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ARTICLE

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Urbanization exacerbates climate sensitivity of eastern United States broadleaf trees

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Abstract

Tree growth is a key mechanism driving carbon sequestration in forest ecosystems. Environmental conditions are important regulators of tree growth that can vary considerably between nearby urban and rural forests. For example, trees growing in cities often experience hotter and drier conditions than their rural counterparts while also being exposed to higher levels of light, pollution, and nutrient inputs. However, the extent to which these intrinsic differences in the growing conditions of trees in urban versus rural forests influence tree growth response to climate is not well known. In this study, we tested for differences in the climate sensitivity of tree growth between urban and rural forests along a latitudinal transect in the eastern United States that included Boston, Massachusetts, New York City, New York, and Baltimore, Maryland. Using dendrochronology analyses of tree cores from 55 white oak trees (*Quercus alba*), 55 red maple trees (*Acer rubrum*), and 41 red oak trees (*Quercus rubra*) we investigated the impacts of heat stress and water stress on the radial growth of individual trees. Across our three-city study, we found that tree growth was more closely correlated with climate stress in the cooler climate cities of Boston and New York than in Baltimore. Furthermore, heat stress was a significant hindrance to tree growth in higher latitudes while the impacts of water stress appeared to be more evenly distributed across latitudes. We also found that the growth of oak trees, but not red maple trees, in the urban sites of Boston and New York City was more adversely impacted by heat stress than their rural counterparts, but we did not see these urban–rural differences in Maryland. Trees provide a wide range of important ecosystem services and increasing tree canopy cover was typically an important component of urban sustainability strategies. In light of our findings that urbanization can influence how tree growth responds to a warming climate, we suggest that municipalities consider these interactions when developing their tree-planting palettes and when estimating the capacity of urban forests to contribute to broader sustainability goals in the future.

KEYWORDS
Acer, climate, climate stress, dendroecology, maple, oak, *Quercus*, tree growth, urban forests, urban heat island

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INTRODUCTION

Temperate broadleaf forests are a critical component of the global carbon (C) cycle, comprising about 60% of the global net C sink (Harris et al., 2021; Pan et al., 2011). Within temperate broadleaf forests, tree growth is often strongly influenced by environmental conditions such as temperature and precipitation (Martin-Benito & Pederson, 2015; Reinmann & Hutyra, 2017). Across the temperate zone, air temperatures are warming and, in many locations, precipitation is becoming more variable in response to climate change (IPCC, 2022). At the same time, urbanization is also altering the growing conditions of trees by increasing exposure to pollution, nitrogen deposition, and light availability, and creating hotter and drier conditions, which can have both positive and negative effects on tree growth (Czaja et al., 2020; Nowak & Walton, 2005; Pendergrass et al., 2017). Globally, urban areas are rapidly expanding (Seto et al., 2012) and urbanization in the United States (US) is expected to subsume 118,318 km^2 of forestland between 2005 and 2050 (Nowak & Walton, 2005). The capacity of temperate forests to remain an important C sink hinges, in part, on how tree growth responds to environmental change. Although both climate change and urbanization are important topics of ecological research, how tree growth and C sequestration respond to the interactive effects of these important facets of environmental change remains a key area of uncertainty.

Across temperate broadleaf forests of the eastern US, climate conditions are important drivers of tree growth, but tree growth response to different climate variables can vary considerably across tree species and as a function of prevailing climate conditions. For example, Martin-Benito and Pederson (2015) found that for red maple (*Acer rubrum*), red oak (*Quercus rubra*), and white oak (*Quercus alba*) trees, wood production was positively correlated with precipitation and negatively correlated with heat stress. In addition, they found that, among these three species, heat stress was a stronger predictor of red maple and white oak growth than that of red oaks. The growth of trees in the northeastern US appears to be more limited by growing season precipitation while tree growth in the southeastern US is more limited by excessive heat during the growing season (Martin-Benito & Pederson, 2015). In contrast, Rollinson et al. (2016) observed a negative correlation between radial tree growth and precipitation for maples and oaks in the eastern US and found that growth of these species peaked at or near the long-term mean maximum growing season air temperatures. They also observed that tree growth sensitivity to climate stress varied by species and concluded that this was a result of interactions between differences in tree size and competition dynamics. Similarly, Reinmann and Hutyra (2017) found that rates of forest-scale aboveground C sequestration in oak-dominated forests were negatively correlated with the number of days during the early growing season when air temperatures exceeded the long-term mean maximum growing season air temperatures. While there has been substantial research dedicated to the relationship between tree growth and climate stress, the extent to which climate conditions might interact with novel conditions in urban environments to augment tree growth is poorly understood.

Urbanization creates unique environmental conditions that can augment tree growth. Compared with rural trees, urban trees are impacted by higher temperatures, increased CO_2 concentrations, modified soil biogeochemistry, increased water stress, and increased vapor pressure deficit (Czaja et al., 2020). As a result of these modifications to growing conditions, urban trees exhibit higher rates of both growth and mortality (Briber et al., 2015; Gregg et al., 2003; Smith et al., 2019; Sonti et al., 2019). For example, white oak trees in urban forests of the northeastern US can grow 42.5% faster than white oak trees in nearby rural forests (Sonti et al., 2019). Smith et al. (2019) reported similar findings for street trees in Boston, Massachusetts (MA), but they also noted that these trees tended to die younger. Gregg et al. (2003) found that higher ozone concentrations in a rural area outside of New York City resulted in reduced growth rates when compared with saplings grown in the urban core of New York City.

