

RESEARCH ARTICLE

Native tree seedling growth and physiology responds to variable soil conditions of urban natural areas

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Soils in urban natural areas can be highly variable due to legacies of land use change that include excavation of existing soils and dumping of construction debris or other anthropogenic materials. As cities undertake large-scale tree planting efforts to sustain and increase forest cover, understanding how urban soil quality influences native tree seedling survival and performance is important. In a greenhouse setting we examined growth and physiology of native silver maple (*Acer saccharinum*), black birch (*Betula lenta*), red oak (*Quercus rubra*), and Canadian serviceberry (*Amelanchier canadensis*) seedlings planted in soils collected from locations across New York, NY, U.S.A. The soils were collected from areas currently undergoing forest restoration, representing a range of soil nutrient quality and anthropogenic disturbance. We measured seedling survival, height growth, leaf chlorosis, and chlorophyll fluorescence for two growing seasons, after which seedlings were harvested to assess biomass allocation and foliar chemistry. Selected variables were standardized and combined to create a seedling stress index. Overall, seedlings performed best in the least disturbed urban soils and had the poorest performance in the more highly disturbed, nutrient-poor urban soil types and a greenhouse mix. Species \times soil type interactions on physiological responses indicate that tree species may not respond to urban soil conditions consistently. Consequently, matching native tree species to soil type could help optimize establishment and growth of urban forest restoration projects. Seedling stress scores from the first growing season were correlated with second year height growth for three of four species, illustrating their utility for managers.

Key words: *Acer saccharinum*, *Amelanchier canadensis*, *Betula lenta*, foliar chemistry, *Quercus rubra*, urban forest restoration

Implications for Practice

- This study highlights the need for gaining a better understanding of species \times soil type interactions specific to urban areas prior to planting.
- Native tree species selection for urban forest restoration planting can benefit from greenhouse trials especially when there are highly disturbed nutrient-poor urban soils involved. For example, red oak seedlings planted in urban fill had high mortality and may not be the best species for restoring those sites.
- Rapid field- or greenhouse-based assessments of seedling health in addition to more traditional survival and growth monitoring can provide useful information for identifying stressful site conditions and predicting future tree performance.

Introduction

Urban forested natural areas can contain a significant proportion of the trees within a city (Pregitzer et al. 2019a). Consequently, forested greenspace in urban areas often provides a disproportionate amount of biophysical ecosystem services to cities (Mexia et al. 2018; Vieira et al. 2018). In addition, we are beginning to learn more about the social ecosystem services forests in cities provide (Botzat et al. 2016). However, forests in cities are frequently lacking a native understory critical to healthy forest regeneration and continued ecosystem service provision (Airola &

Bucholz 1984; Massad et al. 2019; Piana et al. 2021). In addition, these critical urban green spaces are often overlooked by policy-makers and given a lower priority in the context of broader urban forest management (Pregitzer et al. 2019c).

Following recognition of their inherent social and ecological value, management concepts focused on forested natural areas in cities are of increasing interest to researchers (Konijnendijk et al. 2006; Duinker et al. 2017; Piana et al. 2021) and practitioners (Pregitzer et al. 2018, 2019c). Lack of natural regeneration and recruitment of native tree species in urban forested natural areas suggests that long-term sustainability of these forests is at risk (Massad et al. 2019; Pregitzer et al. 2019b; Piana et al. 2021). However, evidence suggests that urban soils can support natural regeneration of native tree species (Pregitzer et al. 2016; Sonti

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et al. 2021). In situations where existing forests are not regenerating and for urban afforestation projects, tree planting is commonly employed in urban forest restoration or management practices (Felson et al. 2013; Pregitzer et al. 2018). Currently, species selection for planting sites is determined by local expert knowledge, strategies to maximize species diversity, or planting stock availability. Rural silvicultural guides and recommendations provide information on which species are likely to grow best on certain soil types (Ashton & Kelty 2018), yet no such guidelines exist for matching tree species with urban natural area soil types.

Traditional silvicultural guidelines may not apply to urban forest restoration efforts due to a suite of anthropogenic factors which can affect soil structure and fertility (Smith et al. 2020; Zuskwert et al. 2021). Human land use legacies have varied impacts on urban soils, resulting in a suite of complex effects and interactions for plant communities (Johnson et al. 2015; Pregitzer et al. 2016). In a review focused on the ecophysiology of tree roots in the urban environment, Day et al. (2010) indicated that little is known about tree growth in contaminated soils and called for more research on this topic. Scharenbroch and Catania (2012) and Scharenbroch et al. (2017) established an urban soil quality index and a rapid urban site index for assessing the quality of street tree planting sites, but similar tools linking urban natural area site conditions and tree performance are lacking. Foliar chemistry of trees in urban natural areas can also provide insight about nutrient cycling and availability, as well as potential toxic effects of urban pollutants (Falxa-Raymond et al. 2014; McDermot et al. 2020; Sonti et al. 2021). However, these studies are limited and focus on larger trees and long-term productivity rather than the early establishment of seedlings.

Given the demonstrated variability in urban soil quality, it is important to develop recommendations that match species to specific soil types and physicochemical properties based on their ability to survive and thrive in the early establishment phase. To answer questions about tree species performance across a wide variety of urban soil types in New York City natural areas, we designed a greenhouse pot study to isolate the impact of these urban soils on tree seedling survival, growth, and physiology. We hypothesized that urban soil type would influence height growth, biomass, and survivorship of native tree species currently used in NYC natural area forest reforestation projects, and that seedlings of different species would exhibit different relative growth and physiology characteristics in and across soil types. We expected that the observed relationships between urban soil type and tree seedling performance from the first growing season would continue (Pregitzer et al. 2016), and that the greater levels of stress seen in more disturbed urban soil types would lead to increasing differences in growth and photosynthetic capacity after a second growing season. Furthermore, we expected to see significant relationships between foliar chemistry and seedling performance that may offer insight into the mechanisms behind these differences in seedling performance.

