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Restoring the iconic *Ulmus americana* to urban landscapes: Early tree growth responds to aboveground conditions

Danielle Mikolajewski [a], Vince D'Amico III [b], Nancy F. Sonti [c], Cornelia C. Pinchot [d], Charles E. Flower [d], Lara A. Roman [e], Tara L.E. Trammell [a,1,*]

[a] *Department of Plant and Soil Sciences, University of Delaware, Newark, DE, USA*
[b] *USDA Forest Service, Northern Research Station, NRS-08, Newark, DE, USA*
[c] *USDA Forest Service, Northern Research Station, NRS-08, Baltimore, MD, USA*
[d] *USDA Forest Service, Northern Research Station, NRS-08, Delaware, OH, USA*
[e] *USDA Forest Service, Northern Research Station, NRS-08, Philadelphia, PA, USA*

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ABSTRACT

Native trees provide a range of benefits, from supporting native wildlife to climate regulation, and many urban natural resource managers prioritize native tree planting and restoration. *Ulmus americana* (American elm) was once widely planted in American cities but has been decimated by Dutch elm disease (DED; *Ophiostoma ulmi*). Our study evaluated *U. americana* establishment and growth across urban landscapes. We planted ramets from three DED-tolerant *U. americana* genotypes (RV16, RV474, and Sunfield) along an urbanization gradient in Newark, DE and Philadelphia, PA, and assessed physiological and morphological responses. We analyzed how *U. americana* clone growth, chlorophyll fluorescence, and foliar chemistry relate to impervious surface area, ozone (O_3) concentrations, and soil characteristics. The one-year post planting mortality rate was low (4%) demonstrating these elms can withstand urban environmental conditions when provided ample water supply and protection from deer. As expected, the elms differed in growth rate, chlorophyll fluorescence, and foliar chemistry between the cities. Elms planted in Philadelphia had greater photosynthetic capacity in July ($F_v/F_m = 0.76$) and September ($F_v/F_m = 0.75$), while Newark elms had greater photosynthetic capacity in August ($F_v/F_m = 0.78$). Depleted foliar $\delta^{13}C$ signatures in Philadelphia suggest elms are experiencing greater fossil-fuel derived atmospheric CO_2 than in Newark, possibly contributing to the greater growth rates observed in Philadelphia compared to Newark. Enriched foliar $\delta^{15}N$ and greater foliar %N in Philadelphia clones suggest they are experiencing greater N deposition from NO_x-derived sources compared to Newark clones. Clones growing in Philadelphia had greater foliar nutrient concentrations despite growing in soils with greater heavy metal concentrations. These foliar-soil chemistry patterns suggest that clones growing in Philadelphia respond positively to urban environmental conditions in a large city, whereas clones growing in Newark may be experiencing N limitation in the first year of growth after planting.

1. Introduction

Urban landscapes provide unique challenges to the organisms living within them. In forested biomes, urban forests and trees provide habitat for biota and a multitude of ecosystem services for residents, such as carbon (C) sequestration, stormwater regulation, and nutrient retention (Livesley et al., 2016). In addition to ecological and environmental benefits, urban forests and trees provide numerous social and economic benefits to the community (Fisher et al., 2015; Song et al., 2018). In response to new greening initiatives and societal support, many municipalities have a renewed interest in tree planting activities to restore urban forests (Eisenman et al., 2021). While planting trees within urban environments is an often-cited approach to promote sustainable cities (Griffin et al., 2018; Wallace and Clarkson, 2019), urban trees must establish and grow in potentially harsh environmental conditions. Urban tree selection focuses on species with traits that can adapt to altered urban environmental conditions, meet specific ecosystem services, and have minimal vulnerabilities to pests and diseases (Laćan and McBride,

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* Correspondence to: Department of Plant and Soil Sciences, University of Delaware, 531S. College Ave, 152 Townsend Hall, Newark 19716, DE, USA.
E-mail address: ttram@udel.edu (T.L.E. Trammell).

[1] ORCID: 0000-0002-5215-4947

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2008; Conway and Vecht, 2015; Sjöman et al., 2018).

Urban trees experience warmer air temperatures than those in surrounding suburban and rural areas (i.e., urban heat island effect; Oke, 1973; Bonan, 2008), which can have a positive effect on urban tree growth (McCarthy et al., 2010; Smith et al., 2019). Similarly, elevated nutrient deposition in urban areas (Rao et al., 2014; Decina et al., 2017, 2018) may be beneficial to urban plants by providing nutrients that are limiting growth. Some urban factors can benefit plant growth (i.e., increased nitrogen deposition, increased CO_2, lack of competition; Idso et al., 2001, 2002; Briber et al., 2015), while other factors can lead to decreased plant growth (i.e., soil compaction, heavy metals; Pouyat et al., 1995; Roy et al., 2020). Contamination of soils with heavy metals, especially legacy soils surrounding previous industrial sites, can make establishment of plants difficult (Cai et al., 2020; Hadjipanagiotou et al., 2020). Furthermore, air pollutants such as O_3, NO_x, and SO_x, can also lead to decreased plant growth (Warren et al., 2007; Kaur, 2016; Kulshrestha and Saxena, 2016). The variety of environmental conditions in urban environments can make tree establishment and growth challenging and difficult to predict.

Ulmus americana (American elm) was once a popular urban tree across the United States due to its fast growth, ability to tolerate drought, poor soil conditions (e.g., compacted soil, salt), and air pollution, as well as its sociopolitical symbolism, with widespread plantings along streets and in parks and yards (Heybroek, 1993; Roman et al., 2018; Bukowski, 2019; Hauer et al., 2020). By the early 20th century, ‘Elm Street’ had become an iconic American landscape (Campanella, 2011). Unfortunately, in the 1930s the accidental importation of Dutch elm disease (DED; *Ophiostoma ulmi*) fungal pathogens and their rapid spread devastated the American elm population (Griffin et al., 2018). Instead of continuing to plant the disease susceptible *U. americana* in monoculture, exotic tree species were introduced from Asian countries that were resistant to DED but still possessed the aesthetic qualities and environmental tolerances provided by *U. americana* that were desirable to urban residents and tree professionals (Dunn, 2000; Hoover et al., 2009; Martín et al., 2018). A new variant of the fungus developed in the 1960s, *Ophiostoma novo-ulmi*, in New England and the upper Midwest that devastated most of the remaining native *U. americana* (Roman et al., 2018; Bukowski, 2019; Hauer et al., 2020). Breeding programs also released *U. americana* varieties of mixed Asian, European, and/or American parentage that exhibited strong DED tolerance, but the search for tolerant American elms continued. Preserving and enhancing the diverse assemblage of native tree species in urban forests can improve ecosystem resilience and maintain critical biotic interactions, such as with Lepidopteran, insect herbivores, and birds (Tallamy and Shropshire, 2009; Narango et al., 2020). Thus, restoring *U. americana* to urban landscapes of North America is highly desirable, leading to breeding programs for native *U. americana* that are tolerant to DED (Pinchot et al., 2016; Flower et al., 2017). Restoring *U. americana* to the urban landscape would reestablish an iconic native tree that can withstand a range of urban conditions and has deep cultural symbolism in the US (Heybroek, 1993).

Our goal was to evaluate physiological and morphological responses of three DED tolerant *U. americana* genotypes to varying urban conditions (e.g., impervious surface cover, soil characteristics) in Philadelphia, PA and Newark, DE. We measured impervious surface cover, soil characteristics, and ozone (O_3) concentrations to represent various urbanization effects on tree growth and function. To understand plant response to these urban conditions, we measured tree growth (height and diameter), leaf mass per area (LMA; g cm^{-2}), foliar chemistry, and chlorophyll fluorescence. Our research addressed the following questions:

1) Do the DED tolerant *U. americana* genotypes differ in growth rates, chlorophyll fluorescence, and foliar chemistry?
2) Are there differences in *U. americana* growth, chlorophyll fluorescence, and foliar chemistry between the cities?
3) How does *U. americana* growth, chlorophyll fluorescence, and foliar chemistry vary with impervious surface, O_3 concentrations, and soil chemical properties?

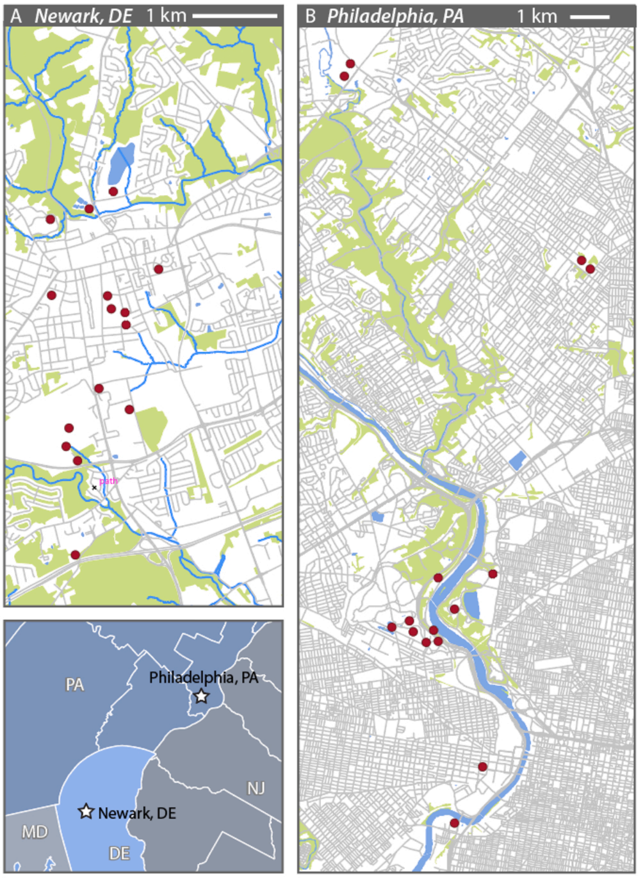

Fig. 1. Planting sites in Newark, DE and Philadelphia, PA.

