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Canopy trees in an urban landscape – viable forests or long-lived gardens?

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Abstract Seedling recruitment shapes tree communities, including those found in altered landscapes such as urban forests. However, little data exists on local- and broad-scale tree seed immigration and recruitment in these communities. Interspecific competition and seed predation are two major causes of recruitment failure for plants. In North American urban forests, these pressures may be exacerbated by an altered disturbance regime and prevalent invasive species combined with dense populations of rodents and browsers. Preliminary investigation in an urban forest on the eastern shore of Lake Erie indicated very low long-term tree seedling recruitment in the mature canopy stands. Our competing hypotheses were that seed establishment (habitat suitability) and seed limitations (seed availability) explained the tree recruitment failure. We tested seed establishment using field experiments (burning and vertebrate herbivore exclosures) and seed limitation by introducing native tree seeds. Moreover, we tested also seed limitation by examining local and regional seed input using seed traps. We found that seedling recruitment increased significantly with experimental reductions in predators and competitors, suggesting strong biotic establishment limitations in the urban forest. In addition, seed rain correlated significantly with immediately proximate parent plants, but no species arrived beyond what occurs within 50 m of the experimental plots. Essentially, then, the existing canopy species are not replacing themselves and extant seeds are not immigrating to replace them. At the patch scale, habitat quality, particularly seed predation and browsing, as well as competition from nonnative understory shrubs, constrained native tree recruitment in the urban forest. At the landscape scale, the evidence of poor long-term seed recruitment and the lack of long-distance seed input also suggest low native tree seed availability. The tree recruitment failure suggests that, in the absence of active management, this urban forest may eventually convert to an invasive-species dominated urban shrubland.

Keywords Brownfield · Dispersal · Landfill · *Populus deltoides* · Recruitment · Urban ecology · Vegetation dynamics

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Introduction

Urban forests often are planned, designed, and managed to maximize environmental, social, and economic benefits for humans. As such, tree population ecology is less known in urban than wildland forests – particularly unmanaged tree establishment. Whereas wildland forests often cover large tracts of land, typically located far from urban centers, urban forests are relatively smaller and occur within highly altered landscapes within urban populations. Essentially, urban forests are green archipelagos in an ocean of urbanized landscape. Given their isolation in an altered landscape, the long-term population viability of urban forests is uncertain, and

little is known about the factors influencing native tree recruitment in urban forests (as noted by Oldfield et al. 2013).

Most plant mortality (90 %) occurs during the earliest life stages (Fenner 1987; Fenner and Kitajima 1999; Harper 1977). As such, recruitment (seedling establishment and survival) is the critical life history stage in determining species distributions and community trajectories (Crawley 2000; Grubb 1977; Turnbull et al. 2000; Warren and Bradford 2011). Successful recruitment can be summarized in a simple dichotomy of establishment (suitable habitat) versus seed (dispersal) limitations, though they are not mutually exclusive. Establishment limitation is present when plant populations are inhibited by habitat availability and quality (Clark et al. 1998; Nathan and Muller-Landau 2000), whereas seed limitation occurs when seeds fail to arrive in necessary densities for recruitment (Nathan and Muller-Landau 2000; Svenning and Wright 2005; Turnbull et al. 2000). Recruitment limitation can undermine forest persistence if existing trees fail to replace themselves due to unsuitable habitat or poor seed availability.

Establishment limitation occurs when plant populations are impeded by unsuitable recruitment habitat (Clark et al. 1998; Nathan and Muller-Landau 2000). Unsuitable habitat conditions can include over-browsing by herbivores (Nuttle et al. 2013; Tyler et al. 2008; Webster et al. 2005; White 2012). Herbivores and granivores may alter plant communities by preferentially feeding on select species, leading to a restructuring of plant community composition and shifts in canopy dominance (Salk et al. 2011; White 2012). In fact, the pressure exerted on plant communities by *O. virginianus* (white-tailed deer) browsing can lead to total recruitment failure for many plant species (Nuttle et al. 2013; Webster et al. 2005; White 2012). Similarly, Tyler et al. (2008) found that seedling survival approximately doubled in the first year of establishment when rodents were excluded from experimental plots, and almost all established seedlings that were protected survived an additional 18 months.

