Received: 16 August 2020 | Revised: 14 December 2020 | Accepted: 20 January 2021

DOI: 10.1111/ppl.13344

ECOPHYSIOLOGY, STRESS AND ADAPTATION

Physiologia Plantarum

Photosynthesis, fluorescence, and biomass responses of white oak seedlings to urban soil and air temperature effects

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Edited by: V. Hurry

Abstract

Urban forest patches can provide critical ecosystem services and their ability to regenerate native tree species is critical to their sustainability. Little is known about native tree seedling establishment and physiological function in urban ecosystems. This growth chamber study examined the effects of urban soil and air temperatures on white oak (*Quercus alba* L.) germination, seedling growth, and leaf-level physiology. A split-plot design tested effects of field collected soils from urban and reference forest sites in Baltimore, Maryland, and warm (urban) versus cool (rural) growth chamber temperature regimes. Seedlings were harvested at the end of the 23-week experiment to assess foliar chemistry and biomass allocation. Seed germination was unaffected by treatments and was high in both soil types and temperature regimes. Urban soils supported significantly higher total seedling biomass and had a significant effect on leaf-level physiological parameters, with seedlings grown in urban soils having greater A_{net}, V_{cmax}, $\mathrm{ETR}_{\mathrm{max}}$, J_{max}, PNUE, g_s, A_{net}/R_d, and $\mathrm{PI}_{\mathrm{abs}}$ (an integrated chlorophyll fluorescence parameter). $\mathrm{PI}_{\mathrm{abs}}$ measurements taken throughout the experiment revealed a significant time × temperature interaction effect. Baltimore urban forest patch soils were higher in nutrients than reference soils, but also higher in heavy metals. Despite higher levels of heavy metals, these results demonstrate that urban forest patch soils are able to support robust white oak seedling growth and enhanced seedling physiological parameters. However, interactions with temperature suggest that warming air temperatures may cause seedling stress and reduced growth.

1 | INTRODUCTION

Biophysical and cultural ecosystem services provided by urban forests have led many municipalities to implement large-scale conservation and reforestation projects (Oldfield et al., 2013). However, few studies have addressed the impact of urban environmental factors on the success of native forest regeneration or restoration efforts (Doroski et al., 2018; Oldfield et al., 2014). Cities are also important ecological analogs for global change, as they exhibit abiotic conditions that are predicted to occur widely in the future (Lahr et al., 2015; Youngsteadt et al., 2014). However, it can be challenging to disentangle the effects of co-occurring and confounding environmental variables and the responses of different focal species (Lahr et al., 2018). Cities experience both regional climate change and pollution effects, as well as locally elevated air temperatures and disturbed soil conditions. These aspects of the urban environment may affect current and future urban tree growth and function. In particular, the impact of these environmental conditions on native seedling establishment and growth has implications for the success of reforestation initiatives and natural regeneration processes critical to the continuation of benefits provided by native forest ecosystems in urban areas.

Decades of urban heat island (UHI) effects have been documented in many cities of the eastern United States where temperate deciduous forests are the dominant native ecosystem type (Brazel et al., 2000; Gaffin et al., 2008; Rosenzweig et al., 2005). However, most urban woodlands or forest patches are not located near downtown weather stations, and UHI effects vary across the urban landscape depending on land use context and tree canopy cover (Gaffin et al., 2008; Heisler et al., 2016; Scott et al., 2017). Still, temperate deciduous trees are likely to have a positive growth response to warming temperatures, as respiration of these tree populations has been shown to acclimate more strongly than photosynthesis (Way & Oren, 2010). The UHI effect is particularly pronounced at night when artificial surfaces slowly radiate heat from solar radiation absorbed during the day (Arnfield, 2003). Experiments from New York City and Baltimore, Maryland, suggests that elevated night-time air temperatures may enhance plant growth, resulting in greater biomass accumulation (George et al., 2009; Searle et al., 2012). In particular, red oak (*Quercus rubra* L.) seedlings grown at elevated urban temperatures allocated more growth to leaves, leading to greater carbon assimilation without any difference in photosynthetic capacity per unit area of foliage (Searle et al., 2012). However, Meineke et al. (2016) found that urban warming was associated with reduced photosynthesis and growth of mature willow oak (*Quercus phellos* L.) trees, likely as a result of drought stress. These results suggest that elevated urban temperatures may be beneficial to oak tree growth provided they do not experience other concomitant stresses such as drought conditions.

Variations in soil quality may also contribute to the health and productivity of urban forest patches. Urban forest soils are often composed of a matrix of remnant natural soils and anthropogenic materials, leading to a high degree of spatial variability (Pouyat et al., 2010). Pouyat et al. (2007, 2010) found that urban soils across a variety of land uses may have sufficient nutrient levels to support plant growth but can also have high concentrations of heavy metals. Urban air may also contain increased concentrations of atmospheric pollutants as well as dust arising from roadways and construction activities, which may lead to higher concentrations of nitrogen (N) and calcium (Ca) in urban forest soils (Lovett et al., 2000; Pouyat et al., 1995; Rao et al., 2014). This greater N availability may lead to higher foliar N concentrations in urban compared to nearby rural forest sites (Falxa-Raymond et al., 2014; Nikula et al., 2010). Forest patch soil quality can be highly variable and the impact of heterogeneous soil composition on native tree health and growth within an urban area is poorly understood, making it important to assess forest patch heterogeneity within a city (Pregitzer et al., 2016). Furthermore, forest soil chemistry and nutrient cycling may respond differently to urbanization gradients depending on spatial patterns of development, parent material, and pollution sources of a particular city (Pouyat et al., 2008, 2009). As a result, the status of urban soil biogeochemistry and resulting impacts on tree growth are dynamic, complex and difficult to predict, both within and between cities.

Despite the attention paid to urban climate and soil biogeochemistry of urban forests, few studies have evaluated the physiological response of plants to these conditions (Cadenasso et al., 2007; Calfapietra et al., 2015). Furthermore, there is an assumption that the urban environment is inherently stressful to plants (Calfapietra et al., 2015), despite some research to the contrary (George et al., 2009; Zhao et al., 2016; Sonti et al., 2019). While increases in N availability, atmospheric carbon dioxide levels, and warmer temperatures found in urban environments may generally enhance photosynthesis, warmer temperatures may also increase rates of respiration and of soil water evaporation, which can lower net photosynthetic carbon gain. Increased leaf N and respiration rates in New York City red oak trees compared to rural trees suggest a need to further explore the interactive effects of urban climate and nutrient availability on tree physiology (Searle et al., 2011).

Oak trees (*Quercus* spp. L.) provide critical ecosystem services in forests of the eastern United States, including forests in urban natural areas (Groffman et al., 2006; Pregitzer et al., 2019; Schuster et al., 2008). However, oaks are failing to regenerate through much of their range, primarily due to over-browsing by white-tailed deer and competition from invasive understory plants (Côté et al., 2004; Doroski et al., 2018; Huebner, 2003; Meekins & McCarthy, 1999; Rooney & Waller, 2003). In particular, analysis of long-term changes in regional forest composition reveals that the slow-growing white oak (*Quercus alba* L.) has declined since European settlement of the eastern United States relative to thin-barked shade tolerant species as well as more disturbance adapted oak species (Abrams, 1998, 2003). However, eastern populations of white oak are not expected to experience additional declines in growth based on anthropogenic climate change, as they are adapted to drought conditions and appear relatively insensitive to climate fluctuations (Abrams, 2003; Goldblum, 2010). White oak is also able to acclimate to conditions of low nutrient availability in infertile soils by increasing nutrient use efficiency (Boerner, 1984; Norby et al., 1986). These results suggest that white oaks may be well adapted to the elevated air temperatures and altered soil properties found in the urban forest patch environment.