To address these questions, we planted 90 trees across 30 sites with varying impervious surface area in a large (Philadelphia, PA) and small (Newark, DE) city. We hypothesized there would be no differences in tree growth, chlorophyll fluorescence, or foliar chemistry between the three genotypes since previous research found they performed similarly in DED field trials (Slavicek and Knight, 2012; Flower et al., 2017; Pinchot et al., 2016). Alternatively, we hypothesized that there would be differences in tree growth, chlorophyll fluorescence, and foliar chemistry between the cities, specifically, we expected trees planted in Newark to have greater radial growth compared to those planted in Philadelphia due to lower environmental stresses in a smaller city. We further hypothesized that tree diameter, height, and LMA would increase with increasing impervious surface and soil nutrients within each city due to warmer temperatures and greater nutrient availability enhancing tree growth. Alternatively, greater O_3 concentrations were expected to reduce tree photosynthetic capacity ultimately depressing plant growth (Kulshrestha and Saxena, 2016).

2. Methods

2.1. Study area

Ulmus americana trees were planted in 15 sites in Newark, DE and 15 sites in Philadelphia, PA (Fig. 1). The mid-Atlantic metropolitan area that encompasses Newark and Philadelphia span Coastal Plain and Piedmont geologic regions with mesophytic forests on the northern edge of a subtropical climate. The planting sites were chosen to capture a gradient of impervious surface cover, which is a common indicator for urbanization intensity and incorporates many potential urban environmental stressors or simulators for plant growth (e.g., Pickett et al., 2011; Sonti et al., 2019; Trammell et al., 2020). Using high-resolution land cover data created for the Delaware River Basin (UV SAL University of Vermont Spatial Analysis Laboratory, 2016), impervious surface area was estimated at 50-m, 100-m, and 500-m circular buffers surrounding each tree planting. The chosen sites in Newark ranged in impervious surface area from 5.8 % to 86.3 % and Philadelphia sites ranged in impervious surface area from 5.8 % to 83.7 %. One individual ramet of each of three *U. americana* genotypes were planted at each site (n = 3 trees * 15 sites = 45 trees per city).

2.2. *Soil sampling*

To quantify belowground conditions that influence plant growth, we measured soil bulk density, pH, organic matter, nutrients, and heavy metals. Prior to planting the elms, two soil cores (5.8 cm diameter) up to 15 cm depth were collected with a AMS soil impact corer within 30 cm of each tree planting location across the 15 sites in Newark and Philadelphia (n = 2 cores * 3 trees * 15 sites * 2 cities = 180 total soil cores). Organic material (i.e., grass or leaf litter) was removed from the soil surface prior to soil collection and soil depth was recorded for each sample (range = 8–15 cm). One soil core at each tree planting location was oven dried at 105 °C for at least 48 h and then analyzed for pH (1:1 soil [15 g] to DI water [15 ml] solution mixed for 30 min), organic matter (loss-on-ignition at 500 °C for 6 h), nutrients (P, K, Ca, S, Mg, Na, Mn, Cu, Fe, B, and Zn), heavy metals (Pb, Cd, Co, Al, As, Cr, and Ni), and cation exchange capacity (CEC) at the University of Delaware Soil Testing Laboratory. We used the Mehlich 3 soil extraction method to analyze soil nutrient and metal concentrations on an ICP-OES (Thermo Iris Intrepid II XSP Duo View ICP). The second soil core collected at each planting location was oven dried at 105 °C for at least 48 h to obtain bulk density (g cm^{-3}).

2.3. *Tree planting and irrigation*

Three genotypes developed for DED tolerance by the USDA Forest Service (FS) Northern Research Station (NRS) Forest Sciences Laboratory in Delaware, OH were selected for tree planting to test the suitability of each DED tolerant elm for use in urban settings. The Sunfield genotype was sourced from a large (DBH ~ 122 cm) survivor elm tree in Sunfield, MI. The RV16 and RV474 genotypes are unique clonal lines developed from seed produced in controlled crosses between known DED tolerant elms sourced from mid continental and northern latitudes. The USDA FS NRS supplied 90 *U. americana* for planting in Newark, DE and Philadelphia, PA research sites. Elms consisted of 1 year-old ramets, root collar diameter ranged from 3.45 mm to 13.04 mm, grown in ~ 7 L pots. In November 2019, one Sunfield, one RV474, and one RV16 ramet was planted at each site with 7-m between the trees to allow sufficient space for tree growth and site maintenance (e.g., mowing). At each planting location, we dug holes ~30 cm in diameter and depth, then gently separated roots and planted the elm with the soil potting mix so that the root crown was slightly above the soil. We poured ~3.5 L of water around the tree to provide immediate access to water. After soil was replaced into the hole around the tree, a pre-soaked (30-min) TreeDiaper® (TD; TD24R, Zynnovation LLC, Ashland, VA, USA; hydrophilic crystals absorb and slowly release water) was placed around the base of each tree to maintain adequate soil moisture and avoid the predominant cause of mortality in newly established trees: lack of soil moisture (Meineke and Frank, 2018). TDs were replaced with rehydrated TDs across all locations once during peak summer dry/drought conditions. We periodically assessed soil moisture using a TD probe to confirm the presence of an adequate water supply during the growing season. TDs were mulched with pine bark nuggets to help diminish evaporation from the TD and surrounding soil. To mitigate deer browse, a cause of significant sapling mortality in our sites and beyond (Griffin et al., 2018; PPR City of Philadelphia Parks and Recreation, 2013), we installed 1.5-m tall wire fence secured to steel fence posts (Everbilt, Model#01154EB) around each tree for protection. Trees were supported to the fence using Arbortie or Velcro ties to maintain tree position (i.e., perpendicular to the ground) and reduce injury due to weak trunk structure or wind. Our study sites were located on a mix of public parks, college campuses, and private arboreta, with varying landscape maintenance regimes. Because such variation could impact tree growth, health, and survival (Hilbert et al., 2019), all planting and irrigation was managed by our research team to promote consistency across study sites, allowing us to focus on differences due to site context and among the three genotypes.

2.4. *Tree size and foliar analyses*

Immediately after planting in November 2019, each elm was measured for height, diameter at breast height (DBH; 137 cm from ground, hereafter D137), and caliper diameter (30 cm from the ground, hereafter D30). Tree height to the hundredth of a meter was measured using an ADIRpro aluminum grade rod (#710–10) and diameter to the tenth of a millimeter was measured using a Mitutoyo caliper (Model#CD-6"ASX). The first year of growth was evaluated by measuring height, D137, and D30 one year later in November 2020. Our precise tree measurements enabled reporting growth during establishment phase of this *U. americana* urban planting (Roman et al., 2015).

During the peak growing season (i.e., July), leaf mass per area (LMA; g cm^{-2}) was measured by randomly collecting 3 sun-lit leaves per tree. The leaf petiole was wrapped in a moist paper towel, and leaves were stored at 4 °C and transported to the lab. Leaves were scanned and area measured using ImageJ Fiji software. Leaves were oven dried at 55 °C for at least 48 h and weighed to calculate LMA.

Leaves were ground to a fine powder using a Retsch Ball Mixer Mill (MM200, Haan, Germany) for foliar chemistry analysis. For foliar nutrients (Al, B, Ca, Cu, Fe, K, Mg, Mn, Na, P, S, and Zn), tissue samples were digested using a CEM MARs5 microwave digestion system (CEM, Matthews, NC) using concentrated nitric acid and 30% hydrogen peroxide at the University of Delaware Soil Testing Laboratory. Digests were then analyzed by inductively coupled plasma optical emission spectroscopy using a ICAP 7600 Duo view Inductively Couple Plasma – Optical Emission Spectrometer (ICP-OES; Thermo Elemental, Madison WI). For foliar heavy metal analysis (As, Cd, Co, Cr, Ni, and Pb), the University of Delaware Soil Testing Laboratory used the same methods as for foliar nutrients. For foliar stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$, respectively), samples were analyzed using an elemental combustion system (4010 CHNSO analyzer, Costech Valencia, CA, USA) interfaced with a Thermo Delta V Ratio Mass Spectrometer (Thermo, Bremen, Germany) at the University of Maryland Central Appalachians Stable Isotope Facility. The natural abundance stable isotope values were expressed relative to the international standards for $\delta^{13}C$ (Vienna Pee-Dee Belemnite) and $\delta^{15}N$ (atmospheric N_2) in the conventional δ-notation.

Chlorophyll fluorescence provides an indication of plant response to urbanization before visible signs of stress occur. Chlorophyll was measured with a Handy Pocket PEA (Hansatech Instruments Ltd., UK) on the same leaves in July, August, and September 2020. Briefly, chlorophyll fluorescence measurements were conducted on three randomly chosen sun-lit leaves devoid of injury. Leaves were dark adapted for thirty minutes prior to measurements (as previously described by Sonti et al., 2019). We analyzed Performance Index (PI), a measure of the efficiency of photosystem I and II which can be thought of how efficiently a leaf can use light for photosynthesis (Hermans et al., 2003), and F_v/F_m, a measure of the efficiency of photosystem II (Hong and Xu, 1999).

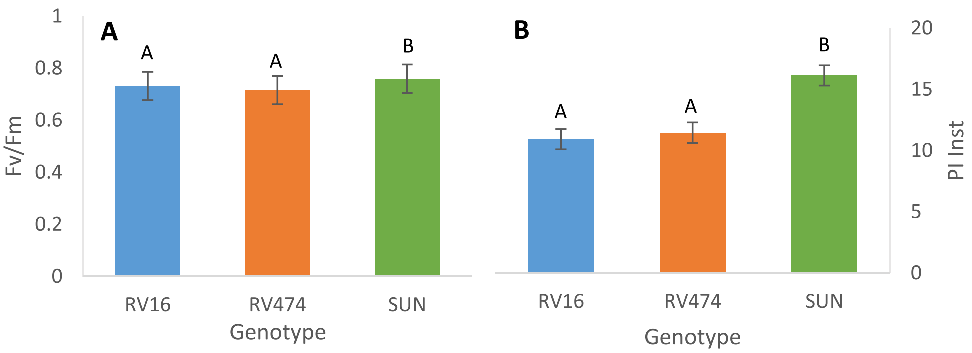

Fig. 2. Differences in photosynthetic capacity between elm tree genotypes in July 2020. The F_v/F_m (efficiency of photosystem II) among genotypes (A) and Photosynthetic Index (PI) among genotypes (B) are shown as mean ± 1 SE. Significant difference between elm genotypes is denoted with letters at $p < 0.05$.

