}, Nicholas G. Smith^{2,3,4}, Susanne S. Hoepfner^{5,6} and Jeffrey S. Dukes^{3,4,7,8}

¹Math and Science Division, Babson College, 231 Forest Street, Wellesley, MA 02481, USA

²Department of Biological Sciences, Texas Tech University, 2901 Main Street, Lubbock, TX 79409, USA

³Department of Forestry and Natural Resources, Purdue University, 715 West State Street, West Lafayette, IN 47907, USA

⁴Purdue Climate Change Research Center, Purdue University, 203 South Martin Jischke Drive, West Lafayette, IN 47907, USA

⁵Department of Psychiatry, Harvard Medical School, 25 Shattuck Street, Boston, MA 02115, USA

⁶Department of Psychiatry, Massachusetts General Hospital, 185 Cambridge Street, Suite 2000, Boston, MA 02114, USA

⁷Department of Biological Sciences, Purdue University, 715 West State Street, West Lafayette, IN 47907, USA

⁸Department of Biology, University of Massachusetts Boston, 100 Morrissey Boulevard, Boston, MA 02125, USA

Received: 11 September 2017 **Editorial decision:** 4 January 2018 **Accepted:** 15 January 2018 **Published:** 17 January 2018

Associate Editor: James F. Cahill

Citation: Rodgers VL, Smith NG, Hoepfner SS, Dukes JS. 2018. Warming increases the sensitivity of seedling growth capacity to rainfall in six temperate deciduous tree species. *AoB PLANTS* 10: ply003; doi: 10.1093/aobpla/ply003

Abstract. Predicting the effects of climate change on tree species and communities is critical for understanding the future state of our forested ecosystems. We used a fully factorial precipitation (three levels; ambient, -50 % ambient, +50 % ambient) by warming (four levels; up to +4 °C) experiment in an old-field ecosystem in the northeastern USA to study the climatic sensitivity of seedlings of six native tree species. We measured whole plant-level responses: survival, total leaf area (TLA), seedling insect herbivory damage, as well as leaf-level responses: specific leaf area (SLA), leaf-level water content (LWC), foliar nitrogen (N) concentration, foliar carbon (C) concentration and C:N ratio of each of these deciduous species in each treatment across a single growing season. We found that canopy warming dramatically increased the sensitivity of plant growth (measured as TLA) to rainfall across all species. Warm, dry conditions consistently reduced TLA and also reduced leaf C:N in four species (*Acer rubrum*, *Betula lenta*, *Prunus serotina*, *Ulmus americana*), primarily as a result of reduced foliar C, not increased foliar N. Interestingly, these conditions also harmed the other two species in different ways, increasing either mortality (*Populus grandidentata*) or herbivory (*Quercus rubra*). Specific leaf area and LWC varied across species, but did not show strong treatment responses. Our results indicate that, in the northeastern USA, dry years in a future warmer environment could have damaging effects on the growth capacity of these early secondary successional forests, through species-specific effects on leaf production (total leaves and leaf C), herbivory and mortality.

Keywords: Boston-Area Climate Experiment (BACE); carbon; climate change; drought; leaf area; nitrogen; tree seedlings; warming.

*Corresponding author's e-mail address: vrodgers@babson.edu

© The Author(s) 2018. Published by Oxford University Press on behalf of the Annals of Botany Company.

This is an Open Access article distributed under the terms of the Creative Commons Attribution License (<http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted reuse, distribution, and reproduction in any medium, provided the original work is properly cited.

Introduction

Climate change is warming air temperatures and shifting precipitation patterns (IPCC 2013; Dai 2013), which will increasingly affect the growth of tree seedlings, leading to long-term changes in the composition and productivity of forests. Many of these changes will be consequences of species- and age-specific sensitivities (Martínez-Vilalta and Lloret 2016). Already, climatic shifts are modifying forest structure and function and have resulted in widespread forest die-back (van Mantgem et al. 2009; Allen et al. 2010; Anderegg et al. 2016). Predicting the effects of climate change on species composition and quantifying how individual tree species respond to climate variability is critical for understanding the future state of our forested ecosystems (Walther et al. 2002; Parmesan and Yohe 2003; Chen et al. 2011; Sittaro et al. 2017).

Studies have shown that plant tolerances and responses to climatic conditions change over the course of development (Cavender-Bares and Bazzaz 2000; Fisichelli et al. 2014). During early development, tree growth is particularly sensitive to external perturbations because the still-shallow root systems have limited access to deep reserves of soil water (Niinemets 2010; Wright et al. 2013). Simple scaling frameworks that fail to account for developmental stages often miss the fact that different age classes use different mechanisms to tolerate drought or warming conditions (Cavender-Bares and Bazzaz 2000). Although some adult trees may be predicted to persist through dramatic shifts in the climate, tree species ranges will eventually contract where tree regeneration fails (Bell et al. 2014).

Field data from multilevel temperature and precipitation experiments can be used to refine or benchmark the processes within current-generation climate models (Smith et al. 2014). The use of plant functional traits within climate models can improve predictions of species distributions (Kearney and Porter 2009; Webb et al. 2010; Van Bodegom et al. 2012; Scheiter et al. 2013). Flexible trait-based models that characterize organisms in terms of their multiple biological attributes allow for changes in the trait distribution (usually measured at the individual level and used comparatively across species) and associated modifications to community composition or ecosystem function to be predicted across time and space (Webb et al. 2010). Whereas the majority of field studies infer changes in trait values by looking across natural environmental gradients that confound differences in populations and species with the environmental variable of interest, in this study we measured functional plant traits under the factorial manipulation of different levels of temperature and precipitation together within a single community.

Total leaf (surface) area (TLA) and specific leaf area (SLA: leaf area per unit leaf mass) are key indicators of a plant's carbon and water balance (Parkhurst and Loucks 1972), serve as important plant functional traits and are well known to vary with climate (Whittaker and Niering 1975). To survive changes in temperature and precipitation regimes, long-lived plants must either be capable of tolerating the new conditions or change physiologically and/or morphologically to accommodate them. Warmer conditions often promote photosynthesis and net primary productivity (Rustad et al. 2001; Wu et al. 2011), unless the warming exceeds metabolic optima or causes soil moisture stress (De Valpine and Harte 2001; Niu et al. 2006; Sage et al. 2008; Zhao et al. 2013).

In general, drier conditions typically suppress TLA, which reduces water loss, and increase biomass allocation to roots, which increases water uptake capacity (Smith and Huston 1989; Aspelmeier and Leuschner 2006; Erice et al. 2010). A number of studies have found reductions in SLA under drought conditions (Ibrahim et al. 1997; Thomas 2000; Valladares and Sánchez-Gómez 2006; Poorter et al. 2009), which is suggestive of an enhanced ability to avoid wilting (Maximov 1929), increasing drought resistance (Valladares and Sánchez-Gómez 2006; Greenwood et al. 2017). Warmer temperatures are likely to enhance drought responses by reducing soil moisture (supply) and increasing atmospheric water demand.

Changes in temperature and precipitation regimes are also known to directly influence rates of plant nutrient uptake and allocation of nutrients to leaf tissue (BassiriRad 2000; Reich and Oleksyn 2004). If photosynthetic carbon gain responds differently to these environmental changes than nitrogen uptake or allocation, leaf tissue chemistry could change. Interestingly, previous studies have found that warming can either increase (Nijs et al. 1996; Oleksyn et al. 2003; Rodgers et al. 2012) or decrease (Yin 1993; Dormann and Woodin 2002; Reich and Oleksyn 2004; Suseela et al. 2015) a plant species' foliar nitrogen concentration. Altered foliar carbon and nitrogen concentrations can affect ecosystem-scale processes by influencing rates of photosynthesis, herbivore forage quality, plant litter chemistry and ultimately carbon and nutrient pathways (Shaver et al. 2001; Aerts et al. 2009).

