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Research paper

Chlorophyll fluorescence parameters, leaf traits and foliar chemistry of white oak and red maple trees in urban forest patches

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The provisioning of critical ecosystem services to cities of the eastern USA depends on the health and physiological function of trees in urban areas. Although we know that the urban environment may be stressful for trees planted in highly developed areas, it is not clear that trees in urban forest patches experience the same stressful environmental impacts. In this study, we examine chlorophyll fluorescence parameters, leaf traits, foliar nutrients and stable isotope signatures of urban forest patch trees compared with trees growing at reference forest sites, in order to characterize physiological response of these native tree species to the urban environment of three major cities arranged along a latitudinal gradient (New York, NY; Philadelphia, PA; Baltimore, MD). Overall, white oaks (*Quercus alba* L.) show more differences in chlorophyll fluorescence parameters and leaf traits by city and site type (urban vs reference) than red maples (*Acer rubrum* L.). The exceptions were $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, which did not vary in white oak foliage but were significantly depleted ($\delta^{13}\text{C}$) and enriched ($\delta^{15}\text{N}$) in urban red maple foliage. Across all sites, red maples had higher thermal tolerance of photosynthesis (T_{crit}) than white oaks, suggesting a greater ability to withstand temperature stress from the urban heat island effect and climate change. However, the highest average values of T_{crit} were found in the Baltimore urban white oaks, suggesting that species suitability and response to the urban environment varies across a latitudinal gradient. Stomatal pore index (SPI) showed inter-specific differences, with red maple SPI being higher in urban trees, whereas white oak SPI was lower in urban trees. These results demonstrate that differences in native tree physiology occur between urban and reference forest patches, but they are site- and species-specific. Data on local site characteristics and tree species performance over time remain necessary to gain insight about urban woodland ecosystem function.

Keywords: *Acer rubrum*, *Quercus alba*, stable isotopes, stomatal pore index, thermal tolerance of photosynthesis, urban forest patch, urban tree physiology.

Introduction

The ability of plants to persist in urban landscapes will determine their capacity to mitigate aspects of the urban environment that are stressful for human inhabitants, including increased air temperature, flooding and pollution (Volder 2010, Calfapietra et al. 2015). In the eastern USA, trees are dominant components of urban ecosystems, providing valuable biophysical

and sociocultural ecosystem services to urban residents. Urban woodlands, or forest patches, make up a significant proportion of many cities' tree canopy cover (e.g., Avins 2013, Pregitzer et al. 2019), and may have a higher capacity to provide critical biophysical ecosystem services than more intensively managed park areas (Vieira et al. 2018). However, the provisioning of these ecosystem services depends on the health

and physiological function of trees in urban forest patches, which may be impacted by the surrounding urban land use (Cadenasso et al. 2007). Although we know that the urban environment can reduce the productivity of trees planted in highly developed areas (O'Rourke and Terjung 1981, Sjöman and Nielsen 2010, Dale and Frank 2014, 2017), it is not clear that trees in urban forest patches experience the same stressful environmental impacts. Furthermore, native wildtype trees found in forest patches may exhibit different physiological function than planted tree cultivars found in highly managed settings (Lahr et al. 2018a).

There is an assumption that the urban environment (i.e., increased air temperatures and pollution) is inherently stressful to plants (Calfapietra et al. 2015), despite some research to the contrary (Zhao et al. 2016). However, warmer nighttime air temperatures at urban sites may allow for higher rates of photosynthesis without causing additional drought stress (George et al. 2009, Searle et al. 2012), and the soils of urban forest patches may actually have greater nutrient availability than reference forest sites (Pouyat et al. 1995, Szlavecz et al. 2006). However, variation in urban forest patch soil quality may lead to differences in native tree growth and physiology within an urban area, making it important to capture forest patch heterogeneity within a city (Pregitzer et al. 2016).

Previous studies have shown evidence of tree physiological responses to the environment of individual cities, but it is not clear whether the same species responds similarly across different urban areas. Pouyat et al. (2008) found that forest soil chemistry responds to urbanization gradients in three different cities, but the nature of the response varies depending on spatial patterns of development, parent material and pollution sources of each particular city. It is possible that native tree physiology has a similarly varied response. Urban environmental impacts vary across different cities and are sure to affect tree species differently according to their inherent growth strategies, nutrient use and tolerance for environmental stress. While increases in CO₂, nitrogen (N) and temperature found in urban environments will generally enhance photosynthesis, warmer temperatures may also increase rates of respiration and of soil water evaporation, which can lower net photosynthetic carbon gain and potentially limit growth. Elevated urban temperatures may also switch from beneficial to harmful in the lower latitudes of a species' range (Ghannoum and Way 2011), making it important to examine species responses to urbanization throughout their range.

Foliar nutrients and leaf-level physiological traits related to the photosynthetic capacity of different tree species can relate to their ability to grow and thrive in urban forest patches. Chlorophyll fluorescence can be used to quickly and easily estimate photosynthetic capacity from recently collected tree foliage (Pontius and Hallett 2014). The critical temperature for functioning of photosystem II (T_{crit}) is an indication of the

thermal tolerance of photosynthesis determined from continuous chlorophyll fluorescence, and is the threshold temperature at which minimal chlorophyll a fluorescence (F_0) rises rapidly indicating disruption of photosystem II (O'Sullivan et al. 2017). Plants in mid-latitude biomes, including the sites studied here, are at the greatest risk of exposure to heat wave temperatures that exceed their thermal tolerance (O'Sullivan et al. 2017), and this risk may be even greater for plants experiencing the urban heat island effect. Specific leaf area (SLA) and stomatal pore index (SPI) are leaf traits related to resource use and drought response (Poorter et al. 2009, Ramírez-Valiente et al. 2018), which are likely to be affected by the urban environment. Stomatal pore index is a good predictor of leaf hydrologic conductance and is associated with maximum rates of gas exchange and carbon assimilation (Sack et al. 2003, Kaproth and Cavender-Bares 2016). Depleted values of foliar $\delta^{13}C$ are associated with higher CO₂ concentrations in the intercellular space of leaves (c_i) and increased water availability (Farquhar et al. 1989). However, stable carbon isotope composition can also reflect proximity to fossil fuel combustion because carbon from fossil fuels released into the atmosphere through combustion is depleted in ¹³C compared with atmospheric CO₂ (Cobley and Pataki 2019). Cities are hotspots of N deposition (Decina et al. 2019), and higher N availability in urban forest patches may lead to enriched foliar N concentration and stable isotope composition ($\delta^{15}N$) compared with nearby rural sites (Nikula et al. 2010, Falxa-Raymond et al. 2014).

The purpose of this study was to examine leaf-level physiological responses of native tree species to the urban environment by measuring chlorophyll fluorescence parameters, leaf traits, foliar nutrients and foliar stable isotope composition of urban forest patch trees compared with trees growing at reference forest sites. White oak (*Quercus alba* L.) and red maple (*Acer rubrum* L.) trees were selected and measured in three major cities of the eastern United States (New York, NY; Philadelphia, PA; Baltimore, MD). The physiological response of these native tree species to urban environmental conditions will provide insight into the future of tree physiology in surrounding rural forests as they are subject to global change impacts such as elevated temperature, atmospheric CO₂ and N deposition (Calfapietra et al. 2015, Lahr et al. 2018b).