2.5. O_3 measurements

O_3 measurements were used as a proxy for potential aboveground stressors related to urban air pollution. Eight Ogawa O_3 samplers (Ogawa Co., Pompano Beach, FL, USA) were deployed according to the Ogawa sampler protocol (Ogawa Company, 2001) in both Newark and Philadelphia with one control sampler deployed in the laboratory at the University of Delaware. Sites were chosen based on their impervious surface buffers and proximity to other sites, choosing sites that comprised the greatest extent of urbanization as well as maximal spatial coverage of each city. O_3 samplers were secured to the fencing surrounding the middle tree at 1.5 m from the ground and placed facing the road. After 14 days of field exposure, the O_3 collection pads were placed in clean Ogawa vials and shipped to the Ogawa Co., where they were analyzed for nitrate with ion chromatography (Dionex Model 2000i equipped with a conductivity detector). The Ogawa collection pads are coated in nitrite, which when exposed to O_3 creates nitrate and atmospheric oxygen, enabling the use of nitrate accumulation as a proxy for O_3.

2.6. Statistical analyses

All statistical analyses were performed in R (Version 3.6.2; R Core Team, 2020). All tests for significance are reported at the $\alpha = 0.05$ critical value, and in a few cases the $\alpha = 0.10$ critical values are reported as marginally significant to identify potential trends in the data.

To determine general differences in clone growth, we conducted ANOVA across the clones and the cities using the ANOVA function in R when data met assumptions of normality and homoscedasticity followed by post hoc Tukey significant difference test. The non-parametric Kruskal-Wallis rank sum test followed by post hoc Nemenyi tests (Pohlert, 2014) were used when assumptions for ANOVA were not met. The growth measurements were height at planting, height after one year, D30 at planting, D30 after one year, D137 at planting, D137 after one year, and absolute growth after one year (each growth measurement after one year subtracted by each growth measurement at planting).

To determine patterns in variation of the soil characteristics in all sampling locations within our 30 sites, we conducted principal components analysis (PCA) using the prcomp function in R. The soil characteristics used in this analysis were pH, buffer pH, SOM, bulk density, nutrient concentrations (P, K, Ca, Mg, Mn, Zn, Cu, Fe, B, S, Na, Al), heavy metal concentrations (As, Cd, Co, Cr, Ni, Pb), cation exchange capacity (CEC), base saturation, and P saturation ratio. We report soil patterns for the first four principal components based upon the proportion of variance explained by each component using the fviz_eig function in the factoextra (Kassambara and Mundt, 2020) and ggfortify (Horikoshi and Tang, 2016) packages. To determine potential predictors of variation across soil characteristics, we used the fviz_add function to overlay impervious at 50-m, 100-m, and 500-m and O_3 at each soil sampling location.

Patterns in variation of the foliar chemistry between all 90 elm ramets were assessed with PCA using the prcomp function in R. The foliar chemistry characteristics used in this analysis were foliar nutrients (Al, B, Ca, Cu, Fe, K, Mg, Mn, Na, P, S, and Zn) and foliar heavy metals (As, Cd, Co, Cr, Ni, and Pb). We report foliar patterns for the first four principal components based upon the proportion of variance explained by each component using the fviz_eig function in the factoextra (Kassambara and Mundt, 2020) and ggfortify (Horikoshi and Tang, 2016) packages. To determine potential predictors of variation across foliar chemistry, we used the fviz_add function to overlay impervious at 50-m, 100-m, and 500-m, O_3, and soil characteristics (i.e., the first four principal components from the soil PCA) at each ramet location.

To determine patterns between our urban predictor variables and plant response factors, linear regression was conducted using the lm function in R. The urban predictor variables were impervious surface at 50-m, 100-m, and 500-m, O_3, and the first four soil characteristic principal components. The plant response factors were tree height, D30, D137, chlorophyll fluorescence, foliar isotopes, and the first four foliar chemistry principal components. We conducted Pearson correlation analysis using the rcorr function in the Hmisc package (Harrell et al., 2019) to determine correlations between our predictor variables and response factors. We also produced correlation matrixes using the corrplot function in the Corrplot package (Wei and Simko, 2017) to determine correlations between the soil and leaf nutrients and heavy metals.

3. Results

3.1. Plant and soil differences among *U. americana* clones

Across the entire study, only four trees died during the first year after planting. This low annual mortality rate (4%) relative to typical establishment mortality of planted urban trees (Hilbert et al., 2019) provides ample data to evaluate *U. americana* genotype health and growth responses across urbanization gradients and cities.

There were significant differences in initial plant size among the clones. RV474 clones were significantly shorter (1.54 ± 0.050 m) than RV16 (1.70 ± 0.034) and Sunfield (1.68 ± 0.029) clones ($p = 0.013$). Similarly, RV474 had smaller D30 (6.17 ± 0.274 mm) and D137 (6.12 ± 0.212 mm) than RV16 clones (D30 = 8.40 ± 0.398 mm, D137 = 7.40 ± 0.397 mm) and Sunfield clones (D30 = 8.42 ± 0.439 mm, D137 = 7.91 ± 0.482 mm; $p < 0.05$). After one year of growth, RV16 clones were significantly taller (2.29 ± 0.1 m) than RV474 (1.83 ± 0.123 m) and Sunfield (1.95 ± 0.106 m) clones, and RV16 clones had significantly greater D30 (16.01 ± 1.033 mm) and D137 (12.04 ± 0.814 mm) than RV474 clones (D30 = 12.87 ± 0.837 mm, D137 = 8.19 ± 0.79 mm) and Sunfield (D30 = 12.18 ± 0.809 mm, D137 = 7.39 ± 0.628 mm) clones ($p < 0.05$). Similarly, there were differences

Table 1
Foliar nutrient concentrations (mg kg^{-1}) in RV16, RV474, and Sunfield genotypes across all planting sites. Significant differences among the genotypes are shown in bold.

Foliar Elements	Genotype RV16	 RV474	 Sunfield
Al	42.98 (± 2.989)	41.56 (± 3.637)	44.45 (± 2.893)
B	**47.15 (± 3.260)** **	**48.85 (± 2.456)** **	**60.22 (± 3.694)** **
Ca	11878 (± 410.7)	12526 (± 392.3)	12830 (± 583.9)
Cr	5.49 (± 0.418)	4.83 (± 0.686)	7.68 (± 1.71)
Cu	**5.86 (± 0.409)** **	**5.53 (± 0.226)** **	**9.01 (± 0.777)** ****
Fe	**96.6 (± 4.95)** **	**94.3 (± 5.550)** **	**113.3 (± 7.76)** **
K	13842 (± 638.7)	12605 (± 552.9)	14994 (± 754.9)
Mg	**3092 (± 88.5)** **	**2615 (± 73.2)** **	**3014 (± 139.7)** ***
Mn	**430.1 (± 35.74)** **	**592.8 (± 41.41)** ***	**522.0 (± 42.74)** **
Na	**49.02 (± 7.617)** **	**48.70 (± 9.643)** **	**132.45 (± 51.010)** ***
Ni	3.44 (± 0.233)	3.30 (± 0.451)	4.65 (± 0.944)
P	2706 (± 127.6)	2721 (± 146.5)	3160 (± 232.0)
S	**1227 (± 50.5)** **	**1206 (± 42.6)** **	**1348 (± 44.5)** **
Zn	**25.02 (± 2.612)** **	**35.32 (± 3.771)** **	**41.44 (± 4.363)** ****

** indicates a p value of less than 0.05
*** indicates a p value of less than 0.01
**** indicates a p value of less than 0.001

between the clones in leaf mass per area (LMA). RV16 had the largest LMA (0.012 ± 0.0014 g cm^{-2}), compared to RV474 (0.010 ± 0.0008 g cm^{-2}) and Sunfield (0.009 ± 0.0007 g cm^{-2}; $p < 0.05$). Overall, Sunfield had the smallest change in D30 (4.96 mm, $p < 0.01$) and D137 (1.3 mm, $p < 0.001$) compared to RV16 (D30 = 8.35 mm, D137 = 4.66 mm; $p < 0.01$) and RV474 (D30 = 7.93 mm, D137 = 3.72 mm; $p < 0.01$).

Chlorophyll fluorescence measurements demonstrated varied responses across *U. americana* clones throughout the growing season. In July, Sunfield clones had significantly greater foliar F_v/F_m and PI than RV16 or RV474 clones ($p = 0.02$; Fig. 2A, B). There were no significant differences in *U. americana* clone chlorophyll fluorescence metrics (F_v/F_m or PI) in August or September 2020 ($p > 0.10$). Similarly, there were no significant differences in clone foliar $\delta^{13}C$, %C, $\delta^{15}N$, or %N ($p > 0.10$). However, there were differences in other foliar chemistry parameters among the *U. americana* clones. The Sunfield clones contained significantly more B, Cu, Fe, Mg, Na, S, and Zn than RV16 and RV474 clones (Table 1). Alternatively, RV474 clones contained significantly more Mn than RV16 and Sunfield clones (Table 1). There were no significant differences in soil characteristics ($p > 0.10$) beneath the *U. americana* clones.

3.2. Plant and soil differences between Newark and Philadelphia

At the city scale, there were significant differences in *U. americana* growth and chlorophyll fluorescence. The trees at the city level were not significantly different in their height, D30, or D137 at the time of planting, however, one year after planting, trees growing in Philadelphia had significantly greater D30 (15.09 ± 0.821 mm) than trees growing in Newark (12.38 ± 0.673 mm; $p < 0.05$). There were no significant differences in height or D137 between the cities ($p > 0.10$). Overall, Philadelphia had significantly higher absolute growth (height growth = 0.49 m, D30 growth = 7.42 mm, D137 growth = 2.57 mm; $p < 0.05$) compared to Newark (height growth = 0.29 m, D30 growth = 4.71 mm, D137 growth = 1.66 mm; $p < 0.05$). There were no significant differences in LMA between trees planted in Newark and Philadelphia ($p > 0.10$). However, chlorophyll fluorescence measurements demonstrated varied responses across cities throughout the growing season. In July and September, trees planted in Philadelphia had significantly greater foliar F_v/F_m and PI than trees planted in Newark ($p < 0.001$; Fig. 3A, B, E, F). However, in August, trees planted in Newark had significantly greater foliar F_v/F_m and PI than trees planted in Philadelphia ($p < 0.001$; Fig. 3C, D).