Across the temperate zone, air temperatures are warming, and, in many locations, precipitation is becoming more variable in response to climate change (IPCC, 2022). These changes in climate will likely have important impacts on tree growth rates, and the sensitivity of tree growth to climate may be increased by the novel growing conditions in urban environments (Czaja et al., 2020; Williams et al., 2010). A key reason for this is the urban heat island (UHI) effect, a climatic phenomenon resulting in urban areas having higher air temperatures than surrounding rural areas because of anthropogenic modifications to the biophysical characteristics of land surfaces and the generation of waste heat (Lee et al., 2014). Reinmann et al. (2020) studied urbanization and forest fragmentation in relation to climate and found that temperate forests adjacent to nonforest land cover sequestered C in aboveground biomass considerably faster than interior forests. Consequently, the highly fragmented nature of many temperate urban forests contributes to them being more productive per unit area than nearby rural forests. Reinmann et al. (2020) also found that the adverse effects of heat stress on forest

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aboveground C sequestration were amplified in urban forests. However, the effects of urbanization on relationships between forest growth and climate remain understudied. Reinmann et al. (2020) conducted their research in Massachusetts, USA and studied forest-scale dynamics, rather focusing on climate sensitivity of individual tree species. While this study compared the climate sensitivity of aboveground growth between urban and rural forests, it is unclear how widespread this phenomenon is both geographically and across different tree species.

Here, we quantify relationships between tree growth and climate conditions for oak and maple trees in urban and nearby rural forests along a transect in the eastern US that includes (from south to north) Baltimore, Maryland (MD), New York City, New York (NY), and Boston, Massachusetts (MA), and spans a 3.6°C and 174 mm range in mean annual temperature and precipitation, respectively. We chose these three cities because both oaks and maples comprise an important component of the native forest types in each city while climate conditions differ. We focus on oaks and maples because they are common across the temperate mixed-deciduous forests of the eastern US, and they exhibit different responses to water stress (Martin-Benito & Pederson, 2015). Red maple trees are isohydric—meaning they close their stomata under relatively low levels of water stress—while white and red oak trees are anisohydric and keep their stomata open under higher levels of water stress (Hochberg et al., 2018; Thomsen et al., 2013; Yi et al., 2017). We hypothesized (1) urban tree growth will be more adversely impacted by heat and water stress than rural tree growth, (2) oak tree growth will be more adversely impacted by heat stress than maple trees, while maple tree growth would be more adversely impacted by water stress, and (3) that the adverse impacts of climate stress on tree growth will increase from north (i.e., cooler climate) to south (i.e., hotter climate).

MATERIALS AND METHODS

Study sites

For this study, we analyzed tree core datasets previously described by Sonti et al. (2019), Reinmann and Hutyra (2017), and Reinmann et al. (2020) (Figure 1). We quantified relationships between climate conditions and basal area increment (BAI) (i.e., radial growth rates) and contrasted these relationships between trees growing in urban forests and nearby (i.e., <90 km) rural forests. For contrasting urban and rural forests in the New York City, New York (NY) area and the Baltimore, Maryland (MD) area we analyzed canopy codominant white oak and red maple trees. In the Boston, Massachusetts (MA) area, canopy codominant white oak and red maple trees were less common, so we analyzed red oak trees. Throughout this manuscript, we use "MD-URB," "NY-URB," and "MA-URB" to refer to the urban forest sites and "MD-RUR," "NY-RUR," and "MA-RUR" to refer to the rural "reference" forest sites (see Table 1 and Figure 1 for specific locations).

The plots in both the urban and rural reference sites in NY and MD had second-growth forests (at least 1.5 ha in size) dominated by white oak and red maple trees (at least 1.5 ha), with slopes <25% and well drained soils of similar soil series (see Appendix S1: Table S1 for more detail). Plots were selected with the intention of finding sites with soil types that were as similar as possible in each urban and rural pairing. The urban plots in NY and MD, with the exception of one plot in MD, were on public parkland or institutional grounds, and most were private estates prior to their current land uses. The rural plots in NY and MD were all protected areas that were established following extensive clear-cutting for timber and/or agricultural purposes through the late 1800s and early 1900s. The plots in both urban and rural MA had second-growth dominated by red oak trees and were also on shallow slopes of stony, well drained soils of sandy loam or fine sandy loam textures (see Appendix S1: Table S1 for more details). The forests in MA developed after agricultural abandonment around the turn of the 20th century. In each of the MA sites, trees were sampled from 200 m^2 plots that were within larger forests. All of the trees in MA, NY, and MD were sampled from the forest interior (i.e., >20 m from the nearest forest edge) to minimize any artifacts from edge effects (Reinmann & Hutyra, 2017).

In MD, forest parks in Baltimore were used for MD-URB and Oregon Ridge Park in Cockeysville, MD, was used for MD-RUR. In NY, forest parks in New York City were used for NY-URB and Black Rock Forest, a 1550-ha research forest in Cornwall, NY, was used for NY-RUR. In MA, forests in the towns of Belmont and Lynn (<15 km of downtown Boston) were used for MA-URB and the Harvard Forest, a 1600-ha research forest in Petersham, MA was used for MA-RUR. Across our sites, there is strong seasonality in air temperatures, but precipitation (1034–1286 mm $year^{-1}$ across sites) is evenly distributed throughout the year. Mean minimum air temperatures in January (i.e., the coldest month; 1981–2010) ranged from −12.2°C at the Harvard Forest to −1.7°C in Baltimore and urban sites are warmer during the winter than rural sites. However, mean maximum temperatures during July (i.e., warmest month), which ranged from 27.2 to 32.2 from north to south, generally