Materials and methods

Study sites

Sites were selected as part of a larger study (Sonti et al. 2019), set in secondary growth oak–hickory forests found in New York, NY, Philadelphia, PA and Baltimore, MD, as well as at reference forest sites outside each metropolitan area (Figure 1). The climate of these eastern US cities is strongly seasonal with warm summers and cold winters and all three cities receive ~1100 mm precipitation annually (see Table S1 available as

Supplementary Data at 'Tree Physiology' Online). The three cities also occupy a latitudinal gradient, with progressively warmer average annual air temperatures as you move south from New York City (NYC) (12.9 °C annual avg.) to Philadelphia (13.3 °C annual avg.) to Baltimore (14.7 °C annual avg.).

In all three metropolitan areas, urban forest patches and reference forest sites were selected based on the presence of red maple and white oak canopy trees and similar soil types within each metropolitan area (NRCS soil survey). All urban sites were within official city limits, and all reference sites were located in protected areas outside of the city surrounded by intermix wildland-urban interface landscapes (Martinuzzi et al. 2015). Reference ecosystems were dominated by mature native trees with minimal management by humans (Reisinger et al. 2016). Within each city, three separate urban forest patches were selected to capture the variation in forest patch site conditions across an individual city. Three reference sites were selected for each city, located within the same protected area considered representative of rural forests of the region.

Previous work has documented differences in air temperature and soil chemistry between these urban and reference forest sites (Sonti et al. 2019). During the 2015 growing season, each city's urban forest patch sites were consistently warmer than reference sites. Daily maximum air temperatures were 3.5, 0.38 and 1.6 °C warmer in urban vs reference forest patches in NYC, Philadelphia and Baltimore, respectively (see Table S1 available as Supplementary Data at 'Tree Physiology' Online). Daily minimum air temperatures were 3.2, 1.6 and 0.8 °C warmer in urban vs reference forest patches in NYC, Philadelphia and Baltimore, respectively. Soil characteristics also varied between urban and reference forest patches of each city (Sonti et al. 2019). Baltimore and NYC had differences in urban vs reference forest soil nutrients, while Philadelphia urban and reference soils were not significantly different from one another. NYC and Baltimore urban soils both had higher Ca, Mg, sand and pH compared with reference soils, while only Baltimore had higher urban soil organic matter, N and phosphorus (P) compared with reference soils. All three cities had higher heavy metal concentrations (aluminium, arsenic, cadmium, chromium, copper, sodium, lead and zinc) in urban soils.

Data collection

Five mature white oak and five mature red maple trees were selected at each site, for a total of 15 reference and 15 urban trees of each species for each city ($n = 180$ trees). White oaks were at least 38.1 cm diameter at breast height (DBH), red maples were at least 25.4 cm DBH, and all trees were dominant or co-dominant canopy trees. The trees had no major trunk cavities and had crown vigor scores of 1 or 2 (<25% overall canopy damage) (Pontius and Hallett 2014).

From early July to early August 2015, ~15 sun leaves were collected from around the periphery of the crown of each

tree with either a shotgun or slingshot. Since the ambient light environment significantly affects leaf morphology and physiological function (Lichtenthaler et al. 2007), and the quantification of the light level received by an individual leaf would have been prohibitively difficult, we limit this study to full sun leaves for consistency and the most robust experimental design. Within 24 h of leaf collection, chlorophyll fluorescence was measured on five leaves from each tree using a continuous excitation Pocket PEA fluorometer equipped with black leaf-clips (Hansatech Instruments Ltd, King's Lynn, UK). Leaves were kept in plastic bags containing moistened paper towels inside a cooler or refrigerator if measurements could not be taken immediately following collection. All 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 and were not affected by several hours of storage in a cooler. The Performance Index (PI_{abs}) parameter calculated by the Pocket PEA was used for subsequent analysis. Performance Index is an integrative chlorophyll fluorescence parameter that reflects the functionality of both photosystems I and II and can indicate stress in plants even before visible symptoms appear on the leaves (Strasser et al. 2004, Christen et al. 2007). Under water stress, PI_{abs} has been found to be more sensitive than the maximum quantum yield of photosystem II (F_V/F_M), and has been shown to be positively correlated with CO_2 assimilation capacity (Van Heerden et al. 2007, Brestič and Živčák 2013).

Within 48 h of leaf collection, chlorophyll fluorescence was assessed under rapidly increasing heat stress to quantify the critical temperature (T_{crit}) at which F_0 rapidly rises and the disruption of both electron transport in photosystem II and respiratory biochemical machinery occurs in organelles (O'Sullivan et al. 2013). Leaves were kept in plastic bags containing moistened paper towels inside a cooler or refrigerator until measurements were taken. F_0 was monitored continuously on one leaf from each tree with a Pulse Amplitude Modulation (PAM-2000) Fluorometer (Heinz-Walz, Effeltrich, Germany) as temperature was increased from 30 °C at the rate of 1 °C min^{-1} using a heating element inside an insulated chamber until maximum F_0 was reached. Temperature was recorded simultaneously with F_0 by the thermocouple in the PAM-2000 leaf clip. T_{crit} values were determined using a change-point analysis, which combines the methods of cumulative sum and bootstrap analysis (Taylor 2000, Rahman et al. 2013).

Three leaves from each tree were pressed and dried immediately after collection. One 10 mm disc was punched out of each leaf and weighed after being dried for a week at 70 °C. The area of the disc was divided by the oven-dried weight of each sample in order to calculate SLA in $cm^2 g^{-1}$. In addition, stomatal density and aperture length were assessed in three spots on each leaf using clear nail polish impressions. For stomatal analysis, clear nail varnish was applied to three locations on the abaxial



Figure 1. Map of the eastern USA showing the location of urban and reference forest patch study sites within each metropolitan area: New York, NY; Philadelphia, PA; and Baltimore, MD.

surface of the leaf between the mid-vein and the leaf margin to create impressions of the leaf epidermis. Stomatal density and aperture length of three stomata were measured in three areas on each leaf impression. Digital image recording and image analysis were performed with the INFINITY ANALYZE software (Lumenera Corporation, Ottawa, Canada). Stomatal pore index was calculated as the stomatal density \times pore length² (Sack et al. 2003). All leaf physiology parameters were averaged for each individual tree.

Remaining oven-dried foliage from ~ 12 leaves per tree was ground to create a composite sample for each tree and

was subsequently digested using a microwave-assisted acid digestion procedure (USEPA Method 3,052) and analyzed for calcium (Ca), potassium (K), magnesium (Mg), manganese (Mn) and P by ICP spectroscopy. Foliar N was determined by combustion with a PerkinElmer 2400 series II CHNS/O analyzer (PerkinElmer, Waltham, MA, USA). Foliar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were analyzed using a Carlo Erba NC2500 elemental analyzer interfaced with a Thermo Delta V+ isotope ratio mass spectrometer. Two USGS standards (USGS 40 and USGS 41) and one secondary standard (acetanilide) were used with precision of 0.12‰ for $\delta^{13}\text{C}$ and 0.11‰ for $\delta^{15}\text{N}$. The natural abundance

stable isotope values were expressed relative to international standards for carbon (Vienna PeeDee Belemnite) and N (air) in the conventional δ -notation.