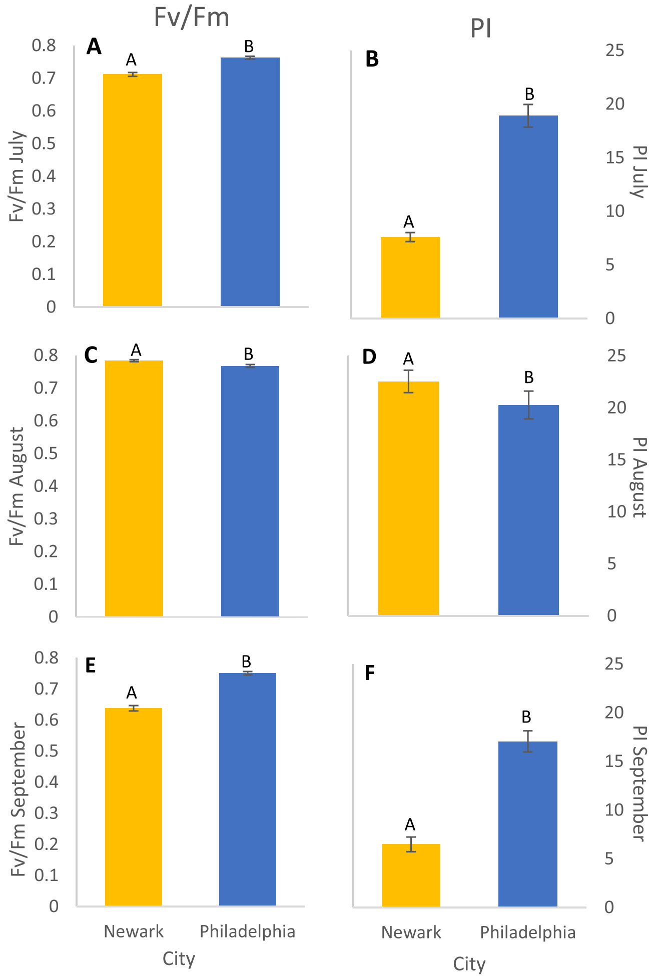

Fig. 3. Differences in photosynthetic capacity between cities in July, August, and September 2020. The F_v/F_m (efficiency of photosystem II) between cities in July (A), August (C), and September (E) and Performance Index (PI) between cities in July (B), August (D), and September (F) are shown as mean ± 1 SE. Significant differences between cities are denoted with letters at $p < 0.05$.

There were significant differences in foliar chemistry in *U. americana* trees growing in Newark compared to those growing in Philadelphia. Specifically, elms in Newark exhibited significantly enriched $\delta^{13}C$ and greater %C than those planted in Philadelphia (Fig. 4A, B), while elms growing in Philadelphia had significantly enriched $\delta^{15}N$ and greater %N than those growing in Newark (Fig. 4C, D). Elms planted in Philadelphia had significantly greater foliar concentrations in B, Ca, Cu, Fe, Mg, Mn, and S than those planted in Newark (Table 2), while elms from Newark had significantly greater foliar concentrations in P and Na than those in Philadelphia (Table 2).

The belowground conditions for *U. americana* trees differed between those growing in Newark versus Philadelphia soils. Newark soils had greater pH, bulk density, soil nutrients (Ca, K, Mg, Mn, B, and Na), and Co and Cr concentrations than Philadelphia soils (Table 3). Alternatively, Philadelphia soils had greater total metal concentrations (Zn, Cu, S, Al, Cd, and Pb) and SOM than Newark soils (Table 3).

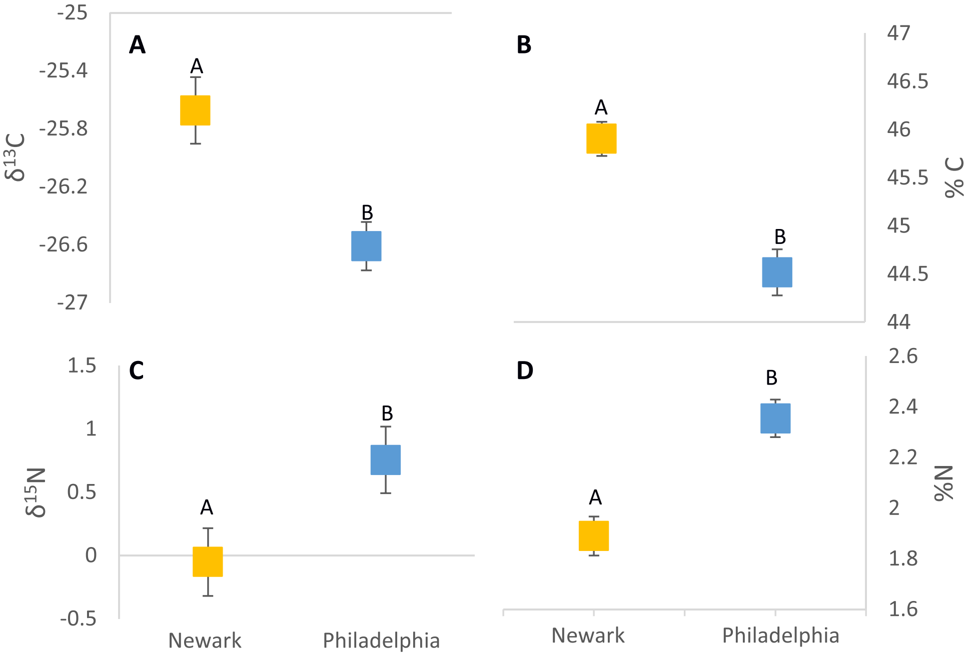

Fig. 4. Differences in foliar isotope concentrations between elms growing in Newark and Philadelphia. $\delta^{13}C$ (A), %C (B), $\delta^{15}N$ (C), and %N (D) are shown as mean ± 1 SE. Significant differences between cities are denoted with letters at $p < 0.05$.

Table 2
Foliar nutrient concentrations (mg kg^{-1}) in RV16, RV474, and Sunfield genotypes across Newark and Philadelphia. Significant differences between the cities are shown in bold.

Foliar Elements	City Newark	Philadelphia
Al	41.82 (± 2.80)	44.21 (± 2.41)
B	**43.83 (± 2.20)******	**60.76 (± 2.59)******
Ca	**11239 (± 285.83)******	**13704 (± 381.95)******
Cr	5.84 (± 0.10)	6.05 (± 1.08)
Cu	**5.76 (± 0.29)******	**7.80 (± 0.60)******
Fe	**94.90 (± 4.50)****	**107.76 (± 5.71)****
K	14277 (± 546.41)	13195 (± 542.74)
Mg	**2746 (± 500.23)*****	**3081 (± 96.73)*****
Mn	**440.7 (± 27.82)*****	**598.4 (± 37.02)*****
Na	**103.61 (± 30.72)******	**41.90 (± 5.93)******
Ni	**3.24 (± 0.027)*****	**4.36 (± 0.67)*****
P	3095 (± 132.57)	2576 (± 143.03)
S	**1149 (± 36.25)******	**39.02 (± 32.32)******
Zn	28.90 (±) 2.08	39.02 (±) 3.96

** indicates a p value of less than 0.05
*** indicates a p value of less than 0.01
**** indicates a p value of less than 0.001

3.3. *Above- and below-ground controls on U. americana clone physiology, morphology, and chemistry*

We found significant relationships between chlorophyll fluorescence and surrounding impervious surface in clones planted in Newark. In September 2020, F_v/F_m significantly decreased with increasing impervious surface area within 500-m of RV16 ($p < 0.05$) and Sunfield ($p < 0.05$) clones (Fig. 5A, E). Similarly, PI significantly decreased with increasing impervious surface within 500-m of RV16 ($p < 0.05$) and RV474 ($p < 0.05$) clones in Newark (Fig. 5B, D). Furthermore, Sunfield clones had significantly decreasing F_v/F_m within increasing impervious surface in August 2020 ($R^2 = 0.533$, $p < 0.05$). However, in July 2020, there were no relationships between chlorophyll fluorescence and impervious surface in Newark ($p > 0.10$). Furthermore, elm clones had no relationship between LMA and impervious surface in Newark ($p > 0.10$).

Table 3
Soil characteristics of the planting sites within the cities. Nutrients and heavy metals are reported in mg kg^{-1}. Significant differences between the cities are shown in bold.