Methods

Experimental Design

To test the impact of urban natural area soils on tree seedling growth and leaf-level physiological function we collected soils from 12 sites within NYC parks (Fig. 1) with either existing or

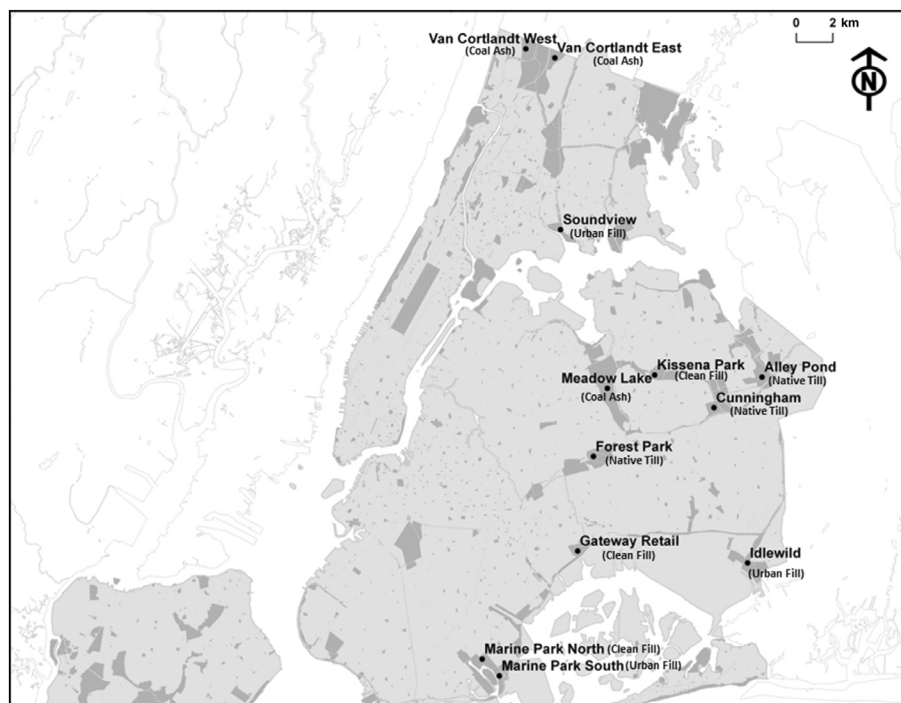


Figure 1. Location of soil collection sites in new York City, NY, U.S.A. NYC is represented in light gray; NYC parks department properties are represented in dark gray. Soil collection sites and soil type categories are labeled.

planned reforestation projects and used one greenhouse soil mix as a control. Sites were selected to ensure a range of soil conditions across common types of natural area soils found in NYC parks (Bounds et al. 2015). Three sites were selected for soil collection within each of the following four general categories (see Pregitzer et al. 2016 for detailed field methods and additional physical and chemical properties of soils):

- (1) Native Glacial Till: Typically, an acidic well-drained sandy loam or loam representative of the native forest soil in the northeastern United States. Pockets of mature native forest exist on soils derived from glacial till in NYC parks, and are dominated by native trees, shrubs, and understory. Mean pH = 6.2.
- (2) Coal Ash: Many current forest restoration sites on NYC parkland fall on 19th and 20th century coal ash dumps that became city parkland. Coal ash has been studied as a possible soil amendment to improve nutrient status. Mean pH = 6.6.
- (3) Clean Fill: This soil originates from excavation projects and is placed over degraded urban fill at afforestation sites. Clean fill is sandy soil without an invasive seed bank that is free of contamination and low in plant available nutrients. Mean pH = 7.6.
- (4) Urban Fill: This soil exists on over 1,000 acres of filled land across NYC parks and usually consists of native soil mixed with anthropogenic waste, such as construction and demolition debris, and/or household trash from regulated or unregulated dumping. Urban fill is known to be highly variable and is thought to be the most degraded of these soil categories. Mean pH = 6.9.
- (5) Greenhouse Soil Mixture: A moderately acidic greenhouse soil mix containing topsoil (50%), sterile peat (35%), and perlite (15%). The NYC Parks Department Greenbelt Native Plant Center uses this mix as the soil for native seed propagation. Mean pH = 6.9.

Soil was collected from each site (Fig. 1) within a 200 m² area to a depth of 25 cm. Soils were homogenized for each site and placed in 1-gal pots for seedling transplant. All soils were

characterized either as Sandy Loam or Loamy Sand (USDA Soil Survey Staff, Natural Resources Conservation Service 2014).

We selected four native tree species that are commonly used in reforestation projects within New York City: silver maple (*Acer saccharinum*), black birch (*Betula lenta*), red oak (*Quercus rubra*), and Canadian serviceberry (*Amelanchier canadensis*). All individuals were grown from seed collected in NYC, except for Canadian serviceberry, which was collected in Cheesecake State Park, NJ, U.S.A. (located just outside New York City limits, across the Raritan Bay from Staten Island). For each species, all seeds used in this study were gathered from the same population. Seedlings were grown in a greenhouse potting soil mix in containers for 2 years (2–0 planting stock) at the NYC Parks Department Greenbelt Native Plant Center. We randomly chose 117 seedlings of each species, transplanting 9 replicates of each species into pots containing soil from one of the 12 soil collection locations or the greenhouse mix ($n = 468$). Once transplanted, all seedlings were placed in a greenhouse and grown under natural light and watered to field capacity twice weekly. Air temperature in the greenhouse was generally kept close to ambient conditions, and averaged 7°C in the winter and 25°C in the summer months.