Data analysis

Linear mixed effects models were used to analyze the effects of city, site type (urban vs reference), tree species and associated interaction effects on tree physiology, foliar nutrients and stable isotope ratios. An average physiological parameter value per tree was used in all linear models. The R function lme in the nlme package allowed the use of site as random effect in each model (R Development Core Team 2008, Pinheiro et al. 2010). Models constructed for each physiological response variable (PI_{abs} , T_{crit} , SPI and SLA) and stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) included city, site type, species and all interaction effects. Assumptions of normality and homoscedasticity of the residuals were verified visually using diagnostic plots, and different variance structures were incorporated into the models using the varIdent function in order to meet assumptions of homoscedasticity (Table 1). Using the function lsmeans, Tukey contrasts were used to test for differences in foliar physiology and chemistry between urban and reference site types within each tree species-city combination and across all city locations. Differences between means were considered significant at $\alpha = 0.05$.

Foliar nutrient data for each species were submitted to principal component analysis (PCA) using the R function prcomp in the package stats v. 3.5.1 (R Core Team 2018). Eigenvalues were used to determine that two principal components should be retained for each foliar nutrients PCA. In the case of both PCAs, a varimax rotation was used to aid in interpretation of the principal components using the function varimax. The first and second rotated principal components (RC1 and RC2) from each foliar nutrients PCA were used as response variables in linear mixed effects models with site as a random effect. Because foliar nutrient RCs were calculated separately for each species, four models were constructed for each RC response variable including city, site type and their interaction. Foliar nutrient RCs were also correlated with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for each species, using the R function rcorr.

Results

All leaf-level physiological variables were significantly different between the two tree species except for foliar stable isotope ratios (Table 1). White oaks tended to have higher values of PI_{abs} , and lower values of SLA, T_{crit} and SPI than red maples (Figure 2a). Average PI_{abs} for white oak foliage was 13.0 compared with 9.2 for red maple, SLA was 133.6 for white oak foliage compared with 155.0 for red maple, T_{crit} was 46.6 °C for white oak compared with 47.1 °C for red maple, and SPI was 0.06 for white oak compared with 0.10 for red maple foliage. No differences were found in these parameters between urban and

Table 1. Results from linear mixed effects models analyzing the effects of tree species, site type and city and their interactions on foliar nutrients and physiology response variables. F-values, denominator degrees of freedom (in parentheses) and P-values are listed for each fixed effect. Species effects are not relevant for foliar nutrients models, which were analyzed separately by tree species. Bold values indicate significant differences ($\alpha = 0.05$): WO, white oak; RM, red maple; RC1 and RC2, first and second rotated principle components

Response variable	Species	Site type	City	City * Site type	Species * Site type	City * species	City * species * Site type	Variance structure
T_{crit}	6.55 (155) 0.01	0.31 (13) 0.59	0.84 (13) 0.45	4.73 (13) 0.03	1.28 (155) 0.26	0.56 (155) 0.57	2.40 (155) 0.09	Species
PI_{abs}	56.88 (155) <0.0001	2.34 (13) 0.15	0.19 (13) 0.83	0.02 (13) 0.98	0.57 (155) 0.45	2.72 (155) 0.07	3.86 (155) 0.02	Species and Site type
SPI	585.29 (155) <0.0001	1.25 (13) 0.28	2.03 (13) 0.17	2.16 (13) 0.16	8.82 (155) 0.003	1.14 (155) 0.32	1.24 (155) 0.29	Species
SLA	26.45 (155) <0.0001	0.01 (13) 0.92	3.98 (13) 0.04	0.61 (13) 0.56	0.67 (155) 0.41	1.88 (155) 0.16	0.79 (155) 0.46	Site type
$\delta^{15}\text{N}$	0.02 (155) 0.89	1.42 (13) 0.25	1.24 (13) 0.32	1.76 (13) 0.21	45.52 0.09	4.58 (155) 0.01	4.42 (155) 0.01	Species and Site type
$\delta^{13}\text{C}$	1.77 (155) 0.19	6.71 (13) 0.02	3.95 (13) 0.05	2.12 (13) 0.16	2.93 (155) 0.09	2.18 (155) 0.12	2.18 (155) 0.80	Site type
WO foliar nutrients RC1		5.68 (12) 0.03	12.18 (12) 0.001	8.48 (12) 0.005				
WO foliar nutrients RC2		0.01 (12) 0.90	0.09 (12) 0.91	3.56 (12) 0.06				
RM foliar nutrients RC1		3.40 (12) 0.09	3.52 (12) 0.06	0.34 (12) 0.71				
RM foliar nutrients RC2		22.47 (12) 0.0005	4.45 (12) 0.04	1.53 (12) 0.26				