	City	
Soil Elements	Newark	Philadelphia
pH	**6.22 (± 0.09)******	**5.35 (± 0.97)****
Buffer pH	7.75 (± 0.02)	7.48 (± 0.03)
Organic Matter (SOM)	**3.26 (± 0.15)******	**5.14 (± 0.17)******
P	34.18 (± 3.76)	27.48 (± 2.03)
Bulk density	**1.13 (± 0.026)*****	**1.08 (± 0.025)*****
K	**134.81 (± 6.96)*****	**106.58 (± 6.20)****
Ca	**1422.45 (± 105.65)******	**869.35 (± 59.37)****
Mg	**225.32 (± 12.47)*****	**170.99 (± 10.10)****
Mn	**62.44 (± 2.82)****	**58.36 (± 3.72)****
Zn	**6.32 (± 1.07)****	**10.72 (± 1.11)******
Cu	**2.61 (± 0.24)****	**4.78 (± 0.25)******
Fe	167.04 (± 4.84)	174.32 (± 7.29)
B	**0.75 (± 0.04)******	**0.59 (± 0.04)****
S	**41.39 (± 7.04)****	**25.80 (± 1.15)****
Na	**60.79 (± 16.24)*****	**17.96 (± 1.97)****
Al	**630.19 (± 14.26)****	**785.17 (± 18.86)******
As	0.31 (± 0.12)	0.33 (± 0.01)
Cd	**0.05 (± 0.004)****	**0.12 (± 0.01)******
Co	**0.89 (± 0.04)******	**0.71 (± 0.05)****
Cr	**0.24 (± 0.02)******	**0.18 (± 0.01)****
Ni	0.86 (± 0.57)	0.82 (± 0.06)
Pb	**6.95 (± 0.54)****	**32.67 (± 2.24)******
CEC	11.55 (± 0.54)	10.20 (± 0.27)
Base Saturation Ratio	78.15 (± 1.91)	56.65 (± 2.61)
P Saturation Ratio	14.56 (± 1.12)	11.58 (± 0.58)

** indicates a p value of less than 0.05
*** indicates a p value of less than 0.01
**** indicates a p value of less than 0.001

In Philadelphia, only Sunfield clones demonstrated a relationship with surrounding impervious surface in Philadelphia. In September 2020, elm clones had significantly increasing F_v/F_m with increasing impervious surface ($R^2 = 0.3182$, $p < 0.05$). Similarly, Sunfield clones had significantly increasing LMA with increasing impervious surface in

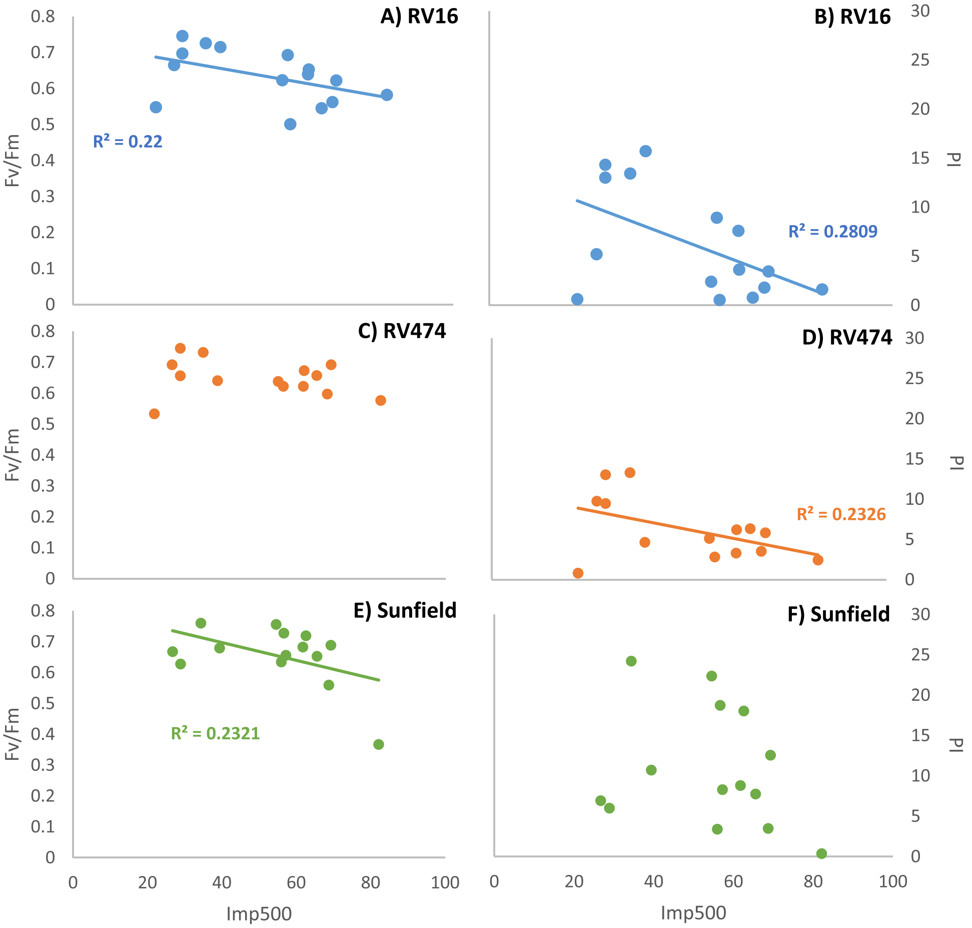

Fig. 5. Linear regression using impervious surface within 500-m to predict photosynthetic capacity, specifically efficiency of photosystem II (F_v/F_m) for RV16 (A), RV474 (C), and Sunfield (E) and photosynthetic index (PI) for RV16 (B), RV474 (D), and Sunfield (F), in Newark in September 2020. Slopes and R^2 are labeled for significant relationships.

Philadelphia ($R^2 = 0.645$, $p < 0.001$). The RV16 and RV474 clones growing in Philadelphia had no significant relationships between chlorophyll fluorescence or LMA and impervious surface ($p > 0.10$). There were no significant relationships between photosynthetic capacity and impervious surface in July or August between the Philadelphia planted clones. Finally, there were no significant relationships between elm growth rates (i.e., changes in height or diameter) and impervious surface gradients or O_3 in either Newark or Philadelphia.

O_3 concentrations represent potential aboveground stressors on *U. americana* foliar responses. While RV16 clones growing in Newark had no relationship between chlorophyll fluorescence and O_3 concentrations (Fig. 6A, B), RV474 clones had significantly increasing F_v/F_m ($p < 0.05$; Fig. 6C) and PI ($p < 0.02$; Fig. 6D) with increasing O_3 concentrations in August and July 2020 ($p = 0.06$). Alternatively, Sunfield clones planted in Newark had significantly decreasing F_v/F_m ($p < 0.04$; Fig. 6E) and PI ($p < 0.01$; Fig. 6F) with increasing O_3 concentrations in August 2020. The only elm genotype to respond to O_3 in Philadelphia was RV16, which had increasing PI with increasing O_3 concentrations in September 2020 ($R^2 = 0.2249$, $p < 0.04$). Finally, there were no significant relationships between elm growth rates and O_3 concentrations in either Newark or Philadelphia.

Belowground conditions important in influencing *U. americana* genotypes differed across Philadelphia and Newark. PCA of soil characteristics across Philadelphia planting locations explained 73.4% of the total variation in soil. Soil characteristics most important in driving separation along Dimension (Dim) 1 were soil pH, Ca, Mg, B, and base saturation (Fig. 7A). Soils with greater pH, Ca, Mg, B, and base saturation were surrounded by more impervious surface within 50-m ($R = 0.69$, $p < 0.001$) and 100-m ($R = 0.51$, $p < 0.001$) of the planting site (Fig. 7C). Soil characteristics that load the strongest along Dim 2 were Mn, Co, OM, and Pb (Fig. 7A). Soil Fe and Cr concentrations had the strongest loading on Dim 3 (Fig. 7B), and soils with greater Fe and Cr concentrations were surrounded by more impervious surface within 500-m of the planting site ($R = -0.45$, $p = 0.002$; Fig. 7D). Finally, soil P concentrations and saturation had the strongest loading on Dim 4 (Fig. 7B).

Principal component analysis of soil characteristics across Newark planting locations explained 71.5% of the total variation in the soil. Soil characteristics most important in driving separation along Dim 1 were soil pH, Ca, Cu, Cd, B, CEC, and base saturation (Fig. 8A) and were surrounded by more impervious surface within 500-m of the planting location ($R= 0.30$, $p = 0.05$; Fig. 8C). Soil characteristics with the strongest loading along Dim 2 were Al and Fe (Fig. 8A) and along Dim 3 were P and P saturation (Fig. 8B). Finally, bulk density (BD) had the strongest loading on Dim 4 (Fig. 8B) and soil BD was related to impervious surface within 50-m ($R= 0.37$, $p = 0.01$) and 100-m ($R = 0.39$, $p = 0.001$) of the planting location (Fig. 8D).

Principal component analysis of leaf nutrients and heavy metals across Philadelphia planting locations explained 71.1% of the total variation in the leaf tissue. Leaf nutrients and heavy metals most important in driving separation along Dimension 1 were Fe, Cr, and Ni (Fig. 9A). Leaves with greater Fe, Cr, Ni, and Co concentrations were surrounded by less impervious surface within 100-m ($R = -0.33$, $p < 0.05$) and 500-m ($R = -0.43$, $p < 0.01$) of the planting location (Fig. 9C). Along Dim 2, foliar chemistry with the strongest loading were Al, S, and K concentrations (Fig. 9A). Along Dim 3, B and P foliar

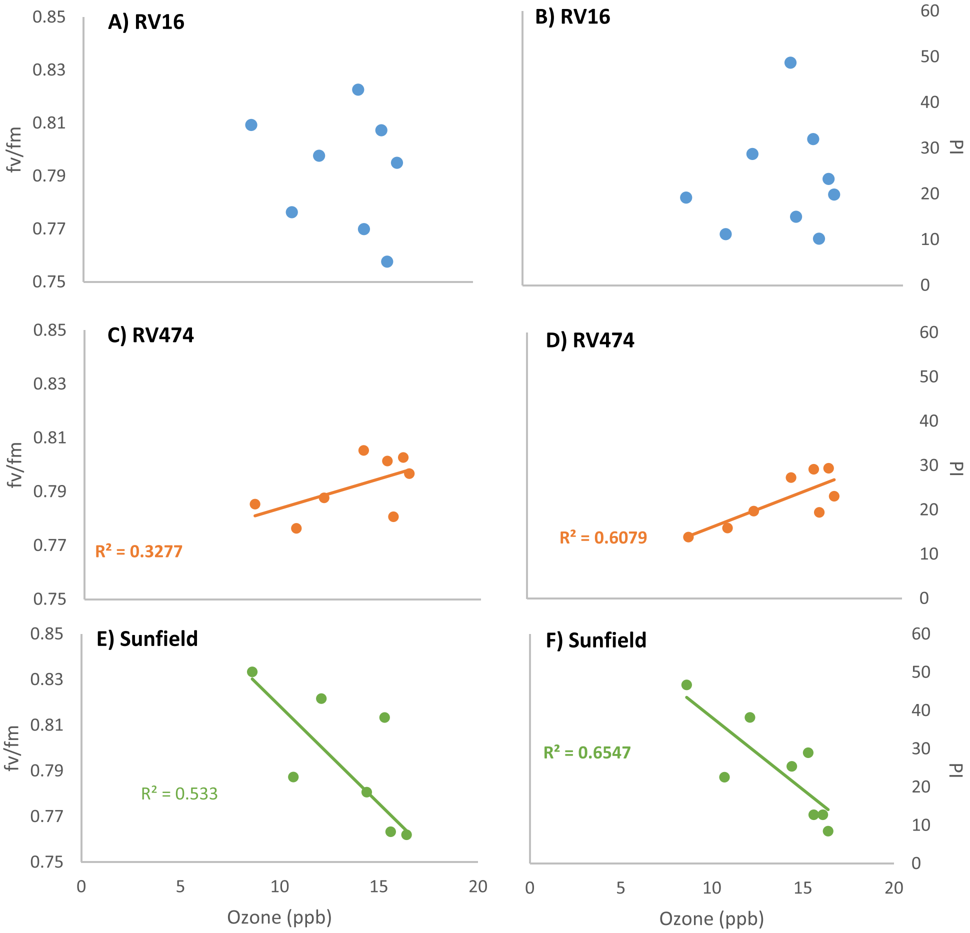

Fig. 6. Linear regression using ozone (O_3) concentration to predict photosynthetic capacity specifically efficiency of photosystem II (F_v/F_m) for RV16 (A), RV474 (C), and Sunfield (E) and photosynthetic index (PI) for RV16 (B), RV474 (D), and Sunfield (F), in Newark in August 2020. Slopes and R^2 are labeled for significant relationships.