In this study, we measured peak season whole plant- and leaf-level responses to warming and altered precipitation across a single growing season in the northeastern USA. Specifically, we measured changes in survival, TLA, leaf-level insect herbivory damage, SLA, leaf-level water content (LWC), and foliar carbon and nitrogen concentration in seedlings of six tree species: *Acer rubrum* (red maple), *Betula lenta* (sweet birch),

Populus grandidentata (big-toothed aspen), *Prunus serotina* (black cherry), *Quercus rubra* (red oak) and *Ulmus americana* (American elm). Most of these species have large current and projected ranges that span much of the eastern and Midwestern USA (Prasad et al. 2007-ongoing; Iverson et al. 2008). However, *B. lenta* is restricted longitudinally, suggesting greater precipitation sensitivity, and *P. grandidentata* is restricted latitudinally, suggesting greater temperature sensitivity (Prasad et al. 2007-ongoing; Iverson et al. 2008). The tree seedlings in this study were grown within a high-light, old-field ecosystem, thereby simulating early secondary successional dynamics. Previous studies at this same experimental field site have found that the precipitation treatments altered heterotrophic soil respiration (Suseela et al. 2012), herbaceous plant water use efficiency (Rodgers et al. 2012) and tree seedling photosynthesis rates (Smith et al. 2016). In contrast, warming has had more limited direct effects, in part because of process acclimation. Warming suppressed the temperature sensitivity of heterotrophic (Suseela et al. 2012) and total soil respiration (Suseela and Dukes 2013), as well as soil nitrogen transformations (Auyeung et al. 2013), but also increased leaf nitrogen concentration in herbaceous plant tissue (Rodgers et al. 2012) and increased the intrinsic water use efficiency of tree seedlings (Smith et al. 2016). The combination of warming and dry conditions suppressed total herbaceous plant production, shoot production and plant species richness (Hoeppe and Dukes 2012), doubled the concentration of total tannins in *A. rubrum* leaf litter (Tharayil et al. 2011) and increased concentrations of other water-stress-related compounds in *Q. rubra* leaves (Suseela et al. 2015).

For this study we formulated hypotheses at the species, whole plant and leaf levels. We expected that responses of individual tree species could be inferred from their climatic niches (Prasad et al. 2007-ongoing; Iverson et al. 2008). We hypothesized that warmer temperatures combined with high levels of precipitation would favour growth of most species. We expected that treatments with drier soil conditions, either from reduced precipitation, warming or the combination, would reduce growth of most species, but added precipitation would counteract the negative effects of soil drying under warmed conditions. The species with the most limited climatic niches were *B. lenta* and *P. grandidentata*; their native ranges are more restricted to cooler and wetter regions (Prasad et al. 2007-ongoing; Iverson et al. 2008). We therefore hypothesized that these two species would be most negatively affected by (1) increased levels of warming, (2) reduced precipitation and (3) the combination of warming and reduced precipitation.

Our whole plant-level hypotheses were related to (i) tree seedling survival, (ii) estimated TLA and (iii) leaf herbivory damage. We expected warming to increase these variables under wet and ambient conditions, but decrease them under drier conditions.

We also tested the following leaf-level hypotheses: (i) LWC will decline across the gradient of increased warming and with reduced precipitation, and will be lowest with the combination of increased warming and drier conditions. (ii) SLA and (iii) foliar N will increase (lowering C:N ratio) with warming and with added precipitation, but will decline with the combination of increased warming and drier conditions.

We expected whole plant- and leaf-level responses to scale linearly with the magnitude of warming.

Methods

Study site and experimental design

This research was conducted at the Boston-Area Climate Experiment (BACE), a multifactorial climate manipulation experiment in an old-field ecosystem at the University of Massachusetts' Suburban Experiment Station in Waltham, MA, USA (42°23'N, 71°13'W). The site experiences a mean annual temperature of 9.3 °C, a mean annual precipitation of 1194 mm year⁻¹ (Auyeung et al. 2013), and features a loam topsoil over a gravelly sandy loam subsoil.

The BACE utilizes a full-factorial, split-plot, randomized block design with the precipitation treatment as the whole-plot factor and the temperature treatments as subplot factors nested within the precipitation treatment. Four levels of warming crossed with three levels of precipitation produced 12 different climate regimes, each of which was replicated three times for a total of 36 plots (2 m × 2 m in size). The four levels of warming were unwarmed (ambient temperature), low warming (+~1.3 °C multi-year average), medium warming (+~2.7 °C multi-year average) and high warming (target of +4.0 °C), and the three levels of precipitation were ambient rainfall, 50 % reduced rainfall (dry) and 50 % increased rainfall during the growing season (wet). Warming values achieved varied by season, leaf angle, heater response time and vegetation cover. Models project that the northeastern USA will warm by 2–3 °C by the end of the 21st century (Hayhoe et al. 2007) with summers experiencing up to a 10 % reduction in precipitation (Rawlins et al. 2012) and winter precipitation projected to increase by 11 to 14 % (Hayhoe et al. 2007).

Warming treatments were applied year-round using ceramic infrared heaters (e.g. Nextthermal FSR) mounted 1 m above the ground at each corner of every plot,

facing towards the centre of the plot and downward at a 45° angle. The wattage varied by treatment: 200, 600 and 1000 W heaters for the low, medium and high warming treatments, respectively. Plant canopy temperatures of all ambient and high warming plots were monitored every 10 s by infrared radiometers (IRR-PN; Apogee Instruments, Logan, UT, USA). For each group of three warmed plots within a precipitation zone, power to all heaters was on a single circuit, and was continually adjusted based on the temperature difference between the unwarmed and high warming plots in that zone. The temperature control algorithms were designed to achieve a 4 °C difference between the unwarmed and high warming treatments when possible. Intermediate treatments received proportionally less warming because the heaters surrounding these plots had lower wattages [see **Supporting Information—Fig. 1**]. [Hoepfner and Dukes \(2012\)](#) reported that the heaters achieved target temperatures much of the time, but for periods during the day and in rainstorms temperatures often dipped below targets, however, a decrease in the diurnal temperature range, is similar to what is projected for the northeastern USA ([Meehl et al. 2007](#)).

Precipitation treatments were achieved using a roof of evenly spaced, clear polycarbonate slats that collected half of the precipitation over the dry treatments (year-round) and immediately delivered it to the wet treatments via an overhead sprinkler system (May–November). Soil moisture was fully recharged to water holding capacity during the winter months in all plots ([Hoepfner and Dukes 2012](#)). In order to adjust for the ~5 % reduction in photosynthetically active radiation (PAR) imposed by the polycarbonate slats, the ambient and wet sections of the greenhouse frames were covered by deer fencing, providing the same reduction in PAR.

Within each precipitation main plot, the four warming split-plots were arranged linearly from ambient to high, and spaced 1 m apart. In 2007, a 0.6 m deep trench was dug around each split-plot, and lined with polyethylene sheets to prevent lateral movement of water and nutrients between split-plots. All treatments were in effect as of July 2008. The herbaceous vegetation within and around the split-plots was clipped twice per growing season. [Hoepfner and Dukes \(2012\)](#) provide further details on the BACE experimental design.

Within each of the 36 split-plots, soil moisture was monitored weekly as relative extractable water (θ_r) using pairs of time-domain reflectometry (TDR) waveguides installed vertically to provide integrated measures of volumetric soil moisture in the top 10 cm and top 30 cm; calculations in [Vicca et al. \(2012\)](#) and [Smith et al. \(2016\)](#). Soil temperature was monitored using custom-made linear temperature sensors placed at 2

and 10 cm below the soil surface. Measurements were recorded every 30 min throughout the year.

Within each of the 36 split-plots, four evenly spaced 0.5 m × 0.5 m subplots were cleared of grasses and forbs and designated for tree seedling planting. One seedling (<20 cm in height) of each of eight tree species was planted into each of these subplots in late April 2011, resulting in a total of 1152 seedlings planted. The eight tree species planted were: *A. rubrum* (red maple), *B. lenta* (sweet birch), *P. grandidentata* (big-toothed aspen), *P. serotina* (black cherry), *Q. rubra* (red oak), *U. americana* (American elm), *Betula populifolia* (grey birch) and *Pinus strobus* (white pine). Due to time and resource limitations *B. populifolia* and *P. strobus* were not measured in this study, leaving six species and 864 tree seedlings that were measured. Whole plant-level measurements (survival, TLA and herbivory) as well as leaf-level responses (SLA, LWC and foliar stoichiometry) were calculated to determine seedling responses to the treatments. All measurements were completed only over the 2011 growing season.

Whole plant-level measurements

Seedling mortality counts were made by comparing the number of seedlings alive in late April as compared to late July. Dead seedlings were not included in the leaf-level analyses. In order to estimate total leaf production without destructively harvesting across the peak growing season, we used length and width measurements to develop species-specific leaf size categories ([Kvet and Marshall 1971](#); [Lu et al. 2004](#)). Before the first measurements began, four distinct leaf size categories (undeveloped, small, medium and large) were established separately for each of the six species. The undeveloped category was used to represent the youngest leaves that had not yet reached the small stage. Ten representative leaves were chosen to represent each size category for each species. The length and width (to the nearest 0.1 cm) of each of these leaves were also measured and mean values were used to confirm visual categories during the sampling. The total number of leaves produced on each tree seedling and the size category for each leaf were determined for plant-level analyses in late July of 2011.

In late July of 2011, the magnitude of leaf-level insect herbivory was assessed as the percent of tissue removed using four categories for damage as previously determined by [Chacon and Armesto \(2006\)](#): 0 %, 1–15 %, 15–50 % and 50–100 %. The herbivory response variable was treated as continuous numbers 0, 1, 15 and 50 (meaning that 50 had 50 times more herbivory than 1). To ensure that visual estimates were consistent, the leaf size estimations and the herbivory levels were all completed by the same person (V.L.R.).