Habitat limitation may also occur through interspecific competition. For example, shrub thickets in forests reduce canopy tree recruitment through shading and altering soil moisture and nutrients (Fagan and Peart 2004; Frappier et al. 2003; Heneghan et al. 2006). Grassland species also can inhibit tree recruitment without disturbance, such as fire, to remove or reduce established grass cover and allow tree recruitment (Bond and Midgley 2001; Jutila and Grace 2002).

Suitable habitat is useless, however, to species that cannot access it. Seed limited recruitment failure occurs when seeds fail to arrive in otherwise suitable habitat (Clark et al. 2007; Nathan and Muller-Landau 2000; Turnbull et al. 2000). Given that introducing seeds to experimental plots generally increases plant populations (Clark et al. 2007; Piqueray et al. 2013) it is likely that unoccupied suitable habitat is common (Pulliam 2000). Spatial scale is crucial in determining

recruitment success. Poor plant dispersers can occupy the same forest stands as stronger dispersers at local scales, but at regional scales, high fecundity in wind-dispersed species reduces the importance of immediate proximity to suitable microsites (Cain et al. 2000; Clark et al. 1998; Nathan and Muller-Landau 2000).

Preliminary data indicated almost complete tree recruitment failure at Tifft Nature Preserve (hereafter, "Tifft") in Buffalo, NY (U.S.), an urban nature preserve with forested patches dominated by mature *Populus deltoides* (eastern cottonwood), and, in an extensive review of the literature, Oldfield et al. (2013) noted a lack of research into tree seedling recruitment in urban forests. These findings prompted our overall objective, which was to investigate tree seedling recruitment in an urban forest.

It is well established that *P. deltoides* does not recruit well in closed-canopy sites because of germination requirements for bare soil and full sunlight (Bradley and Smith 1986; Engstrom 1948); however, forest cover at Tifft is patchy with abundant edge habitat. Furthermore, shade-tolerant seedlings of middle- to late-successional native tree species generally are present in mature forests (Abrams and Orwig 1996; Bonser and Aarssen 1994), but absent at Tifft. We explore two hypotheses predicting failed recruitment at Tifft. Given that 90 % of plants die in the recruitment stage (Fenner and Kitajima 1999; Harper 1977), we hypothesized that establishment (habitat) limitation would best explain failed recruitment. However, habitat limitations are of little consequence if the seeds fail to arrive, so we also tested the alternative hypothesis that native tree recruitment failure is best explained by limited seed availability. We tested seed establishment using field experiments (burning and vertebrate herbivore exclosures) and seed limitation by introducing native tree seeds. We also we tested also seed limitation by examining local and regional seed input using seed traps.

Materials and methods

Study site

Tifft Nature Preserve is a 107 ha urban nature preserve administered by the Buffalo Museum of Science (ESM_1.pdf). The preserve is a former brownfield south of Buffalo which was used for industrial activities as well as refuse dumping until the early 1970s. Tifft (42°50′38.67″ N, 78°51′17.27″ W) lies close (~160 m) to the western shore of Lake Erie (elev.183 m), and it is surrounded by former industrial sites, a limited access highway and active railroad yards. Past industrial dredging and dumping created a soil base composed of natural and artificial materials, and the forest soils contain a thin layer of humus above mineral soil mixed with industrial dredge and residential refuse (Spiering 2009). Historic aerial photos

indicate that trees began establishing at Tifft in the 1950s when industrial and residential dumping was still occurring. The dominant canopy species in the forest is *P. deltoides* (eastern cottonwood), but other woody genera are present, including the exotic invasive *Rhamnus cathartica* (common buckthorn) and *Pinus* spp. (pines). *Populus deltoides* trees are relatively short-lived, only surviving about 80 years (USDA 2016), so the Tifft cottonwood forest can be considered a mature canopy. Treefall gaps at Tifft are dominated by *R. cathartica*.