Seedling Data Collection

Seedling measurements were taken for two growing seasons (Year 1 and Year 2) and the number of surviving seedlings was recorded at the end of each growing season. Total height and basal stem diameter (taken just above the root collar) of each live seedling was recorded at the beginning and end of each growing season to calculate total growth during each year of the experiment. Leaf discoloration and chlorophyll fluorescence measurements were also made at the end of each growing season.

Chlorophyll fluorescence measurements were made on three leaves per tree using the Handy PEA (Plant Efficiency Analyzer) chlorophyll fluorescence meter (Hansatech Instruments Ltd., England, U.K.). Leaves were dark adapted in situ for 30 minutes prior to measurement. We used Performance

Table 1. Results from linear mixed effects models analyzing the effects of soil type, species, and their interaction on seedling growth and physiology. Initial height was not included in root:shoot, seedling stress, PI_{ABS}, or foliar C:N models. *F*-values, denominator degrees of freedom (in parentheses), and *p*-values are listed for each fixed effect. Bold *p*-values indicate significant differences ($\alpha = 0.05$).

Response Variable	Soil Type	Species	Soil Type × Species	Initial Height
Total height growth	2.65 (8) 0.11	76.57 (388) <0.0001	2.04 (388) 0.02	4.74 (390) 0.03
Total biomass	5.10 (8) 0.02	50.68 (370) <0.0001	3.39 (370) 0.0001	36.07 (371) <0.0001
Root:shoot	1.38 (8) 0.32	92.52 (370) <0.0001	2.56 (370) 0.003	
Year 2 seedling stress (<i>z</i> -score)	1.60 (8) 0.27	27.60 (388) <0.0001	2.14 (388) 0.01	
Year 2 PI _{ABS}	1.50 (8) 0.29	76.08 (389) <0.0001	3.33 (389) 0.0001	
Year 2 foliar C:N	1.37 (8) 0.33	96.20 (388) <0.0001	15.01 (388) <0.0001	