concentrations had the strongest loading (Fig. 9B) and were related to soil PC1 ($R = 0.53$, $p < 0.001$) and soil PC2 ($R = 0.38$, $p = 0.02$; Fig. 9D). Finally, foliar Na and Cu concentrations had the strongest loading on Dim 4 (Fig. 9B). There were no significant relationships between the soil PCA dimensions and foliar photosynthetic capacity (i.e., F_v/F_m or PI) of elms in Philadelphia.

Principal component analysis of leaf nutrients and heavy metals across Newark planting locations explained 71.3% of the total variation in the leaf tissue. Leaf nutrients and heavy metals most important in driving separation along Dimension 1 were Fe, Cr, and Ni (Fig. 10A). Along Dim 2, foliar chemistry with the strongest loadings were Cu, K, and S concentrations (Fig. 10A). Along Dim 3, foliar chemistry with the strongest loadings were Ca and Mn concentrations (Fig. 10B). Along Dim 4, foliar chemistry with the strongest loadings were Zn, Na, and Mg concentrations (Fig. 10B), and leaves with more Zn and Na and less Mg were surrounded by more impervious surface within 100-m ($R = 0.30$, $p < 0.05$) of the planting locations (Fig. 10D). In Newark elms, variation in foliar chemistry was not related to dimension scores in the soil PCA (Fig. 10C, D). Similarly, there were no significant relationships between the soil PCA dimensions and foliar photosynthetic capacity (i.e., F_v/F_m or PI) of elms in Newark. Finally, foliar nutrients were not correlated with soil nutrients across Philadelphia and Newark (Fig. 11).

4. Discussion

The three *U. americana* genotypes planted in a small (Newark, DE) and a large (Philadelphia, PA) city for this study demonstrated different morphological, physiological, and chemical characteristics. Contrary to our expectations, the elm clones had differing chlorophyll fluorescence responses to urbanization gradients across the growing season resulting in significantly different growth across the first year. While we observed differences in elm genotype growth, foliar chemistry, chlorophyll fluorescence, and soil characteristics between Newark and Philadelphia as expected, the elm genotype response (e.g., growth) was not enhanced in Newark as predicted. Instead, elms planted in Philadelphia demonstrated greater growth rates and photosynthetic capacity than those planted in Newark. Specific differences in tree growth, foliar chlorophyll fluorescence, and foliar chemistry elucidate the potential mechanisms causing differential responses between the genotypes and the cities.

4.1. Differential growth and photosynthetic capacity between the genotypes

Contrary to our expectations, after one year growing in urban environments, the *U. americana* clones had significantly different growth rates. While the smallest clone at the time of planting remained the smallest one year later (RV474), the clone with the greatest absolute growth (RV16) was not the largest clone at planting (Sunfield). Interestingly, Sunfield had the greatest photosynthetic capacity early in the growing season (i.e., July; Fig. 2), yet there were no differences between the clones in photosynthetic capacity later in the growing season (i.e., August and September). The early enhanced photosynthetic capacity in Sunfield clones and greater foliar nutrient content (Table 1), yet slower growth rate than RV16 and RV474, suggests potential genetic differences influencing clone response to urbanization conditions across the growing season. Previous research on *U. americana* clones planted in

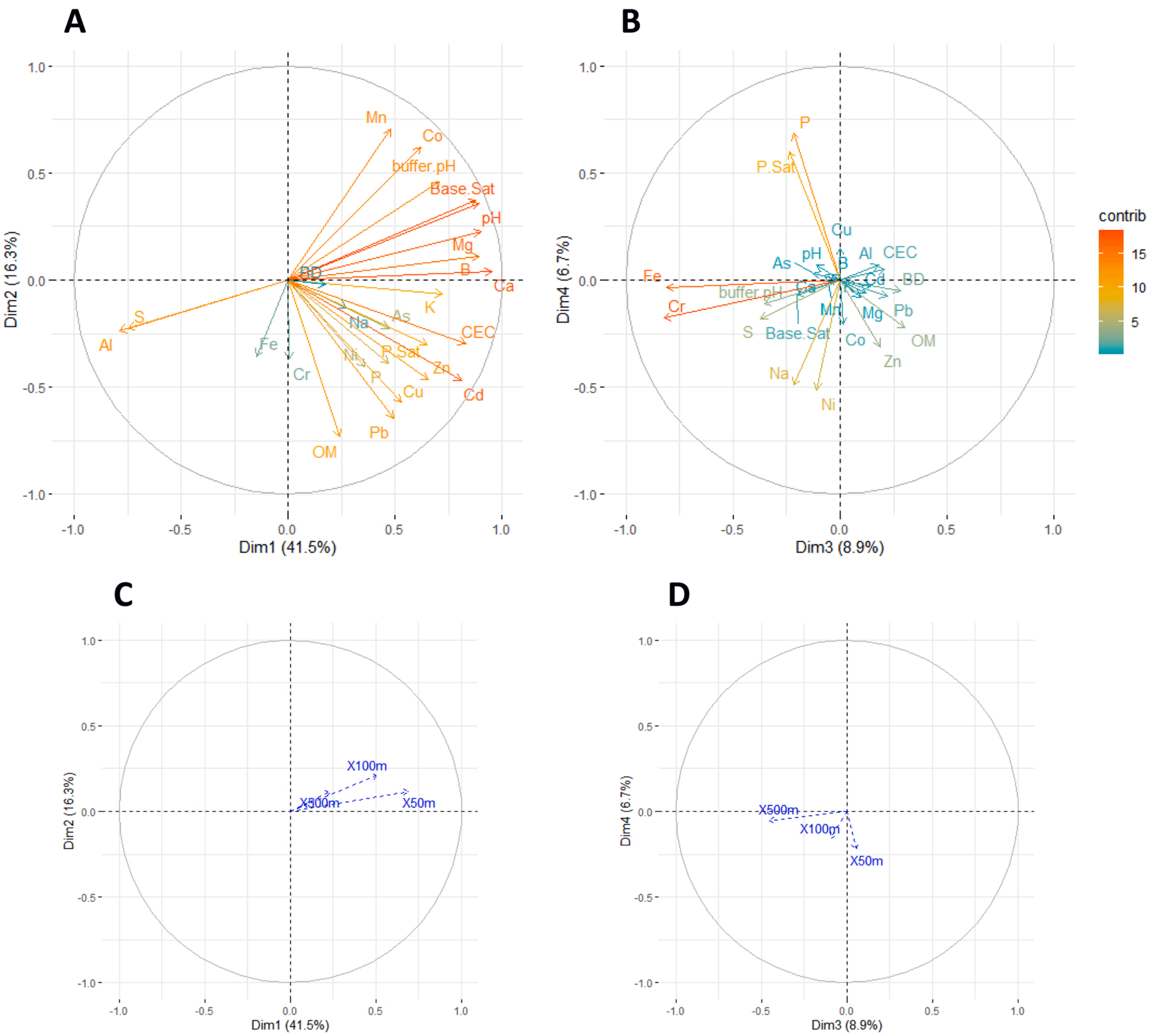

Fig. 7. Principal component analysis of soil nutrients and heavy metals in Philadelphia. Dimension 1 explained 41.5% and dimension 2 explained 16.3% of the variation in soils in Philadelphia (A). Dimension 3 explained 8.9% and 4 explained 6.7% of variation in soils across Philadelphia (B). Urban predictors (impervious surface area at 50 m, 100 m, and 500 m, and O_3) for Philadelphia laid over soil Dim 1 and 2 (C) and soil Dim 3 and 4 (D).

field and greenhouse settings found no differences in canopy decline during a DED tolerance study (Slavicek and Knight, 2012; Flower et al., 2017; Pinchot et al., 2016). Underlying genetic differences between tree selections from different origins have long been observed in common garden experiments (Fahlvik et al., 2019; Heilig et al., 2021) and may underlie some of the differences observed in this study. This study, the first to report growth rates in these elms in urban conditions, showed that elm genotypes have differential responses to urban growing conditions, which further supports that underlying genetic differences may control elm genotype response to urban conditions.

4.2. *Differential genotype growth, photosynthetic capacity, and foliar chemistry between the cities*

As expected, *U. americana* genotypes planted in Philadelphia had different growth rates, photosynthetic capacity, and foliar chemistry than genotypes planted in Newark, however, the direction of the response to the city environments was opposite from our expectations. Philadelphia trees had greater photosynthetic capacity in July and September, whereas Newark trees had greater photosynthetic capacity in August. In the peak summer heat (i.e., July), greater foliar nutrients and depleted foliar $\delta^{13}C$ suggests Philadelphia trees may have additional resources to enhance photosynthesis in comparison to trees growing in Newark. There is a long-recognized CO_2 dome effect in urban areas (Idso et al., 2001, 2002), thus, it is reasonable to expect that a larger city, like Philadelphia, will have a larger CO_2 dome effect than a smaller city, like Newark. Philadelphia elm leaves had significantly depleted foliar $\delta^{13}C$ which suggests elevated CO_2 from fossil fuel sources (e.g., Lichtfouse et al., 2003). Alternatively, the enriched foliar $\delta^{13}C$ in Newark trees could be an indication of water stress (Farquhar et al., 1989; Boutton, 1996). However, since the trees had similar water supply, it is more likely the Philadelphia trees experienced greater fossil fuel-derived CO_2 sources contributing to the observed greater growth rates.