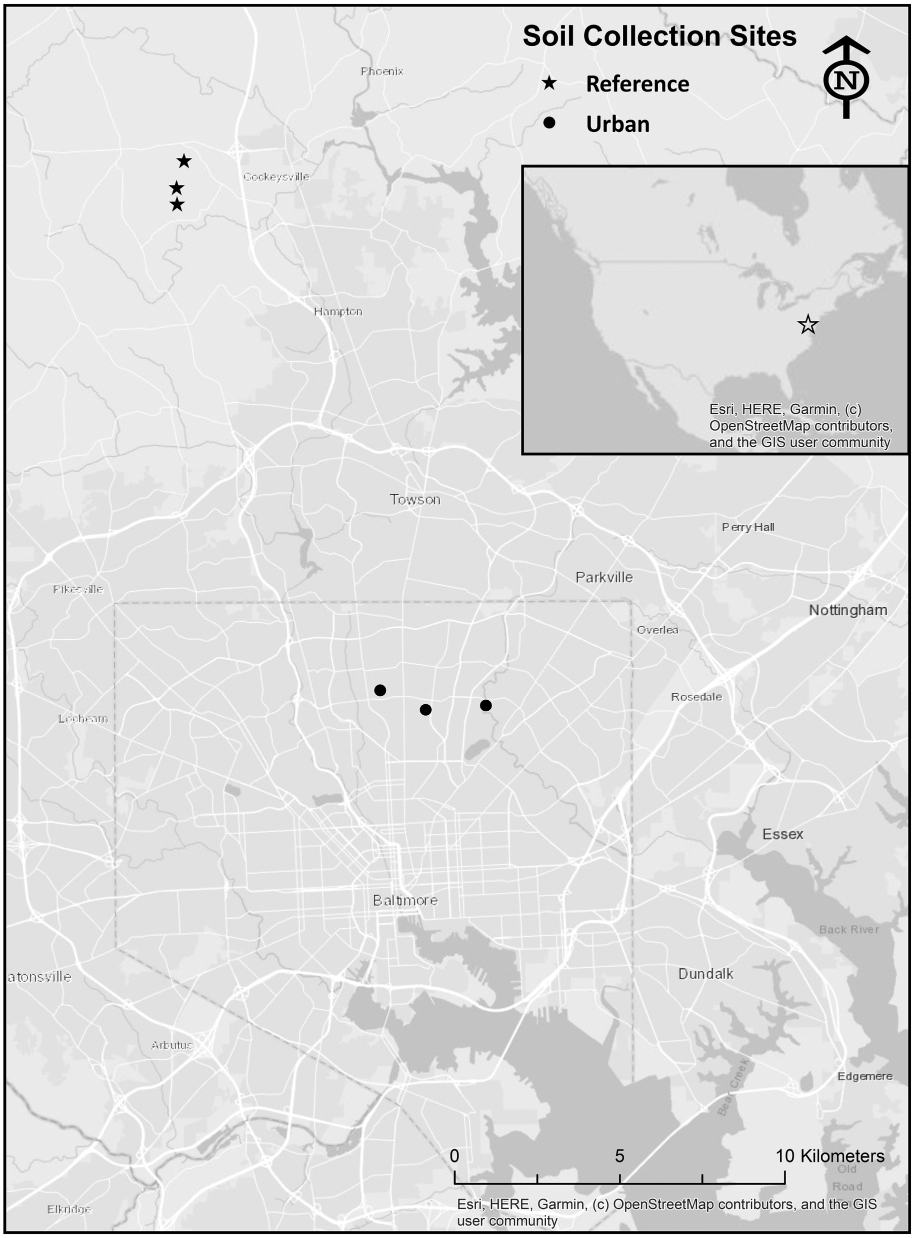
Baltimore, Maryland, is among a growing list of cities advocating for the preservation and restoration of urban woodlands or forest patches (Barron, 2018; City of Seattle, 2013; Lautar & Avins, 2017). These are sites with relatively unmanaged understories comprised of decomposing leaf litter and naturally occurring vegetation. Successful seedling establishment and growth in urban forest patch conditions are important for both processes of natural regeneration as well as the success of costly reforestation activities, which often focus on restoration of oak-dominated ecosystems. A long-term study of Baltimore's forest patches reveals that white oak is one of the most dominant canopy tree species (Templeton et al., 2019), and it is common in urban woodlands of other cities in the eastern United States (Nowak et al., 2016; Pregitzer et al., 2019).

In this study, we use a controlled growth chamber experiment to examine the effects of field collected urban forest patch soils and elevated urban air temperatures (compared to reference forest soils and rural air temperatures) on early stages of white oak regeneration (i.e., germination and seedling performance). We set out to answer the following questions: (1) What are the effects of urban vs. reference forest soils and elevated urban air temperature on white oak germination rates? (2) What are the effects of urban versus reference forest soils, elevated urban air temperature and their interaction on white oak seedling photosynthesis, respiration, chlorophyll fluorescence, and biomass allocation, and foliar chemistry during their first year of growth? This experiment was designed to answer key questions about white oak seedling establishment and performance in urban forest patches in an effort to inform sustainable management of this important keystone species throughout urban and rural natural areas of the region.

2 | MATERIAL AND METHODS

2.1 | Growth chamber study design

Acorns were collected in October 2015 from beneath a stand of white oak trees at a rural forest site used by the Baltimore County nursery for oak propagation. After collection, acorns that floated in a bucket of water were removed from the sample collection, and 600 viable acorns were weighed and planted in Baltimore soils collected from three urban and three reference sites (Figure 1). Soils were collected from below white oak stands and from the top 25 cm below the leaf litter layer. To capture spatial variation, urban soil collection sites were located within forest patches on a variety of land uses within Baltimore City limits. The three urban sites included city parkland, museum grounds, and undeveloped vacant land approximately 5 km from the city center. The reference sites were all located within the 1000-acre Oregon Ridge Park in Baltimore County, approximately 30 km from the Baltimore City center. This location was chosen as a representative reference ecosystem for the region, dominated by mature native trees with minimal management by humans (Reisinger et al., 2016). All soil collection sites were on similar soils of Typic Hapludults with slopes less than 25% and were located beneath mature stands of



Esri, HERE, Garmin, (c) OpenStreetMap contributors, and the GIS user community

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FIGURE 1 Map of reference and urban forest patch soil collection sites in Baltimore, Maryland, USA

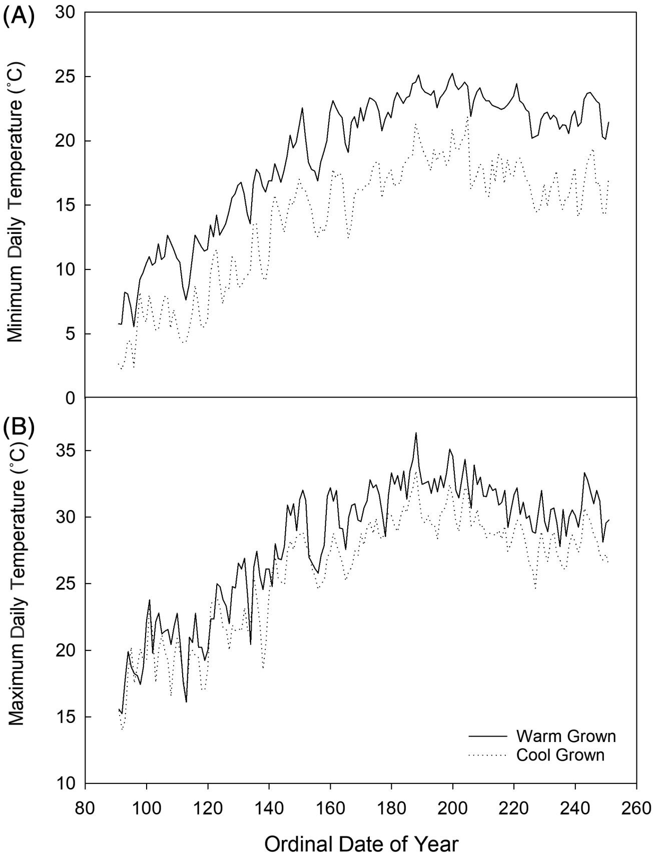

FIGURE 2 Five-year (April–September, 2010–2014) mean daily (A) minimum and (B) maximum air temperatures from urban (Maryland Science Center Station in Baltimore City) and reference (Millers, MD Station in Carroll County) locations in Maryland, used for warm and cool temperature treatments, respectively. Data from NOAA Climate Data Online (https://www.ncdc.noaa.gov/cdo-web/)

white oak trees. At each site, leaf litter and surface vegetation were removed before approximately 38 l of soil was collected and homogenized.

