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### Forest Sustainability in an Altered Landscape Requires Human Intervention

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Forest Sustainability in an Altered Landscape Requires Human Intervention

by

Adam C. Labatore

An Abstract of a Thesis

in

Biology

Submitted in Partial Fulfillment  
of the Requirements  
for the Degree of

Master of Arts

May 2015

Buffalo State College  
State University of New York  
Department of Biology

## ABSTRACT OF THESIS

### Forest Sustainability in an Altered Landscape Requires Human Intervention

Recruitment success determines the abundance and composition of plant communities. Successful recruitment can be summarized as a simple dichotomy of establishment versus seed limitations. Establishment limitation occurs when plant populations are inhibited by habitat availability and quality, whereas seed limitation occurs when seeds fail to arrive in necessary densities. Recruitment failure undermines overstory sustainability if the existing trees cannot replace themselves. Preliminary analysis indicated tree recruitment failure at an urban nature preserve with too few tree seedlings to replace mature canopy trees. These data suggested that the urban forest was not sustainable. The overarching goal of the study was to test whether establishment or seed limitation explained the recruitment failure. Given that 90% of seeds are killed by unsuitable habitat conditions it was hypothesized that establishment limitation would best explain the limited recruitment. This hypothesis was tested using field experiments with introduced native tree seeds. However, environmental limitations are of little consequence if the seeds fail to arrive. This alternative hypothesis was tested using seed traps to capture dispersed seeds. Seedling recruitment varied by tree species, and it increased significantly with herbivore/granivore exclusion in experimental plots. Seed rain correlated significantly with immediately proximate parent plants, but seeds from species beyond 50 m of the experimental plots were not present in seed traps. These results suggested that habitat quality, particularly granivory and competition, limited recruitment at local scales in the urban forest whereas long-distance dispersal limited seed availability beyond local species.

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## Introduction

Urban forests are planned, designed, and managed on municipal lands to maximize environmental, social, and economic benefits for humans (Johnson et al. 1990). Whereas rural forests often cover large tracts of land, typically located far from urban centers, urban forests are smaller and occur within highly altered landscapes closer to urban populations (DEC 2014). We can think of urban forests as green islands in an archipelago of other green landscapes surrounded by an ocean of developed areas. Given their isolation in an altered landscape, the viability of urban forest canopy regeneration is doubtful, but unknown (Oldfield et al. 2013). Are they sustainable forests or long-lived gardens (requiring constant management)? Urban forest canopy sustainability may be defined by the regenerative capacity of the existing canopy trees (Wiersum 1995), but there is a paucity of scientific studies investigating the growth, survival, and regeneration of native urban forest trees – particularly those investigating seed recruitment dynamics (Oldfield et al. 2013).

Most plant mortality (90%) occurs during the earliest life stages (Harper 1977; Fenner & Kitajima 1999). As such, recruitment (seedling establishment and survival) is the critical life history stage in determining species distributions and community trajectories (Grubb 1977; Eriksson & Ehrlén 1992; Crawley 2000; Turnbull et al. 2000; Warren & Bradford 2011). Successful recruitment can be summarized in a simple dichotomy of establishment (suitable habitat) versus seed (dispersal) limitations. Establishment limitation is present when plant populations are inhibited by habitat availability and quality (Clark et al. 1998; Nathan & Muller-Landau 2000), whereas seed limitation occurs when seeds fail to arrive in necessary densities for recruitment (Eriksson & Ehrlén 1992; Nathan & Muller-Landau 2000; Turnbull et al. 2000; Svenning & Wright 2005). Recruitment limitation can undermine overstory sustainability 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 & Muller-Landau 2000). This can be the result of over-browsing by herbivores (Pastor et al. 1993; Webster et al. 2005; Tyler et al. 2008; White 2012; Nuttle et al. 2013). Herbivores may alter plant communities by preferentially feeding on select species (Pastor et al. 1993; White 2012) 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 *Odocoileus virginianus* (white-tailed deer) browsing can lead to total recruitment failure for many plant species (Pastor et al. 1993; Webster et al. 2005; White 2012; Nuttle et al. 2013). White (2012) found that unprotected planted species preferred by *O. virginianus* suffered near complete recruitment failure, whereas conspecifics that were protected in enclosures showed significant recruitment success. This effect also occurs with rodents. For example, 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. Competition for space (Yodzis 1978; Roughgarden & Iwasa 1985; Hughes et al. 1991) and resources such as light and nitrogen can impact recruitment (Tilman 1987; Zeiter et al. 2006; MacDougall & Wilson 2007). Shrub thickets in forests reduce canopy tree recruitment (Frappier et al. 2003; Fagan & Peart 2004) through shading, altering soil moisture, pH, carbon, and nitrogen dynamics (Heneghan et al. 2006). Grasslands are dominated by species of grasses that have traits that inhibit canopy species, such as dense, fibrous root networks that outcompete woody species for nutrients (Pärtel & Wilson 2002). Grasses typically outcompete trees in the seedling and sapling stage when trees and grasses share the same belowground rooting space (Bond 2008).