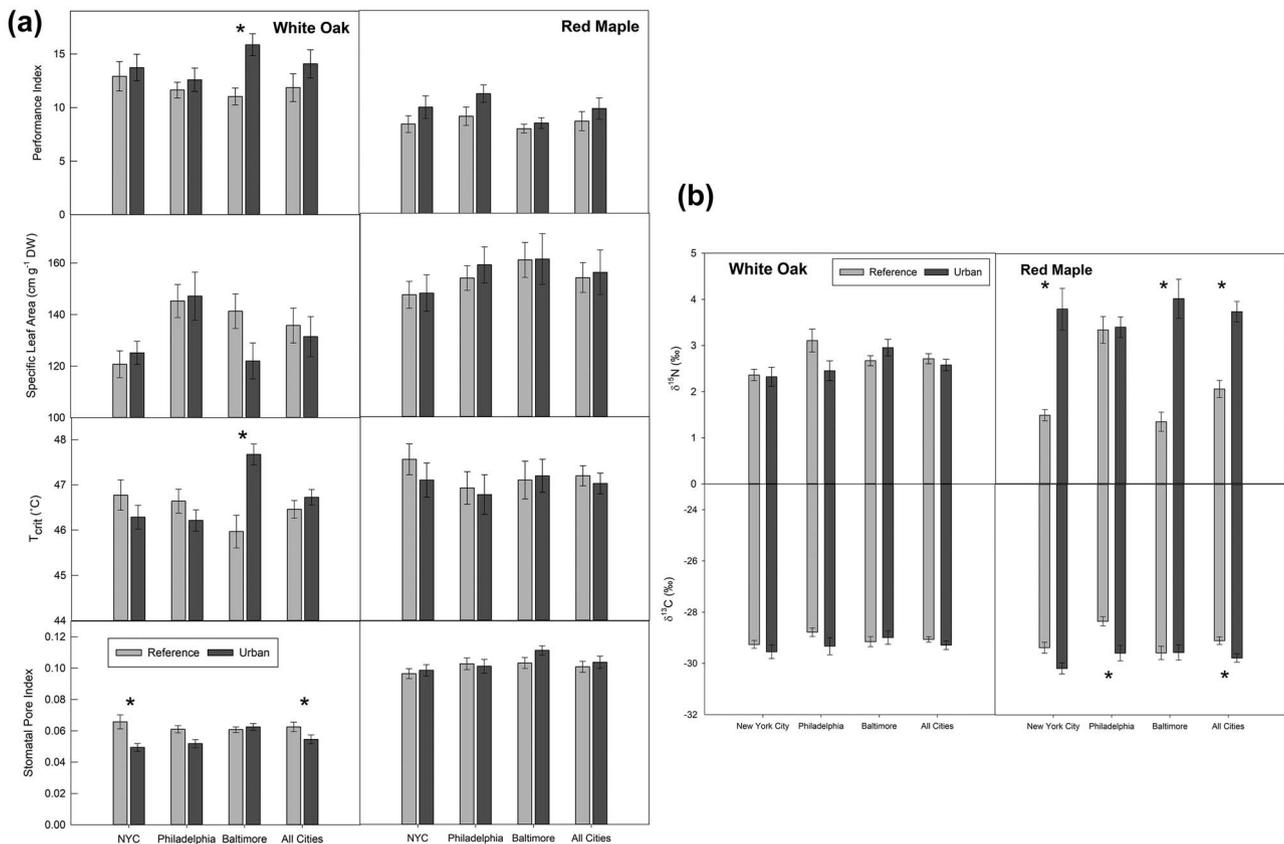


Figure 2. White oak and red maple (a) foliar physiology variables and (b) foliar stable isotope composition by city and site type. Error bars show mean \pm standard error of the mean (SEM). Asterisks indicate significant difference between urban and reference values within each city and averaged across all cities ($P < 0.05$). DW, dry weight.

reference sites in red maple, but significant interaction effects were observed in white oak. Pl_{abs} and T_{crit} increased only in Baltimore urban compared with reference sites, while SPI was significantly lower in NYC and across all urban sites (Figure 2a).

The three-way interaction of city \times species \times site type had a significant effect on foliar $\delta^{15}N$, as did the two-way species \times site type and city \times species interaction effects (Table 1). In contrast to Pl_{abs} , T_{crit} and SPI, red maple trees had greater differences in urban vs reference foliar isotopic composition than white oaks. Urban red maple $\delta^{15}N$ was enriched compared with reference trees in both NYC and Baltimore, while red maple $\delta^{13}C$ was significantly depleted in Philadelphia urban vs reference sites (Figure 2b).

In the white oak foliar nutrients PCA, 52% of the variation was explained by the first two varimax rotated components, with RC1 accounting for 31% of the variation and RC2 21% (Figure 3a). Positive loadings of RC1 corresponded to foliar N, P and K and negative loadings to foliar Mn, whereas positive loadings of RC2 corresponded to foliar Ca and Mg (see Table S2 available as Supplementary Data at 'Tree Physiology' Online). Linear mixed effects models revealed a significant city \times site type interaction effect on white oak foliar nutrients RC1 (Table 1). Inspection of the scatterplot for RC1 and RC2 shows a clustering of Baltimore

reference sites to the left and Philadelphia reference sites to the right (negative vs positive loadings of RC1 or concentrations of foliar N, P, K and Mn). There appears to be less separation of white oak foliar nutrients RC2 by city and site type.

In the red maple foliar nutrients PCA, 59% of the variation was explained by the first two varimax rotated components, with RC1 accounting for 30% of the variation and RC2 29% (Figure 3b). Positive loadings of RC1 corresponded to foliar N, P and K, whereas positive loadings of RC2 corresponded to foliar Ca and Mg (see Table S2 available as Supplementary Data at 'Tree Physiology' Online). Linear mixed effects models revealed a significant effect of city on red maple foliar nutrients RC1, and significant effects of site type and city on RC2 (Table 1). Inspection of the scatterplot for RC1 and RC2 shows a general clustering of urban sites to the upper right and reference sites to the bottom left, indicating that urban red maple foliage is higher in nutrients than reference foliage. In particular, NYC reference sites cluster toward the bottom (negative loadings of RC2 or concentrations of foliar Ca and Mg) and Baltimore reference sites cluster toward the left (negative loadings of RC1 or concentrations of foliar N, P and K).

White oak foliar $\delta^{15}N$ was not significantly correlated with the foliar nutrient RCs, but $\delta^{13}C$ was significantly negatively

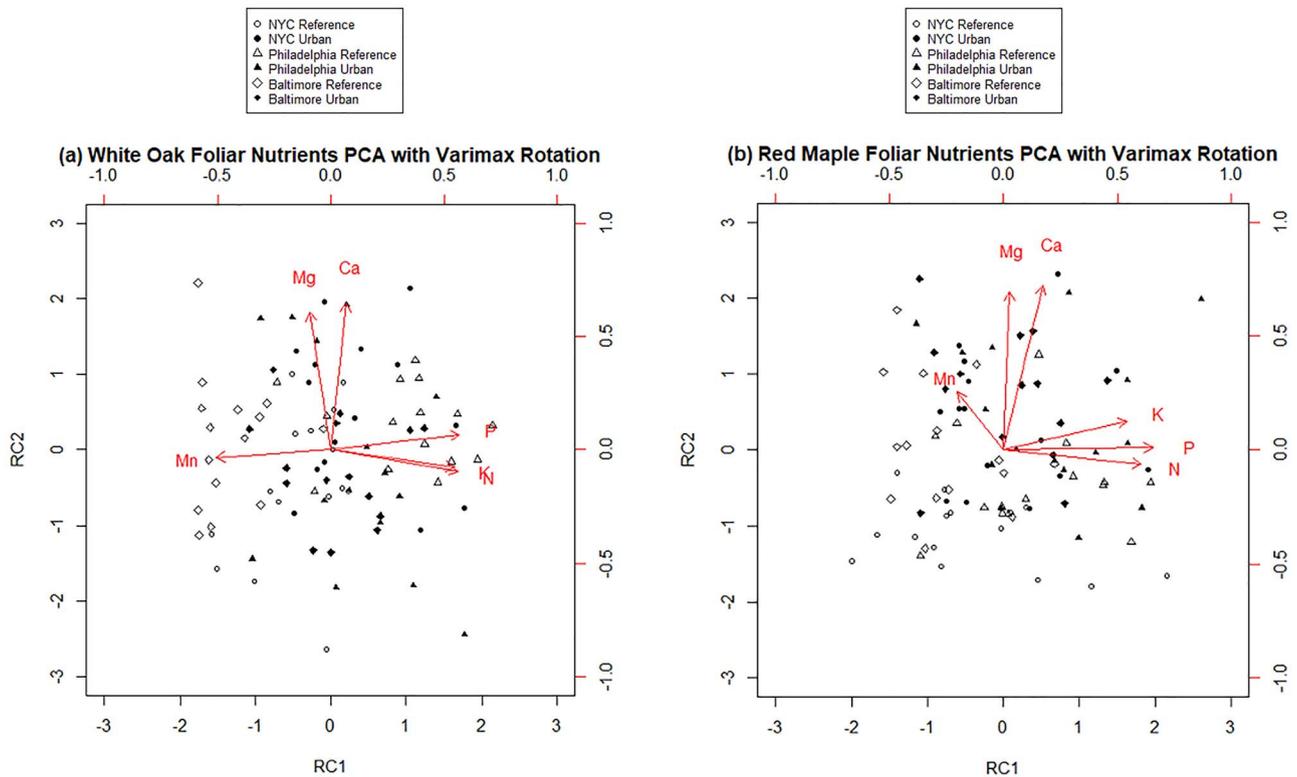


Figure 3. (a) Biplot of white oak foliar nutrients principal components 1 and 2 after Varimax rotation (31% and 21% of variance), (b) Biplot of red maple foliar nutrients principal components 1 and 2 after Varimax rotation (30% and 29% of variance). Trees from urban forest patches are represented by solid symbols and trees from reference forest sites are represented by clear symbols; shapes are used to differentiate trees from New York City (circles), Philadelphia (triangles) and Baltimore (diamonds).