Acorns were initially planted in propagation trays and placed in a growth chamber at 4°C for three months (Environmental Growth Chambers Model M40, Chagrin Falls). After this stratification period, the acorns were divided into two growth chambers, one set at Baltimore City air temperatures ("warm grown") and one set at rural Maryland temperatures ("cool grown"). Long-term temperature records were not available for the forest patch soil collection sites at the time of the experiment, so climate records from urban and rural sites in the Baltimore region were used to set growth chamber temperatures. Chamber temperature regimes were adjusted each week based on 2010–2014 NOAA (National Oceanic and Atmospheric Administration) climate records from the Maryland Science Center station in Baltimore City's Inner Harbor and the Millers, MD station in northern Carroll County, about 50 km north of Baltimore City (Figure 2). Minimum, maximum, and mean air temperatures were averaged for 7-day periods for the duration of the 23-week experiment, which spanned early April to early September temperatures. Daily temperature fluctuations were calculated for six time-steps using maximum, minimum, and mean temperatures. The warm temperature treatment had an average maximum daily temperature of 2.2°C warmer than the cool treatment, while average minimum daily temperature was 5.0°C warmer.

The acorns remained in the initial two growth chambers for 40 days until germination was complete. At this point, successfully germinated acorns were replanted into larger pots of the same soil (freshly collected from the same sites) and randomly placed in four growth chambers: two at warm temperature regimes and two at cool temperature regimes. This setup created a split-plot design where each growth chamber contained 48 seedlings: 24 in urban soils and 24 in reference soils (eight replicates from each soil collection site). Pots were randomly moved around each chamber every two weeks to reduce the influence of microclimate variation (light, temperature, humidity) within the chamber on seedling growth and physiology. During cold storage and germination, the seedlings were kept in moist soil to improve chances of germination success. During the remainder of the experiment, the seedlings received uniform watering two times per week. Relative humidity in the growth chambers was maintained at 50% at all temperatures. Light levels in the chambers were between 200–250 μmol m^{-2} s^{-1} of photosynthetically active radiation (PAR), measured at the top of the canopy.

2.2 | Data collection

Nine samples of homogenized soil per site were analyzed for physical and chemical properties. Each sample was air-dried and screened to remove particles >2 mm. Samples were analyzed for pH in 0.01 M $CaCl_2$, organic content was estimated by loss-on-ignition (LOI), and soil texture was determined using the hydrometer method (Day, 1965). Plant available elements, including Al, As, Ca, Cd, Cr, Cu, K, Mg, N, Na, P, Pb, and Zn, were determined by extracting soil using a modified Morgan's solution (NH_4OAC, pH 4.8, McIntosh, 1969). These extracts were analyzed for plant available elements with inductively coupled plasma (ICP) spectroscopy.

Chlorophyll fluorescence was measured four times throughout growing season on the same leaf using a Hansatech Pocket PEA continuous excitation chlorophyll fluorometer. Leaves were dark adapted for at least 30 min before measurements were taken. Preliminary trials demonstrated that chlorophyll fluorescence parameters did not change after additional dark adaptation beyond 30 min. Measurements of the integrative Performance Index (PI_{abs}) parameter were taken during week 11 (mid-June for seedlings), week 15 (mid-July), week 19 (early August), and week 23 (early September). PI_{abs} reflects the functionality of both photosystems I and II and can indicate stress in plants even before visible symptoms appear on the leaves (Christen et al., 2007; Strasser et al., 2000, 2004).

During weeks 18–20 (early August), net photosynthesis (A_{net}), dark respiration (R_d), and electron transport rates (ETR) were measured on 24 seedlings from each growth chamber (four replicates of each soil), for a total of 96 seedlings. Replicate seedlings were chosen randomly, excluding seedlings whose leaves were senescing. A_{net}, R_d, and ETR measurements were made on the healthiest fully expanded leaf of the first flush of each seedling, or on a fully expanded leaf from the second flush if necessary. A_{net} and R_d measurements were made using a LI-6400 (Li-Cor). Measurements of net photosynthesis rates were made at 25°C over 10 CO_2 levels (400, 300, 200, 100, 75, 50, 400, 400, 500, 600, 750, 1000 μmol CO_2 mol^{-1}). Relative humidity was controlled at 50%–60% and light intensity was set to 600 μmol m^{-2} s^{-1} PAR after photosynthetic response to light was found to be saturated at that level of intensity. The response of A_{net} to c_i (intercellular CO_2 concentration) was fit with the model and software provided by Sharkey et al. (2007) to predict the maximum light-saturated rate of electron transport for RuBP regeneration (J_{max}) and the maximum rate of Rubisco carboxylation (V_{cmax}). Reported values of A_{net} and stomatal conductance (g_s) are measured at 400 μmol CO_2 mol^{-1}. R_d rates were averaged over 20 s at 25°C and 400 μmol CO_2 mol^{-1} after leaves acclimated to the cuvette conditions for at least 3 min.

A portable Walz PAM-2000 pulse-amplitude-modulated chlorophyll fluorometer was used to measure the in situ ETR during rapid light curves (RLC). RLCs were obtained by exposing leaves (not pretreated with a dark treatment) to 10 increasing steps of incident PAR ranging from 7 to 2000 μmol m^{-2} s^{-1}. The maximum rate of electron transport (ETR_{max}) of light reactions of photosynthesis was determined from the point of light saturation of a plot of ETR against the ambient PAR using a nonlinear curve fitting function in the JMP software (JMP, Version 11. SAS Institute Inc., Cary, NC, 1989–2007). Once RLCs and gas exchange measurements were completed, each leaf was removed and analyzed on a leaf area meter (LI-3100, Li-Cor).

At the end of the growth chamber experiment, stems of all remaining seedlings were clipped at the base. Coarse and fine roots were removed from the pots and carefully washed to remove soil particles. Leaf, stem, and root tissues were then bagged separately and dried in an oven at 50°C for one week. All dry tissues were then weighed. Root, stem, and leaf mass were summed for total plant biomass. Individual leaves used for RLCs and gas exchange measurements were dried, weighed, and analyzed separately for carbon and N content to determine photosynthetic N use efficiency (PNUE). PNUE is the photosynthetic capacity per unit N and is calculated as the ratio between A_{net} and leaf N content.

Remaining oven-dried foliage was ground to create a composite sample for each seedling and was subsequently digested using a microwave-assisted acid digestion procedure (USEPA Method 3052) and analyzed for Ca, K, Mg, Mn, and P by ICP spectroscopy. Foliar N was determined by combustion with a PerkinElmer 2400 series II CHNS/O analyzer (PerkinElmer).

2.3 | Data analysis

Linear mixed effects models in the nlme R package were used to analyze the effects of soil type (urban vs. reference) and temperature regime (warm grown vs. cool grown) and their interactions on seedling physiology and biomass allocation (R Development Core Team, 2008; Pinheiro et al., 2010). To account for the split-plot experimental design, temperature treatment was analyzed as a plot effect and soil type as a subplot effect. Acorn weight was included as a covariate in the biomass models. The lme function allowed the use of soil collection site as a random variable in each model, as well as seedling as a random variable to account for repeated chlorophyll fluorescence measurements on the same seedling over time. In addition, different variance structures were incorporated into some of the models using the varIdent function to meet assumptions of homoscedasticity (Table 1). Differences between means were considered significant at $\alpha = 0.05$.