Disturbance, such as fire, can disrupt competitive advantages by removing or reducing established grass cover and freeing up the resources required for tree recruitment (Keeley 1977; Pickett & White 1985; Bond & Midgley 2001; Jutila & 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 (Eriksson & Ehrlén 1992, Nathan & Muller-Landau 2000, Turnbull et al. 2000, Clark et al. 2007). Two forms of seed limitation occur: (1) source limitation, in which not enough seeds are produced for successful recruitment (Clark et al. 2007), and (2) dispersal limitation, in which seeds do not reach suitable habitat in spite of plentiful production (Clark et al. 2007). Given that introducing seeds to experimental plots generally increases plant populations (Eriksson & Ehrlén 1992; Primack & Miao 1992; van der Meijden et al. 1992; Crawley & Brown 1995; Ackerman et al. 1996; Clark et al. 1998; Coulson et al. 2002; Clark et al. 2007; Piqueray et al. 2013) it is likely that unoccupied suitable habitat is common (Pulliam 2000).

If seed source is an important factor in limiting recruitment, understanding the influence spatial scales have on seed availability becomes critical. We need to know how different species' seed sources at local and broad scales determine success in recruitment. For example, at local levels, in the same habitat, woody species incapable of saturating the forest floor with seeds, such as *Carya* (hickories), *Cornus* (dogwoods), *Nyssa* (tupelos), and *Oxydendrum* (sorrels), may occupy the same stands as species capable of completely covering the forest floor with seeds, such as *Acer* (maples), *Betula* (alders), and *Liriodendron* (tuliptrees [Clark et al. 1998]). At regional scales, however, high fecundity in wind-dispersed species reduces the importance of immediate proximity to suitable microsites compared to short distance dispersers that lack

sufficient long distance dispersal (Clark et al. 1998; Cain et al. 2000; Nathan & Muller-Landau 2000).

Given that preliminary analysis indicated tree recruitment failure at Tifft Nature Preserve in Buffalo, NY (USA), an urban nature preserve dominated by a mature cottonwood forest canopy, I investigated the mechanisms that might explain forest sustainability. These data suggested that the urban forest was not sustainable with too few seedlings to replace mature canopy trees. Although cottonwoods do not recruit well in mature canopies due to germination requirements for bare soil and full sunlight (Engstrom 1948; Bradley & Smith 1986), shade tolerant seedlings of middle to late successional tree species should be present (Bonser & Aarsen 1994; Abrams & Orwig 1996). The overarching goal of this study was to test whether establishment or seed limitation explained recruitment failure at Tifft Nature Preserve. Given that 90% of seeds are killed by unsuitable habitat conditions, it was hypothesized that establishment limitation would best explain the limited recruitment. This hypothesis was tested using manipulative (herbivory exclusion and burning) field experiments with experimentally planted tree seeds (three species). Given that habitat limitations are of little consequence if the seeds fail to arrive, I also tested whether the urban forest's canopy was seed limited using seed traps.

## **Methods**

### *Study site*

Tifft Nature Preserve (hereafter, "Tifft") is a 107 ha urban nature preserve administered by the Buffalo Museum of Science. The preserve is a former brownfield (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 at an elevation of 183 m and it is surrounded by former industrial sites, railyards, and other intensely developed areas. The site receives strong winds all year-round due to its proximity to the western shore of Lake Erie. Tifft contains two major habitats — deciduous forest (“woodlands”) and grassland (“grasslands”) — used in this study. The dominant canopy species in the woodlands is *Populus deltoides* (eastern cottonwood), but other genera are present, including *Pinus* (pines), *Acer*, *Salix* (willows), *Ailanthus* (tree of heaven), and *Rhamnus cathartica* (common buckthorn), a woody invasive that dominates the shrub-layer. The grasslands consist of rolling hills covering a sealed landfill (Spiering 2009). It is dominated by grasses, but a few tree and shrub species are present, such as *P. deltoides* and *R. cathartica*. Past industrial dredging and dumping has resulted in a soil base composed of natural and artificial materials, resulting in variable soil composition throughout the preserve that can change radically over short distances, horizontally and vertically (Spiering 2009). The soil is shallow with an underlying mixture of industrial waste, generally alkaline (pH: 7.6-7.8), and it contains high levels of potassium, magnesium, calcium, and varying levels of phosphorus (Klips et al. 1993).