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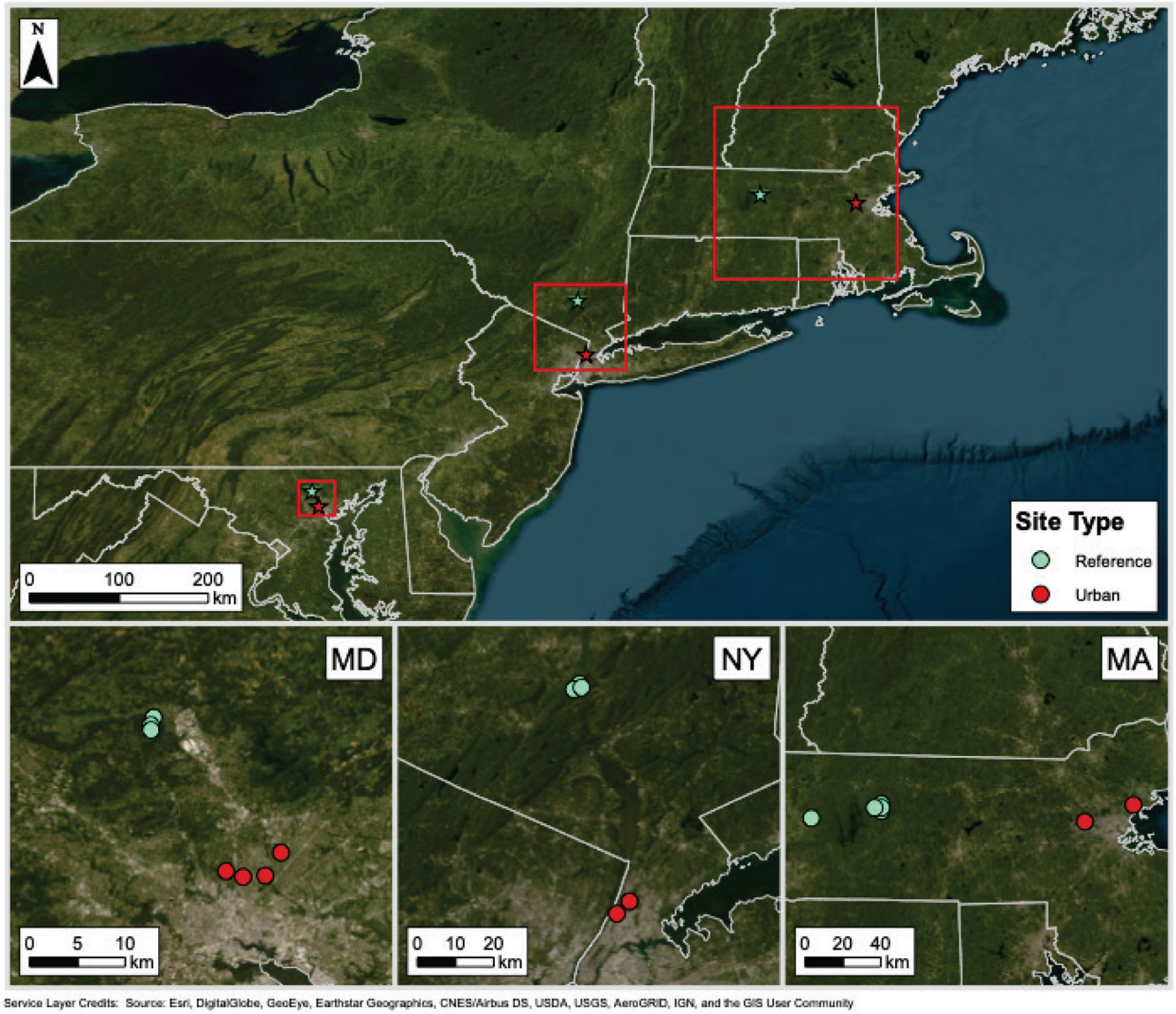

FIGURE 1 Locations of urban (red symbols) and rural reference (blue symbols) study sites in Massachusetts, New York, and Maryland. The map extent covers 38°16′ N to 44°18′ N and 68°02′ W to 79°51′ W.

differ by <1°C between pairs of urban and rural sites. Mean climate conditions (1981–2010) for each study site are summarized in Table 1.

Tree core data

In MA-URB, 21 red oak trees were sampled across eight plots and in MA-RUR 20 red oak trees were sampled across six plots at the Harvard Forest. In NY-URB we used a total of 10 white oak trees and a total of 10 red maple trees sampled across two plots (we initially planned to sample 15 trees of each species, but permission was not granted to core trees at a third plot in NYC). In NY-RUR, a total of 15 white oak trees and a total of 15 red maple trees were sampled across three plots at Black Rock Forest (BRF). In MD-URB, a total of 15 white oak and a total of 15 red maple trees were sampled across four plots. In MD-RUR, a total of 15 white oak and 15 red maple trees were sampled across three plots. A total of 41 trees in MA, 50 trees in NY, and 60 trees in MD were cored ($n = 151$ trees, 302 cores).

In NY and MD, we collected tree cores during fall 2015 through summer 2016 from white oak trees >35 cm diameter at breast height (dbh; 1.4 m) and red maple trees >25 cm dbh (the trees selected for measurement were either dominant or codominant with healthy crowns). For each plot in Massachusetts, we cored dominant or codominant red oak trees >30 cm dbh during 2015 and 2016. For all trees at each site, two 5.15-mm

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TABLE 1 Climate data for each study site from the weather station closest to our study sites with historical climate means from the period of 1981–2010.