Table 2. Pearson correlation coefficients (r^2) and associated P -values for the correlations between white oak and red maple foliar nutrients varimax rotated principal components (RCs) and foliar stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$). Bold values indicate significant differences ($\alpha = 0.05$)

	Foliar Chem RC1	Foliar Chem RC2
White oak		
$\delta^{13}\text{C}$	-0.05 (0.66)	-0.26 (0.01)
$\delta^{15}\text{N}$	-0.05 (0.67)	0.12 (0.24)
Red maple		
$\delta^{13}\text{C}$	0.15 (0.17)	-0.25 (0.02)
$\delta^{15}\text{N}$	0.23 (0.03)	0.24 (0.02)

correlated with RC2 (Ca and Mg) (Table 2). Red maple foliar $\delta^{15}\text{N}$ was significantly positively correlated with both RC1 (N, P and K) and RC2 (Ca and Mg), while foliar $\delta^{13}\text{C}$ was significantly negatively correlated with RC2 (Ca and Mg) (Table 2).

Discussion

In this study, leaf-level physiology of native tree species in urban and reference forests indicates that urban forest patches do not necessarily provide a more difficult growing environment than nearby reference forests, despite the ecological disturbances

caused by urbanization. The results of this study demonstrate that white oak chlorophyll fluorescence parameters and leaf traits vary by city and site type, whereas red maples show greater variation in foliar stable isotope composition across sites. The findings are consistent with previous work showing a modest response of red maple leaf physiology to changes in environmental conditions compared with co-occurring oak species (Turnbull et al. 2001), and with Abrams' (1998) assertion that the widespread expansion of red maple is not easily explained by its leaf physiology.

Overall, red maple trees in this study had higher values of T_{crit} than white oaks, suggesting higher photosynthetic tolerance for the warmer conditions of urban forest patches. We also find that white oaks in Baltimore urban forest patches, which experience the warmest temperatures of any site in this study, have the highest average T_{crit} . Perhaps these warm temperatures have surpassed a threshold causing the oaks to acclimate and increase their thermal tolerance of photosynthesis (O'Sullivan et al. 2017). Overall growth and survival of urban trees and their photosynthetic thermal tolerance may not be correlated because photosynthesis occurs only when environmental conditions are favorable (Knight and Ackerly 2003). If favorable conditions occur frequently enough despite episodes of high temperature stress, there may not be pressure for acclimation (i.e., increased T_{crit}). However, urban tree canopy temperatures can be as much

as 10 °C warmer than ambient temperatures (Leuzinger et al. 2010), so these tree canopies will likely approach or reach T_{crit} more frequently under future warming scenarios with more frequent extreme temperature events. Furthermore, species suitability and response to the urban environment vary across a latitudinal gradient, and further research on these species at their southern range limits may reveal greater temperature stress due to urban heat island effects (Kendal et al. 2018).

White oak physiology appeared to respond differently to the urban environment of Baltimore compared with NYC or Philadelphia, which may be due to the warmer average temperatures found in Baltimore compared with the other two urban areas. In addition to higher T_{crit} , Baltimore urban white oaks also have a higher average PI_{abs} and lower SLA compared with reference trees, possibly indicating lower overall stress and higher photosynthetic capacity (Poorter et al. 2009), while differences in these physiological variables between urban and reference trees are not as strong in NYC or Philadelphia. There is a documented atmospheric CO₂ gradient in Baltimore that may contribute to lower urban vs reference SLA in Baltimore white oaks, although we do not see this difference in red maples (George et al. 2007, Poorter et al. 2009).

Baltimore white oaks may also be responding to strong differences in nutrient availability between urban and reference sites revealed by the separation in values of foliar nutrients RC1 (corresponding to higher concentrations of foliar N, P and K, and lower concentrations of Mn). This pattern is driven by P deficiency in white oak foliage from the Baltimore reference site (see Table S3 available as Supplementary Data at 'Tree Physiology' Online; Ward and Bowersox 1970, Davis et al. 1995, Mellert and Göttlein 2012) and may be contributing to the significantly lower PI_{abs} of Baltimore reference white oaks compared with urban trees. Previous research has shown that these Baltimore urban forest patch soils have more Ca, Mg, N, P and soil organic matter than the reference forest site (Sonti et al. 2019). Overall, both species' foliar N concentrations are below the levels associated with maximum growth rates (Mitchell and Chandler 1939), making them both likely to benefit from the increased N availability of urban forest soils. Manganese is more readily available at lower soil pH, and within each city we do find higher white oak foliar Mn at sites with lower pH (NYC reference, Philadelphia urban and Baltimore reference) (Sonti et al. 2019). However, there does not appear to be Mn deficiency or toxicity in the trees studied here (see Table S3 available as Supplementary Data at 'Tree Physiology' Online; Hallett et al. 2006).

Differences in water availability across sites may impact the physiological responses of isohydric red maples and anisohydric white oaks to drought stress. Abrams (2003) has predicted that climate change may benefit white oak due to its drought tolerance relative to other hardwood species, although red maple may have a greater safety margin for hydraulic failure than white oak under drought conditions (Choat et al. 2012). Urban

red maple foliage was depleted in ¹³C compared with reference foliage, which may be due to the increased precipitation in these urban areas, leading to reduced drought stress compared with reference forest sites (Warren et al. 2001). Water stress has been suggested to drive patterns of $\delta^{13}C$ in urban vegetation across residential landscapes (Cobley and Pataki 2019), and intrinsic water-use efficiency of isohydric species (i.e., red maple) is generally more sensitive to environmental conditions than that of anisohydric species (i.e., white oak; Yi et al. 2019). Average SPI of urban white oaks in NYC and Philadelphia was lower than reference trees, while in Baltimore there was no difference between urban and reference SPI. A lower SPI may indicate drought conditions (Ramírez-Valiente et al. 2018), so it is possible that Baltimore's urban white oaks are experiencing less drought stress relative to reference sites compared with trees of the other cities' urban forest patches. The difference in total annual precipitation between urban and reference sites is the least pronounced in Baltimore (see Table S1 available as Supplementary Data at 'Tree Physiology' Online), but other site conditions may affect forest patch hydrology and soil moisture conditions.