Tifft also contains a grassland that covers rolling hills above a sealed landfill and is dominated by native cool-season grasses such as *Festuca rubra* (red fescue) and *Bromus inermis* (smooth brome), *Agrostis gigantea* (red top) as well as nonnative forbs such as *Coronilla varia* (crown vetch) and *Lotus corniculatus* (bird's foot trefoil) (Huff et al. 2015; Spiering 2009).

Survey plots

Tree size class distributions can be linked with demographic patterns to infer population trajectories (Shimano 2000). For example, because plant mortality is highest in the recruitment stage, a viable population requires far more seedlings than adults to replace mortality (Crawley 2000; Grubb 1977; Turnbull et al. 2000; Warren and Bradford 2011). Class size distributions also capture long-term forest dynamics so that if, for example, seedling recruitment is pulsed, the temporal variability would be consolidated into the smaller size classes.

Three transects were established in forest and grassland patches ($n = 6$ total transects) with 1 m^2 plots spaced at 50-m intervals along each transect. Areas with active management (e.g., invasive species eradication) and tree plantings were systematically avoided by moving plots 50 m further along the transects. No plots were located within 50 m of habitat borders. We measured woody abundance, species richness and basal area in August 2013 to determine overstory composition and structure. Overstory (DBH > 10 cm) and understory (DBH < 10 cm) abundances were sampled using the point-centered quarter method (Dix 1960) up to 50 m from 1 m^2 plots. We also sampled each plot for seedling abundance and cover for all woody species within the 1 m^2 plots.

Experimental plots

Twelve randomly stratified experimental grids ($n = 6$ in woodlands and $n = 6$ in grasslands) were established in May 2014 to measure tree recruitment success. Each grid included four, 0.25 m^2 treatment plots separated by 0.5 m (ESM_2.pdf). Each treatment plot included three subplots planted with one of three species: *P. deltoides*, *Pinus strobus* (eastern white pine), and *Acer saccharum* (sugar maple) in random arrangements. *Populous deltoides* was included in the study because it dominates forest patches at Tifft Nature Preserve. *Acer saccharum* was chosen for this study as it is a shade tolerant late-successional species (Bonser and Aarssen 1994), whereas *Pinus strobus* is associated with early- and mid- succession forests (Abrams and Orwig 1996). Seeds were pre-mixed and dampened in ~20 g of commercial potting soil. A 15.2 cm circular PVC cylinder was used to create a 15.2 cm diameter × 2.5 cm deep depression in each subplot where the seeds were packed with potting soil. Each plot was then covered with a wood fiber seed blanket held down with landscape pins to hold the seeds in place until germination. Twenty seeds of each species were planted in each treatment ($n = 960$ total seeds). Inspections of the grids for emerging seedlings were conducted every two weeks from May 2014 to the end of the growing season in October 2014. Following the end of the growing season, all aboveground biomass in the plots was removed, dried at 65 °C for 48 h, and weighed.

We examined the impacts of interspecific competition and seedling herbivory on the native tree recruitment using a randomized, factorial understory removal and vertebrate herbivore exclusion experiment to test the influence of habitat limitation on native tree recruitment. The treatments were: burning (entire 0.25 m^2 treatment plot was burned with a propane torch [VT 3–30 C propane torch, Flame Engineering Inc., Lacrosse, KS, USA]) in May 2014, exclusion (PVC frame secured to the ground with rebar and covered by 2 cm flexible nylon netting) and burning + exclusion. The exclusion treatment was designed to deter deer herbivory as the populations are very high at Tifft and site management efforts toward tree establishment only succeed with deer exclusion (Spiering, *pers. Obs.*). The seed matting and plot netting may have deterred some granivores, particularly birds, but we cut openings in the netting sides so that birds could escape if trapped, and the large pore size and loose application of the netting were unlikely to deter anything except large mammals.