Study site	NOAA Weather Station location	Latitude (°N)	Longitude (°W)	Elevation (m)	July maximum temperature (°C)	January minimum temperature (°C)	Precipitation (mm year^{-1})
MA-URB	Boston, MA	42.36057	71.00975	6	27.2	−5.6	1112
MA-RUR	Athol, MA	42.53311	72.18968	410	28.3	−12.2	1187
NY-URB	New York, NY	40.779	73.9693	41	29.4	−2.2	1174
NY-RUR	West Point, NY	41.410031	74.027131	318	29.4	−6.7	1286
MD-URB	Baltimore, MD	39.1733	76.684	48	31.7	−1.7	1034
MD-RUR	Conowingo, MD	39.6556	76.1751	12	32.2	−5.6	1205

Note: Historical climate means were retrieved from usclimaterecrods.com (data accessed on 23 February 2023).
Abbreviations: MA-RUR, Rural Massachusetts; MA-URB, Urban Massachusetts; MD-RUR, Rural Maryland; MD-URB, Urban Maryland; NOAA, National Atmospheric and Oceanic Administration; NY-RUR, Rural New York; NY-URB, Urban New York.

tree cores were collected at breast height. All tree cores were dried, mounted to grooved wood boards, and sanded to a smooth, flat finish using a belt sander. Then they were digitized using high-resolution scanners. Ring increments were measured to 0.001 mm using CooRecorder or WinDENDRO 2012 (Regent Instruments, Inc.) image analysis software. Cross-dating of the cores was performed visually with statistical assistance from COFECHA (Larsson, 2003). The average growth increment of the two cores from each tree was used to calculate BAI. BAI is calculated from:

$$\left(\left(R_2{}^2\right)\right) - \left(\pi\left(\left(R_1{}^2\right)\right)\right), \quad (1)$$

where R_1 is the tree's radius at the beginning of the year and R_2 is the tree's radius at the end of the year and is measured in square millimeters. For our analyses, we used the tree growth data for the period of 1990–2014 for all tree cores.

Climate data

To characterize relationships between BAI and climate stress, we used archived weather station data for the period 1990–2014 from the National Oceanic and Atmospheric (NOAA) National Climate Data Center (NCDC; accessed via Climate Data Online in 2021), except when noted otherwise. Here, climate stress was separated into two categories: heat stress and water stress. Heat stress was quantified using two different metrics: (1) heat stress days, defined as the number of days more than 27°C (Reinmann & Hutyra, 2017) and (2) mean daily maximum temperature. We used SPEI_2 (i.e., a metric of water stress on a two-month timescale) as a proxy for water stress and data were derived from the 1° × 1° SPEI Global Drought Monitor (Vicente-Serrano et al., 2010). With the exception of NY-RUR and MA-RUR, we used NCDC data collected from unique weather stations for each of our sites, as summarized in Table 1. Heat stress data for NY-RUR were from a weather station located at BRF (The Virtual Forest Initiative, 2021), and heat stress data for the MA-RUR sites were collected from a weather station located at the Harvard Forest (see Reinmann et al., 2020). Because of missing data at the BRF weather station, heat stress analyses for NY-RUR included the years 1996–1998 and 2000–2014.

Data analysis

We performed data analyses using R (version 1.3.9; https://cran.r-project.org/). Climate stress as a driver of interannual variability in tree growth (i.e., BAI) across all sites was quantified using linear regression analyses. Climate variables (i.e., metrics of heat stress and SPEI_2) and their interactions were aggregated by month or groups of months for each year and used as the fixed effects. "Summer" was defined as June through August and "early summer" was defined as June and July. Analyses of the number of heat stress days were conducted for four time periods during the growing season: May through July ("MJJ"), May through August ("MJJA"), June and July ("JJ"), and June through August ("JJA"). Statistical significance (alpha = 0.05), r^2, and slope values were used to assess the climate sensitivity of BAI. Unless otherwise indicated, all values reported are means and standard error (SE). For simplicity, the figures we present illustrate the tree growth–climate relationships with the strongest correlations out of all the significant

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relationships we found. A summary of all statistics for all variables and relationships quantified is reported in Appendix S2: Table S1.

RESULTS

Climate data

For the period of 1990–2014, the average summer maximum temperatures and the number of heat stress days increased from north to south (Appendix S1: Tables S2 and S3). Urban sites had warmer mean summer maximum temperatures than rural sites in both Massachusetts (urban: 26.4 ± 0.2°C, rural: 25.3 ± 0.2°C) and New York (urban: 28.2 ± 0.2°C, rural: 26.8 ± 0.3°C) but not in Maryland (urban: 29.9 ± 0.2°C, rural: 30.2 ± 0.4°C) (Appendix S1: Table S2). June and July SPEI_2 values were lower (i.e., drier) in Maryland (urban: −0.12 ± 0.2, rural: −0.09 ± 0.2) than in both Massachusetts (urban: 0.03 ± 0.2, rural: 0.03 ± 0.2) and New York (urban: 0.07 ± 0.2, rural: 0.24 ± 0.2) (Appendix S1: Table S4). In both Maryland and Massachusetts, the urban and rural sites fall within the same SPEI_2 Global Drought Monitor grid cell, precluding the detection of differences between these locations. In New York, NY-RUR tended to be wetter than NY-URB (Appendix S1: Table S4).