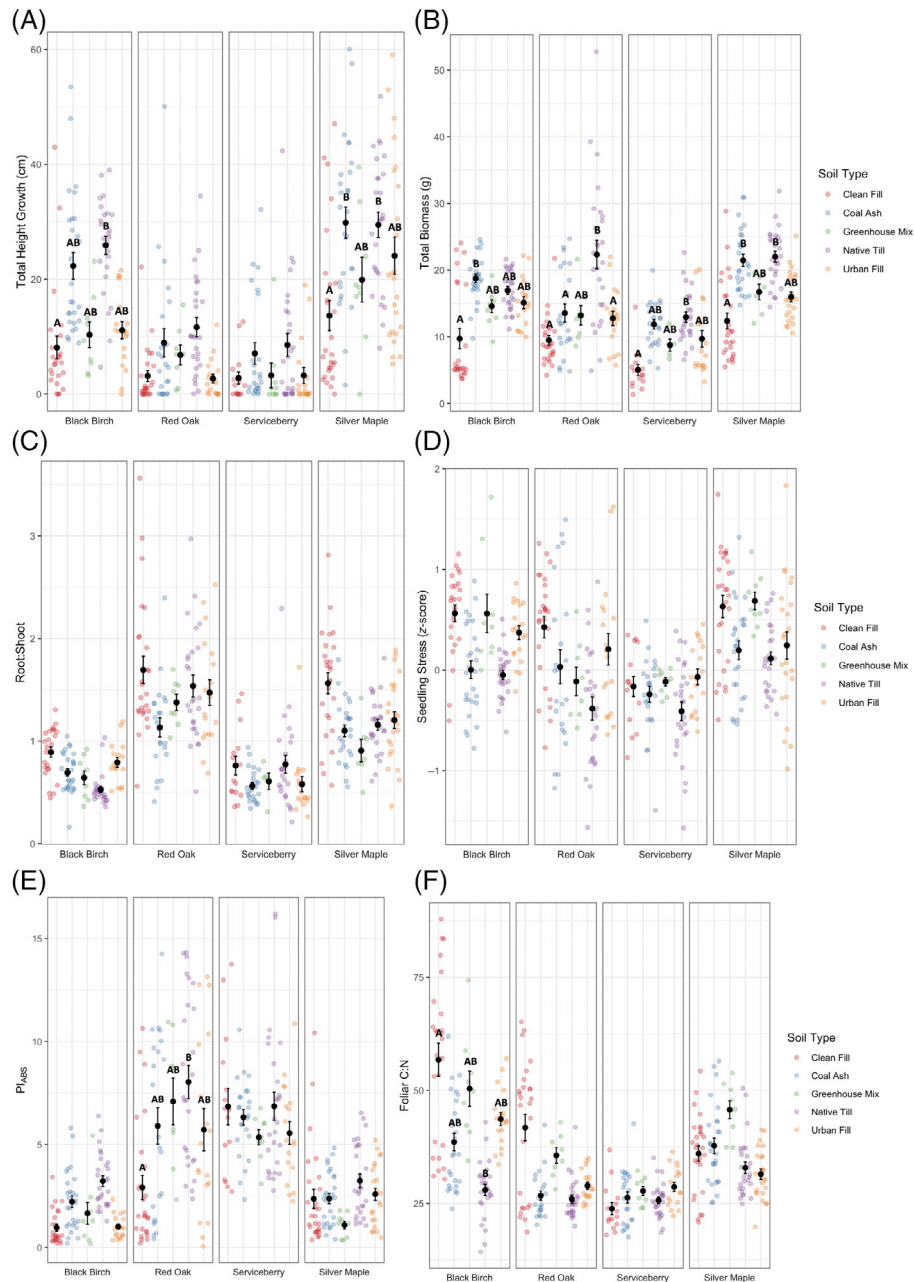


Figure 2. Growth and physiology responses of four native tree species planted in different urban soil types. Each point represents the individual tree response and the mean of that species in each soil type is represented by the black dot (\pm SE). A different growth or physiology response is represented in each panel including (A) total height growth, (B) total biomass, (C) root:shoot ratio, (D) seedling stress score, (E) PI_{ABS} , and (F) foliar C:N ratio. Letters show significant differences between soil types within each species ($P < 0.05$).

Index (PI_{ABS}) and F_V/F_M for our analyses. PI_{ABS} is a measure of how efficiently a leaf can use light for photosynthesis (Hermans et al. 2003) and F_V/F_M is a measure of the efficiency in photosystem II (Hong & Xu 1999). We incorporated the average PI_{ABS} and F_V/F_M values from each seedling into the final health calculations described below. Leaf discoloration was assessed by making an ocular estimate of the percent total leaf tissue with color change using the following classes: Class 1 = 0%

discoloration; Class 2 = 1–25% discoloration; Class 3 = 26–50% discoloration; Class 4 = 51–75% discoloration; and Class 5 = 76–100% discoloration.

At the end of the experiment, stems were clipped at the base. Coarse and fine roots were removed from the pots and carefully washed to remove soil particles. Leaf, stem, and root tissues were bagged separately and dried in an oven at 50°C for 1 week. All dry tissues were then weighed. Root, stem, and leaf mass

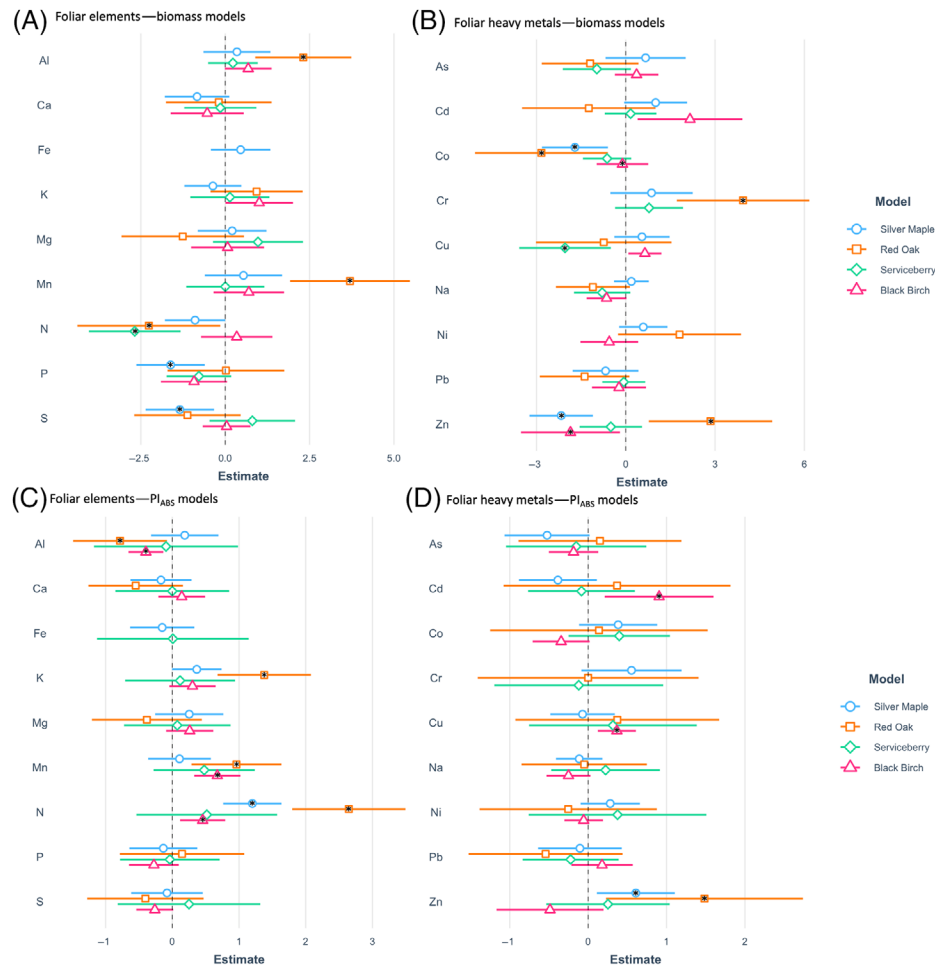


Figure 3. The relationship between (A) foliar elements and seedling biomass, (B) foliar heavy metals and seedling biomass, (C) foliar elements and PI_{ABS} , and (D) foliar heavy metals and PI_{ABS} . Standardized estimates (coefficients) \pm SE are displayed for each foliar element or heavy metal; asterisks on each coefficient indicate statistically significant effects ($\alpha = 0.05$).

were summed for total plant biomass. Oven-dried foliage was ground to create a composite sample for each seedling and was subsequently digested using a microwave-assisted acid digestion procedure (US EPA Method 3052) and analyzed for Al, As, Ca, Cd, Cr, Cu, Fe, K, Mg, Mn, Na, Ni, P, Pb, S, and Zn by ICP spectroscopy. Foliar N was determined by combustion with a PerkinElmer 2,400 series II CHNS/O analyzer (PerkinElmer, Waltham, MA, U.S.A.). Foliar chemistry outlier values were excluded from analysis when concentrations were more than double the next highest value in the dataset, suggesting an error in sample processing. These included three foliar Na values (two silver maple and one serviceberry sample) and three foliar Al values (two serviceberry and one red oak sample).