Leaf-level measurements

After all plant-level analyses were completed, four green, representative leaves were collected from each of the tree seedlings for leaf-level analyses. When possible, the leaf samples were chosen to include at least one leaf from each of the small, medium and large size categories. For tree seedlings with limited leaf production, we took up to, but no more than, half of the leaves present. Each leaf collected was immediately weighed and scanned for leaf area using a CI-202 Portable Area Meter (CID Bio-Science, Camas, WA, USA). The mean leaf area for each size category of each species was calculated across all individuals. The estimated TLA for each individual tree seedling was then calculated as the number of leaves observed within each size category multiplied by the species-specific measured mean leaf area for each category, and summed across size categories.

Leaf samples were dried to a constant mass at 65 °C to determine dry weight and leaf-level water content (LWC) was calculated by subtracting dry weight from wet weight, and dividing by wet weight. Specific leaf area was measured as leaf area divided by dry weight. One small size category, dried leaf sample from each tree seedling was then ground and analysed for carbon and nitrogen concentration on a Costech ECS 4010 elemental analyzer (Costech Analytical Technologies Inc., Valencia, CA, USA).

Data analysis and statistics

Seedling mortality, estimated TLA (m²), SLA (cm² g⁻¹), leaf herbivory (%), LWC (%), leaf tissue percent nitrogen by weight (%N) and leaf C:N ratio (g g⁻¹) were analysed for all species together using linear mixed-effects models. Specific leaf area, LWC and herbivory were averaged for each individual tree. The mixed-effects models included a fully factorial combination of precipitation treatment, warming treatment and species as fixed effects. Block, precipitation treatment within block and warming treatment within precipitation treatment within block were included as random effects in each model to represent the experimental design of BACE. For model fitting, we used the ‘lmer’ function from the *lme4* package (Bates et al. 2015) in the statistical programming environment R (R Core Development Team 2015). As seedling mortality was binomial (died or survived), we used a logit-link binomial generalized linear model, implemented with function ‘glmer’ in *lme4*. Model convergence could not be achieved for the mortality model with all species included, due to the low mortality of some species. Therefore, a separate seedling mortality model was run for each species with >15 % total mortality (*A. rubrum*, *P. grandidentata* and *P. serotina*). To evaluate the level of significance for each fixed effect, we calculated a Wald

χ^2 statistic and performed a Type-II Wald test using the ‘ANOVA’ function in the ‘car’ package (Fox and Weisberg 2011) in R. *Post hoc* comparison of means was done using Tukey’s least squared difference tests utilizing the ‘lsmeans’ package (Lenth 2016) in R.

Results

Treatment effects on seedling mortality

Over the course of this experiment and throughout all plots *B. lenta*, *U. americana* and *Q. rubra* had low (<13.2 %) tree mortality; only 7, 8 and 19, respectively, out of 144 each. *Prunus serotina* and *A. rubrum* had moderate levels of mortality (43.1 and 45.8 %) with 82 and 78 of each species surviving. The highest mortality rate (61.9 %) was in *P. grandidentata*; only 55 out of the 144 seedlings survived. Among the species with >15 % mortality, only *P. grandidentata* showed a significant response to the treatments. Both warming and reduced precipitation caused greater *P. grandidentata* mortality (Fig. 1).

Total leaf area

Total leaf area was reduced by 83 % under the combination of reduced precipitation and warming as compared to controls (warming by precipitation interaction; $P < 0.001$; see Supporting Information—Fig. S2). There were also significant species by warming ($P < 0.05$; Table 1) and species by precipitation ($P < 0.05$; Table 1)

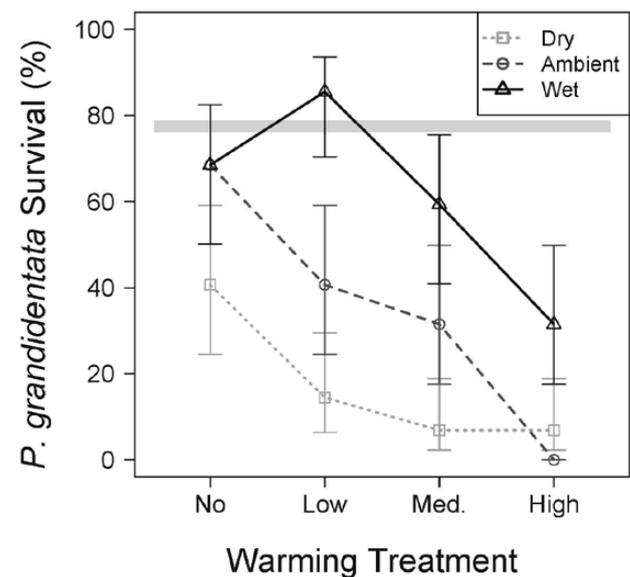


Figure 1. Probability of survival (\pm SE) from initial of planting (early spring) to sampling date (late July) for *P. grandidentata* in the wet (dark grey triangles), ambient (grey circles) and dry (light grey squares) precipitation treatments across the four warming treatments. The grey horizontal bar represents the mean survival (\pm SE) for the other five species combined.

interactions. *Post hoc* analyses revealed that TLA was 49 and 51 % lower in reduced precipitation compared to added precipitation for *B. lenta* and *U. americana*, respectively (both $P < 0.05$; Fig. 2; [see [Supporting Information—Table S1](#)]), but precipitation did not have an effect on other species (precipitation by species: $P < 0.05$). Total leaf area was 19 and 58% lower in medium and high warming, respectively, compared to no warming in *B. lenta*, but warming did not have a direct effect in other species (warming by species: $P < 0.05$; Fig. 2; [see [Supporting Information—Table S2](#)]).

Insect herbivory

A significant three-way interaction between species, warming treatment and precipitation treatment ($P < 0.05$; Table 1) indicated that *Q. rubra* was unique from the rest of the species (Fig. 3). *Quercus rubra* experienced over four times more herbivory damage than the species with the second highest rates, *A. rubrum* ($P < 0.05$; [see [Supporting Information—Fig. S3](#)]). Rates of herbivory on *Q. rubra* were greatest in the combined reduced precipitation, high warming plots, showing an increase of 137 % as compared to the ambient precipitation, no warming plots ($P < 0.05$; Fig. 3).

SLA and LWC

Specific leaf area varied by species, with the highest values seen in *B. lenta*, followed by *P. serotina*, *A. rubrum*, *U. americana*, *P. grandidentata* and *Q. rubra* [see [Supporting Information—Table S3](#)]. However, SLA did not respond to the warming or precipitation treatments in any of these species ($P > 0.05$ for all main effects and interactions; Table 1; see [Supporting Information—Fig. S4](#)).

In general, LWC was relatively unaffected by the treatments. However, dry treatments reduced LWC of *Q. rubra* by 35 % ($P < 0.05$; [see [Supporting Information—Table S1](#); Fig. S5]). In addition, the highest level of

warming reduced the LWC of *B. lenta* by 21 % as compared to the unwarmed plots ($P < 0.05$; [see [Supporting Information—Table S2](#); Fig. S5]).

Foliar stoichiometry

Foliar percent N responded inconsistently to the climate treatments, with only *U. americana* increasing leaf N by 84 % in the driest and warmest plots compared to plots with reduced precipitation ($P < 0.05$; Table 1; Fig. 4). Foliar carbon content was relatively stable across the treatments (Table 1), except for a large increase in the high warmed, dry treatments for *B. lenta* [see [Supporting Information—Fig. S6](#)]. Four of the six species, *P. serotina*, *B. lenta*, *A. rubrum* and *U. americana*, had higher C:N in plots receiving greater precipitation ($P < 0.05$; Fig. 5), while *Q. rubra* and *P. grandidentata* had no change with the precipitation treatment ($P > 0.05$; Fig. 5; see [Supporting Information—Table S1](#)). *Ulmus americana* was also the only species to respond significantly ($P < 0.05$; Fig. 5) to warming, with the high heating reducing leaf C:N by 10 % as compared to the unwarmed plots [see [Supporting Information—Table S2](#)].

Discussion

Seedling mortality of *P. grandidentata* increased in warmer and drier conditions, and this species showed limited plasticity in leaf-level responses to the manipulations. The combination of warming and reduced precipitation suppressed TLA across species, and strongly in the most productive species, *B. lenta* and *U. americana*. Herbivory primarily affected *Q. rubra*, with the highest rates occurring in the warmest, driest plots. At the leaf level, SLA and foliar N were rarely affected by the treatments, while leaf C:N increased in wetter plots, most notably in *B. lenta*, *A. rubrum*, *P. serotina* and *U. americana*.