In the peak growing season, greater resource availability for photosynthesis is a plausible explanation for greater photosynthetic capacity in Philadelphia. However, greater photosynthetic capacity in

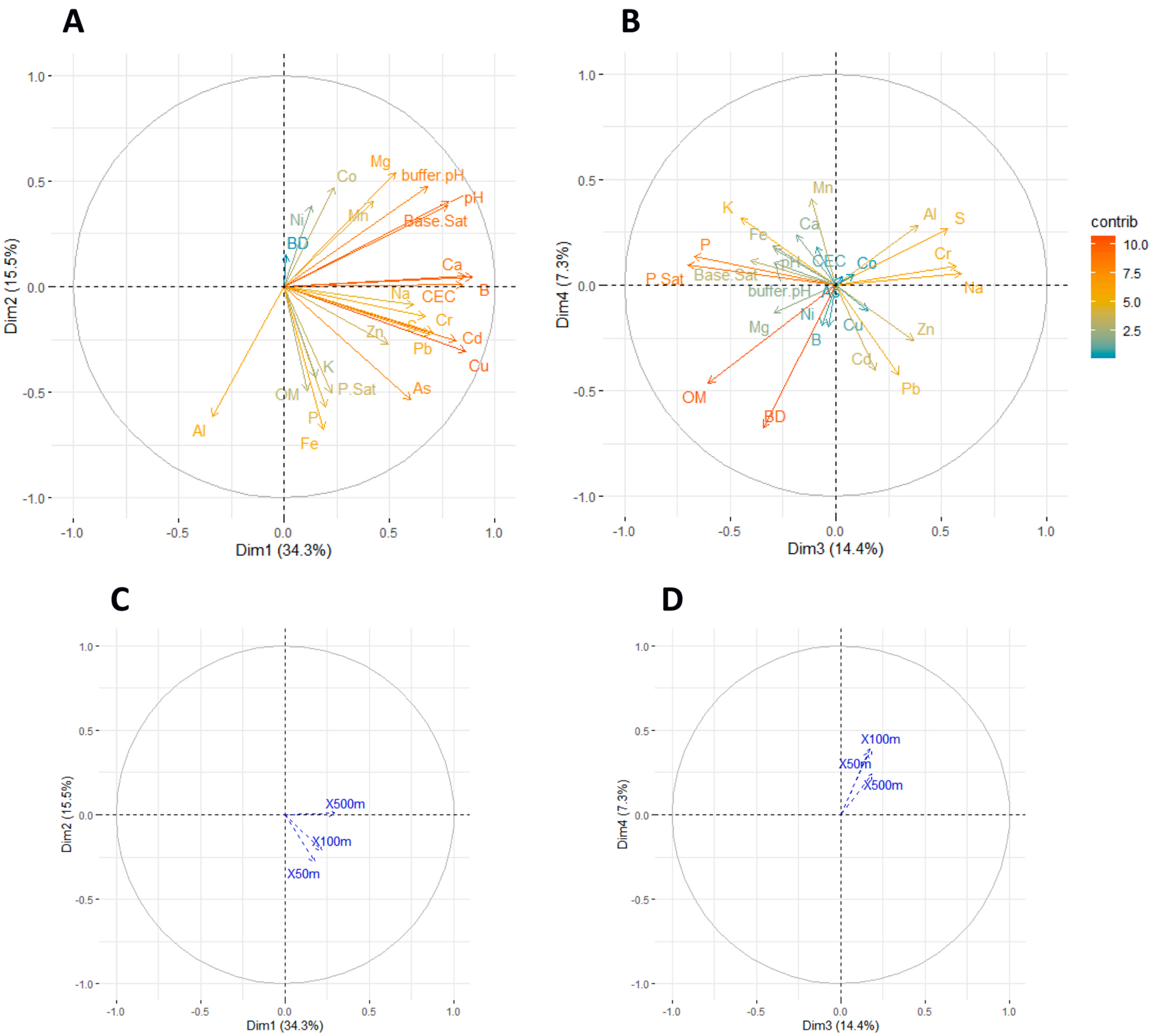

Fig. 8. Principal component analysis of soil nutrients and heavy metals in Newark. Dimension 1 explained 34.3% and dimension 2 explained 15.5% of the variation in the soils in Newark (A). Dimension 3 explained 14.4% and dimension 4 explained 7.3% of the variation in the soils in Newark (B). Urban predictors (impervious surface area at 50 m, 100 m, and 500 m, and O_3) for Newark laid over soil Dim 1 and 2 (C) and soil Dim 3 and 4 (D).

Philadelphia during the early fall could either be due to enhanced resources or due to differences in fall phenology between the cities. Warmer temperatures associated with the urban heat island effect are linked with changes in plant phenology, such as canopy duration (Neil and Wu, 2006; Jochner and Menzel, 2015). Philadelphia was on average 1 °C warmer (21 °C) compared to Newark (20 °C) throughout September 2020 (NOAA, 2020). Thus, it is possible the elm trees in Newark are showing earlier signs of fall leaf senescence than elm trees in Philadelphia.

The differences between Philadelphia and Newark photosynthetic capacity may also be a result of differing nitrogen dynamics across the cities. Elms planted in Philadelphia had greater foliar %N and enriched δ^{15}N (Fig. 4C, D), a similar pattern to differences observed in red maple trees in Philadelphia and Newark forests (McDermot et al., 2020). Greater fossil fuel combustion associated with urbanization activities, specifically mobile sources, leads to greater N deposition that is highly variable across cities (Lovett et al., 2000; Decina et al., 2020). Thus, greater foliar %N in Philadelphia elms is expected because it is a larger city than Newark. Enriched foliar δ^{15}N observed in the Philadelphia elms is an indication of elevated N deposition from fossil fuel combustion sources and/or enhanced soil N cycling rates (e.g., Trammell et al., 2016). In atmospheric N sources, enriched δ^{15}N correlates with fossil fuel combustion from mobile and stationary N sources, whereas depleted δ^{15}N correlates with agricultural and urban excretory wastes (Xiao and Liu, 2002; Elliott et al., 2007; Kendall et al., 2007). Alternatively, enhanced soil N cycling rates can result in enriched soil N available for plant uptake, which can also explain the enriched foliar δ^{15}N in Philadelphia relative to Newark (Pardo et al., 2006, 2007; Högberg et al., 2010). Future research on the N resorption in these elms could provide an indication of differing N availability in Newark compared to Philadelphia (Yuan and Chen, 2015).

The observed differences in soil chemistry between Philadelphia and Newark were not reflected in foliar chemistry differences between the cities. Though Philadelphia elms had higher foliar nutrients than those in Newark, the soils had greater heavy metals and SOM than Newark (Tables 1–3). In contrast, Newark soils had greater nutrients than

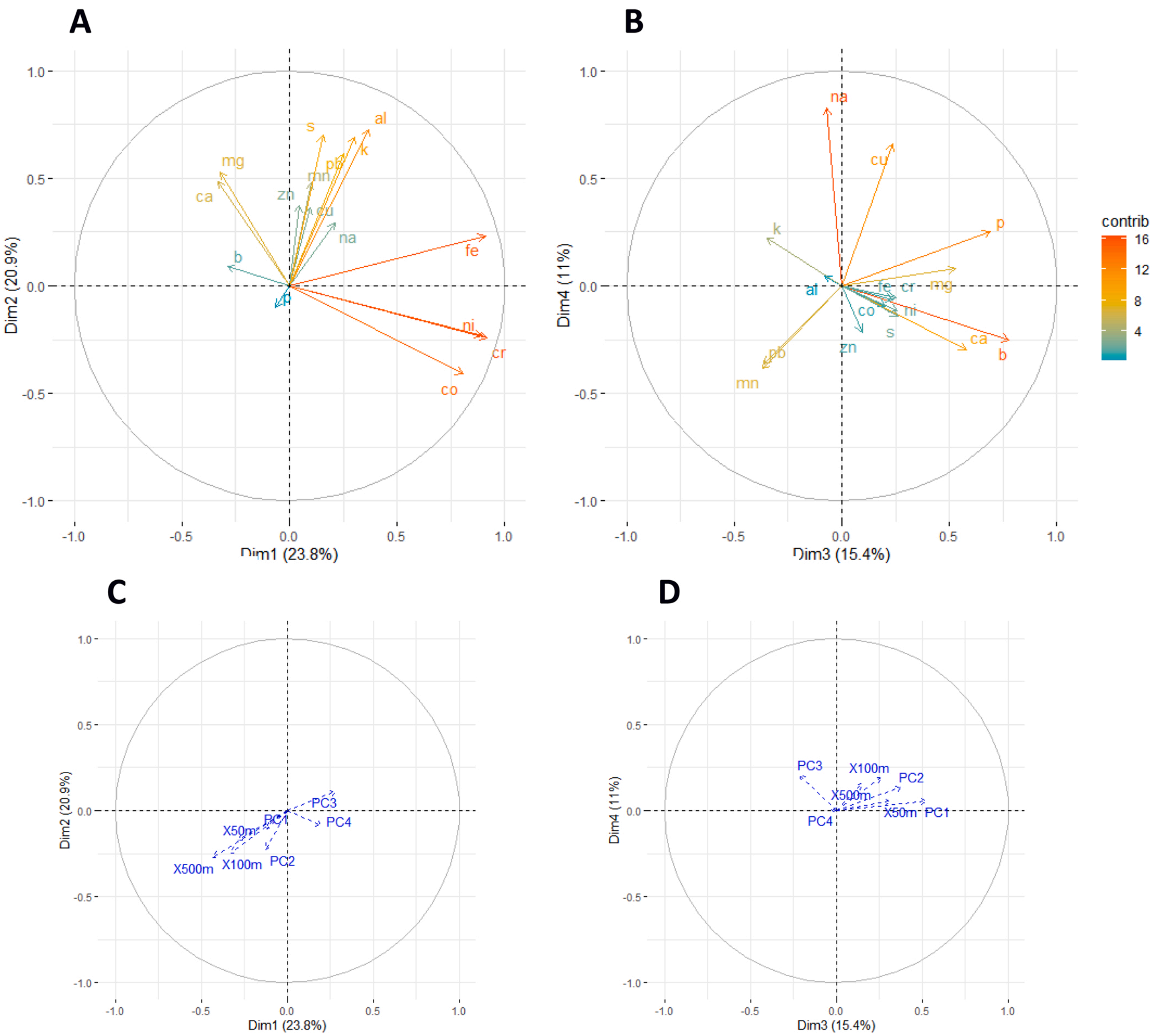

Fig. 9. Principal component analysis of leaf nutrients and heavy metals in Philadelphia. Dimension 1 explained 23.8% and dimension 2 explained 20.9% of the variation in the leaf tissue in Philadelphia (A). Dimension 3 explained 15.4% and dimension 4 explained 11% of the variation in the leaf tissue in Philadelphia (B). Urban predictors (impervious surface area at 50 m, 100 m, and 500 m, and O_3) and dimension scores for Philadelphia soil PCA for Philadelphia laid over leaf Dim 1 and 2 (C) and leaf Dim 3 and 4 (D).