Statistical Analysis

To compare seedling health across all soil types and species during both years of the experiment, we created a single tree stress index using z -scores (Green 1979) calculated from the following

variables: diameter growth, height growth, discoloration, PI_{ABS} , and F_V/F_M (Pontius & Hallett 2014; Pregitzer et al. 2016).

Our seedlings were planted in a multifactorial design with tree species and soil type as the main effects. Linear mixed effects models in the lme4 R package were used to analyze the effects of soil type, tree species, and their interactions on leaf-level physiology and growth response variables (R Development Core Team 2018; Bates et al. 2015). Initial height was included as a covariate in the growth and biomass models (Table 1). The lmer function allowed the use of soil collection site as a random effect in each model, and p -values for each model were obtained using the lmerTest package (Kuznetsova et al. 2017). Using the function lsmeans, Tukey contrasts were used to determine significance among soil types within each species. Linear mixed effects models were also used to analyze the effects of foliar chemistry (nutrients and heavy metals) on seedling biomass and chlorophyll fluorescence (PI_{ABS}), with soil collection site used as a random effect. For each foliar chemistry model, we tested all independent variables for collinearity and removed variables when the square roots of the variance inflation factors

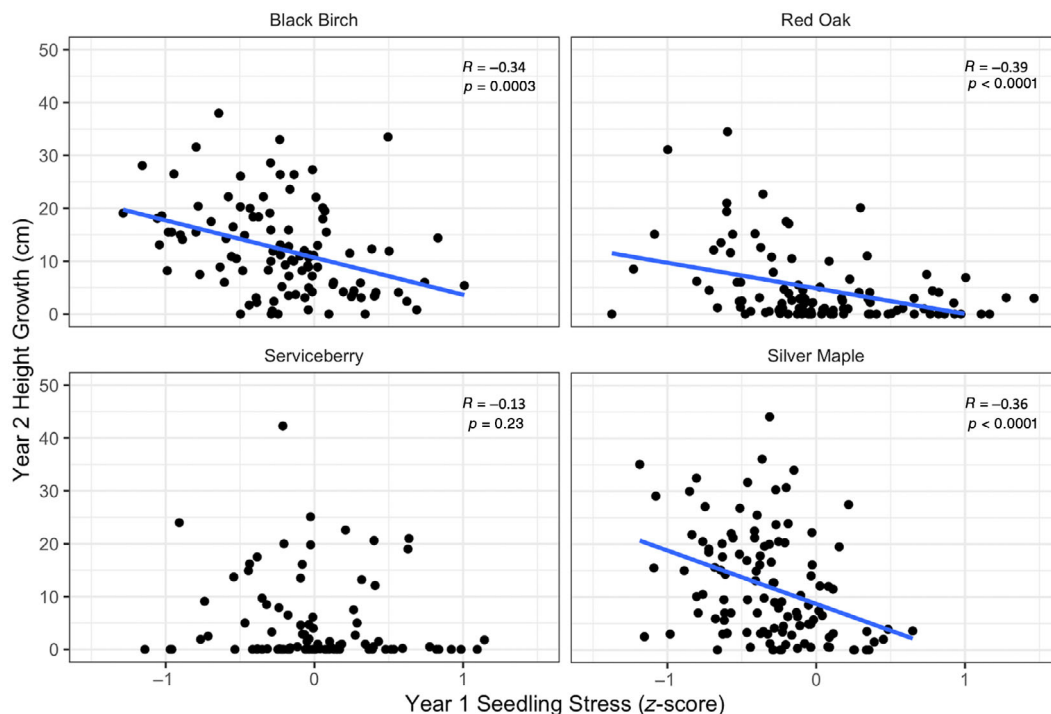


Figure 4. Pearson correlation coefficients and p -values for correlations between year 1 seedling stress and Year 2 height growth.

were >2 . The estimated variance explained by calculating R^2 values for each model follows methods of Nakagawa and Schielzeth (2013). Finally, Year 1 stress index values were correlated with Year 2 growth and physiology variables using Pearson's correlation in the R function `rcorr` in the package `Hmisc` v. 4.4-0 (Harrell 2019). Correlations were performed for each species separately to determine the utility of the stress z -score in predicting future seedling performance. Significant differences between were determined at $\alpha = 0.05$.

Results

Seedling survival after two growing seasons was generally high, but there was considerable variation among species and soil types. Individual species survival ranged from 0 to 100% depending on the soil collection location (Table S1). Native till soil supported 100% seedling survival across all tree species, while clean fill and the greenhouse mix supported 97% survival, and coal ash soil supported 96% survival across all species. Seedlings grown in urban fill soil had an 80% survival rate, driven by one soil collection location (Idlewild) with only 39% of seedlings surviving. Species grown in soils collected from Idlewild (Fig. 1) had varying survival rates, with 100% of silver maple seedlings surviving and 0% red oak seedling survival. Across all soils, silver maple seedlings had a 100% survival rate, serviceberry had 96% survival, black birch had 91% survival, and red oak had 87% survival.