Table 1. Mixed model results for estimated TLA, leaf herbivory damage, SLA, LWC, leaf carbon (%C), leaf nitrogen (%N) and leaf C:N. *P*-values < 0.05 and 0.10 are bolded and italicized, respectively. Df, degrees of freedom; χ^2 , Wald's chi-squared statistic.

	Df	TLA		Herbivory		SLA		LWC		Leaf C		Leaf N		Leaf C:N	
		χ^2	<i>P</i> -value	χ^2	<i>P</i> -value	χ^2	<i>P</i> -value	χ^2	<i>P</i> -value	χ^2	<i>P</i> -value	χ^2	<i>P</i> -value	χ^2	<i>P</i> -value
Precipitation (P)	2	8.96	0.011	2.31	0.314	2.39	0.303	3.91	0.141	0.80	0.671	10.91	0.004	22.68	<0.001
Warming (W)	3	23.78	<0.001	4.40	0.221	0.83	0.842	2.41	0.491	3.36	0.340	3.16	0.368	5.30	0.151
Species (S)	5	993.15	<0.001	207.19	<0.001	238.98	<0.001	89.00	<0.001	224.96	<0.001	184.79	<0.001	212.22	<0.001
P × W	6	21.84	0.001	14.08	0.029	5.15	0.524	6.98	0.323	8.38	0.212	2.30	0.890	3.70	0.717
P × S	10	57.73	<0.001	44.59	<0.001	17.75	0.059	40.18	<0.001	19.36	0.036	43.19	<0.001	38.28	<0.001
W × S	15	110.11	<0.001	38.88	0.001	10.25	0.804	29.98	0.012	10.82	0.765	25.63	0.042	31.75	0.007
P × W × S	30	30.60	0.435	153.60	<0.001	34.22	0.272	41.43	0.080	39.93	0.106	44.23	0.045	15.35	0.988

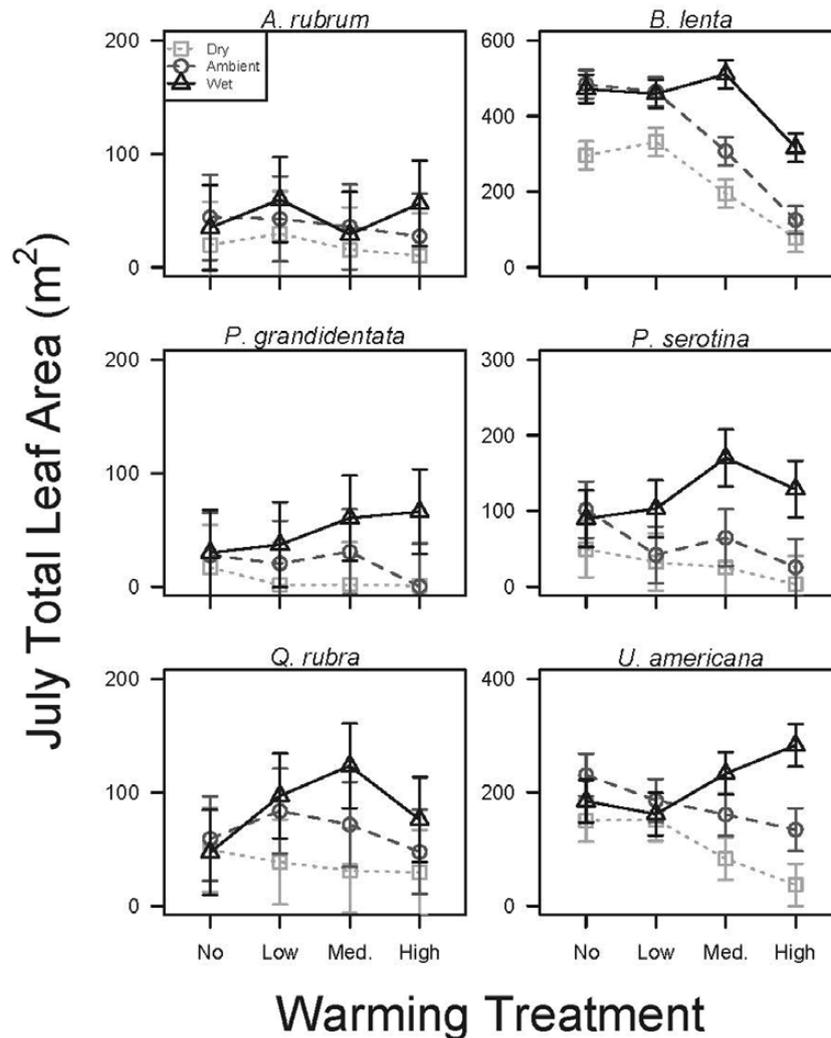


Figure 2. Estimated TLA in late July (mean \pm SE) for *A. rubrum*, *B. lenta*, *P. grandidentata*, *P. serotina*, *Q. rubra* and *U. americana* in the wet (dark grey triangles), ambient (grey circles) and dry (light grey squares) precipitation treatments across the four warming treatments.

Consistent with our expectations, the warming treatments combined with either ambient or reduced precipitation progressively reduced estimated TLA of most species, likely as a response to whole-plant water stress induced by warming-driven increases in water demand (i.e. vapour pressure deficit) and reductions in water supply (i.e. soil moisture) (Smith et al., 2016). This was likely to be especially pronounced in our study based upon the warm and dry background conditions prior to sampling date (Fig. 6). Using four of the same tree species, and also at BACE, Smith et al. (2016) found that net photosynthesis and transpiration rates decreased with warming as a consequence of the indirect effect of the warming treatments on soil moisture. Our results highlight two possible strategies for reducing whole-plant water loss in combined warm, dry conditions: reduced growth or the shedding of leaves. That the TLA response was greatest in the warmest, driest plots, but the physiological responses occurred in response to warming and

drying alone (Smith et al., 2016) suggesting that leaf area reduction later in the growing season could potentially be a secondary response to drought in these species. The interactions of temperature with the reduced precipitation treatment on insect damage in *Q. rubra* were particularly complex and the fluctuations between no, low and medium warming are difficult to explain biologically (Fig. 3). However, the combined high temperature, dry treatment dramatically increased herbivory damage (Fig. 3), suggesting that leaves grown in hot, dry conditions are more favourable for oak herbivores. Although the effects of temperature on insect performance differ greatly in different habitats, host plants, insect life history strategies and complex trophic interactions, there is much data to suggest that temperature itself enhances localized insect herbivores through survival, abundance and development (review in Bale et al., 2002). Interestingly, Carnicer et al. (2011) found trends of increased crown defoliation in southern European

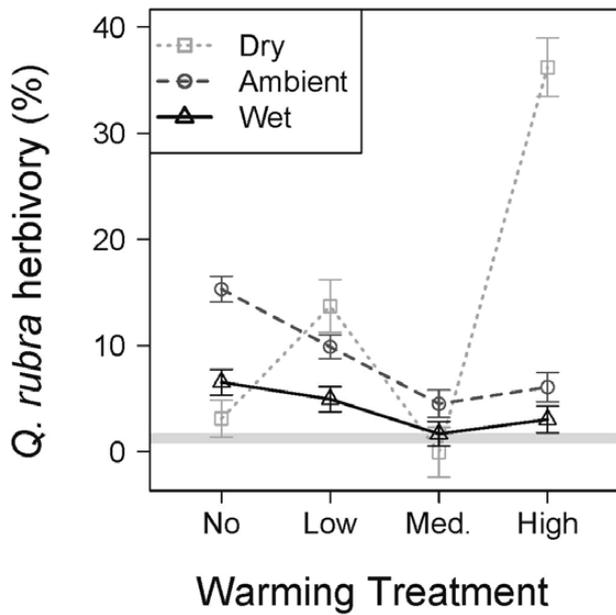


Figure 3. Mean percent leaf level insect herbivory (\pm SE) for *Q. rubra* in the wet (dark grey triangles), ambient (grey circles) and dry (light grey squares) precipitation treatments across the four warming treatments measured in late July. The grey horizontal bar represents the mean percent herbivory for the other five species combined.

forests after periods of severe drought, which they suggest is due to different species-specific responses to increased water deficit pressures within complex food webs.

As we did not measure what types of insect herbivores were consuming the leaves, we cannot be sure whether they were attracted to the leaves or present in higher numbers within the high temperature, dry plots. In a study of *Q. rubra* leaf metabolite responses at BACE, Suseela et al. (2015) found that both warmed and drier conditions increased the concentration of soluble proteins in green leaf tissue by over 75 % as compared to controls. Leaves in the dry, high warming treatment of that study also had a markedly different metabolite profile and the highest tannin concentrations. The increased damage we observed could suggest that some herbivores may be able to detect the enhanced nutritional quality of these climate-stressed plants and tolerate the higher tannin content—but could also suggest greater consumption by the herbivore individuals that were present.