BAI and climate data analysis

Water stress

We found that BAI was generally positively correlated with water availability during the early growing season (June and July) across our sites (urban and rural) and the species we sampled (Figure 2). The only exception to this was for white oaks in both MD-RUR and MD-URB where we observed BAI decreases in response to increased water availability. In MA-URB, red oak tree growth was significantly positively correlated with June, July, and JJ (June and July average) SPEI_2, with July SPEI_2 being the strongest predictor of tree response to climate (July SPEI_2: $p = 0.0001$, $r^2 = 0.46$, slope = 276.25 mm^2 wood SPEI $unit^{-1}$; Figure 3). BAI of white oak trees in both NY-URB and NY-RUR exhibited significant positive correlations with JJ SPEI_2 ($p = 0.004$ and $p = 0.04$, respectively; Figure 3). We found significant positive correlations between NY-URB white oak BAI with June, July, and JJ SPEI_2, with JJ SPEI_2 being the strongest predictor of tree response to climate stress (JJ SPEI_2: $r^2 = 0.30$, slope = 220.60 mm^2 wood SPEI $unit^{-1}$; Figure 3). In NY-RUR, white oak BAI was significantly positively correlated only with JJ SPEI_2 ($r^2 = 0.21$, slope = 99.26 mm^2 wood SPEI $unit^{-1}$; Figure 3). Red maple BAI in NY-RUR was significantly positively correlated with July SPEI_2 ($p = 0.023$; $r^2 = 0.26$, slope = 78.93 mm^2 wood SPEI $unit^{-1}$; Figure 3) while NY-URB red maple BAI was not significantly correlated with SPEI_2. In MD-RUR, we found a significant positive correlation between red maple BAI and SPEI_2 in June, July, JJ, and August, but June SPEI_2 was the strongest predictor of tree growth (June SPEI_2: $p = 0.013$, $r^2 = 0.23$, slope = 118.01 mm^2 wood SPEI $unit^{-1}$; Figure 3). We did not find a significant correlation between red maple BAI and SPEI_2 in MD-URB. Similarly, white oak BAI was not significantly correlated with SPEI_2 in MD-URB or MD-RUR (Figure 3).

Heat stress

While water stress appears to be an important climatic control on tree growth across our cities, we find that urbanization and heat stress impact growth differently across latitudes (Figure 2). For example, urbanization exacerbates declines in tree growth from heat stress at our cooler northern sites of MA and NY, but not at our warmest and most southern sites in MD (Figure 4). We found significant negative correlations between the BAI of white oak trees in NY-URB and each of our measures of heat stress, but early summer mean temperature was the strongest predictor of BAI ($p = 0.002$, $r^2 = 0.34$, slope = −190.1 mm^2 BAI $°C^{-1}$ increase in mean temperature; Figure 4). We did not find significant correlations between our different metrics of heat stress and BAI for either white oak or red maple in NY-RUR. While heat stress was a significant predictor of white oak BAI in NY-URB, no metric of heat stress was a significant predictor of red maple BAI ($p > 0.3$). In MA-URB, we found significant correlations between red oak BAI and the number of heat stress days (i.e., days with maximum temperature above 27°C) in MJJA (May–August), MJJ (May–July), JJ (June–July), and JJA (June–August), but the number of heat stress days in JJ explained the highest amount of interannual variability in BAI (JJ heat stress: $p = 0.014$, $r^2 = 0.23$, slope = −33.9 mm^2 BAI heat stress day^{-1}; Figure 4). Furthermore, we found that both the strength of the correlation (i.e., r^2) between red oak BAI and JJ heat stress and magnitude of growth decline were substantially higher in MA-URB ($p = 0.014$, $r^2 = 0.23$, slope = −33.9 mm^2 BAI heat stress day^{-1}; Figure 4) than MA-RUR ($p = 0.08$, $r^2 = 0.13$, slope = −20.9 mm^2 BAI heat stress day^{-1}; Figure 4). Red maple and white oak BAI were not significantly correlated with heat stress in either MD-URB or MD-RUR.

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Hypothesis		(1) Urban trees will be more adversely impacted by heat and water stress than rural trees (2) Oak trees will be more adversely impacted by heat stress than maple trees while maple trees would be more adversely impacted by water stress (3) The adverse impacts of climate stress on tree growth will increase from north (i.e., cooler climate) to south (i.e., hotter climate).									
Location by Latitude (North to South)		Heat stress						Water stress			
		Early summer temp	Summer temp	MJJA Heat Stress	MJJ Heat Stress	JJ Heat Stress	JJA Heat Stress	June SPEI	July SPEI	Aug SPEI	June-July SPEI
Boston	Rural										
	Urban										
NYC	Rural										
	Urban										
Baltimore	Rural										
	Urban										

FIGURE 2 Visualization of hypothesis and findings across all sites, with leaf icons representing locations where correlations were significant (the  icon represents red maple trees, the  icon represents red oak trees, and the  icon represents white oak trees).

DISCUSSION

Our study illustrates important differences in tree growth sensitivity to climate stress between urban and rural forests, but our results suggest that this response differs across cities (which vary in climate conditions) and tree species. We explored the roles of water stress (using SPEI_2 as a proxy) and exposure to heat stress to improve understanding of the relative importance of water and temperature as mediators of tree growth in urban and rural temperate broadleaf forests. Heat stress significantly influences tree growth in the higher latitude and cooler climates of New York and Massachusetts, but not the lower latitude and warmer climate of Maryland. By contrast, the adverse impacts of water stress, as represented by SPEI_2, are ubiquitous across these cities spanning a range in climate and latitude. Similar to other recent studies in the eastern US (D'Orangeville et al., 2018; Martin-Benito & Pederson, 2015; Reinmann et al., 2020; Reinmann & Hutyra, 2017), we also observed that tree growth was most sensitive to climate stress during the early growing season. Furthermore, we found that the growth of oak trees in urban forests of New York and Massachusetts is more adversely impacted by heat stress than oak trees in rural forests. However, of the trees we sampled, the growth of white and red oak trees more consistently responded to climate stress than red maple trees.