Initial height had a significant effect on total height growth and biomass (Table 1). Species had a significant effect on all response variables, with silver maple generally having the highest total height growth and biomass, followed by black birch, and serviceberry having the lowest total height growth and biomass (Table 1; Fig. 2A & 2B). Black birch and silver maple seedlings had the highest average stress scores, despite these species having the greatest total height growth and biomass response, while serviceberry had the lowest stress scores (Fig. 2D). Average root:shoot ratio values were highest in red oak seedlings and lowest in serviceberry seedlings, while the C:N ratio was highest in black birch foliage and lowest in serviceberry foliage (Fig. 2C & 2F). Soil type had a significant effect on seedling biomass, which was highest in native till and coal ash soils and lowest in clean fill and urban fill soils (Table 1; Fig. 2B).

A significant soil type \times species interaction reflected variation in the species' physiology and growth responses across the different soil types (Table 1). Black birch and silver maple had the greatest amount of total height growth and lowest stress scores in native till and coal ash soils, whereas these differences by soil type were much less apparent in the other two species. There were more significant differences in seedling biomass across soil types, with native till and/or coal ash soils supporting significantly higher biomass than clean fill soils. However, red oak biomass had a slightly different pattern with much higher biomass in native till compared to all other soil types including coal ash. In addition, red oak PI_{ABS} varied significantly by soil type with seedlings grown in native till having higher

photosynthetic capacity than clean fill, whereas we did not see the same differentiation by soil type in other species. Similarly, black birch seedlings in native till had a lower foliar C:N ratio than those in clean fill, whereas other species did not have significant differences between soil types.

Seedlings demonstrated differences in foliar chemistry by species and soil type (Table S3). However, there were only a few significant relationships between foliar elements and seedling biomass or PI_{ABS} of different species (Fig. 3; Table S2a, b). Foliar N had a negative effect on red oak and serviceberry biomass, whereas this pattern was not significant for silver maple or black birch. Foliar Al was positively correlated with red oak and silver maple biomass, Mn had a positive effect on red oak biomass, and P and S had negative effects on silver maple biomass. Foliar Ca, Fe, K, and Mg did not significantly impact seedling biomass of any species. Foliar N had a significant positive effect on PI_{ABS} of all species except serviceberry, whereas foliar Al had a positive effect on silver maple PI_{ABS} , but a negative effect on red oak and black birch. Foliar K only had a positive effect on red oak PI_{ABS} , and foliar Mn only had a positive effect on black birch and red oak PI_{ABS} . Foliar Ca, Fe, Mg, P, and S did not have a significant association with PI_{ABS} of any species.

Among foliar heavy metal concentrations, only Co, Cr, Cu, and Zn had any significant effects on seedling biomass, with different patterns observed between species (Fig. 3; Table S2c). Foliar Co had a negative effect on biomass of all species except serviceberry, while foliar Cu only had a negative effect on serviceberry biomass. Foliar Cr and Zn had positive effects on red oak biomass, whereas foliar Zn had a negative effect on black birch and silver maple biomass. There were very few significant effects of foliar heavy metals on PI_{ABS} of any species (Table S2d). Foliar Cd and Cu had positive effects on black birch PI_{ABS} , whereas foliar Zn had a positive effect on red oak and silver maple PI_{ABS} .

Stress z -scores from the first year of the experiment were significantly negatively correlated with second year height growth of black birch, red oak, and silver maple (Fig. 4).

Discussion

Seedling Survival, Growth, and Physiology

During this 2-year greenhouse study, we observed significant interactions of native tree species and urban soil types collected from various New York City forest restoration sites on seedling survival, physiology and growth. Overall survival patterns among soil types and species were relatively consistent, with red oak seedlings and seedlings grown in urban fill having the highest mortality rates over both growing seasons. The overall seedling mortality rate during the second growing season was comparable to that of the first growing season. Transplant shock likely had less of an effect during the second growing season, but some of the effects of soil chemistry on seedling performance may have become stronger over time.

Clean fill soils supported the lowest amount of seedling biomass and total height growth, while native till supported the

greatest amount of height growth and biomass, followed by coal ash soils. That pattern is consistent with the high stress z -scores of seedlings grown in clean fill and comparatively lower stress observed in native till seedlings. Seedlings grown in native till generally had higher PI_{ABS} and lower foliar C:N than those grown in clean fill, reflecting greater nitrogen availability and associated photosynthetic capacity. There were no significant differences in the root:shoot ratio by soil type within each species, though red oak and silver maple root:shoot ratio was higher in clean fill soils than in other soil types. Previous work has established the lack of nutrients in this soil type (Pregitzer et al. 2016), which may have led seedlings to put on additional root biomass to seek out nutrients (McKee 1995; Qu et al. 2003).

The relatively high values of foliar C:N in black birch grown in clean fill and greenhouse mix reflect the lack of nitrogen availability in those soils. Black birch seedlings grow larger when nitrate is more readily available (Crabtree & Bazzaz 1992), and previous work has found a substantial black birch growth response following forest disturbances associated with an increase in nitrogen cycling (Jenkins et al. 1999; Falxa-Raymond et al. 2012). This species may be well-suited to take advantage of the increased nitrogen availability in urban forest soils.

Red oak PI_{ABS} showed the most variation between soil types compared to the other species, yet red oak total height growth was not significantly different between soil types. This result illustrates the value of incorporating different physiological metrics into an overall stress score (Pontius & Hallett 2014). However, the opposing patterns in PI_{ABS} and height growth may have contributed to the lack of significant differences in stress scores by soil type, and so there is also values in considering each metric individually.