### *Survey data*

Tree size class distributions can be linked with demographic patterns in tree stands to infer population trajectories (Shimano 2000). For example, sustainable overstories require far more seedlings than the mature canopy trees they may one day replace. Tree abundance, species richness, and basal area were measured in the woodlands and grasslands habitats in August 2013 to determine overstory composition and structure. Three random transects were established in each of the woodlands and grasslands areas ( $n = 6$  total transects) with 1 m<sup>2</sup> 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. To avoid edge effects, no plot was located within 50 m of habitat borders, man-made trails, or preserve boundaries. Each plot was sampled for seedling abundance and cover for all woody species within the 1 m<sup>2</sup> plots. Overstory (DBH > 10 cm) and understory (DBH < 10 cm) abundances were sampled using point-centered quarter method (Dix 1960) up to 50 m from 1 m<sup>2</sup> plots.

#### *Seed introduction and habitat manipulation*

Twelve randomly stratified experimental grids ( $n = 6$  in woodlands and  $n = 6$  in grasslands) were established in May 2014 to measure recruitment success in canopy species. Each grid included four, 0.25 m<sup>2</sup> treatment plots separated by 0.5 m (Fig. 1). Each treatment plot included three subplots planted with one of three study trees: *Populus deltoides*, *Pinus strobus* (eastern white pine), and *Acer saccharum* (sugar maple) in random arrangements. *Populus deltoides* was included in the study because it represents the dominant canopy species at Tiff Nature Preserve. *Acer saccharum* was chosen for this study as it is a shade tolerant late-successional species (Bonser & Aarsen 1994). *Pinus strobus* represents a canopy species that is successful in both early and middle successional habitats (Abrams & Orwig 1996) and it has a high germination rate. The seeds were pre-mixed with, and dampened in, approximately 20 g of commercial potting soil. A 15.2 cm circular PVC cylinder was used to create a 15.2 cm diameter x 2.5 cm deep depression in each subplot where the seeds were packed with potting soil (Fig. 1). 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 species<sup>-1</sup>). Inspections of the grids for emerging seedlings were conducted every two weeks May 2014 to October 2014. All plant material in the plots was removed in October, dried at 65° C for 48 hours, and weighed to determine above ground plant biomass and assess the competitive environment.

Field manipulations were conducted to test habitat limitations on the recruitment of each study species in a classic factorial design (Fig. 1). The treatments were: burning (entire 0.25 m<sup>2</sup> treatment plot was burned with a propane torch [VT 3-30 C propane torch, Flame Engineering Inc., Lacrosse, KS, USA]) in May 2014, herbivore exclusion (PVC frame secured to the ground with rebar and covered by netting), and burning + herbivore exclusion. Each grid also included a control plot with no treatments. The spatial arrangement of treatments was randomized.

#### *Seed rain*

Tree seed rain was measured to assess seed availability. Twenty-four, 0.25 m<sup>2</sup> x 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/>). Collection of seeds occurred every two weeks May 2014 to October 2014 to capture variation in seed dispersal phenology. In addition, point-centered quarter method (Dix 1960) was used to survey trees 50 m around seed traps in order to compare seed rain species composition with standing overstory and understory woody composition.

#### *Habitat conditions*

Available diffuse light 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 percentage 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 at each plot in both habitats in conjunction with the measurements for volumetric soil moisture percentage to measure soil temperature.