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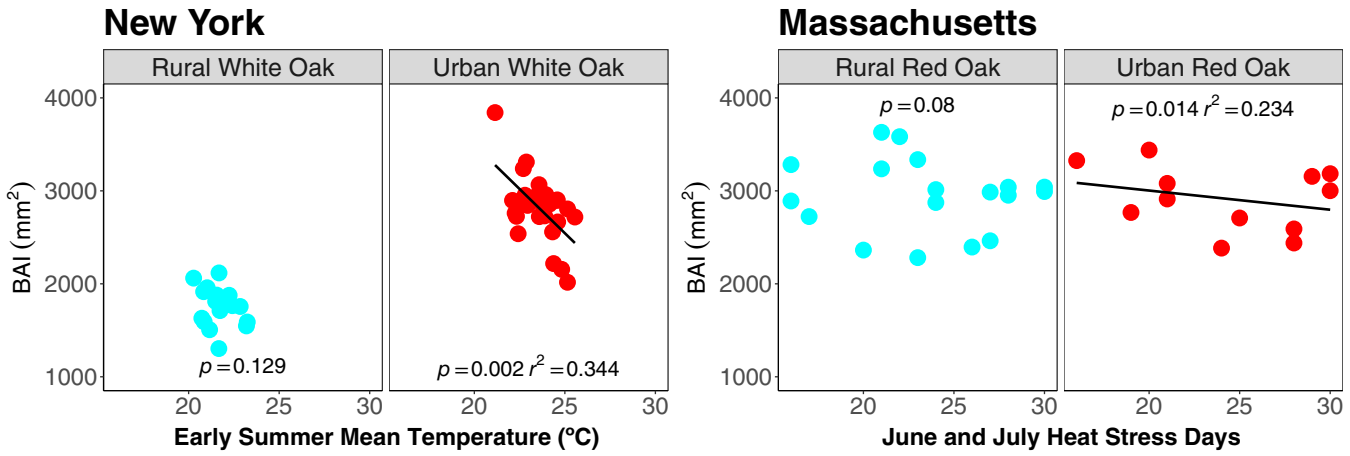

FIGURE 3 Relationships between tree basal area increment (BAI) and SPEI_2 during the early growing season for urban (red symbols) and rural reference (blue symbols) sites. Regression lines are only included for sites with a significant relationship ($p < 0.1$). For each site, we only include the time period within the early growing season with relationships that were either significant and had the best fit (determined from r^2 values) or analogous to other sites that are significant (for comparison). We did not find significant results for red maples in NY-URB and MD-URB, white oaks in MD-URB, and red oaks in MA-RUR.

Tree growth in temperate broadleaf forests of the eastern US tends to be positively correlated with growing season precipitation and negatively correlated with water stress and excessive heat during the growing season (Martin-Benito & Pederson, 2015; Rollinson et al., 2016), which our findings reflect. Reinmann and Hutyra (2017) also found temperate forest growth to be negatively impacted by heat stress during the early growing season. We found the growth of oak trees to be more responsive to climate stress than red maple, but the responses observed in other studies have been mixed. For example, although oak tree growth in temperate broadleaf forests generally exhibits a clear sensitivity to growing season climate, Rollinson et al. (2016) found that red maples in the central Appalachians were generally unresponsive to gradients in mean summer temperature while Martin-Benito and Pederson (2015) found that growth of red maple trees from a broad latitudinal range in the eastern US was negatively correlated with maximum July temperatures. It is likely that geography, site conditions, and local competition dynamics collectively mediate the extent to which red maple growth exhibits strong climate sensitivities. In our study, we made a concerted effort to select red maple and oak trees in similar canopy positions. However, our findings regarding these forests (Sonti et al., 2019) and those reported by others (e.g., Urbanski et al., 2007) are that oaks tend to grow faster and outcompete co-occurring red maples, which could limit maple growth sensitivity to climate (Clark et al., 2014). Given warming climate conditions throughout our study region (IPCC, 2022) and the larger adverse impacts of heat stress on oak growth than red maple growth, it might seem counterintuitive that oaks outcompete co-occurring maples across much of the region. However, oaks often have higher photosynthetic capacities than red maples (e.g., Bassow & Bazzaz, 1997; Reinmann et al., 2023) and the oaks at our sites consistently grow faster than co-occurring maples, even in years with more climate stress. We found that climate–tree growth relationships were more similar among trees in New York and Massachusetts than with trees from Maryland. This finding is similar to Martin-Benito and Pederson (2015) who reported that the climate–tree growth relationships for trees in Maryland were grouped with southern populations of trees while those in New York were grouped with northern populations.

Cross-city comparisons across the eastern US

Tree growth response to interannual variations in climate varied across our cities, but in the opposite direction of what we expected. It is possible that the generally hotter growing season conditions in Maryland compared with New York and Massachusetts could have induced an adaptive response that has made the trees less adversely impacted by heat. Although we studied the same tree species in New York and Maryland, it was also possible that they were from genetically distinct populations with different tolerances for climate stress. Past studies have found variations in adaptations to stressors across unique genetic provenances of temperate tree species. For example, Russell and Dawson (1995) observed that red oaks in the southeastern US tend to have thicker bark than red oaks in the northeastern US because of selective pressure from fires. Schaberg et al. (2022) also observed that