Seed rain

Seed rain was measured to assess the availability of native tree seeds in the vicinity the experimental plots. Twenty-four, 0.25 m^2 × 1 m high seed traps (2 per grid, $n = 24$ total) were placed 2 m from the experimental plots (May 2014). The design of these traps was based on the seed trap model provided by the Smithsonian Tropical Research Institute (http://www.ctfs.si.edu/floss/page/methods/). Seed collection occurred every two weeks May to October 2014. In addition, point-centered quarter method (Dix 1960) was used to survey woody species 50 m around each seed trap in order to compare the species composition of collected seeds with the surrounding woody plant community.

Habitat conditions

Light availability was measured by calculating the difference between understory photosynthetically active radiation (PAR; wavelength: 400–700 nm) at each plot and a fully exposed PAR reference site. Plot-level PAR was measured in August 2014 using a 0.5 m handheld AccuPAR ceptometer (Decagon Devices, Inc., Pullman, WA, USA), and reference PAR was measured using a LI-200 spherical PAR sensor (LiCor, Inc., Lincoln, NE, USA) placed in an open field. Volumetric soil moisture (10 cm) was measured in every plot using a handheld Hydrosense Soil Water Content Measurement System (Campbell Scientific, Inc., Logan, UT, USA) six times from July to September 2014. Temperature probes (Taylor Precision Products, Oak Brook, IL, USA) were placed in conjunction with soil moisture measurements.

Data analysis

A canopy size-class distribution for Tifft was built using tree DBH data with seedlings as the smallest class. Experimental recruitment success was analyzed in two stages: germination success (germination/20 seeds planted) and seedling survival (survived seedlings/germinated seeds). Germination and survival success were analyzed as binomial proportions using generalized linear models (GLM) assuming a binomial error distribution using the R statistical software (R Development Core Team 2015). Habitat (woodlands, grasslands), treatments (burn, exclusion, control, burn + exclusion), species (*P. deltoides*, *A. saccharum*, *P. strobus*) and their interactions terms were included as explanatory variables. Given that both models were overdispersed ($\phi > 2.5$), quasibinomial error distributions were used. The "car" package (Fox and Weisberg 2011) was used to test for collinearity (variance inflation) in the models. The coefficients for fitted GLM models were analyzed using analysis of deviance (ANODEV) with Chi-square tests. GLM ANODEV models were also used to evaluate germination and survival as a function of plot vegetation biomass assuming quasibinomial error distributions ($\phi > 2.5$). The composition and quantity of seed rain was evaluated as a function of woody basal area (canopy and understory) using a linear regression.

Results

Tree survey

Expectedly, forest patches contained greater density of trees (mean ± SE, 3.3 ± 0.2 stems m^{-2}) and greater basal area (10.3 m$^2 \pm 1.6$ m^{-2}) than grassland patches (1.5 ± 0.2 stems m^{-2}; 2.6 m$^2 \pm 0.5$ basal area m^{-2}). In both forested and grassland patches, mid-sized trees (80–120 dbh) dominated the size class distribution with *P.deltoides* (32 % of all stems) and *R. cathartica* (31 %) the most common woody species, followed by *Pinus* spp. (10 %), *Cornus amomum* (6 %) and ten other species (~21 %). There were far fewer seedlings and saplings than adult trees, and most woodland trees were mid-sized (Fig. 1). The grassland plots had twice the light but less than half the soil moisture as the woodland plots (Table 1). Woody basal area was 10× higher in the woodland than grassland, and herbaceous biomass was 10× higher in the grassland than woodland.

Seed germination and seedling survival

A significant habitat x species interaction (*df* = 2, *deviance* = 75.787, *residual df* = 135, *p-value* < 0.001) indicated that germination success was greater in the woodland than grassland habitat for *P. strobus*, but not for *P. deltoides* or *A. saccharum* (ESM_3.pdf). A significant treatment x species interaction (*df* = 6, *deviance* = 107.343, *residual df* = 129, *p-value* < 0.001) also indicated species-specific treatment responses (ESM_3.pdf). *Acer saccharum* germination was much lower than the other two species, and it differed little between treatments. *Pinus strobus* germination was significantly higher with exclusion than the other treatments. *Populus deltoides* germinate was significantly higher in the Burn and Burn + Exclusion plots. A significant habitat x treatment interaction (*df* = 3, *deviance* = 19.405, *residual df* = 126, *p-value* < 0.05) indicated that, though germination was higher in the woodlands than grasslands, germination success was highest in the Burn + Exclusion plots in the grasslands but highest in the Exclusion plots in the woodlands (ESM_4.pdf).