Both SPI and $\delta^{13}C$ may be impacted by atmospheric pollution in addition to drought stress, complicating interpretation of these parameters. Lower values of urban red maple $\delta^{13}C$ may reflect the depleted ¹³C signature of fossil fuel emissions that are more prevalent in urban areas (Lichtfouse et al. 2003, Wang and Pataki 2012). Higher levels of atmospheric CO₂ may result in lower stomatal density, whereas elevated atmospheric ozone can lead to higher stomatal density (Paoletti and Grukke 2005). However, white oak is not sensitive to ozone (Davis and Skelly 1992), and previous research indicates that Baltimore has a stronger urban–rural gradient of elevated CO₂ than NYC (George et al. 2007, Hsueh 2009), which does not support the differences in white oak stomatal characteristics found here. Thus, our results do not indicate that the CO₂ gradient between Baltimore urban and reference sites was physiologically meaningful to the trees in this study.

Variation in foliar nutrients RC1 (N, P and K) and $\delta^{15}N$ reveal differences in N use across species, cities and site types. Red maple associates with vesicular arbuscular mycorrhizal species, which does not strongly discriminate against ¹⁵N during uptake (Vallano and Sparks 2013). As a result, the N isotope signature of red maple foliage is likely to reflect the surrounding environmental conditions more strongly than that of white oak, whose ectomycorrhizal associations would be expected to show a greater degree of isotopic fractionation during root N uptake from the soil N pool (Hobbie and Hobbie 2008). This may explain why white oak leaf $\delta^{15}N$ is not significantly correlated with foliar nutrients, and why this species' N isotope signature does not vary significantly between urban and reference forest sites. In contrast, enriched red maple foliar $\delta^{15}N$ in Baltimore and NYC urban versus

reference forests may be due to pollution-derived N deposition, which tends to be isotopically enriched (Ammann et al. 1999, Pearson et al. 2000, Díaz-Alvarez et al. 2016). In addition, the increased N availability, warmer temperatures and higher rates of precipitation in urban forest patches may lead to enriched N isotope signatures resulting from an opening of the tightly regulated N cycle often found in N-limited eastern deciduous forests (Pardo and Nadelhoffer 2010, West et al. 2010, Falxa-Raymond et al. 2014).

Heterogeneous forest soil characteristics may impact nutrient availability to white oak and red maple trees within a site. For example, given the values of RC2 (Ca and Mg) found here it is possible that urban white oaks in NYC and urban red maples in Baltimore are located near construction debris leading to particularly high availability of Ca and Mg in surrounding soils compared with reference sites. However, this difference is unlikely to impact tree productivity since there do not seem to be Ca or Mg deficiencies in any of the trees studied here (see Table S3 available as Supplementary Data at 'Tree Physiology' Online; Davis et al. 1995). Leaf $\delta^{13}\text{C}$ is also significantly negatively correlated with foliar nutrients RC2 (Ca, Mg) in both species. These two aspects of foliar chemistry may be independently driven by co-occurring processes of atmospheric pollution and soil disturbance across and within urban forest sites. Foliar $\delta^{13}\text{C}$ may also be linked with Ca and Mg concentrations, since these nutrients may improve or inhibit stomatal conductance under stress conditions (Rao et al. 1987, Borer et al. 2005, Liu et al. 2015).

Previous research on growth rates of the same trees used in this study found higher basal area increment of urban white oaks compared with reference trees in NYC and Baltimore, and higher basal area increment of urban red maples compared with reference trees in Philadelphia and Baltimore in recent decades (Sonti et al. 2019). These differences are not clearly reflected in the leaf-level physiology characterized here, suggesting that leaf-level physiology measurements may not always provide the most direct assessment of overall ecosystem function and service provision. Likely, trees in urban forest patches are putting on more aboveground biomass, increasing overall capacity for carbon fixation without necessarily altering leaf-level photosynthesis (Searle et al. 2012). For example, it is not surprising that PI_{abs} did not vary more strongly across cities and site types given that healthy trees were chosen for this study and PI_{abs} is an indication of stress. It is possible that including trees from a spectrum of stress levels would increase the differences between urban and reference trees, particularly if trees in urban forest patches are better able to avoid nutrient deficiencies than trees in nearby reference forest sites (Falxa-Raymond et al. 2014). The small but consistent differences in PI_{abs} found here may reflect the higher productivity of urban trees compared with reference trees (Sonti et al. 2019), as chlorophyll fluorescence

has been found to be correlated with plant growth and gas exchange rates (Brestič and Živčák 2013, Sonti 2019).

This study included healthy canopy trees across urban and reference forest sites. However, biotic and abiotic stresses may impact the health of native tree populations in urban and reference forests, leading to differences in overall site productivity and ecosystem service provision that are not apparent when examining only physiology of healthy individuals. Urban environmental conditions may also influence the susceptibility of native trees to damage from pests and pathogens, with implications for the long-term health of urban forest patches.

Conclusions

The ecophysiological results from this study suggest that the urban environment is not inherently stressful for native trees, and may allow for greater physiological function, depending on the species and city. Both white oak and red maple are widespread species in the eastern USA, but the past century has seen a decline in white oak and an increase in red maple throughout forests of the region (Abrams 1998, 2003, McEwan et al. 2011). Although both species are able to thrive in a variety of site conditions, our data suggest that red maple may have a greater ability to withstand temperature stress from the urban heat island effect and climate change and may acclimate even more readily than white oak to the urban forest patch environment. The ability to acclimate to present and future urban environmental conditions will allow for continued photosynthetic activity and associated ecosystem functions of healthy and productive urban forest patches. A greater understanding of the physiological function that underlies the growth and productivity of these trees will allow for the continuation of critical ecosystem services in urban areas.

Supplementary Data

Supplementary Data for this article are available at *Tree Physiology* Online.

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Conflict of interest

None declared.