Under favourable conditions (e.g. warm and wet), plants tend to produce higher SLA (Poorter et al. 2009).

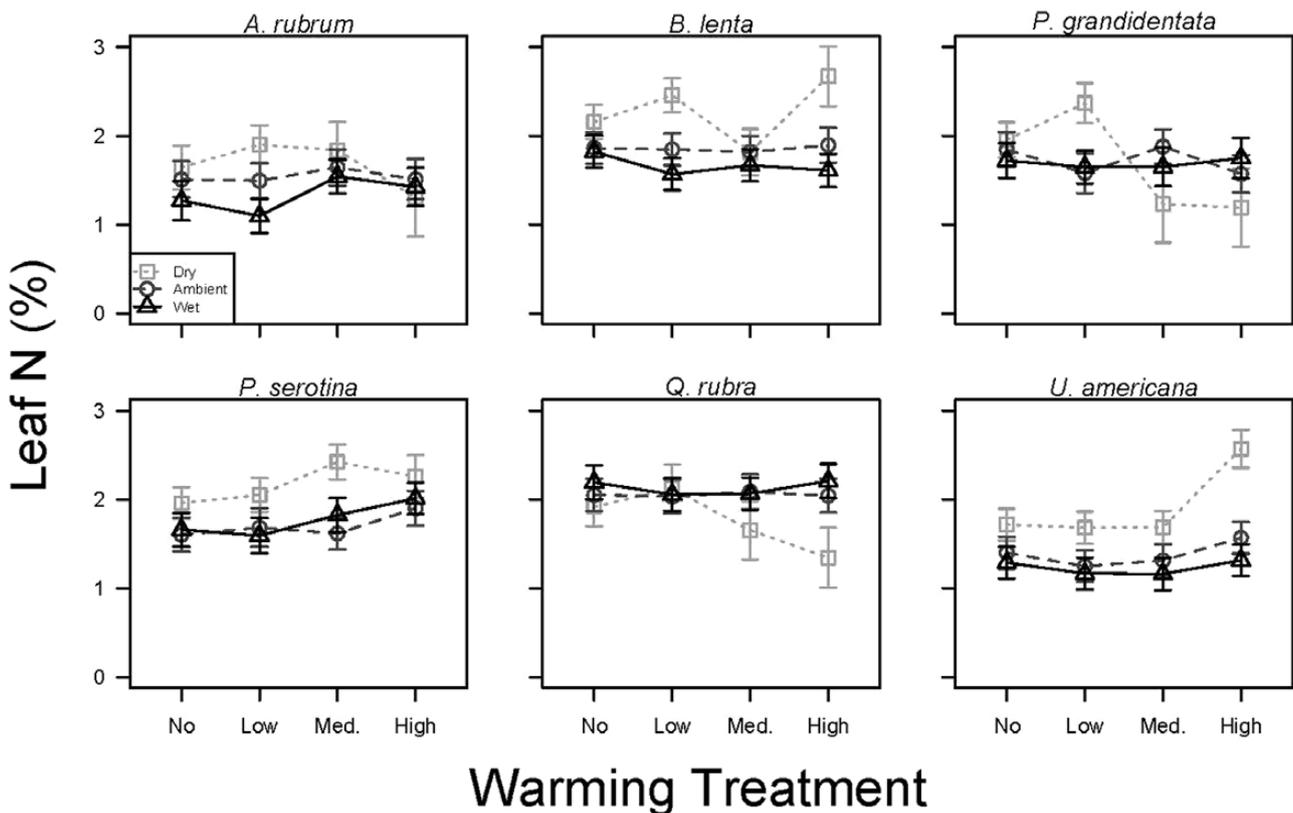


Figure 4. Foliar nitrogen by weight (percent; mean \pm SE) of *A. rubrum*, *B. lenta*, *P. grandidentata*, *P. serotina*, *Q. rubra* and *U. americana* in the wet (dark triangles), ambient (grey circles) and dry (light squares) precipitation treatments across the four warming treatments measured in late July.

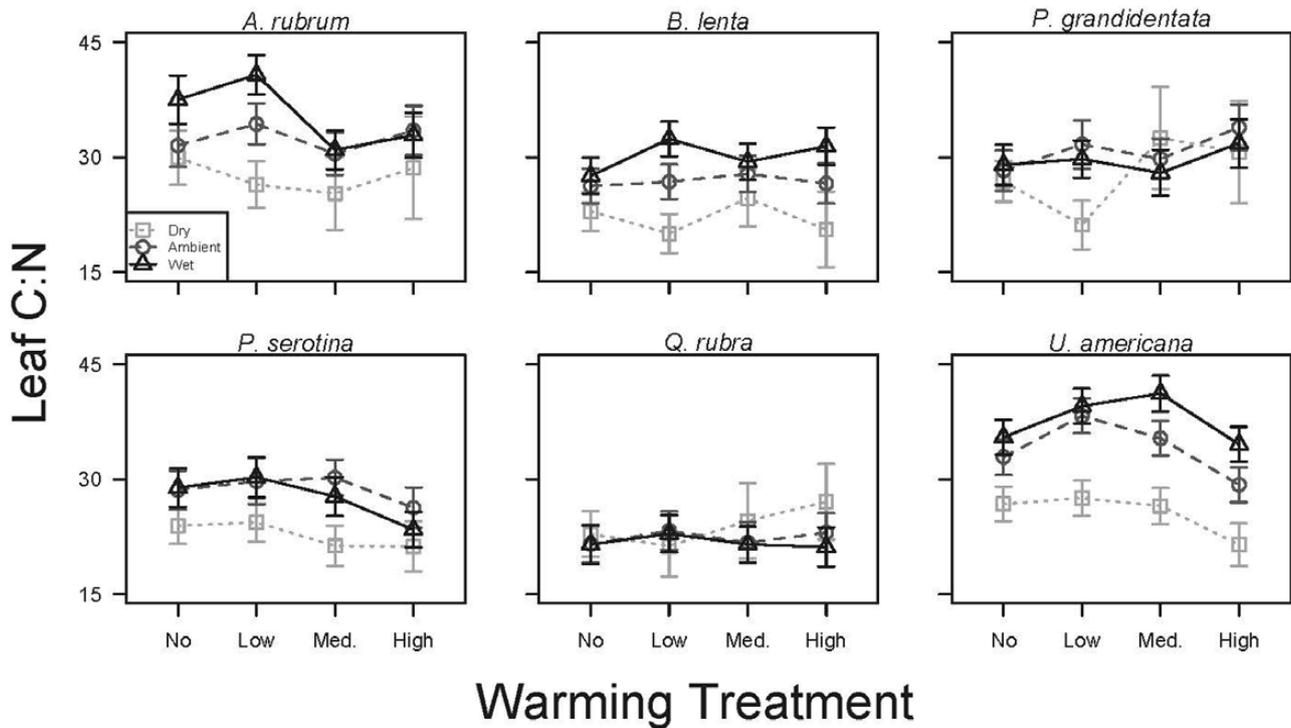


Figure 5. Leaf carbon:nitrogen ratio (\pm SE) for *A. rubrum*, *B. lenta*, *P. grandidentata*, *P. serotina*, *Q. rubra* and *U. americana* in the wet (dark grey triangles), ambient (grey circles) and dry (light grey squares) precipitation treatments across the four warming treatments measured in late July.

However, we found little consistent response of SLA to the climate treatment manipulations we imposed (Table 1). This suggests that, in these deciduous species, the primary means of response to climatic change is not through alterations of leaf morphology, but through a change in canopy properties, namely leaf area. In this experiment, the individuals were planted in each plot before leaf onset in the spring, but had not been acclimated to the treatments over multiple growing seasons. As such, our results suggest that, within a single growing season, leaf morphology is generally less plastic than TLA.

We expected foliar N to increase (and foliar C:N to decrease) with warming and added precipitation. However, the treatments had no consistent effect on foliar percent N (Table 1). *Ulmus americana* had the overall lowest foliar N level, and was the only species to respond to the treatments, with greater leaf N concentrations in the warmer and drier plots. Auyeung (2012) found the availability of summer soil ammonium and nitrate to be highest in the dry treatment at BACE. Other work at BACE found that warming increased foliar N in herbaceous plant tissue (Rodgers et al. 2012) but had little effect on soil N cycling rates (Auyeung et al. 2013).