Foliar chemistry and soil nutrients and heavy metals were submitted to principal component analysis (PCA) using the R function prcomp in the package stats v. 3.5.1 (R Core Team, 2008). Here, "nutrients" indicate soil properties essential to plant growth, including ppm of N, P, K, Ca, and Mg; percent sand and clay; pH; and soil organic matter (SOM). "Heavy metals" indicate elements that may inhibit plant growth and function, including Al, As, Cd, Cr, Cu, Na, Pb, and Zn (Appenroth, 2010). Al concentrations in soil samples from most sites were found to be at a potentially toxic level (Amacher et al., 2007), and Na was thought to be potentially toxic due to urban pollution, and so both elements were included as heavy metals. Eigenvalues were used to determine that two principal components should be retained for each PCA. A varimax rotation was used to aid in interpretation of the principal components using the varimax function. The first and second rotated principal components (RC1 and RC2) from each PCA were used as response variables in linear mixed effects models as described above. Finally, biomass and leaf-level physiology variables were correlated with foliar nutrients using Pearson's correlation in the R function rcorr in the package Hmisc v. 4.4–0 (Harrell, 2020).

3 | RESULTS

Germination rate was 87% across all temperature regimes and soil types. Acorn weight had a significant effect on total seedling biomass (Table 1). Soil type also had a significant effect on total seedling biomass, with seedlings grown in urban soils having 20% greater total biomass than seedlings grown in reference soils (Figure 3A). However, root:shoot ratio was not significantly impacted by soil type (Table 1; Figure 3B). Soil type also had a significant effect on all leaf-level physiological variables except for R_d, and there was a significant interaction effect on V_{cmax}, ETR_{max}, and g_s where differences between soil types were only observed in one temperature treatment (Table 1; Figure 4). Repeated measures analysis revealed that soil and temperature treatment effects on PI_{abs} changed significantly throughout the growing season (Table 2; Figure 5).

PI_{abs} values taken in August were significantly positively correlated with other photosynthetic parameters measured during the same part of the growing season, suggesting that the rapid chlorophyll fluorescence parameter may be a good proxy for more time intensive gas exchange measurements. Pearson correlation coefficients are as

TABLE 1 Results from linear mixed effects models analyzing the effects of urban versus reference forest soils and warm versus cool grown temperature treatment and their interactions on seedling growth and leaf level physiology

Response variable	Soil type	Temperature	Soil type × temperature	Acorn weight	Variance structure
Total biomass	11.12	2.49	2.72	49.45	
	0.004	0.26	0.12	**<0.0001**	
Root:shoot	0.10	1.41	1.79	3.00	Temperature treatment
	0.75	0.36	0.12	0.09	
A_{net}	48.33	0.001	1.41		
	<0.0001	0.98	0.25		
J_{max}	24.45	1.45	2.45		
	0.0001	0.35	0.13		
V_{cmax}	18.17	0.45	4.07		
	0.0005	0.57	**0.058**		
ETR_{max}	24.54	0.08	4.07		Temperature treatment and soil type
	0.0001	0.80	**0.058**		
PNUE	42.37	0.003	1.37		Soil type
	<0.0001	0.86	0.26		
R_{d}	0.03	0.65	1.86		Chamber
	0.8629	0.50	0.19		
g_{s}	13.85	0.59	7.93		Chamber
	0.0016	0.52	**0.01**		
$A_{\text{net}}/R_{\text{d}}$	37.61	0.04	0.03		Soil type
	<0.0001	0.87	0.87		
Foliar chemistry RC1	18.18	0.04	1.93		
	0.0005	0.85	0.18		
Foliar chemistry RC2	30.99	5.85	0.05		
	<0.0001	0.14	0.83		

Note: Acorn weight was not included in leaf level physiology models (indicated by gray cells). *F*-values and *P*-values are listed for each fixed effect, and bold *P*-values indicate significant differences ($\alpha = 0.05$). Variance structures included in each model are listed where applicable.

follows: $A_{\text{net}} = 0.54$, $J_{\text{max}} = 0.50$, $V_{\text{cmax}} = 0.40$, $\text{ETR}_{\text{max}} = 0.58$, and $A_{\text{net}}/R_{\text{d}} = 0.57$ ($n = 96$; $P < 0.001$ for all correlations).

In the foliar chemistry PCA, 50% of the variation was explained by the first two varimax rotated components, with RC1 accounting for 27% of the variation and RC2 23% (Figure 6). Positive loadings of RC1 corresponded to foliar Ca and Mg, whereas positive loadings of RC2 corresponded to foliar P and negative loadings to foliar Mn (Table S1). Linear mixed effect models revealed a significant effect of soil type on foliar chemistry RC1 and RC2 (Table 1). Inspection of the scatterplot for RC1 and RC2 shows a clustering of foliar chemistry grown in urban soils to the top right and foliage grown in reference soils to the bottom left, meaning that foliage from seedlings grown in urban soils is likely to be higher in Ca, Mg, and P, and lower in Mn than foliage from seedlings grown in reference soils. There is no clear separation of foliar chemistry by temperature treatment.

Total biomass was positively correlated with foliar P and Ca and negatively correlated with foliar Mn (Table 3). Root:shoot ratio was correlated with foliar N, P, and Mn. Leaf-level parameters related to photosynthetic performance (A_{net}, J_{max}, V_{cmax}, ETR_{max}, and $A_{\text{net}}/R_{\text{d}}$) were most strongly associated with foliar P concentration, but also positively correlated with foliar N and negatively correlated with foliar Mn. $A_{\text{net}}/R_{\text{d}}$ was also positively correlated with foliar Mg. R_{d} was not significantly correlated with any foliar nutrients, and g_{s} was only correlated with foliar P. PNUE was positively correlated with foliar N and P, and negatively correlated with foliar Mn.

In the soil nutrients PCA, 86% of the variation was explained by the first two varimax rotated components, with RC1 accounting for 57% of the variation and RC2 29% (Figure 7A). Positive loadings of soil nutrients RC1 corresponded most strongly to SOM, N, P, K, Ca, and Mg, and negative loadings to pH. Positive loadings of soil nutrients RC2 corresponded to SOM and % sand and negative loadings to % clay (Table S2). Inspection of the scatterplot for soil nutrients RC1 and RC2 showed a greater clustering of reference sites to the left (negative loadings of RC1 or lower pH and lower concentrations of SOM, N, P, K, Ca, and Mg) compared to urban sites. The scatterplot also suggests that there is more variation in urban soil nutrients compared to reference soils, and that the greater clustering of urban soil collection sites reveals that they are less similar to one another than the reference sites. Linear mixed effects models revealed a significant effect of soil type on soil nutrients RC1, but not RC2 (Table 4).

In the soil heavy metals PCA, 89% of the variation was explained by the first two varimax rotated components, with RC1 accounting for 54% of the variation and RC2 35% (Figure 7B). Positive loadings of soil heavy metals RC1 corresponded most strongly to As, Cd, Cr, Cu, Na, Pb, and Zn, while positive loadings of soil heavy metals RC2