### *Data Analysis*

A canopy size-class distribution for Tiffy was built using tree DBH data with seedlings as the smallest class. Recruitment success was considered in two parts: Germination success (successful germination/20 seeds planted) and seedling survival success (survived seedlings/germinated seeds). Student's *t*-tests were used to determine the difference between canopy stems and basal area per habitat. Germination and survival success as a function of habitat and experimental treatments 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). Given that both models were overdispersed ( $\phi > 2.5$ ), quasibinomial error distributions were used. The germination and survival models included habitat (woodlands, grasslands), treatments (burn, exclusion, control, burn + exclusion), species (*A. saccharum*, *P. deltoides*, *P. strobus*), and interactions terms (habitat x treatment, habitat x

species, and treatment x species.) The “car” package (Fox & 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

### *Survey Data*

Mid-sized trees dominated the size class distribution. There were far fewer seedlings and saplings than mid-sized trees (Fig. 2a). *Populus deltoides* (62%) was by far the most common canopy species, followed by *P. strobus* (18%), *Fraxinus pennsylvanica* (green ash, 5%), *Rhus typhina* (sumac, 4%), and then ten other species (~11%). Significantly greater stems per plot ( $t$ -value = 5.743,  $df$  = 50.682,  $p$ -value < 0.001) were found in the woodland habitat (mean  $\pm$ SE, 3.3  $\pm$  0.2 stems) than in the grassland habitat (1.5  $\pm$  0.2 stems). Standing canopy vegetation comprised significantly higher amounts of basal area per plot ( $t$ -value = 4.623,  $df$  = 29.697,  $p$ -value < 0.001) in the woodlands (10.3 m<sup>2</sup>  $\pm$  1.6) than in the grasslands (2.6 m<sup>2</sup>  $\pm$  0.5).

### *Seed introduction and habitat manipulation*

A significant habitat x species interaction term ( $df$  = 2, deviance = 75.787, residual  $df$  = 135,  $p$ -value < 0.001) indicated that germination success was higher in the woodlands than grasslands habitat for *P. strobus*, but not for either *P. deltoides* or *A. saccharum* (Fig 3). A significant

treatment x species interaction term ( $df = 6$ ,  $deviance = 107.343$ ,  $residual\ df = 129$ ,  $p\text{-value} < 0.001$ ) also indicated species specific treatment responses. *Acer saccharum* germination was lower than the other two species, but differed little between treatments (Fig. 4). *Pinus strobus* germination was higher than *A. rubrum*, and it did much better with herbivore exclusion than the other treatments. *Populus deltoides* germination was much greater in the burn treatments (burn and burn + exclusion) where it also exhibited far greater germination success than the other tree species. The habitat x treatment interaction also was significant for germination ( $df = 3$ ,  $deviance = 19.405$ ,  $residual\ df = 126$ ,  $p\text{-value} < 0.05$ ). Germination under all treatments except burn + exclusion was higher in the woodlands than grasslands (Fig. 5). Germination success significantly correlated negatively ( $coeff. = -0.006367$ ,  $SE = 0.001892$ ,  $t\text{-value} = -3.364$ ,  $p\text{-value} < 0.001$ ) with increased competitor biomass (Fig. 6). This effect, however, did not convey a significant impact on seedling survival ( $coeff. = -0.002723$ ,  $SE = 0.003185$ ,  $t\text{-value} = -0.855$ ,  $p\text{-value} = 0.396$ ).

Seedling survival was species specific ( $df = 2$ ,  $deviance = 16.615$ ,  $residual\ df = 52$ ,  $p\text{-value} < 0.05$ ), with *A. saccharum* surviving at higher rates than *P. deltoides* but no difference between *P. strobus* and the other two species (Fig. 7). Survival was significantly higher for all species in the exclusion treatments than burn treatment or control ( $df = 3$ ,  $deviance = 47.072$ ,  $residual\ df = 54$ ,  $p\text{-value} < 0.001$ ; Fig. 8). Survival did not change with habitat ( $df = 1$ ,  $deviance = 2.007$ ,  $residual\ df = 57$ ,  $p\text{-value} = 0.346$ ).

### Seed rain

Seed rain abundance was significantly dependent on woody basal area ( $coeff. = 33.35$ ,  $SE = 10.63$ ,  $t\text{-value} = 3.137$ ,  $p\text{-value} < 0.05$ ) with higher amounts of seeds found in plots with more

large trees and shrubs (Fig. 9). Only four species of woody plants (Table 1) were found in the seed traps (*R. cathartica*, *P. deltoides*, *R. typhina*, *Cornus* spp.), and all of them occur at Tifft.