While we did not see a strong response of leaf N to the treatments (Fig. 4), leaf C:N tended to decrease in drier plots in all species except *P. grandidentata* and *Q. rubra*

(Fig. 5), indicating a reduction in foliar C in dry conditions (Table 1). Combined with a reduction in TLA in these plots, this result suggests that seedlings grown under dry conditions are likely to take up and store less carbon, at least in their leaves. Interestingly, the two species that did not show C:N changes, *P. grandidentata* and *Q. rubra*, showed unique whole-plant increases in mortality and herbivory, respectively, in response to warm, dry conditions.

We had hypothesized that *B. lenta* and *P. grandidentata* would be more negatively affected by the warmed and dry treatments than the other species because their climatic niches and range sizes are smaller, and their ranges lie farther north and east. This hypothesis was supported, but in somewhat different ways for each species. Our results confirm the low drought tolerance of *P. grandidentata* with large percentages of these seedlings dying in both the dry and warmed conditions (Fig. 1), whereas other species' seedlings had much higher survivorship. Although *B. lenta* seedlings survived environmental conditions in all of the treatments, drier conditions reduced leaf production of *B. lenta* (along with *U. americana*) more strongly than the other species, and *B. lenta* TLA was most strongly suppressed by warming (Fig. 2). This suppression of TLA could be a consequence of limited C inputs; working with seedlings of four of the same tree species at BACE, Smith et al. (2016) found that

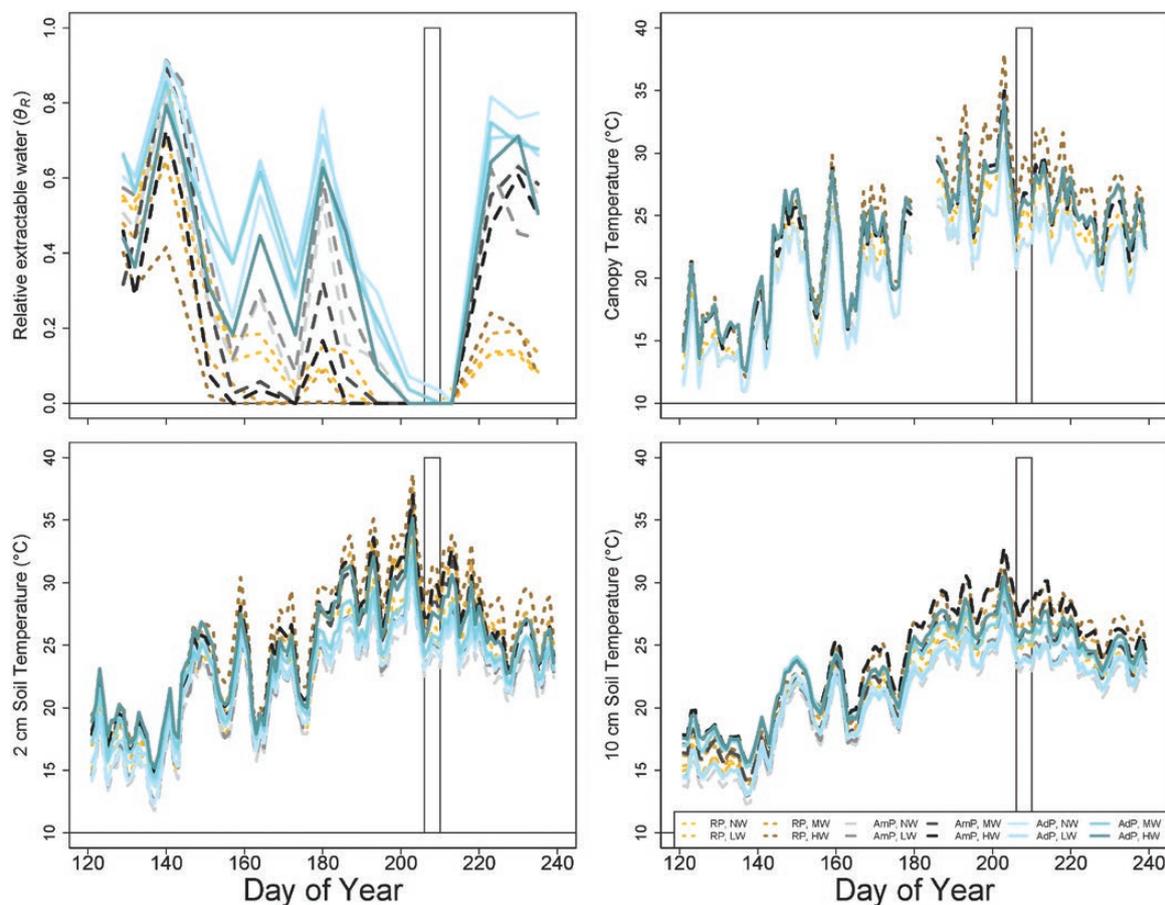


Figure 6. Mean relative extractable water (θ_R ; unitless; top left), canopy temperature (top right), soil temperature at 2 cm depth (bottom left), soil temperature at 10 cm depth (bottom right) in the added precipitation (AdP; blue, solid lines), ambient precipitation (AmP; grey and black, dashed lines) and reduced precipitation (brown, dotted lines) over the course of the experiment. Darker colours within each precipitation treatment indicate higher levels of warming (NW, no warming; LW, low warming; MW, medium warming; HW, high warming). Means are for each plot type during each measurement date ($n = 3$). White box indicates the plant measurement dates.

the leaf gas exchange rates of *B. lenta* were more sensitive to soil moisture than the gas exchange rates of *P. serotina*, *Q. rubra* or *U. americana*. Taking these results together with the trend towards increasing leaf N content [see [Supporting Information—Table S2](#)], *B. lenta* appears to be more conservative when stressed and could be considered one of the more isohydric species we studied. The USDA plants database classifies *P. grandidentata* and *Q. rubra* as having low tolerance to drought, while *A. rubrum*, *B. lenta*, *P. serotina* and *U. americana* are listed as having a medium level (USDA 2017). The two low-tolerance species each had unique responses to the driest treatments in this study, with high seedling mortality in *P. grandidentata* (Fig. 1) and high herbivory in *Q. rubra* (Fig. 3). However, responses of growth (measured at TLA) and other leaf properties did not clearly distinguish these species from the other four (Fig. 2). We would not expect our measurements to perfectly classify species' drought tolerances, as we measured these trees

only as seedlings, although the seedling stage may be the most critical for determining long-term persistence of a tree species.

Our findings that plants generally responded more strongly to the reduced precipitation treatment than to warming, and that warming and reduced precipitation together had the strongest effects (Table 1; see [Supporting Information—Fig. S2](#)), parallel those of other studies from the BACE site (Tharayil et al. 2011; Hoeppe and Dukes 2012; Rodgers et al. 2012; Suseela et al. 2012; Suseela et al. 2015; Smith et al. 2016). Interestingly, there is little evidence of added precipitation ameliorating any negative responses to the high warming treatment. Taken together, these studies suggest that future projected warming conditions in the northeastern USA (Hayhoe et al. 2007) in combination with extended dry periods over the growing season (Rawlins et al. 2012) may result in substantial shifts in species composition, declines in whole-plant growth and altered leaf-level health.

Conclusions

Warm and dry conditions suppressed seedling growth in these six common New England tree species, as measured by TLA. These conditions also increased mortality and herbivory of *P. grandidentata* and *Q. rubra*, respectively. For the other four species, warm, dry conditions decreased foliar C and C:N. This study indicates that climatic warming is likely to increase the sensitivity of carbon uptake to precipitation in young trees. Dry years in a warming climate are likely to increasingly suppress production through species-specific combinations of mortality, herbivory, reduced leaf area and reduced per-leaf C uptake.

Sources of Funding

The Boston-Area Climate Experiment was constructed with funding from the National Science Foundation (grant # DEB-0546670), with further support from NSF (DEB-1146279) and the U.S. Department of Energy's Office of Science (BER), through the Terrestrial Ecosystem Science programme and the Northeastern Regional Center of the National Institute for Climatic Change Research. Faculty and student summer research funds were provided by the Babson Faculty Research Fund. Partial support for J.S.D.'s participation in this project was provided by the USDA's National Institute of Food and Agriculture, through Hatch project 1000026 and AFRI grant 2015-67003-23485. This is paper no. 1821 of the Purdue Climate Change Research Center (PCCRC).

Contributions by the Authors

V.L.R., S.S.H. and J.S.D. conceived of the project. V.L.R., N.G.S. and S.S.H. took the field measurements. V.L.R. prepped lab samples. N.G.S. and S.S.H. analysed the data. All authors contributed to the writing of the article.

Conflict of Interest

None declared.

Acknowledgements

We thank C. Goranson, R. McNellis, G. Pold, T. Lancaster, M. Kapotsis and J. Schaefer for field and laboratory assistance. We also thank D. Flynn for assistance in initial data analysis.