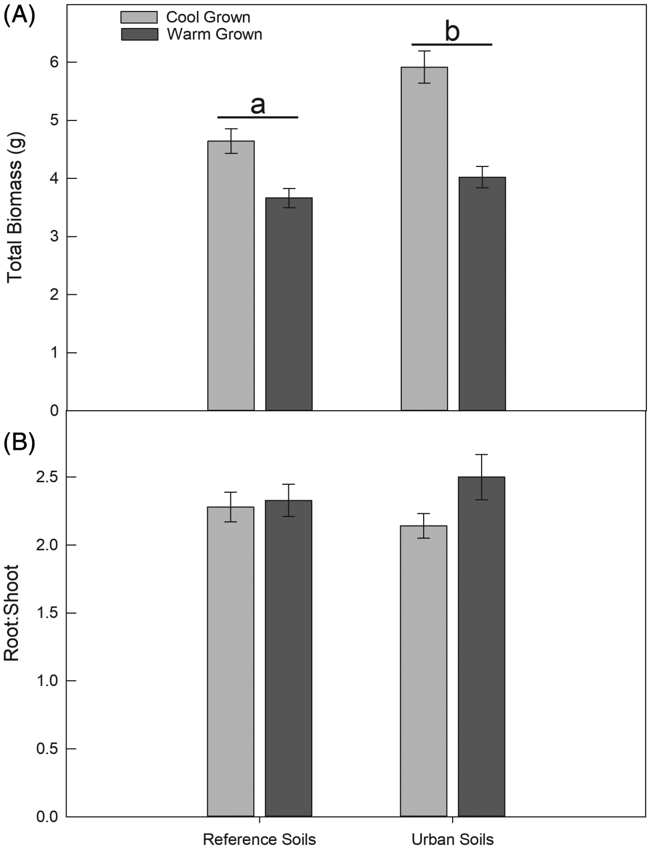

FIGURE 3 White oak seedling biomass allocation by soil type and temperature treatment: (A) total biomass and (B) root:shoot ratio. Values shown are mean ± standard error (*n* = 192). Letters show significant differences between soil types (*P* = 0.004)

corresponded to Al, Cr, Cu, Pb, and Zn (Table S2). Inspection of the scatterplot for soil heavy metals RC1 and RC2 showed a greater clustering of reference sites to the bottom left (negative loadings of RC1 and RC2 or lower concentrations of all heavy metals) compared to urban sites. The scatterplot also suggests that there is more variation in concentrations of heavy metals in urban soils compared to reference soils, and that the greater clustering of urban soil collection sites reveals that they are less similar to one another than the reference soil collection sites. Linear mixed effects models revealed a significant effect of soil type on soil heavy metals RC1, but not RC2 (Table 4).

4 | DISCUSSION

The results of this growth chamber experiment indicate that while urban forest patch soils and elevated air temperatures did not impact white oak germination, seedling photosynthetic capacity and biomass accumulation were increased in urban soils compared to reference soils. The nutrients provided by urban soils may have led to increased biomass via enhanced leaf level physiological parameters including $\mathrm{PI_{abs}}$, A_{net}, $J_{\max}$, V_{cmax}, $\mathrm{ETR_{max}}$, $A_{\mathrm{net}}/R_{\mathrm{d}}$, PNUE, and g_{s}. In contrast, nutrient poor reference soils led to reduced seedling growth and photosynthetic capacity. Our findings are consistent with previous work indicating elevated soil nutrient and heavy metal concentrations in urban forest patch soils (Pouyat et al., 2008; Sonti et al., 2019) or tree foliage (Sonti et al., 2021) due to nearby anthropogenic activities (Kaye et al., 2006; Weathers et al., 2001). Furthermore, native till soils from intact urban forest patches in New York City were found to support greater native seedling growth and lower physiological stress than a greenhouse soil mix, likely due to the higher nutrient availability in these soils (Pregitzer et al., 2016). While urban soils across a range of land use and site types may be highly disturbed or nutrient-poor, there is growing evidence that soils from intact forest patches in urban areas can support robust native tree growth.

Soil physical and chemical analysis revealed that although there is some variation among urban forest patch soils, they are clearly distinct from reference soils. On average, urban soils were higher in nutrients and SOM than reference soils, consistent with previous soil analyzes from the same field sites (Sonti et al., 2019). The higher SOM in the urban soils appears to be driven by one site (Springfield Woods), and may increase water holding capacity and nutrient supply to those seedlings (Table S3). All of the seedlings were somewhat P deficient, but the seedlings grown in reference soils were more deficient (Table S4; Norby & O'Neill, 1989, Birge et al., 2006, Mellert & Göttlein, 2012). Foliar P was significantly correlated with total biomass, g_{s}, and all leaf-level photosynthetic parameters, suggesting that the greater availability of P in urban forest patch soils is benefitting white oak seedling growth. In addition, seedlings grown in one of the reference soils (Oregon Ridge 3) have foliage that is N deficient (Norby & O'Neill, 1989). None of the average foliar N concentrations in this study are in the surplus range for mature oak trees (Mellert & Göttlein, 2012; Mitchell & Chandler, 1939), and the higher PNUE of seedlings grown in urban soils suggests that they are still experiencing N limitation. Furthermore, foliar N was significantly correlated with A_{net}, $J_{\max}$, and V_{cmax}, suggesting that additional N is enhancing photosynthesis rates at the leaf level. Although foliar N concentration was not significantly correlated with total biomass, the larger seedlings are likely to have greater overall N content.

Although foliar Ca and Mg were not in deficient ranges for mature oaks (Table S4; Mellert & Göttlein, 2012), higher availability in urban soils may also benefit white oak seedling growth, as foliar Ca concentration was significantly correlated with total biomass, and foliar Mg was correlated with $A_{\mathrm{net}}/R_{\mathrm{d}}$. Calcium additions to rural white oak stands have been found to improve diameter growth (Ward & Bowersox, 1970), and Mg is an essential micronutrient required for chlorophyll formation (Farhat et al., 2016). Urban soils are known to experience elevated Ca availability as a result of cement dust (Lovett et al., 2000). Values of foliar Mn found in reference seedlings are high compared to naturally occurring levels (Table S4; Davis et al., 1995), but white oak seedlings are considered tolerant to excess Mn resulting in foliar concentrations of at least 5000 ppm (St.Clair & Lynch, 2005), so we do not necessarily suspect Mn toxicity in our reference seedlings. While we found foliar Mn to be negatively correlated with total seedling biomass,