## Discussion

Tree canopy recruitment at Tifft is limited by habitat quality at local scales and seed limitation at larger scales. Herbivore exclusion and fire disturbance helped establish experimentally planted regionally common tree species in both woodland and grassland habitats where they are otherwise uncommon. Hence, Tifft only receives local seed rain that lands in habitat made unsuitable by high levels of granivory and competition. These results suggest that urban forest habitat is not sustainable without anthropogenic management.

Seedling recruitment starts with germination, and I found tree germination highly dependent on burning for two of the three introduced species (Fig. 4). The need for habitat disturbance for tree germination is well documented (Henry & Swan 1974; Runkle 1982; Armesto & Pickett 1985; Canham & Marks 1985; Rankin & Pickett 1989; Peroni 1994; Elliot et al. 1997; Hubbell et al. 1999; Warren et al. 2004). *Pinus strobus* germination increased by 25% when sown in a forested habitat as compared to the grassland (Fig. 3), and *P. deltoides* increased germination 15-17% when fire disturbance removed vegetation (Fig. 4). Both species are epigeal and generally germinate successfully under full sun exposure (Engstrom 1948; Balmer & Williston 1983) and thus grass cover appeared to create unfavorable conditions for germination.

Seeds are an important component of many mammal diets (Jameson 1952; Drożdż 1966; Abbott & Quink 1970; Everett et al. 1978; Merritt & Merritt 1978; Price & Jenkins 1986; Kelt et al. 1996; Sivy et al. 2011; Connolly et al. 2014; Lobo 2014). As such, seed predator behavior influences post dispersal plant recruitment (Abbott 1961; Radvanyi 1970; Reichman 1979;

Inouye et al. 1980; Sullivan & Sullivan 1982; Schupp & Fuentes 1995; Côté et al. 2003; Peters et al. 2004). Whereas granivorous mammals typically act as generalists due to the widely strewn and irregular quality and quantity of available seeds (Hulme & Benkman 2002), seed mass generally serves as a proxy for nutritional content that drives small mammals to prefer larger seeds (Vander Wall 2010; Hulme 1998; Wang & Chen 2009). In this study, germination rates for the relatively larger *A. saccharum* and *P. strobus* seeds were higher when protected inside enclosures, but protecting the much smaller *P. deltoides* seeds did little for germination, even in optimal conditions of bare soil and direct sunlight (Table 2).

Herbivores pose large impacts on plants that make it to the seeding stage (Pastor et al. 1993; Webster et al. 2005; Tyler et al. 2008; Salk et al. 2011; White 2012; Nuttle et al. 2013). Seedlings of the introduced tree species generally survived at higher rates (18-23%) when protected from browsers (Fig. 8) indicating that survival is linked with reduced herbivory. A large *O. virginianus* population dominates the study site (Spiering 2009, pers. obs.). Herbivory by *O. virginianus*, as displayed in previous studies (Pastor et al. 1993; Stromayer & Wilson 1997; Rooney et al. 2002; MacDougall & Wilson 2007; Gill & Morgan 2010; White 2012) may account for differences in survival rates among protected and unprotected plots. Survival also differed between species indicating preferential browsing may be present (Fig. 7). Although seedling size differences and detectability could account for the species-specific survival rates, in this case using size as a proxy for preference was unlikely. *A. saccharum* and *P. strobus* seedlings were much larger and more apparent within the plots than *P. deltoides* seedlings (Table 2), though the latter species had the lowest survival rate.

Whereas habitat quality limited recruitment, Tiffet also lacked availability of seed emigration by successional tree species. *Populus deltoides* constituted 100% of seeds by

abundance in grasslands seed traps and 99% of seeds by abundance in woodlands seed traps, indicating this species was a better disperser than any other tree at Tifft (Table 1). These results demonstrate that influx of this species may represent a consistent source of seeds. However, neither a persistent nor a transient seed reserve of middle to late successional species was able to accumulate, indicating a poor outlook for sustaining the canopy (Baskin & Baskin; Thompson & Grime 1979). These characteristics do not necessarily apply to species, like *P. deltoides*, that are characterized by long-distance dispersal (> 500 m, Cain et al. 2000; maximum 1000 m, Feekes 1936), high fecundity (~400 seeds cm<sup>-2</sup> basal area, Cain et al. 2000), and rapid growth, in open canopies and disturbed habitat. Urban green spaces rely heavily on existing localized individuals for seed source, as availability of nearby sources of short range seed dispersers are virtually non-existent due to the isolated, “island-like” nature of these forests (Sullivan et al. 2009).