Supporting Information

The following additional information is available in the online version of this article—

Table S1. Results from *post hoc* Tukey's tests for TLA, LWC and C:N across precipitation treatments. Key: SE, standard error of the least square means; Ddf, denominator degrees of freedom; lowerCL, lower confidence limit; upperCL, upper confidence limit; Group, indicates statistically different mean values for treatment within species based on Tukey's HSD ($\alpha = 0.05$). Ambient denotes treatments receiving ambient precipitation.

Table S2. Results from *post hoc* Tukey's tests for TLA, LWC and C:N across warming treatments. Key: SE, standard error of the least square means; Ddf, denominator degrees of freedom; lowerCL, lower confidence limit; upperCL, upper confidence limit; Group, indicates statistically different mean values for treatment within species based on Tukey's HSD ($\alpha = 0.05$). Control denotes the unwarmed treatments.

Table S3. Specific leaf area (SLA) by species (mean \pm SE) with different lower case letters indicating significant differences ($P < 0.05$) from a Tukey's HSD test.

Figure S1. Hourly canopy temperature averaged across plot type for DOY 121-239 in the added precipitation (AdP; blue, solid lines), ambient precipitation (AmP; grey and black, dashed lines) and reduced precipitation (brown, dotted lines) over the course of the experiment. Darker colours within each precipitation treatment indicate higher levels of warming (NW, no warming; HW, high warming). Means are for the three plot types over 119 days ($n = 357$).

Figure S2. Estimated total leaf (surface) area in late July (\pm SE) for all species averaged together in the wet (dark grey triangles), ambient (grey circles) and dry (light grey squares) precipitation treatments across the four warming treatments.

Figure S3. Leaf level insect herbivory (percent; mean \pm SE) for *A. rubrum*, *B. lenta*, *P. grandidentata*, *P. serotina*, *Q. rubra* and *U. americana* in the wet (dark triangles), ambient (grey circles) and dry (light squares) precipitation treatments across the four warming treatments measured in late July.

Figure S4. Specific leaf area (mean \pm SE) for *A. rubrum*, *B. lenta*, *P. grandidentata*, *P. serotina*, *Q. rubra* and *U. americana* in the wet (dark triangles), ambient (grey circles) and dry (light squares) precipitation treatments across the four warming treatments measured in late July.

Figure S5. Leaf-level water content (percent; mean \pm SE) of *A. rubrum*, *B. lenta*, *P. grandidentata*, *P. serotina*, *Q. rubra* and *U. americana* in the wet (dark triangles), ambient (grey circles) and dry (light squares) precipitation treatments across the four warming treatments measured in late July.

Figure S6. Foliar carbon by weight (percent; mean \pm SE) of *A. rubrum*, *B. lenta*, *P. grandidentata*, *P. serotina*,

Q. rubra and *U. americana* in the wet (dark triangles), ambient (grey circles) and dry (light squares) precipitation treatments across the four warming treatments measured in late July.

Literature Cited

- Aerts R, Callaghan TV, Dorrepaal E, van Logtestijn RSP, Cornelissen JHC. 2009. Seasonal climate manipulations result in species-specific changes in leaf nutrient levels and isotopic composition in a sub-arctic bog. *Functional Ecology* **23**:680–688.
- Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshears DD, Hog EH, Gonzalez P, Fensham R, Zhang Z, Castro J, Demidova N, Lim J-H, Allard G, Running S, Semerci A, Cobb N. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management* **259**:660–684.
- Anderegg WR, Klein T, Bartlett M, Sack L, Pellegrini AF, Choat B, Jansen S. 2016. Meta-analysis reveals that hydraulic traits explain cross-species patterns of drought-induced tree mortality across the globe. *Proceedings of the National Academy of Sciences of the United States of America* **113**:5024–5029.
- Aspelmeier S, Leuschner C. 2006. Genotypic variation in drought response of silver birch (*Betula pendula* Roth): leaf and root morphology and carbon partitioning. *Trees* **20**:42–52.
- Auyeung DSN. 2012. *Responses of nitrogen cycling and ammonia-oxidizing communities to warming and altered precipitation in a New England old field*. PhD Thesis, Purdue University, West Lafayette, IN.
- Auyeung DSN, Suseela V, Dukes JS. 2013. Warming and drought reduce temperature sensitivity of nitrogen transformations. *Global Change Biology* **19**:662–676.
- Bale JS, Masters GJ, Hodkinson ID, Awmack C, Bezemer TM, Brown VK, Butterfield J, Buse A, Coulson JC, Farrar J, Good JEG, Harrington R, Hartley S, Jones TH, Lindroth RL, Press MC, Symrnioudis I, Watt AD, Whittaker JB. (2002). Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology* **8**:1–16.
- BassiriRad H. 2000. Kinetics of nutrient uptake by roots: responses to global change. *New Phytologist* **147**:155–169.
- Bates D, Maechler M, Bolker B, Walker S. 2015. lme4: Linear Mixed-Effects Models Using Eigen and S4. R package version 1.1-10. <http://CRAN.R-project.org/package=lme4>.
- Bell DM, Bradford JB, Lauenroth WK. 2014. Early indicators of change: divergent climate envelopes between tree life stages imply range shifts in the western United States. *Global Ecology and Biogeography* **23**:168–180.
- Carnicer J, Coll M, Ninyerola M, Pons X, Sanchez G, Penuelas J. 2011. Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *Proceedings of the National Academy of Sciences* **108**:1474–1478.
- Cavender-Bares J, Bazzaz FA. 2000. Changes in drought response strategies with ontogeny in *Quercus rubra*: implications for scaling from seedlings to mature trees. *Oecologia* **124**:8–18.
- Chacon P, Armesto JJ. 2006. Do carbon-based defences reduce foliar damage? Habitat-related effects on tree seedling performance in a temperate rainforest of Chiloé Island, Chile. *Oecologia* **146**:555–565.
- Chen IC, Hill JK, Ohlemüller R, Roy DB, Thomas CD. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* **333**:1024–1026.
- Dai A. 2013. Increasing drought under global warming in observations and models. *Nature Climate Change* **3**:52–58.
- De Valpine P, Harte J. 2001. Plant responses to experimental warming in a montane meadow. *Ecology* **82**:637–648.
- Dormann CF, Woodin SJ. 2002. Climate change in the Arctic: using plant functional types in a meta-analysis of field experiments. *Functional Ecology* **16**:4–17.
- Erice G, Louahia S, Irigoyen JJ, Sanchez-Diaz M, Avice JC. 2010. Biomass partitioning, morphology and water status of four alfalfa genotypes submitted to progressive drought and subsequent recovery. *Journal of Plant Physiology* **167**:114–120.
- Fisichelli N, Wright A, Rice K, Mau A, Buschena C, Reich PB. 2014. First-year seedlings and climate change: species-specific responses of 15 North American tree species. *Oikos* **123**:1331–1340.
- Fox J, Weisberg S. 2011. *An (R) companion to applied regression*, 2nd edn. Thousand Oaks, CA: Sage. <http://socserv.mcmaster.ca/jfox/Books/Companion/index.html> (9 June 2017).
- Greenwood S, Ruiz-Benito P, Martinez-Vilalta J, Lloret F, Kitzberger T, Allen CD, Fensham R, Laughlin DC, Kattge J, Bönisch G, Kraft NJ, Jump AS. 2017. Tree mortality across biomes is promoted by drought intensity, lower wood density and higher specific leaf area. *Ecology Letters* **20**:539–553.
- Hayhoe K, Wake C, Huntington T, Luo L, Schwartz M, Sheffield J, Wood E, Anderson B, Bradbury J, DeGaetano A, Troy T, Wolfe D. 2007. Past and future changes in climate and hydrological indicators in the US Northeast. *Climate Dynamics* **28**:381–407.
- Hoepfner SS, Dukes JS. 2012. Interactive responses of old-field plant growth and composition to warming and precipitation. *Global Change Biology* **18**:1754–1768.
- Ibrahim L, Proe MF, Cameron AD. 1997. Main effects of nitrogen supply nad drought stress upon whole-plant carbon allocation in poplar. *Canadian Journal of Forest Research* **27**:1413–1419.
- IPCC. 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*. New York, NY: Cambridge University Press.
- Iverson LR, Prasad AM, Matthews SN, Peters M. 2008. Estimating potential habitat for 134 eastern US tree species under six climate scenarios. *Forest Ecology and Management* **254**:390–406.
- Kearney M, Porter W. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters* **12**:334–350.
- Kvet J, Marshall JK. 1971. Assessment of leaf area and other assimilating plant surfaces. In: Sestak Z, Catsky J, Jarvis PG, eds. *Plant photosynthetic production manual of methods*. The Hague, The Netherlands: Junk Publishers, 517–555.
- Lenth RV. 2016. Least-squares means: the R package lmeans. *Journal of Statistical Software* **69**:1–33.
- Lu HY, Lu CT, Wei ML, Chan LF. 2004. Comparison of different models for nondestructive leaf area estimation in taro. *Agronomy Journal* **96**:448–453.
- van Mantgem PJ, Stephenson NL, Byrne JC, Daniels LD, Franklin JF, Fulé PZ, Harmon ME, Larson AJ, Smith JM, Taylor AH, Veblen TT.