References

- Abrams MD (1998) The red maple paradox. *Bioscience* 48:355–364.
- Abrams MD (2003) Where has all the white oak gone? *Bioscience* 53: 927–939.
- Ammann M, Seigwolf R, Pichlmayer F, Suter M, Saurer M, Brunold C (1999) Estimating the uptake of traffic-derived NO₂ from ¹⁵N abundance in Norway spruce needles. *Oecologia* 118:124–131.
- Avins M (2013) Baltimore's forest patches: emerald assets for ecosystem Services. Baltimore Green Space, Baltimore, Maryland, USA, p 34.
- Borer CH, Schaberg PG, DeHayes DH (2005) Acidic mist reduces foliar membrane-associated calcium and impairs stomatal responsiveness in red spruce. *Tree Physiol* 25:673–680.
- Brestič M, Živčák M (2013) PSII fluorescence techniques for measurement of drought and high temperature stress signal in crop plants: protocols and applications. In: Rout GR, Das AB (eds) *Molecular stress physiology of plants*. Springer, India, pp 87–131.
- Cadenasso ML, Pickett STA, McDonnell MJ, Pouyat RV (2007) Forest vegetation along an urban-rural gradient in the New York City metropolitan area: patterns and relationships to ecosystem processes. *Trans Linnean Soc NY* 10:79–99.
- Calfapietra C, Peñuelas J, Niinemets Ü (2015) Urban plant physiology: adaptation-mitigation strategies under permanent stress. *Trends Plant Sci* 20:72–i75.
- Choat B, Jansen S, Brodribb TJ et al. (2012) Global convergence in the vulnerability of forests to drought. *Nature* 491:752–755.
- Christen D, Schönmann S, Jermini M, Strasser RJ, Défago G (2007) Characterization and early detection of grapevine (*Vitis vinifera*) stress responses to esca disease by in situ chlorophyll fluorescence and comparison with drought stress. *Environ Exp Bot* 60: 504–514.
- Cobley LAE, Pataki DE (2019) Vehicle emissions and fertilizer impact the leaf chemistry of urban trees in salt Lake Valley, UT. *Environ Pollut* 254:112984.
- Dale AG, Frank SD (2014) The effects of urban warming on herbivore abundance and street tree condition. *PLoS One* 9:e102996.
- Dale AG, Frank SD (2017) Warming and drought combine to increase pest insect fitness on urban trees. *PLoS ONE* 12: e0173844.
- Davis DD, Skelly JM (1992) Foliar sensitivity of eight eastern hardwood tree species to ozone. *Water Air Soil Pollut* 62:269–277.
- Davis DD, Skelly JM, Nash BL (1995) Oak in relation to atmospheric deposition in Pennsylvania. In: *Proceedings 10th Annual Central Hardwood Conference*, Lakeview Resort and Conference Center, Morgantown, WV, March 5–8, pp. 188–195.
- Decina SM, Hutrya LR, Templer PH (2019) Hotspots of nitrogen deposition in the world's urban areas: a global data synthesis. *Front Ecol Environ*. doi: 10.1002/fee.2143.
- Díaz-Alvarez EA, Reyes-García C, de la Barrera E (2016) A $\delta^{15}\text{N}$ assessment of nitrogen deposition for the endangered epiphytic orchid *Laelia speciosa* from a city and an oak forest in Mexico. *J Plant Res* 129:863–872.
- Falxa-Raymond N, Palmer MI, McPhearson T, Griffin KL (2014) Foliar nitrogen characteristics of four tree species planted in New York City reforestation sites. *Urban Ecosyst* 17:807–824.
- Farquhar GD, Ehleringer JR, Hubick KT (1989) Carbon isotope discrimination and photosynthesis. *Annu Rev Plant Physiol Plant Mol Biol* 40:503–537.
- George K, Ziska LH, Bunce JA, Quebedeaux B (2007) Elevated atmospheric CO₂ concentration and temperature across an urban-rural transect. *Atmos Environ* 41:7654–7665.
- George K, Ziska LH, Bunce JA, Quebedeaux B, Hom JL, Wolf J, Teasdale JR (2009) Macroclimate associated with urbanization increases the rate of secondary succession from fallow soil. *Oecologia* 159:637–647.
- Ghannoum O, Way DA (2011) On the role of ecological adaptation and geographic distribution in the response of trees to climate change. *Tree Physiol* 31:1273–1276.
- Hallett RA, Bailey SW, Horsley SB, Long RP (2006) Influence of nutrition and stress on sugar maple at a regional scale. *Can J For Res* 36:2235–2246.
- Hobbie EA, Hobbie JE (2008) Natural abundance of ¹⁵N in nitrogen-limited forests and tundra can estimate nitrogen cycling through mycorrhizal fungi: a review. *Ecosystems* 11:815–830.
- Hsueh D (2009) New York City's metropolitan dome: past and present CO₂ concentration patterns from an urban to rural gradient. Masters Thesis. Department of Ecology Evolution and Environmental Biology, Columbia University, New York, pp 1–101.
- Kaproth M, Cavender-Bares J (2016) Drought tolerance and climatic distributions of the American oaks. *International Oaks* 27:49–60.
- Kendal D, Dobbs C, Gallagher RV, Beaumont LJ, Baumann J, Williams NS, Livesley SJ (2018) A global comparison of the climatic niches of urban and native tree populations. *Glob Ecol Biogeogr* 27:629–637.
- Knight CA, Ackerly DD (2003) Evolution and plasticity of photosynthetic thermal tolerance, specific leaf area and leaf size: congeneric species from desert and coastal environments. *New Phytol* 160:337–347.
- Lahr EC, Dunn RR, Frank SD (2018a) Variation in photosynthesis and stomatal conductance among red maple (*Acer rubrum*) urban planted cultivars and wildtype trees in the southeastern United States. *PLoS One* 13: e0197866.
- Lahr EC, Dunn RR, Frank SD (2018b) Getting ahead of the curve: cities as surrogates for global change. *Proc R Soc B: Biol Sci* 285:20180643.
- Leuzinger S, Vogt R, Körner C (2010) Tree surface temperature in an urban environment. *Agric For Meteorol* 150:56–62.
- Lichtenthaler HK, Ač A, Marek MV, Kalina J, Urban O (2007) Differences in pigment composition, photosynthetic rates and chlorophyll fluorescence images of sun and shade leaves of four tree species. *Plant Physiol Biochem* 45:577–588.
- Lichtfouse E, Lichtfouse M, Jaffrezic A (2003) $\delta^{13}\text{C}$ values of grasses as a novel indicator of pollution by fossil-fuel-derived greenhouse gas CO₂ in urban areas. *Environ Sci Tech* 37:87–89.
- Liu YF, Zhang GX, Qi MF, Li TL (2015) Effects of calcium on photosynthesis, antioxidant system, and chloroplast ultrastructure in tomato leaves under low night temperature stress. *J Plant Growth Regulat* 34:263–273.
- Martinuzzi S, Stewart SI, Helmers DP, Mockrin MH, Hammer RB, Radeloff VC (2015) The 2010 wildland-urban interface of the conterminous United States. Research Map NRS-8. Newtown Square. Department of Agriculture, Forest Service, Northern Research Station, PA, USA, p 124.
- McEwan RW, Dyer JM, Pederson N (2011) Multiple interacting ecosystem drivers: toward an encompassing hypothesis of oak forest dynamics across eastern North America. *Ecography* 34:244–256.
- Mellert KH, Göttele A (2012) Comparison of new foliar nutrient thresholds derived from van den Burg's literature compilation with established central European references. *Eur J For Res* 131: 1461–1472.
- Mitchell HL, Chandler RF (1939) The nitrogen nutrition and growth of certain deciduous trees of Northeastern United States. *Black Rock Forest Bull* 11:1–94.
- Nikula S, Vapaavuori E, Manninen S (2010) Urbanization-related changes in European aspen (*Populus tremula* L.): leaf traits and litter decomposition. *Environ Pollut* 158:2132–2142.
- NOAA Global Historical Climate Network (GHCN) (2018) <https://www.ncdc.noaa.gov/cdo-web/> (31 August 2020, date last accessed).