Furthermore, Clark et al. (1998) correlated fecundity (seed production per cm<sup>2</sup> basal area) positively to mean dispersal distance for 14 canopy species indicating, as this study verifies, that seedling recruitment of many species in a particular location is restricted by proximity to reproducing adults.

Establishing whether recruitment in plant populations is seed or habitat limited is crucial to understanding population trajectories. If a landscape receives sufficient seed input, then failures in recruitment may be due to limitations in habitat via interspecific competition or by seed predators and herbivores (Crawley & Ross 1990). If it does not receive seeds, then the quality of habitat is irrelevant (Eriksson & Ehrlén 1992, Nathan & Muller-Landau 2000, Turnbull et al. 2000, Clark et al. 2007). The results presented here suggest that urban forest recruitment was limited by a combination of both seed and establishment limitation, as is recruitment in many non-urban systems (Eriksson and Ehrlén 1992, Clark et al. 2007, Poulsen et

al. 2007, Warren et al. 2012). However, due to the diverse mechanisms at work limiting seedling recruitment here and the relatively short duration of this study (~1 year), it may be worth exploring each mechanism in deeper detail over longer periods of time in future research to help discern differences in the intensities of limiting factors at similar urban landscapes.

Whereas the regeneration of the existing canopy is required for sustainability, other successional trajectories could be considered without management intervention. Simple models of succession indicate that short-lived overstory species with rapid growth rates, such as *P. deltoides*, should initially dominate forest canopies, but later successions should be characterized by slower growing trees (Crawley 1997). With this type of succession later successional tree species have lower mortality than the non-native and pioneer species so that they eventually become the dominant overstory species (Crawley 1997). The initial colonization of the Tifft forest occurred immediately after landfill capping in conditions of bare soil and very little competition for newly established seedlings (Spiering 2009). At the current trajectory, without management intervention, Tifft's succession is headed toward a grass and shrub dominated landscape with few trees to close a canopy.

The continued growth of cities (UN 2014) will place increased needs and strains on urban forests (Wania et al. 2006; McKinney 2008; Shen et al. 2008). Urban forests typically have lower abundance and lower emigration of native tree species than their rural counterparts (Burton et al. 2005; Pennington et al 2010; Michalak 2011; Trammell & Carreiro 2011; Overdyck & Clarkson 2012). Tree recruitment failure suggests that urban forest canopy species have limited sustainability. Long-distance dispersal recruitment failure indicates that 'natural' recruitment rescue is unlikely. These results demonstrate that urban forest recruitment is limited



on several fronts, from local to regional scales, so that sustaining man-made forests require man-made interventions.

## References

- Abbott, H.G. 1961. White pine seed consumption by small mammals. *Journal of Forestry* 59:197-201.
- Abbott, H.G., Quink, T.F. 1970. Ecology of eastern white pine seed caches made by small mammals. *Ecology* 51:271-278.
- Abrams, M.D., Orwig, D.A. 1996. A 300-year history of disturbance and canopy recruitment for co-occurring white pine and hemlock on Allegheny Plateau, USA. *Journal of Ecology* 84(3):353-363.
- Ackerman, J.D., Sabat, A., Zimmerman, J.K. 1996. Seedling establishment in an epiphytic orchid: an experimental study of seed limitation. *Oecologia* 106(2):192-198.
- Albrecht, M.A., McCarthy, B.C. 2009. Seedling establishment shapes the distribution of shade-adapted forest herbs across a topographical moisture gradient. *Journal of Ecology* 97:1037-10.
- Anderson, W.P., Kanaroglou, P.S., Miller, E.J. 1996. Urban form, energy and the environment: a review of issues, evidence and policy. *Urban Studies* 33:7-35.
- Armesto, J.J., Pickett, S.T.A. 1985. Experiments on disturbance in old-field plant communities: impact on species richness and abundances. *Ecology* 66:230-240.
- Baskin, J.M., Baskin, C.C. 1978. The seed bank in a population of endemic plant species and its ecological significance. *Biological Conservation* 14:125-130.
- Bakker, J.P., Poshchod, P., Strykstra, R.J., Bekker, R.M., Thompson, K. 1996. Seed banks and seed dispersal: important topics in restoration ecology. *Acta Botanica Neerlandica* 45:461-490.
- Balmer, W.E., Williston, H.L. 1983. Managing eastern white pine in the Southeast. USDA Forest Service, Forestry Report R8-FR1. Southern Region. 11p; Robert W. Wilson and William F. McQuilkin. 1965. In *Silvics of Forest Trees of the United States*. Pp. 329-337. In H.A. Fowells, comp. U.S. Department of Agriculture, Agriculture Handbook 271. Washington, D.C.