Seedling survival was species specific (*df* = 2, *deviance* = 16.615, *residual df* = 52, *p-value* < 0.05), with *A. saccharum* surviving at higher rates than *P. deltoides* but no difference between *P. strobus* and the other two species (Fig. 2a). Survival was significantly higher for all species in the exclusion treatments than burn treatment or control (*df* = 3, *deviance* = 47.072, *residual df* = 54, *p-value* < 0.001; Fig. 2b). Survival did not change with habitat (*df* = 1, *deviance* = 2.007, *residual df* = 57, *p-value* = 0.346).

Plot biomass

Germination success decreased significantly with increased understory biomass (*coeff.* = −0.006367, *SE* = 0.001892, *t-value* = −3.364, *p-value* < 0.001), but seedling survival was unaffected by co-occurring plant biomass (coeff. = −0.002723, *SE* = 0.003185, *t-value* = −0.855, *p-value* = 0.396).

Fig. 1 Canopy size class distribution of all canopy species at Tifft Nature Preserve (Buffalo, NY, U.S.) with the first size class representing seedlings. Viable forests should have a size class distribution a right-skewed, inverse-J pattern (Kimmins 1987; Shimano 2000), indicating future canopy replacement by seedlings and saplings
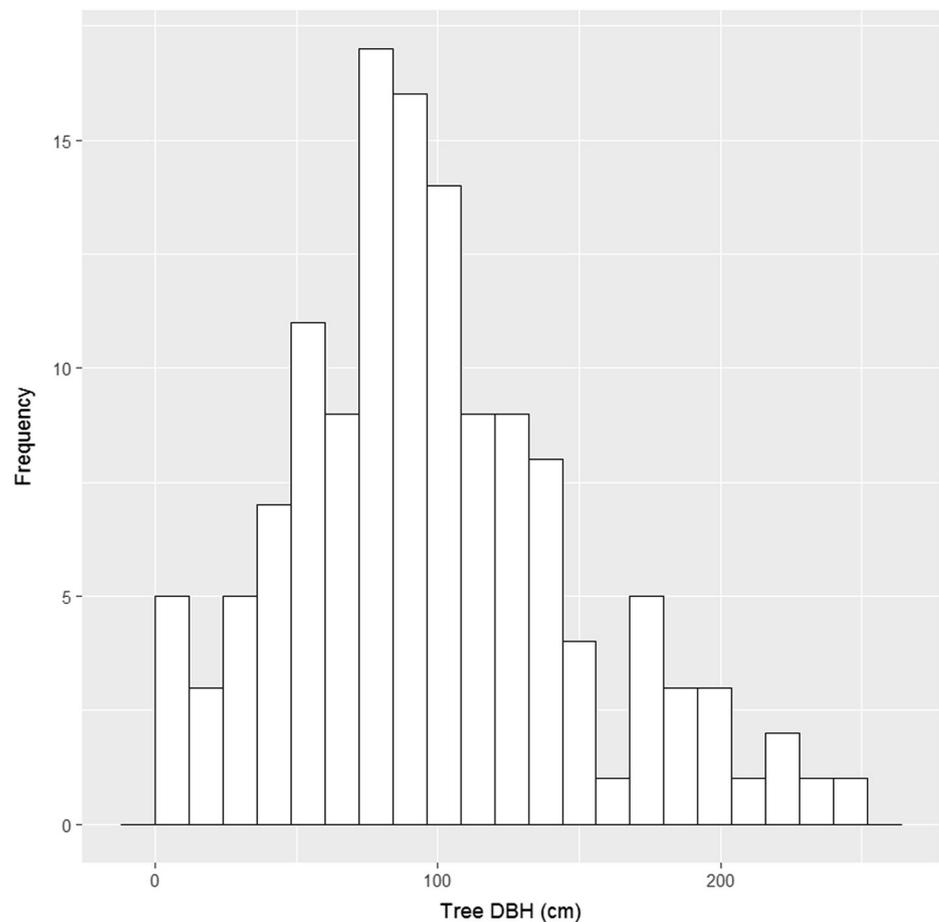
Seed rain