2009. Widespread increase of tree mortality rates in the western United States. *Science* **323**:521–524.
- Martinez-Vilalta J, Lloret F. 2016. Drought-induced vegetation shifts in terrestrial ecosystems: the key role of regeneration dynamics. *Global and Planetary Change* **144**:94–108.
- Maximov NA. 1929. *The plant in relation to water: a study of the physiological basis of drought resistance*. London: Allen & Unwin.
- Meehl GA, Stocker TF, Collins WD, Friedlingstein P, Gaye AT, Gregory JM, Kitoh A, Knutti R, Murphy JM, Noda A, Raper SCB, Watterson IG, Weaver AJ, Zhao Z-C. 2007. *Global climate projections*. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL, eds. *Climate 2007: the physical science basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change*. New York, NY: Cambridge University Press.
- Niinemets Ü. 2010. Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: past stress history, stress interactions, tolerance and acclimation. *Forest Ecology Management* **260**:1623–1639.
- Nijs I, Teughels H, Blum H, Hendrey G, Impens I. 1996. Simulation of climate change with infrared heaters reduces the productivity of *Lolium perenne* L. in summer. *Environmental and Experimental Botany* **36**:271–280.
- Niu G, Rodriguez DS, Wang YT. 2006. Impact of drought and temperature on growth and leaf gas exchange of six bedding plant species under greenhouse conditions. *HortScience* **41**:1408–1411.
- Oleksyn J, Reich PB, Zytowski R, Karolewski P, Tjoelker MG. 2003. Nutrient conservation increases with latitude of origin in European *Pinus sylvestris* populations. *Oecologia* **136**:220–235.
- Parkhurst DF, Loucks OL. 1972. Optimal leaf size in relation to environment. *Journal of Ecology* **60**:505–537.
- Parmesan C, Yohe G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**:37–42.
- Poorter H, Niinemets U, Poorter L, Wright IJ, Villar R. 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *The New Phytologist* **182**:565–588.
- Prasad AM, Iverson LR., Matthews S, Peters M. 2007-ongoing. *A climate change atlas for 134 forest tree species of the Eastern United States [database]*. Delaware, OH: Northern Research Station, USDA Forest Service. <https://www.nrs.fs.fed.us/atlas/tree> (15 May 2017).
- R Core Team. 2015. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. <http://www.R-project.org/>.
- Rawlins MA, Bradley RS, Diaz HF. 2012. Assessment of regional climate model simulation estimates over the northeast United States. *Journal of Geophysical Research* **117**:D23112.
- Reich PB, Oleksyn J. 2004. Global patterns of plant leaf N and P in relation to temperature and latitude. *Proceedings of the National Academy of Sciences of the United States of America* **101**:11001–11006.
- Rodgers VL, Hoeppe SS, Daley MD, Dukes JD. 2012. Leaf level gas exchange and foliar chemistry of common old field species, responding to warming and precipitation treatments. *International Journal of Plant Sciences* **173**:957–970.
- Rustad L, Campbell J, Marion G, Norby R, Mitchell M, Hartley A, Cornelissen J, Gurevitch J. 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia* **126**:543–562.
- Sage RF, Way DA, Kubien DS. 2008. Rubisco, rubisco activase, and global climate change. *Journal of Experimental Botany* **59**:1581–1595.
- Scheiter S, Langan L, Higgins SI. 2013. Next-generation dynamic global vegetation models: learning from community ecology. *The New Phytologist* **198**:957–969.
- Shaver GR, Bret-Harte SM, Jones MH, Johnstone J, Gough L, Laundre J, Chapin FS. 2001. Species composition interacts with fertilizer to control long-term change in tundra productivity. *Ecology* **82**:3163–3181.
- Sittaro F, Paquette A, Messier C, Nock CA. 2017. Tree range expansion in eastern North America fails to keep pace with climate warming at northern range limits. *Global Change Biology* **23**:3292–3301.
- Smith TM, Huston MA. 1989. A theory of the spatial and temporal dynamics of plant communities. *Vegetation* **83**:49–69.
- Smith NG, Pold G, Goranson C, Dukes JS. 2016. Characterizing the drivers of seedling leaf gas exchange responses to warming and altered precipitation: indirect and direct effects. *AoB PLANTS* **8**:plw066.
- Smith NG, Rodgers VL, Brzostek E, Kulmatiski A, Avolio ML, Koerner SE, Hoover D, Grant K, Jentshe A, Fatichi S, Niyogi D. 2014. Towards a better integration of biological data from precipitation manipulation experiments into Earth system models. *Reviews of Geophysics* **52**:412–434.
- Suseela V, Conant RT, Wallenstein MD, Dukes JS. 2012. Effects of soil moisture on the temperature sensitivity of heterotrophic respiration vary seasonally in an old-field climate change experiment. *Global Change Biology* **18**:336–348.
- Suseela V, Dukes JS. 2013. The responses of soil and rhizosphere respiration to simulated climatic changes vary by season. *Ecology* **94**:403–413.
- Suseela V, Tharayil N, Xing B, Dukes JS. 2015. Warming and drought differentially influence the production and resorption of elemental and metabolic nitrogen pools in *Quercus rubra*. *Global Change Biology* **21**:4177–4195.
- Tharayil N, Suseela V, Triebwasser DJ, Preston CM, Gerard PD, Dukes JS. 2011. Changes in the structural composition and reactivity of *Acer rubrum* leaf litter tannins exposed to warming and altered precipitation: climatic stress-induced tannins are more reactive. *The New Phytologist* **191**:132–145.
- Thomas FM. 2000. Growth and water relations of four deciduous tree species (*Fagus sylvatica* L., *Quercus petraea* [Matt.] Liebl., *Q. pubescens* Willd., *Sorbusaria* [L.] Cr.) occurring at Central-European tree-line sites on shallow calcareous soils: physiological reactions of seedlings to severe drought. *Flora* **195**:104–115.
- USDA United States Department of Agriculture, Natural Resources Conservation Service. 2017. *Plants database*. <https://plants.usda.gov/java/> (27 April 2017).
- Valladares F, Sánchez-Gómez D. 2006. Ecophysiological traits associated with drought in Mediterranean tree seedlings: individual responses versus interspecific trends in eleven species. *Plant Biology* **8**:688–697.
- Van Bodegom PM, Douma JC, Witte JPM, Ordóñez JC, Bartholomeus RP, Aerts R. 2012. Going beyond limitations of plant functional types when predicting global ecosystem-atmosphere fluxes: exploring the merits of traits-based approaches. *Global Ecology and Biogeography* **21**:625–636.

- Vicca S, Gilgen AK, Camino Serrano M, Dreesen FE, Dukes JS, Estiarte M, Gray SB, Guidolotti G, Hoepfner SS, Leakey AD, Ogaya R, Ort DR, Ostrogovic MZ, Rambal S, Sardans J, Schmitt M, Siebers M, van der Linden L, van Straaten O, Granier A. 2012. Urgent need for a common metric to make precipitation manipulation experiments comparable. *The New Phytologist* **195**:518–522.
- Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJ, Fromentin JM, Hoegh-Guldberg O, Bairlein F. 2002. Ecological responses to recent climate change. *Nature* **416**:389–395.
- Webb CT, Hoeting JA, Ames GM, Pyne MI, LeRoy Poff N. 2010. A structured and dynamic framework to advance traits-based theory and prediction in ecology. *Ecology Letters* **13**:267–283.
- Whittaker RH, Niering WA. 1975. Vegetation of the Santa Catalina Mountains, Arizona. V. Biomass, production and diversity along the elevation gradient. *Ecology* **56**:771–790.
- Wright A, Schnitzer SA, Dickie IA, Gunderson AR, Pinter GA, Mangan SA, Reich PB. 2013. Complex facilitation and competition in a temperate grassland: loss of plant diversity and elevated CO₂ have divergent and opposite effects on oak establishment. *Oecologia* **171**:449–458.
- Wu Z, Dijkstra P, Koch GW, Peñuelas J, Hungate BA. 2011. Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. *Global Change Biology* **17**:927–942.
- Yin XW. 1993. Variation in foliar nitrogen concentration by forest type and climatic gradients in North America. *Canadian Journal of Forest Research* **23**:1587–1602.
- Zhao J, Hartmann H, Trumbore S, Ziegler W, Zhang Y. 2013. High temperature causes negative whole-plant carbon balance under mild drought. *The New Phytologist* **200**:330–339.