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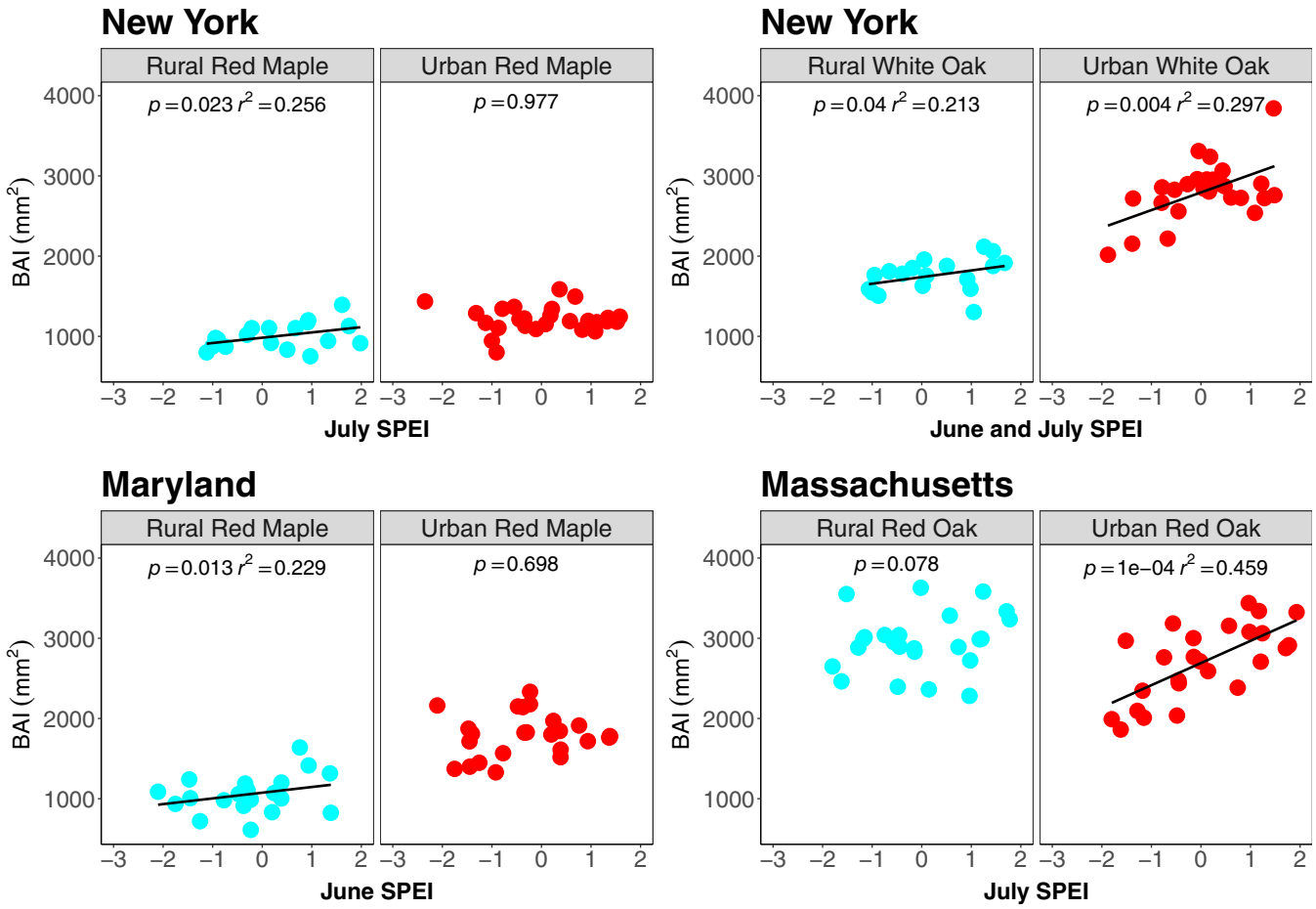

FIGURE 4 Relationships between tree basal area increment (BAI) and heat stress data during the early growing season for urban (red symbols) and rural reference (blue symbols) sites. Regression lines are only included for sites with a significant relationship ($p < 0.1$). For each site, we only include the time period within the early growing season with relationships that were either significant and had the best fit (determined from r^2 values) or analogous to other sites that are significant (for comparison). We did not find significant results for red maples in NY-URB, NY-RUR, MD-URB and MD-RUR, white oaks in NY-RUR, MD-URB and MD-RUR, and red oaks in MA-RUR.

American chestnut (*Castanea dentata*) trees from warm climate genetic populations tended to break bud earlier and experience greater spring leaf frost damage than trees from colder climate zones. Differences in genetic provenance may also explain previous observations that tree growth relationships with climate were similar among trees within warm temperate climates and similar among trees within cool temperate climates in the eastern US (Martin-Benito & Pederson, 2015).

Urban versus rural differences

Urbanization is well known to impact growing conditions for trees by altering important variables such as the light environment, growing season length and temperature, competition dynamics, exposure to pollution, and soil characteristics (Czaja et al., 2020). Previous work has demonstrated that these altered conditions can increase the rates of both tree growth (Smith et al., 2019; Sonti et al., 2019) and rates of mortality (Smith et al., 2019). We found that urbanization can also increase the sensitivity of oak tree growth to climate stress in both Massachusetts and New York. We found steeper declines in oak tree growth in response to heat stress for white oak trees in New York City than for red oak trees in Boston, but the role of geography and magnitude of urbanization versus species differences remains unknown. Reinmann et al. (2020) found that urbanization exacerbated the negative effects of early growing season heat stress on rates of forest aboveground C sequestration in mixed-broadleaf forests of Massachusetts, USA. However, we do not know of any other study that contrasts the effects of urbanization on tree-level or species-specific relationships between growth and climate.

Here we tested for differences in tree growth sensitivity to climate stress between urban and rural forests, but the exact mechanisms behind the patterns we observed remain unclear. Trees in urban environments are