Seed rain abundance increased significantly with local tree and shrub area to approximately 4.3 cm^2 ha^{-1} but a marginally significant second-order term indicated that it steadied and decreased with even higher basal area (*coeff.* = 98.108, *SE* = 32.734, *t-value* = 2.997, p-value <0.015; *coeff^2*. = −9.297, *SE* = 4.509, *t-value* = −2.062, p-value <0.069, R^2 = 65.8 %) (Fig. 3). Only four species of woody plants were found in the seed traps (*R. cathartica*, *P. deltoides*, *R. typhina*,

Cornus spp.), and all of them occur at Tifft. Only *P. deltoides* seeds were found in the grassland.

Discussion

Native tree recruitment in the urban forest required localized burning and herbivore exclusion, suggesting unsuitable habitat conditions for current tree replacement, and a lack of seed rain from outside the urban forest boundaries indicate limited input by species that would find the habitat suitable, such as mid-successional tree species. Hence, the urban forest recruitment was limited by habitat at the local scale and seed dispersal at larger scales, suggesting that urban forest viability and biodiversity may depend upon management intervention.

Seedling recruitment starts with germination, and many trees require vegetation disturbance for successful germination (Elliott et al. 1997; Hubbell et al. 1999; Peroni 1994; Warren et al. 2004). We found that the seed germination for three widespread native tree species was negatively correlated with understory plant biomass, but increased with vegetation disturbance, suggesting a lack of light or space. Interestingly,

Table 1 Mean (±SE) abiotic and biomass values for grassland and woodland habitats

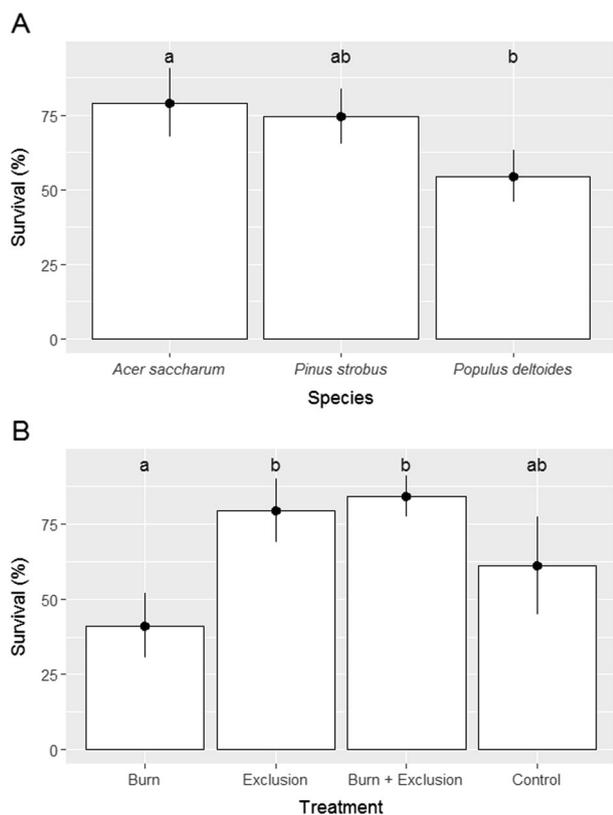|	Grassland	Woodland
Photosynthetically active radiation (%)	97.0 ± 0.6	46.0 ± 0.5
Soil moisture (%)	18.2 ± 0.3	46.8 ± 0.9
Soil temperature (°C)	17.5 ± 0.2	17.1 ± 0.2
Herbaceous layer biomass (g m^{-2})	807.2 ± 19.9	78.5 ± 7.6
Undertory woody basal area (m^2 ha^{-1})	0.2 ± 0.1	0.7 ± 0.1
Overstory woody basal area (m^2 ha^{-1})	2.2 ± 1.8	21.5 ± 2.8