- O'Rourke PA, Terjung WH (1981) Relative influence of city structure on canopy photosynthesis. *Int J Biometeorol* 25:1–19.
- O'Sullivan OS, Weerasinghe KWLK, Evans JR, Egerton JGG, Tjoelker MG, Atkin OK (2013) High-resolution temperature responses of leaf respiration in snow gum (*Eucalyptus pauciflora*) reveal high-temperature limits to respiratory function. *Plant Cell Environ* 36:1268–1284.
- O'Sullivan OS, Heskell MA, Reich PB et al. (2017) Thermal limits of leaf metabolism across biomes. *Glob Chang Biol* 36:209–223.
- Paoletti E, Grulke NE (2005) Does living in elevated CO₂ ameliorate tree response to ozone? A review on stomatal responses. *Environ Pollut* 137:483–493.
- Pardo L, Nadelhoffer K (2010) Using nitrogen stable isotope ratios to assess terrestrial ecosystems at regional and global scales. In: West JB, Bowen GJ, Dawson TE, Tu KP (eds) *Isoscapes: understanding movement, pattern, and process on earth through isotope mapping*. Springer, New York, pp 221–249.
- Pearson J, Wells DM, Sella KJ, Bennett A, Soares A, Woodall J, Ingrouille MJ (2000) Traffic exposure increases natural ¹⁵N and heavy metal concentrations in mosses. *New Phytol* 147:317–326.
- Pinheiro J, Bates D, DebRoy S, Sarkar S, The R Development Core Team (2010) NLME: linear and nonlinear mixed effects models. R Package Version 3, pp 1–97.
- Pontius J, Hallett R (2014) Comprehensive methods for earlier detection and monitoring of forest decline. *Forest Sci* 60:1156–1163.
- Poorter H, Niinemets U, Poorter L, Wright IJ, Villar R (2009) Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytol* 182:565–588.
- Pouyat RV, McDonnell MJ, Pickett STA (1995) Soil characteristics of oak stands along an urban-rural land-use gradient. *J Environ Qual* 24:516–526.
- Pouyat RV, Yesilonis ID, Szlavecz K, Csuzdi C, Hornung E, Korsós Z, Russell-Anelli J, Giorgio V (2008) Response of forest soil properties to urbanization gradients in three metropolitan areas. *Landsc Ecol* 23:1187–1203.
- Pregitzer CC, Charlop-Powers S, Bibbo S, Forgiione HM, Gunther B, Hallett RA, Bradford MA (2019) A city-scale assessment reveals that native forest types and overstory species dominate New York City forests. *Ecol Appl* 29: e01819.
- Pregitzer CC, Sonti NF, Hallett RA (2016) Variability in Urban soils influences the health and growth of native tree seedlings. *Ecol Restor* 34:106–116.
- R Development Core Team (2008) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.
- Rahman AF, Dragoni D, Didan K, Barreto-Munoz A, Hutabarat JA (2013) Detecting large scale conversion of mangroves to aquaculture with change point and mixed-pixel analyses of high-fidelity MODIS data. *Remote Sens Environ* 130:96–107.
- Ramirez-Valiente JA, Deacon NJ, Etterson J, Center A, Sparks JP, Sparks KL, Longwell T, Pilz G, Cavender-Bares J (2018) Natural selection and neutral evolutionary processes contribute to genetic divergence in leaf traits across a precipitation gradient in the tropical oak *Quercus oleoides*. *Mol Ecol* 27:2176–2192.
- Rao IM, Sharp RE, Boyer JS (1987) Leaf magnesium alters photosynthetic response to low water potentials in sunflower. *Plant Physiol* 84:1214–1219.
- Reisinger AJ, Groffman PM, Rosi-Marshall EJ (2016) Nitrogen cycling process rates across urban ecosystems. *FEMS Microbiology Ecology* 92:fiw198.
- Sack L, Cowan PD, Jaikumar N, Holbrook NM (2003) The 'hydrology' of leaves: co-ordination of structure and function in temperate woody species. *Plant Cell Environ* 26:1343–1356.
- Searle SY, Turnbull MH, Boelman NT, Schuster WSF, Yakir D, Griffin KL (2012) Urban environment of New York City promotes growth in northern red oak seedlings. *Tree Physiol* 32:389–400.
- Sjöman H, Nielsen AB (2010) Selecting trees for urban paved sites in Scandinavia—a review of information on stress tolerance and its relation to the requirements of tree planners. *Urban Forestry Urban Greening* 9:281–293.
- Sonti NF (2019) Ecophysiological and social functions of urban forest patches. Doctoral Dissertation. University of Maryland, MD, College Park, Maryland, USA.
- Sonti NF, Hallett RA, Griffin KL, Sullivan JH (2019) White oak and red maple tree ring analysis reveals enhanced productivity in urban forest patches. *For Ecol Manage* 453:117626.
- Strasser RJ, Tsimilli-Michael M, Srivastava A (2004) Analysis of the fluorescence transient. In: George C, Papageorgiou C, Govindjee (eds) *Chlorophyll fluorescence: a signature of photosynthesis. Advances in photosynthesis and respiration series*. Springer, Dordrecht, pp 321–362.
- Szlavecz K, Placella SA, Pouyat RV, Groffman PM, Csuzdi C, & Yesilonis I (2006). Invasive earthworm species and nitrogen cycling in remnant forest patches. *Appl Soil Ecol* 32:54–62.
- Taylor WA (2000) Change-point analysis: a powerful new tool for detecting changes. <http://www.variation.com/cpa/tech/changepoint.html> (31 August 2020, date last accessed).
- Turnbull MH, Whitehead D, Tissue DT, Schuster WS, Brown KJ, Griffin KL (2001) Responses of leaf respiration to temperature and leaf characteristics in three deciduous tree species vary with site water availability. *Tree Physiol* 21:571–578.
- Vallano DM, Sparks JP (2013) Foliar δ¹⁵N is affected by foliar nitrogen uptake, soil nitrogen, and mycorrhizae along a nitrogen deposition gradient. *Oecologia* 172:47–58.
- van Heerden PDR, Swanepoel JW, Krüger GHJ (2007) Modulation of photosynthesis by drought in two desert scrub species exhibiting C₃-mode CO₂ assimilation. *Environ Exp Bot* 61:124–136.
- Vieira J, Matos P, Mexia T et al. (2018) Green spaces are not all the same for the provision of air purification and climate regulation services: the case of urban parks. *Environ Res* 160:306–313.
- Volder A. 2010. Urban plant ecology. In: Aitkenhead-Peterson J, Volder A (eds) *Urban ecosystem ecology*. American Society of Agronomy: Crop Science Society of America: Soil Science Society of America, Madison, WI, USA.
- Wang W, Pataki DE (2012) Drivers of spatial variability in urban plant and soil isotopic composition in the Los Angeles basin. *Plant Soil* 350:323–338.
- Ward WW, Bowersox TW (1970) Upland oak response to fertilization with nitrogen, phosphorus, and calcium. *Forest Sci* 16:113–120.
- Warren CR, McGrath JF, Adams MA (2001) Water availability and carbon isotope discrimination in conifers. *Oecologia* 127:476–486.
- West JB, Bowen GJ, Dawson TE, Tu KP (2010) Isoscapes: understanding movement, pattern, and process on earth through isotope mapping. Springer, New York, p 487.
- Yi K, Maxwell JT, Wenzel MK, Roman DT, Sauer PE, Phillips RP, Novick KA (2019) Linking variation in intrinsic water-use efficiency to isohydricity: a comparison at multiple spatiotemporal scales. *New Phytol* 221:195–208.
- Zhao S, Liu, S, Zhou D (2016) Prevalent vegetation growth enhancement in urban environment. *Proc Natl Acad Sci USA* 113:6313–6318.