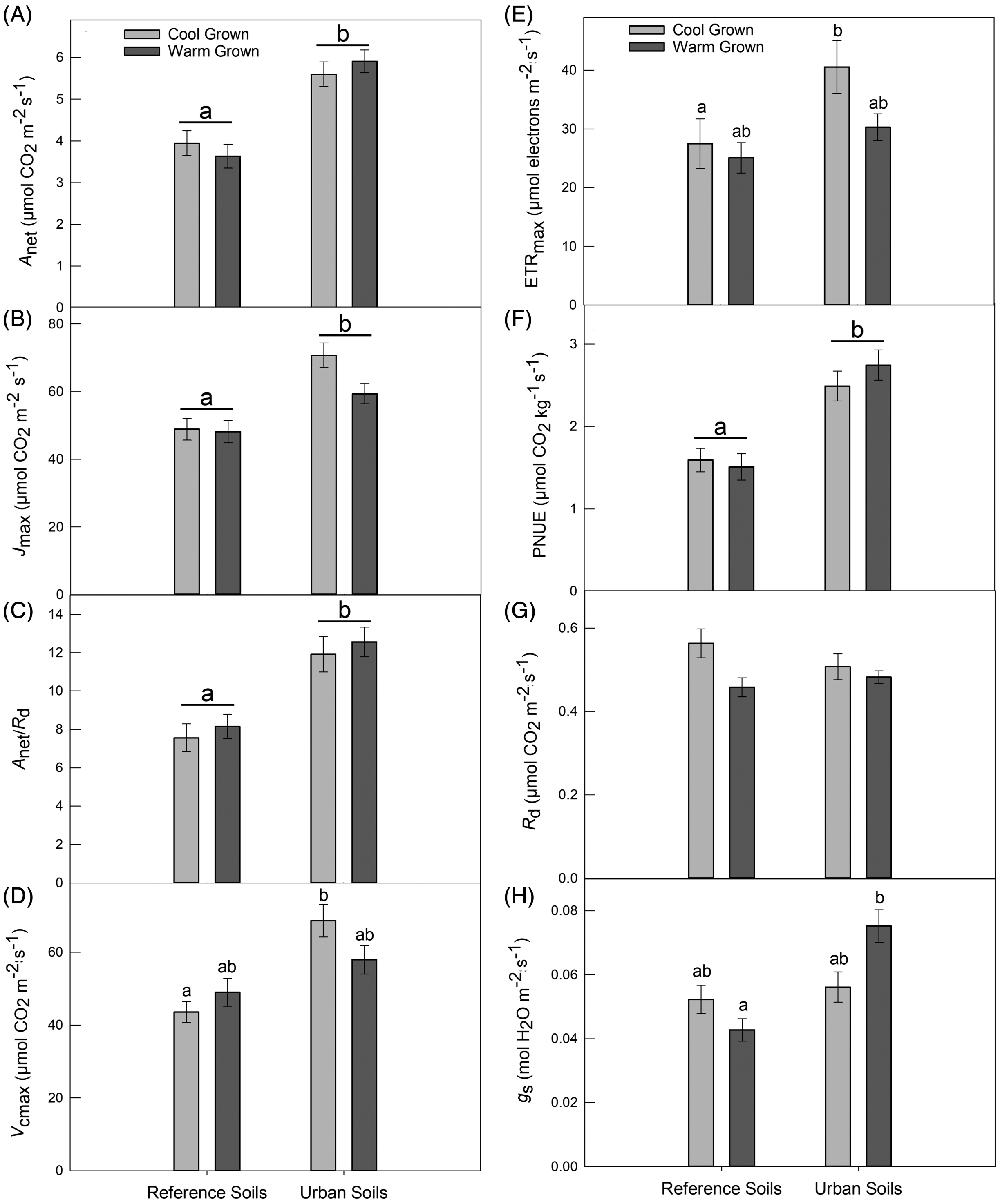

FIGURE 4 Leaf level physiological parameters of white oak seedlings by soil type and temperature treatment: (A) net photosynthesis measured at [CO_2] of 400 µmol mol^{-1}; (B) maximum light-saturated rate of electron transport for RuBP regeneration; (C) ratio of A_{net} to R_d; (D) maximum rate of Rubisco carboxylation; (E) maximum rate of electron transport of light reactions of photosynthesis; (F) photosynthetic nitrogen use efficiency; (G) dark respiration measured at [CO_2] of 400 µmol mol^{-1}; (H) stomatal conductance measured at [CO_2] of 400 µmol mol^{-1}. Values shown are mean ± standard error (*n* = 96). Letters show significant differences between soil types, or soil-temperature combinations ($P < 0.05$)

A_{net}, J_{max}, ETR_{max}, and PNUE, it was positively correlated with root: shoot ratio despite the potential for excess Mn to inhibit root growth (McQuattie & Schier, 2000).

Urban forest patch soils from all sites were higher in plant available heavy metals than reference soils, but the levels were likely not high enough to negatively impact plant growth (Table S3; Sonti

TABLE 2 Results from linear mixed effects model analyzing the effects of urban versus reference forest soils and warm versus cool grown temperature treatment over time and their interactions on Performance Index (PI_{abs})

Response variable	Soil type	Temperature	Time	Soil type × temperature	Temperature × time	Soil type × time	Soil type × temperature × time	Variance structure
PI_{abs}	113.91 **<0.0001**	0.01 0.92	16.81 **<0.0001**	1.59 0.22	25.29 **<0.0001**	15.03 **<0.0001**	5.16 **0.0016**	Soil type and chamber

Note: F-values and *P*-values are listed for each fixed effect, and bold *P*-values indicate significant differences ($\alpha = 0.05$).

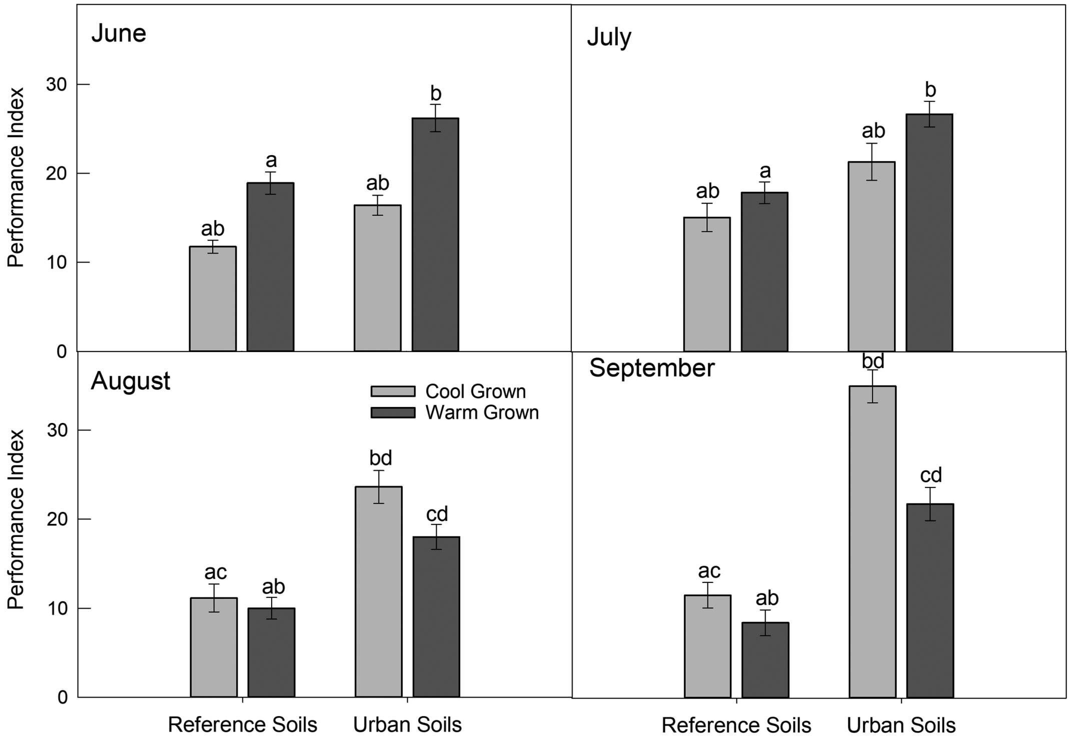

FIGURE 5 Performance Index (PI_{abs}) of white oak seedling foliage by soil type and temperature treatment throughout the growing season. Values shown are mean ± standard error ($n = 192$). Letters show significant differences between soil-temperature treatment combinations within each time period ($P < 0.05$)

et al., 2019). Heavy metals are known to disrupt physiological processes in tree species of the eastern United States (Balsberg-Påhlsson, 1989), but there is little research relating tree growth and physiological response to soil concentrations of plant available heavy metals (Amacher et al., 2007), particularly in deciduous tree species. The photosynthetic capacity of gray birch (*Betula populifolia* Marsh.) is robust to exposure to heavy metal contaminated soils in urban areas, although tolerance to climatic stress may be reduced (Salisbury et al., 2018). It is likely that the differences found here in growth and photosynthetic performance of white oak seedlings grown in urban and reference soils are due to increased nutrient availability in urban soils, but further research could identify specific markers of heavy metal stress (Gawel et al., 1996).

Cool grown seedlings attained greater total biomass than warm grown seedlings, although the effect was not significant, possibly due to the low replication of the temperature treatment. There was also no difference in root:shoot ratio between temperature treatments or soil types. These results contradict those of Searle et al. (2012) who found greater total leaf area and lower root:shoot ratio in northern red oak (*Quercus rubra* L.) seedlings grown at urban versus rural temperatures from the New York City region. However, Wertin et al. (2011) observed a negative growth response of northern red oak to elevated temperatures near the southern limit of the species range. Deciduous tree species growing near their warm range limits exhibit reductions in net photosynthesis and growth, whereas species near their cold range limit respond positively to warming (Reich et al., 2015). Although Baltimore, Maryland, is not currently near the southern range limit of white oak, it is possible that the elevated downtown air temperatures used in this experiment are high enough to negatively impact seedling growth. Indeed, white oak is projected to be less prevalent in the Baltimore region under future climate scenarios as the species' range shifts north (Prasad et al., 2014).