Fig. 2 Mean (±SE) seedling survival by species (A) and treatment (B) at Tifft Nature Preserve (Buffalo, NY, U.S.). *Acer saccharum* had a higher survival rate than *P. deltoides,* though there was no significant difference between the *P. strobus* and *A. saccharum* or *P. strobus* and *P. deltoides* (a). The Burn + Exclusion treatment and Exclusion treatments yielded higher survival rates than the Burn treatment, but none differed from the control (b). Responses that are not significantly different share the same letter
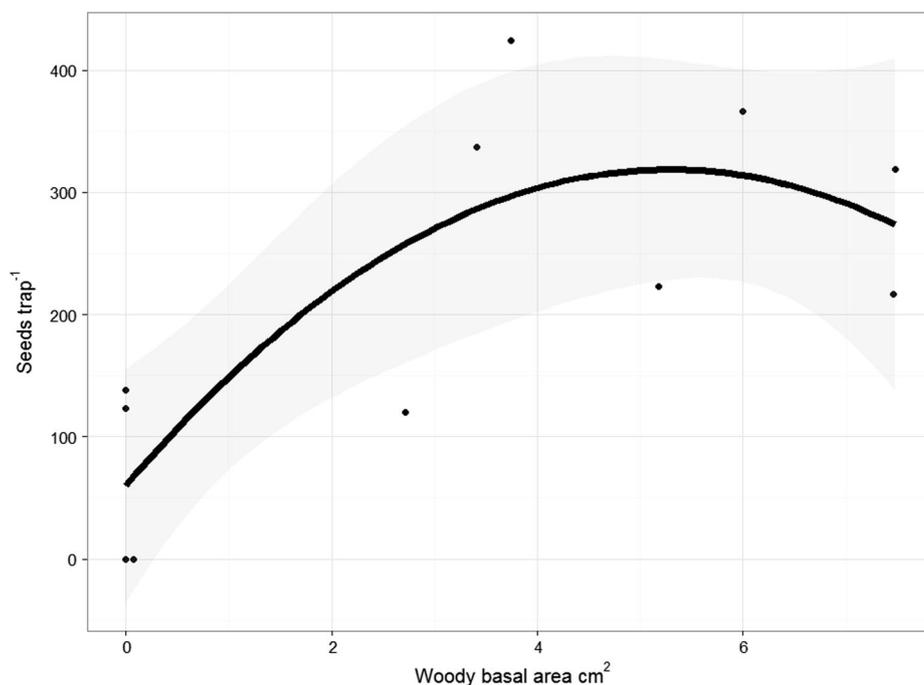
P. strobus germination increased by 25 % in forested compared to grassland habitat, but *P. deltoides* did not increase in the forest, which may reflect abiotic microhabitat differences, such as higher forest soil moisture. Both species are epigeal and require sun exposure for germination (Engstrom 1948), but *P. strobus* germinated much better in exclusion plots whereas *P. deltoides* did better with burning. These results suggest that the grasslands may contain a seed or seedling predator that targets *P. strobus* whereas interspecific competition appears more limiting for *P. deltoides*, which has considerably smaller seeds than the other study species.

Seeds are an important component of many mammal diets (Connolly et al. 2014; Lobo 2014; Sivy et al. 2011). As such, seed predators inhibit plant recruitment (Côté et al. 2003; Peters et al. 2004). Whereas granivorous mammals typically are seed generalists due to the irregular quality and quantity of available seeds (Hulme and Benkman 2002), seed mass generally serves as a proxy for nutritional content, and small mammals prefer larger seeds (Hulme 1998; Wang and Chen 2009). We found that recruitment for the relatively larger *A. saccharum* and *P. strobus* seeds were greater when protected inside enclosures, but protecting the much smaller *P. deltoides* seeds did little, even in optimal conditions of bare soil and direct sunlight, suggesting that the exclusion treatment also inhibited small mammals.