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typically exposed to elevated levels of pollutants such as nitrogen oxides, particulates, and heavy metals that are known to have damaging effects on different aspects of plant physiology (e.g., photosynthesis) and induce mechanical disruptions such as stomatal occlusion (Czaja et al., 2020; Tatsumi et al., 2023). Despite increased exposure to environmental stressors, urban trees have been observed to grow faster than their rural counterparts (Smith et al., 2019; Sonti et al., 2019), at least under mean climate conditions. Perhaps paradoxically, we find that the growth of these urban trees is also more adversely impacted by climate stress than their rural counterparts. These findings may suggest that the presence of adverse effects of environmental and climate stressors on tree growth in cities is compounded. For example, tropospheric ozone pollution is a photochemical process that accelerates under conditions of high light and air temperature. Additionally, to the extent that particulates in cities occlude stomata (Czaja et al., 2020), transpiration and related foliar cooling could be limited which could exacerbate the adverse effects of high air temperatures on photosynthesis (Teskey et al., 2015). Urban soils can also be drier than rural soils (e.g., Garvey et al., 2022), which coupled with typically higher vapor pressure deficits in cities could increase water stress during hot conditions and potentially further limit the capacity of transpiration to cool leaves. Similarly, lower rates of root colonization by mycorrhizal symbionts in urban forests (Tatsumi et al., 2023) could further impair tree uptake of water and nutrients during periods of climate stress (Schlesinger et al., 2016). Last, although we were intentional about selecting paired urban and rural sites with similar soil textures, slope, and land-use histories, it is possible that other characteristics (e.g., nutrient availability, organic matter, etc.) not considered could have varied. However, it is not clear which soil variables could support higher tree growth under mean climate conditions yet cause more adverse impacts on tree growth during times of climate stress. We suggest gaining a mechanistic understanding of climate controls on tree growth in cities as a key frontier in urban ecology and global change research that is critical for advancing urban forest management techniques and efforts to create more sustainable cities.

Species differences

The results from our study regarding climate responses across different species can inform urban sustainability strategies and tree-planting decisions. The growth of oak trees in our study tended to be more responsive to climate stress than the growth of red maple trees, which could be attributed to the interspecific differences in physiology and/or abilities to compete for resources (e.g., Rollinson et al., 2016). In the forests we studied, oaks grew faster and tended to be larger than co-occurring red maples (Sonti et al., 2019). It is possible that these differences in competitiveness made red maple trees more light-limited than the oaks which may limit the climate sensitivity of tree growth (Clark et al., 2014). The tendency of oaks to be more competitive as an overstory species than maples, and oak's tendency as an anisohydric species to take more water usage risks than the isohydric maples, could result in greater reductions in oak tree growth under high heat (and presumably high vapor pressure deficit) conditions than maples (Rollinson et al., 2016). In turn, the tendency of mature maples to be less competitive than mature oaks and to have less risky water usage strategies may reduce growth variability between years and help to explain why fewer maples were found to have significant relationships with climate stress (Rollinson et al., 2016), particularly in urban areas where these stressors may be stronger. Ford et al. (2017) found that the growth of trees in environments with low competitive pressure was more responsive to climate conditions than trees growing in environments with high competitive pressure. Additionally, in contrast with maples, oaks are well known to produce large quantities of isoprene in response to heat stress (Loreto et al., 1998), the production of which can divert fixed carbon away from growth. For example, isoprene production during high heat events has been shown to be equivalent to 15% or more of oak tree photosynthate (Sharkey et al., 1991) and may contribute to heat-related declines in oak tree growth. Our findings are consistent with Turnbull et al. (2001), who illustrated an increased response of leaf physiology to changes in environmental conditions in oaks compared with co-occurring maples, as well as Sonti, Hallett, et al. (2021), who found greater variation in leaf physiology of oaks than maples across our cities. Similarly, Royer-Tardif et al. (2021) found that of 26 tree species native to the northeastern US, red maples exhibited the greatest adaptive capacity to climate change. Our findings and these past studies suggest that red maples tend to acclimate and perform more consistently than oaks in a wide variety of ecological conditions (Abrams, 1998). In terms of intraspecies trait variability, there is still a general lack of understanding of these dynamics that demands further research, with one potential approach being a tree provenance silviculture study.

CONCLUSIONS

Collectively, the findings from our study provide important new insights into how climate conditions and landscape contexts (i.e., urban and rural areas) interact with each other to influence tree growth. In the eastern US,

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heat stress and variation in precipitation are expected to increase in response to climate change (IPCC, 2022) and these shifts in climate are expected to have significant impacts on tree growth (Babst et al., 2019) and forest C sequestration (Finzi et al., 2020; Harris et al., 2021). Recent trends illustrate longer growing seasons positively affect ecosystem carbon sequestration. However the mounting evidence that climate stress can negatively affect tree growth suggests that these positive effects on carbon sequestration may decline as the frequency and severity of climate stress increases (Finzi et al., 2020; Reinmann & Hutyra, 2017). At the same time, expanding urban areas will increase the total forest land area exposed to urban conditions (Nowak & Walton, 2005; Seto et al., 2012). Urban forest managers have the daunting task of managing a myriad of ecosystem services that trees provide (e.g., cooling, air quality, recreation, carbon sequestration) as well as threats to urban forest health such as invasive species and air pollution. There is a rapidly growing interest in increasing urban tree canopy cover using native species, which may involve considering trade-offs between species performance in urban environments and the services they provide. We focused on native oak and maple species here and although we found that the growth of oak trees appeared to be more adversely impacted by climate stress than the growth of maples, oak trees still tended to grow faster. As such, our findings do not necessarily point to maples as a more "climate-friendly" tree to plant in cities of the eastern US, but rather should be used to temper expectations of the capacity of certain tree species (oaks in this case) to sequester carbon as the climate continues to warm. To support urban forest managers, our findings suggest that it is imperative that we broaden our understanding of how climate change and urbanization might interact to impact forest productivity and associated ecosystem services. Although the exact mechanisms remain to be elucidated, we show that urbanization impacts tree growth response to climate in ways that are not predictable from our understanding of rural forest trees. Globally, cities are increasingly looking to their forests as a nature-based solution to environmental problems and to support ambitious sustainability goals (Hobbie & Grimm, 2020). From our findings, we suggest that when developing tree-planting palettes to increase climate resiliency and projecting contributions of urban forests to sustainability goals, municipalities and forest managers consider interactions among climate change, urbanization, and tree species physiology.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and related metadata files (Warner et al., 2024) are available through the Environmental Data Initiative at https://doi.org/10.6073/pasta/03e494f2812f8f042202e120f10ecfc0.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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