Leaf physiological traits varied by treatment conditions and provide useful insights into the mechanistic control of seedling growth. For example, only cool grown seedlings had significantly higher V_{cmax} and ETR_{max} in urban versus reference soils. Warm grown seedlings may be experiencing physiological stress that prevents them from taking advantage of the greater nutrient concentrations. Cool grown seedlings in urban soils have the greatest total biomass and photosynthetic capacity, demonstrating that this treatment combination provides a better growing environment and less physiological stress compared to warm temperatures and relatively nutrient-poor reference soils. Warm grown seedlings in urban soils had the highest rates of g_s, which were significantly different from that of warm grown seedlings in reference soils. This finding suggests that warm grown seedlings in this experiment were not drought stressed or CO_2 limited, at least when grown in urban soils. There were no significant soil type or temperature treatment effects on dark R_d. However, the lack of differences in total respiration may conceal greater allocation of respiratory function to growth over maintenance as suggested by the findings of Searle et al. (2011, 2012). The increase in A_{net}/R_d suggests that seedlings grown in urban soils are becoming more efficient, leading to increased growth. Overall, these physiological parameters suggest urban soils are not limiting white oak seedling growth, particularly if temperatures remain moderate. These data provide a much-needed mechanistic basis for assessing urban forest restoration programs that hope to increase ecosystem services in urban areas.

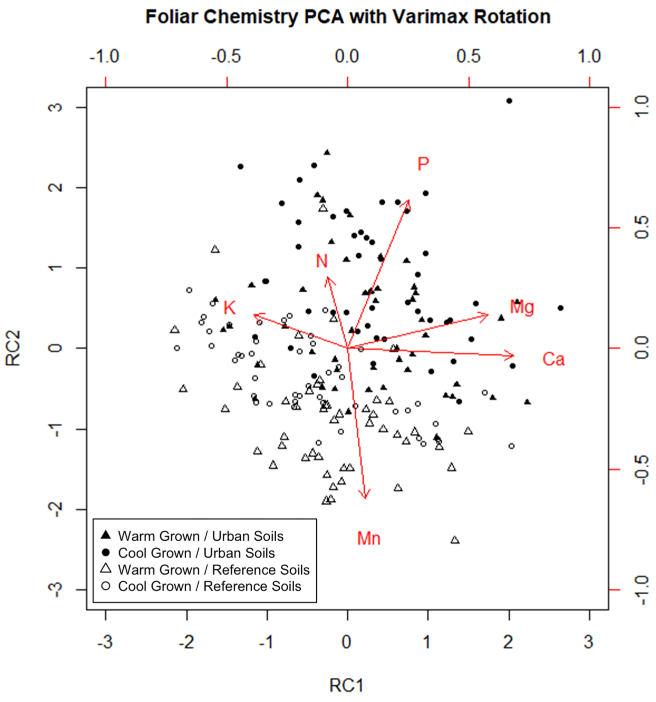

FIGURE 6 Biplot of white oak seedling foliar chemistry principal components 1 and 2 after varimax rotation (27% and 23% of variance). Seedlings grown in urban soils are represented by solid symbols and seedlings grown in reference soils are represented by clear symbols. Warm grown seedlings are represented by triangles and cool grown seedlings are represented by circles. Top and right axes in red refer to variable loadings indicated by red arrows

Measurements of the chlorophyll fluorescence parameter PI_{abs} taken throughout the growing season show consistently higher photosynthetic performance of seedlings grown in urban soils compared to reference soils. In addition, warm grown seedlings start out with higher values of PI_{abs} at the beginning of the growing season but drop over time to become lower than cool grown seedlings by the end of the experiment. Early in the growing season (June and July), only warm grown seedlings show significant soil type differences in PI_{abs}. However, in August and September there are significant differences by soil type within both temperature treatments, indicating that urban soils are better able to support continued photosynthetic activity late in the growing season when urban and rural temperature differences are greatest. Although not statistically significant, the difference in PI_{abs} between warm and cool grown seedlings in urban soils at the end of the growing season suggests a decrease in photochemical efficiency in warm grown seedlings compared to cool grown seedlings. PI_{abs} of seedlings in reference soils is much lower, and it may be too nutrient stressed to show any difference by temperature treatment. PI_{abs} values taken in August were significantly positively correlated with other photosynthetic parameters measured during the same part

TABLE 3 Correlation matrix of physiological parameters and foliar chemistry (Pearson correlation coefficients)

Parameters	Foliar N (leaf)	Foliar N	Foliar P	Foliar K	Foliar Ca	Foliar Mg	Foliar Mn
Total biomass	NA	−0.03	**0.28**	−0.07	**0.18**	0.09	**−0.30**
Root:shoot	NA	**0.17**	**0.19**	−0.05	0.04	−0.05	**0.20**
A_{net}	**0.28**	**0.25**	**0.52**	−0.03	0.13	0.12	**−0.29**
J_{max}	**0.23**	0.12	**0.55**	−0.08	0.10	0.11	**−0.27**
V_{cmax}	**0.23**	0.05	**0.52**	−0.10	0.06	0.02	−0.18
ETR_{max}	0.19	**0.24**	**0.39**	0.12	0.00	0.18	**−0.25**
A_{net}/R_d	**0.28**	**0.29**	**0.46**	−0.06	0.10	**0.20**	**−0.25**
R_d	−0.11	−0.18	−0.03	0.05	−0.01	−0.19	0.01
g_s	0.12	0.17	**0.22**	−0.04	0.11	0.00	−0.11
PNUE	**0.53**	**0.38**	**0.51**	−0.04	0.13	0.13	**−0.23**

Note: Total biomass and root:shoot correlations are based on 192 replicate seedlings and leaf-level parameter correlations are based on 96 replicate seedlings. Foliar N values are averaged for entire plant, while foliar N (leaf) values are for the individual leaf measured. All values in bold print indicate significant correlations (α = 0.05).