Herbivores impose large impacts on plants that make it to the seeding stage (Nuttle et al. 2013; Salk et al. 2011; Tyler et al. 2008; Webster et al. 2005; White 2012). We found that tree seedlings generally survived better (18–23 %) when protected from browsers. Tifft is home to a large population

Fig. 3 Effect of woody basal area (cm^2 ha^{-1}) on seeds (seed trap^{-1}) at Tifft Nature Preserve (Buffalo, NY). Seeds increased significantly with larger woody area up to approximately 4 cm^2 ha^{-1}, but declined with greater woody area

of *O. virginianus* (Spiering 2009, *pers. Obs.*), and intense herbivory by *O. virginianus* is well documented in other studies (Gill and Morgan 2010; MacDougall and Turkington 2007; Rooney et al. 2002; White 2012). Hence, deer browsing also likely contributed to the difference in seedling survival between protected and unprotected plots.

Habitat quality limited recruitment, but Tifft also lacked seed emigration by mid-successional tree species. Instead, the dominant canopy tree, *P. deltoides,* which is an early successional species, constituted 100 % of seeds in the grassland seed traps and 99 % of the seeds in forest traps. The other dominant woody species, e.g., *R. catharctica* and *C. amomum*, were found in the seed traps, though no *Pinus* spp. were captured. Certainly, the seed collection was confounded by time of year, and temporal variations in mast output. *Populus deltoides* produces very small, downy seeds that are very capable of long-distance dispersal in great numbers (Cain et al. 2000). Urban forests rely heavily on local seed sources due to their isolated, "island-like" placement in an otherwise human-dominated landscape (Sullivan et al. 2009). Mid- to late-successional tree species generally produce fewer, larger seeds which are less likely to disperse long distances (Chen et al. 2014; Dalling et al. 1998). Hence, urban forests may initiate relatively easily through the long-distance dispersal of early successional trees, but may not progress to a typical and species diverse mature forest without receiving the poor-dispersing mid-successional tree species harbored in distant wildland forests (Manion and Griffin 2001; Runkle 2000). At Tifft, our observations suggest that canopy gaps are filled by invasive shrubs with no indication of native tree recruitment.

In the absence of ongoing tree recruitment, the urban forest canopy structure will shift to a different vegetation structure with time. A widely-held conceptual model of succession predicts that following disturbance, short-lived species with rapid growth rates, such as *P. deltoides*, should initially dominate forest canopies, but later successional stages include slower growing, shade-tolerant trees that come to dominate with time (e.g., Crawley and Ross 1990). Industrial disturbances at Tifft exposed large areas of bare soil and newly established *P. deltoides* seedlings experienced little competition (Spiering 2009). Moreover, this sparsely vegetated post-industrial urban landscape initially harbored few herbivores and granivores. With trees came tree seed and seedling predators, and competing vegetation, which appear to create an impenetrable recruitment barrier for the trees. Without active management such as tree plantings that are protected from browsers, as well as the suppression of nonnative understory shrubs, the forested patches may transition from tree-dominated to (invasive) shrub-dominated in the coming decades.

Current management activities at Tifft include efforts to control invasive species, such as *R. catharctica,* and introduce native woody species, such as *Quercus* spp. With invasive species removal and protection from early browsers, native tree species introductions are successful at Tifft (*see* Grunzweig et al. 2015). Hence, the only input of native diversity has occurred through active management. The continued growth of cities places increased needs and strains on urban forests (McKinney 2008; Shen et al. 2008; Wania et al. 2006). Urban forests typically have lower abundance and lower emigration of native tree species than their wildland counterparts (Michalak 2011; Overdyck and Clarkson 2012; Pennington et al. 2010; Trammell and Carreiro 2011) and tree recruitment failure without rescue from long-distance dispersal suggests that urban forests have limited 'natural' viability. Hence, anthropogenic forest viability and diversity may require anthropogenic intervention.

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