Clean fill and urban fill may still be suitable for native forest restoration using appropriate species choices and with the expectation of slower seedling growth rates. Despite high stress scores and slow growth rates, seedling survival in clean fill soils was high. Soil amendments may be helpful to support long-term tree growth in these nutrient-poor soils (Oldfield et al. 2015; Pregitzer et al. 2016). Urban fill soils may not be suitable for all native tree species, given the high mortality rates observed in this study. However, silver maple seedlings had a 100% survival rate in urban fill, and similar performance to native till soils, demonstrating that some species are capable of early establishment and growth in nutrient poor urban edaphic conditions. The species \times soil type interaction is illustrated by the strong biomass response of red oak to native till soils, a pattern that is not as apparent in the other species. Red oak frequently occurs on nutrient-poor acidic soils where its growth is limited by ammonium availability (Bigelow & Canham 2007), and so the species may be able to take advantage of the relatively undisturbed native till soils with elevated nitrogen availability compared to rural forest conditions.

Patterns of species growth were relatively stable over time, although black birch put on more height growth than silver maple during the second growing season, resulting in a smaller overall difference between those two species. Both are fast-growing species that may be successful at outcompeting

invasive plants across a variety of urban site types. However, continued research in urban field conditions and over a longer time horizon would provide further insight into the most beneficial growth strategies in urban soils. For example, both red oak and silver maple have the highest root:shoot ratio, yet red oak is slow growing with low total height growth and silver maple is fast growing with greater height growth. It is possible that red oak may be more resilient to future stresses compared to silver maple, despite its lower productivity in greenhouse conditions. Red oak is an anisohydric species and may be able to withstand drought conditions better than the isohydric silver maple that generally grows on moist alluvial soils and may have benefitted from the regular watering in our experiment (Burns & Honkala 1990). Similarly, as the most shade-intolerant species in our study, black birch may not be able to compete as well in restoration contexts with existing canopy cover from other vegetation (Burns & Honkala 1990).

Contrary to expectations, patterns of seedling performance by soil type changed somewhat between the first and second growing seasons. Clean fill led to consistently low growth and high stress z -scores, whereas native till consistently supported the greatest amount of growth and lowest seedling stress. However, seedlings in urban fill soils performed relatively better during the second growing season, whereas those grown in the greenhouse mix performed relatively worse over time. In the second growing season, seedling height growth in urban fill was almost equivalent to that of seedlings in native till and coal ash, whereas seedlings in the greenhouse mix and clean fill soils attained much lower height growth. Similarly, the stress z -scores for seedlings grown in the greenhouse mix were relatively higher during the second growing season, appearing more similar to clean fill stress scores rather than coal ash and native till. The lack of nutrients in clean fill and greenhouse mix soils is likely leading to their declining ability to support seedling growth over time (Pregitzer et al. 2016). In addition, these soils likely lack established and diverse mycorrhizal symbionts that would enhance growth of native tree species (Baxter et al. 1999; Karpatis et al. 2011). Without soil amendments, continued growth in these soils might lead to further reduction of seedling growth and even mortality. It is unclear whether seedling performance in urban fill would continue to improve over time. The high mortality rates of black birch, red oak, and serviceberry in urban fill soil collected from the Idlewild location caused the most stressed trees in this soil type to drop out of the dataset completely. However, if seedlings can survive in urban fill soils, the contaminants or other disturbances present may not prevent successful establishment and growth over time.

Foliar Chemistry

Across all species, foliar N concentrations were consistently highest in seedlings grown in native till soils, and foliar N had a significant positive effect on PI_{ABS} on all tree species except serviceberry. The black birch, red oak, and silver maple seedling foliar N concentrations were lower than published values or thresholds for deficiency (Pardo et al. 2004; Castro et al. 2007; Showalter et al. 2010), while serviceberry foliar N was

comparable to published values found in saplings at New York City restoration sites and elsewhere (Pardo et al. 2004; Wibiralske et al. 2004; Falxa-Raymond et al. 2014). However, foliar N did not have a positive effect on seedling biomass of any species and had a significant negative effect on red oak and serviceberry biomass (primarily driven by declines in foliar biomass). Foliar N is generally highly correlated with photosynthesis rates, but its relationship with plant biomass is more complex, and the plasticity of different species' growth responses to N availability may vary based on their inherent growth rates (Niinemets et al. 2002). Nitrogen availability may impact foliar biomass and productivity without significant changes in foliar N concentrations (Luxmoore 1991). This may explain the lack of correlation in our data between foliar N and overall biomass, despite the likely N limitation of all species except serviceberry.

We found foliar Mn to have a significant positive effect on red oak PI_{ABS} and biomass, and on black birch PI_{ABS} . Black birch and red oak foliage appear to have low Mn concentrations compared to previously published values from undisturbed rural forest conditions (Pardo et al. 2004; St Clair & Lynch 2005; Jordan et al. 2019) and both species show the same patterns of foliar Mn by soil type, with the highest levels in the greenhouse mix, followed by native till, coal ash, and then the lowest levels in urban fill and clean fill. Given that Mn availability is somewhat pH dependent (Foy 1984) with deficiencies for some species occurring at pH values greater than 7.29 (Zukswert et al. 2021), the pH values of the soils in this study are high enough where they may limit Mn availability causing deficiency (Van Sambeek et al. 2017; Marek & Richardson 2020).