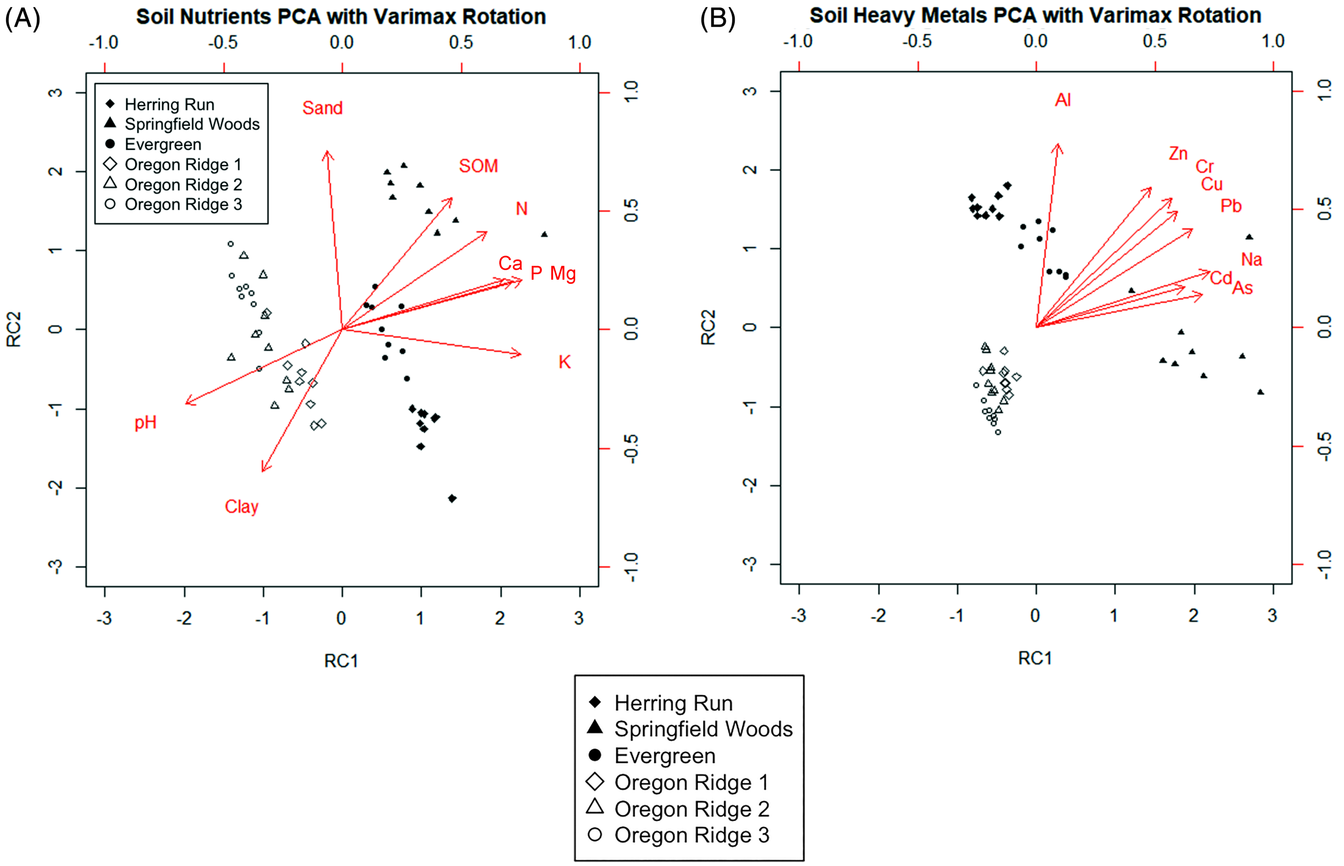

FIGURE 7 Biplots of (A) soil nutrients principal components 1 and 2 after varimax rotation (57% and 29% of variance) and (B) soil heavy metals principal components 1 and 2 after varimax rotation (54% and 35% of variance). Seedlings grown in urban soils are represented by solid symbols and seedlings grown in reference soils are represented by clear symbols; shapes represent soil collection sites. Top and right axes in red refer to variable loadings indicated by red arrows

TABLE 4 Linear mixed effects model summaries for soil nutrients and heavy metals varimax rotated principal components (RC) response variables

Response variable	Soil type	Variance structure
Soil nutrients RC1	15.18 **0.02**	Soil collection site
Soil nutrients RC2	0.65 0.46	Soil collection site
Soil heavy metals RC1	25.42 **0.007**	Soil collection site
Soil heavy metals RC2	0.57 0.49	Soil collection site

Note: *F*-values and *P*-values are listed for each fixed effect, and bold *P*-values indicate significant differences ($\alpha = 0.05$).

of the growing season, suggesting that this rapid chlorophyll fluorescence parameter may be considered a good proxy for more time intensive gas exchange measurements that are not feasible to include in assessments of urban forest restoration projects.

In this experiment, we were able to isolate the effects of air temperature and soil on native seedling performance but were unable to account for other aspects of the urban environment that warrant further study. For example, urban forest patches may experience flashier hydrology and increased drought conditions due to the UHI effect and surrounding impervious surfaces (Jacobson, 2011; Lahr et al., 2018). In addition, urban areas may experience different levels of atmospheric CO_2, ozone, and other air pollutants compared to surrounding rural areas, with important implications for plant growth (Gregg et al., 2003; Lahr et al., 2015; Locosselli et al., 2019; Ziska et al., 2004). Finally, many important biotic factors excluded from this experiment affect seedling growth in urban and reference forest patches, including deer, invasive plants, insect pests, soil invertebrates, and mycorrhizal fungi (e.g., Cregg & Dix, 2001; Schmidt et al., 2017; Szlavecz et al., 2006; Templeton et al., 2019). Despite these limitations in evaluating the complex urban environment, this study establishes that urban forest soils may support robust seedling establishment and growth and are not inherently stressful for native trees.

The physiological parameters measured in this experiment provide evidence that enhanced leaf level photosynthetic performance of seedlings grown in urban soils leads to greater total biomass. However, elevated urban temperatures may not enhance seedling growth, and repeated chlorophyll fluorescence measurements show that soil and temperature treatment effects change throughout the growing season. Mature white oak trees growing at the urban forest patch soil collection sites used in this study were found to have greater basal area increment, higher values of PI_{abs} and greater thermal tolerance of photosynthesis relative to reference forest sites, attributed to elevated air temperatures and higher availability of soil nutrients (Sonti et al., 2019, 2021). Daily maximum and minimum air temperature differences between the urban and reference forest patches are smaller than those used in this growth chamber experiment, which are based on NOAA climate records from downtown Baltimore (Sonti et al., 2019). Therefore, the results of this study may indicate future impacts of a warming urban climate on native tree establishment and growth. In addition, white oak foliage collected from mature trees growing at the reference forest site had lower levels of foliar Mn and higher foliar P than the seedlings in this study (Sonti et al., 2021). Mature trees can access much deeper soil and may not be as heavily impacted by nutrient imbalances in surface soil. Tolerance of mature trees to environmental stress may be also greater than that of seedlings (Niinemets, 2010). However, seedling establishment and growth in surface soils is critical to forest regeneration and replacement of aging canopy trees.

5 | CONCLUSIONS

Urban forest patches of the eastern United States are largely made up of native canopy species (Groffman et al., 2006; Pregitzer et al., 2019; Templeton et al., 2019; Trammell et al., 2020), which may provide the seed source for natural forest regeneration. Furthermore, urban forest restoration plantings are costly, and many cities are not able to support these activities on a regular basis (Pregitzer et al., 2019). Therefore, successful germination and growth of oak seedlings is critical to the work of natural resource managers in establishing and enhancing native forest canopies in urban and rural areas.

In this growth chamber experiment, we find that urban soils and elevated temperatures do not impact germination rates of white oak acorns. Importantly, soils collected from Baltimore City forest patches support enhanced growth and photosynthesis, particularly in cool grown seedlings. Although temperature treatment did not have a significant effect on response variables, warm grown seedlings attained a lower average total biomass than cool grown seedlings despite earlier germination. Elevated air temperatures resulting from regional climate change may interact with relatively nutrient poor soils to impact future tree seedling performance in rural forests of the eastern United States Nutrient deficiency in eastern deciduous forests is not uncommon, given decades of harvesting and atmospheric pollution (Adams et al., 2000). In addition, forest reserves are often located on nutrient poor sites, as more productive areas have long since been developed for farmland and human settlement (Huston, 2005). Infertile rural forest sites have also been more susceptible to further nutrient loss and soil cation imbalances due to acid deposition (Bailey et al., 2005; Horsley et al., 2000; Sullivan et al., 2013). Seedlings of some native tree species may have difficulty establishing in these conditions when they are also under heat stress predicted in future climate scenarios. Urban seedlings will also have to survive in warmer climatic conditions, but the nutrients available in urban forest patch soils may help mitigate some environmental stress. Additional field research on these interacting environmental factors will help ensure successful forest patch regeneration under continued conditions of global change.

ACKNOWLEDGMENTS

The authors thank Domenic Bello, Jillie Drutz, Jenifer Mallinoff, Michelle Lincoln, Laura Templeton, and Tiffany Wong for assistance with data collection and sample processing and Dr. Maile Neel for feedback on an earlier draft. Support for this project was provided by the USDA Forest Service Northern Research Station.

AUTHOR CONTRIBUTIONS

Nancy F. Sonti conceived and designed the research with input from Kevin L. Griffin, Richard A. Hallett, and Joe H. Sullivan. Nancy F. Sonti performed the experiments. Richard A. Hallett oversaw soil and foliage elemental analysis. Nancy F. Sonti analyzed data and drafted the manuscript. All authors contributed to data interpretation, reviewed, edited, and approved the final manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

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

How to cite this article: Sonti NF, Griffin KL, Hallett RA, Sullivan JH. Photosynthesis, fluorescence, and biomass responses of white oak seedlings to urban soil and air temperature effects. *Physiologia Plantarum*. 2021;172: 1535–1549. https://doi.org/10.1111/ppl.13344