Philadelphia (Tables 1–3). SOM increases nutrient content in the soil and increases nutrient availability for plant uptake (Muniraj et al., 2018). Thus, greater soil SOM in Philadelphia may contribute to the observed greater foliar nutrient concentrations compared to Newark. The disconnection between foliar and soil chemistry in both cities may be due to the elm roots not accessing the soil at the planting locations within their first year of growth, instead utilizing the residual potting soil. Alternatively, previous research on established trees similarly demonstrated laboratory soil analyses slightly improved predictions on tree performance (Scharenbroch et al., 2017), and soil texture, pH, and OM were most important in correlating with tree performance (Scharenbroch and Cantania, 2012). Incorporating a suite of soil nutrients and heavy metals in our study did not strengthen the relationship between tree growth in early establishment with soil chemistry. Since elm photosynthetic capacity and growth rates were not related to the soil chemical properties, this further supports that the local urban soil is not influencing urban trees during this early establishment phase. Additional years of research will help further explain these relationships, and assess whether similar patterns between soil chemistry (specifically heavy metals) and urban tree growth remain as the trees age.

5. Conclusion

Early establishment and survival of new DED tolerant elms planted across Newark and Philadelphia suggests these genotypes, not yet sold commercially, show potential for strong performance in urban conditions. Long-term study of the growth and survival of these elm trees will further elucidate the success of these genotypes in restoring the iconic American elm to our urban landscapes. During establishment, we observed differences in the *U. americana* genotypes growing in urban conditions, specifically, Sunfield had the greatest photosynthetic capacity early in the season, yet the lowest annual growth, suggesting carbon gain was utilized for maintenance versus growth for this genotype. While our results demonstrated observable differences in growing

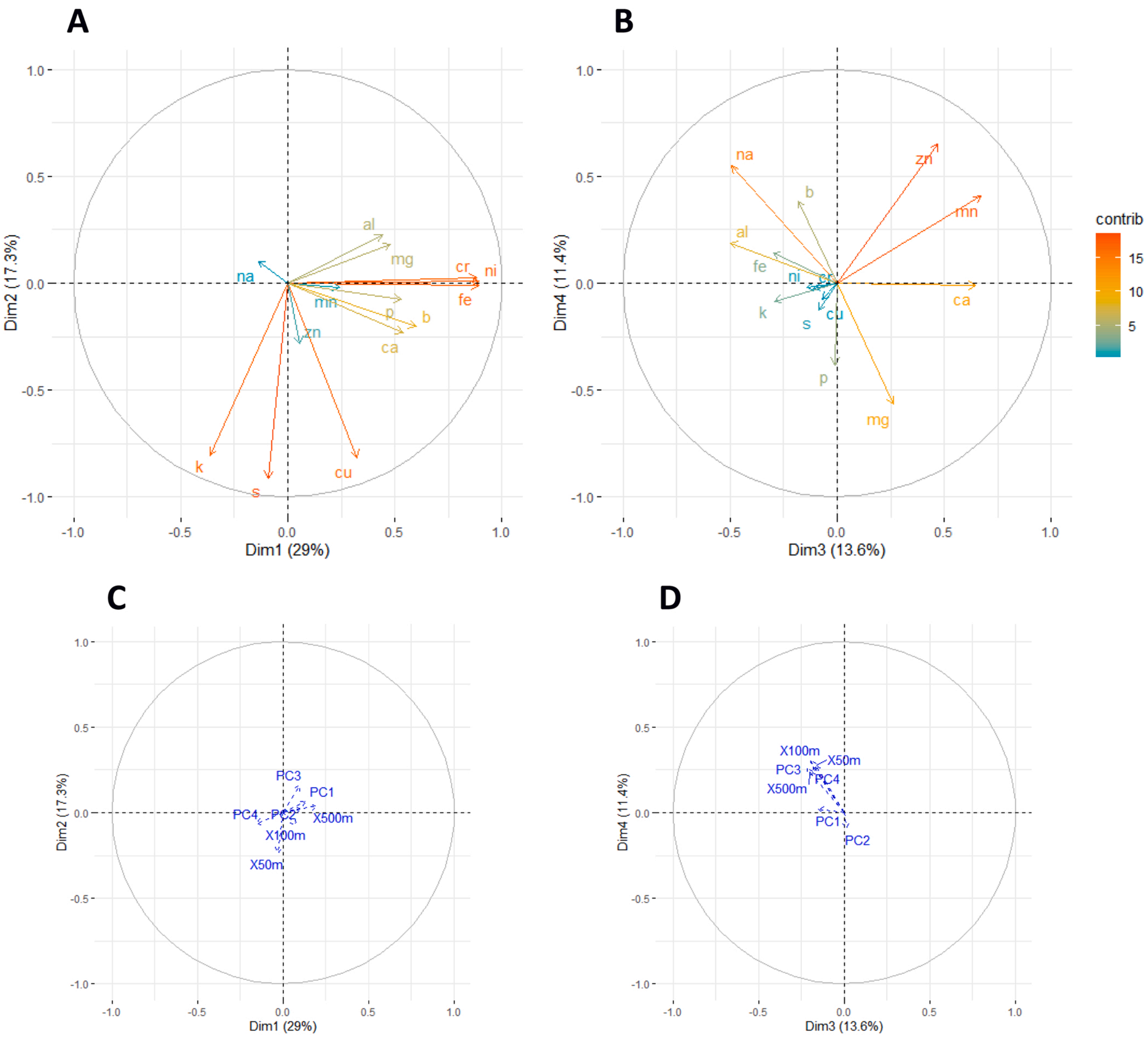

Fig. 10. Principal component analysis of leaf nutrient and heavy metals in Newark. Dimension 1 explained 29% and dimension 2 explained 17.3% of the variation in the leaf tissue in Newark (A). Dimension 3 explained 13.6% and dimension 4 explained 11.4% of the variation in the leaf tissue in Newark (B). Urban predictors (impervious surface area at 50 m, 100 m, and 500 m, and O_3) for Newark laid over leaf Dim 1 and 2 (C) and leaf Dim 3 and 4 (D).

conditions between Newark and Philadelphia, elms survived and grew in both cities. We observed greater growth rates and chlorophyll fluorescence in elms planted in Philadelphia during the first year of growth suggesting the trees were positively responding to beneficial aboveground conditions, such as warmer temperatures, greater CO_2 concentrations, and higher N deposition. However, as the trees grow and mature, it is possible the observed greater heavy metal concentrations in Philadelphia soils could suppress elm growth in future years relative to elms growing in Newark. Our study provides insight into early establishment of trees growing across urban conditions provided ample water is supplied and trees are protected from deer browse. Determining urban conditions these elm genotypes can endure provides information needed to further American elm restoration (Knight et al., 2017) across our cities and towns.

CRediT authorship contribution statement

Danielle Mikolajewski: Methodology, Data curation, Formal analysis, Investigation, Validation, Visualization, Writing – original draft. **Vince D'Amico III:** Conceptualization, Data curation, Funding acquisition, Project administration, Supervision, Visualization. **Nancy Sonti:** Conceptualization, Methodology, Resources, Writing – review & editing. **Cornelia C. Pinchot:** Conceptualization, Funding acquisition, Writing – review & editing. **Charles E. Flower:** Conceptualization, Writing – review & editing. **Lara A. Roman:** Conceptualization, Writing – review & editing. **Tara L.E. Trammell:** Conceptualization, Methodology, Data curation, Formal analysis, Funding acquisition, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft.

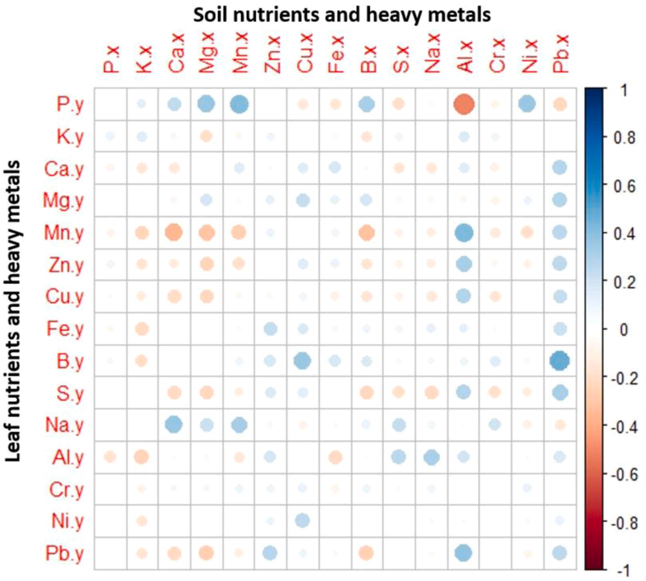

Fig. 11. Soil nutrient and leaf nutrient correlation matrix.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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