All species appeared to have foliar P concentrations above thresholds for deficiency (Pardo et al. 2004; Zatylny & St-Pierre 2006; Block et al. 2013). In addition, none of the species seem to be Ca or Mg limited based on the available literature (Kopinga & van den Burg 1995; Pardo et al. 2004; Showalter et al. 2010), which is consistent with elevated levels of Ca found in urban soils (Lovett et al. 2000). Foliar K only had a significant positive effect on PI_{ABS} of red oak, which may be somewhat K deficient (Pardo et al. 2004; Showalter et al. 2010). Red oak is adapted to acid forest soils in rural forests (Hallett & Hornbeck 1997) consequently the higher pH of the soils in this study (5.5–8.0; Pregitzer et al. 2016) could cause K limitations as was found by Zukswert et al. (2021) for other tree species adapted to acid forest soils. Aluminum becomes more available as soil pH decreases and can damage fine roots and interfere with cation uptake (Cronan & Grigal 1995). This may explain the negative correlation found between foliar Al and PI_{ABS} in red oak and black birch. However, the red oak foliar Al in this study is comparable to other published values of healthy red oak foliage (Joslin & Wolfe 1989; Hallett & Hornbeck 1997) and foliar Ca/Al values were above 4, indicating that Al is not likely high enough to have toxic effects (Kelly et al. 1990). The positive association found between foliar Al and red oak biomass may reflect the availability of other nutrients associated with Al availability in certain soil conditions. There is limited available literature on foliar Fe or S in these species or genera, and so it is difficult to interpret the significant effects observed in this study.

Our foliar chemistry models suggest limited negative impacts of foliar heavy metal concentrations on total biomass or PI_{ABS} . However, the lack of literature on toxic thresholds of foliar heavy metals in the tree species studied here limits our ability to interpret whether the urban soils in this study have harmful levels of these elements that may be inhibiting seedling growth and/or photosynthetic activity (Assche & Clijsters 1983). In particular, foliar Cu has a negative effect on serviceberry and red oak biomass (although it is only significant in the serviceberry model) and may have reached a toxic level in these species grown in coal ash and urban fill soils (Zatylny & St.-Pierre 2006; Beyer et al. 2013; Tanentzap 2015). Silver maple foliar Cu does not appear to exceed normal levels, except perhaps in urban fill soils where it is comparable to seedlings grown in mining soils (Roth et al. 1982; Nkongolo et al. 2017). Foliar Co also has a significant negative effect on biomass of all species except for serviceberry, and the available literature suggests that it may have reached toxic levels in red oak seedlings grown in coal ash and urban fill soils (Tran et al. 2014; Tanentzap 2015).

The lack of literature on black birch foliar heavy metal concentrations, makes it difficult to interpret the positive effect of foliar Cd and Cu on PI_{ABS} of this species. Red oak foliar Zn in our study is clearly below published toxic ranges for the species (Jordan 1975), and so the high levels associated with native till and coal ash soils appears to have a positive rather than a negative impact on biomass and PI_{ABS} . Red oak foliar Cr also has a significant positive effect on biomass though it is in a range similar to red oak foliage found at a contaminated site in France (Migeon et al. 2009). Because Cr is toxic, this result implies that the heavy metal may not be present in levels high enough to damage seedling growth and that available Cr may correlate with another element that is beneficial for seedling growth. Foliar Zn has a significant negative effect on black birch and silver maple biomass, but silver maple foliar Zn seems to be in a normal range (Smith & Brennan 1984). Zn and Cu are micronutrients, which may explain their positive effect on seedling performance when present below toxic ranges.

Overall, the relatively high pH in these soils will tend to make heavy metals less available for plant uptake (Kahle 1993) including those that are micronutrients (e.g. Cu, Zn, Mn). Decreased availability of micronutrients may explain the positive correlations between Cu, Zn, and Mn and PI_{ABS} and biomass for some species in this study.

Urban soils exhibit a high degree of variability, a phenomenon encountered in rural forest restoration activities as well. However, urban soils not only vary in macronutrient availability but also in heavy metal concentrations and other contaminants due to the wide variety of development and land management practices implemented on small parcels of urban land. We found that different soils collected from NYC parks impacted survival, growth, and health of four tree species commonly used in NYC's restoration projects. In addition to variability between urban soils we found variability in how species fared in each soil type. A stark example of this is Idlewild Park soils where red oak had 100% mortality, while serviceberry and black birch had greater than 50% mortality, and all silver maple survived.

This study highlights the need for gaining a better understanding of species-site interactions specific to urban areas prior to planting. This approach is relied on by rural silvicultural techniques which use decades of research and practice to guide species selection (Ashton & Kelty 2018). Currently, urban practitioners largely rely on expert local knowledge and empirical evidence for species selection for a given site. Given that the planning and site preparation phases for urban restoration or afforestation projects can take at least 2 years (Bounds et al. 2015), it may be possible to set up controlled greenhouse trials during planning stages to identify tree and shrub species that will establish and perform well in soils from specific restoration sites. Tree planting in urban natural areas can be very costly (\$75,000–\$162,000 per acre including the cost of labor; Bounds et al. 2015), making survival important in order to maximize limited budgets for natural resource management and potentially justifying additional time and effort spent to match native tree species to site conditions. The assessment techniques used in this study could also be used in post-planting monitoring efforts. With additional time for variation in seedling growth to become apparent, the stress score may prove even more useful in predicting future performance, alerting land managers to potentially stressful site conditions that may need to be remediated to forestall mortality or ensure maximum growth and productivity.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Seedling survival by soil type (bold), soil collection location, and species after 2 years in the greenhouse.

Table S2. Results from linear mixed effects models analyzing the effects of foliar nutrients and heavy metals on seedling biomass and photosynthetic capacity (PI_{ABS}).

Table S3. Mean ± SE of foliar chemistry values from seedlings grown in field collected soils. Values are reported in parts per million (mg/kg).