- Bond, W.J. 2008. What limits trees in C<sub>4</sub> grasslands and savannas? *Annual Review of Ecology, Evolution, and Systematics* 39:641-659.
- Bonser, S.P., Aarssen, L.W. 1994. Plastic allometry in young sugar maple (*Acer saccharum*): adaptive responses to light availability. *American Journal of Botany* 81(4):400-406.
- Bond, W.J., Midgeley, J.J. 2001. Ecology of sprouting in woody plants: the persistence of niche. *Trends in Ecology and Evolution* 16(1):45-51.
- Brack, C.L. 2002. Pollution mitigation and carbon sequestration by an urban forest. *Environmental Pollution* 115(1):S195-S200.
- Bradley, C.E., Smith, D.G. 1986. Plains cottonwood recruitment and survival on a prairie meandering river floodplain, Milk River, southern Alberta and northern Montana. *Canadian Journal of Botany* 64:1433-1442.
- Brown, J.H., Heske, E.J. 1990. Control of a desert-grassland transition by a keystone rodent guild. *Science* 250:1705-1707.
- Burton, M., Samuelson, L., Pan, S. 2005. Riparian woody plant diversity and forest structure along an urban-rural gradient. *Urban Ecosystems* 8:93-106.
- Cain, M.L., Milligan, B.G., Strand A.E. 2000. Long-distance dispersal in plant populations. *American Journal of Botany* 87(9):1217-1227.
- Canham, C.D., Marks, P.L. 1985. The response of woody plants to disturbance: patterns of establishment and growth. Pp. 201-216. In S.T.A. Pickett and P.S. White (eds.) *The Ecology of Natural Disturbances and Patch Dynamics*. Academic Press, Orlando, FL, USA.
- Chourmert, J., Salanié, J. 2008. Provision of urban green spaces: some insights from economics. *Landscape Research* 33:331-345.
- Clark, J.S., Macklin, E., Wood, L. 1998. Stages and spatial scales of recruitment limitation in southern Appalachian forests. *Ecological Monographs* 68:213-235.
- Clark, C.J., Poulsen, J.R., Levey, D.J., Osenber, C.W. 2007. Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. *American Naturalist* 170(1):128-142.
- Connolly, B.M., Pearson, D.E., Mack, R.N. 2014. Granivory of invasive, naturalized, and native plants in communities differentially susceptible to invasion. *Ecology* 95:1759-1769.

- Côté, M., Ferron, J., Gagnon, R. 2003. Impact of seed and seedling predation by small rodents on early regeneration establishment of black spruce. *Canadian Journal of Forest Research* 33:2362-2371.
- Cottrell, T.R. 2004. Seed rain traps for forest lands: consideration for trap construction and study design. *Journal of Ecosystems and Management* 5(1):1-6.
- Coulson, S.J., Bullock, J.M., Stevenson, M.J., Pywell, R.F. 2002. Colonization of grassland by sown species: dispersal versus microsite limitation in responses to management. *Journal of Applied Ecology* 38:204-216.
- Crawley, M.J. 2000. Seed predators and plant population dynamics. Pp. 167-183. In M. Fenner (ed.) *Seeds: ecology of regeneration in plant communities*. CABI.
- Crawley, M.J., Brown, S.L. 1995. Seed limitation and the dynamics of feral oilseed rape on the M25 motorway. *Proceedings of the Royal Society of London: Biological Sciences* 259(1354):49-54.
- Crawley, M.J., Ross, G.J.S. 1990. The population dynamics of plants. *Philosophical Transactions of the Royal Society of London: Biological Sciences* 330:125-140.
- Dalling, J.W., Hubbell, S.P. 2002. Seed size, growth rate and gap microsite conditions as determinants of recruitment success for pioneer species. *Journal of Ecology* 90:557-568.
- DeCalesta, D.S. 1994. Deer and diversity in Allegheny hardwood forests: managing an unlikely challenge. *Landscape and Urban Planning* 28:47-53.
- Department of Environmental Conservation. 2013. Urban and community forestry report.
- Dix, R.L. 1960. An application of the point-centered quarter method to sampling of grassland vegetation. *Journal of Range Management* 14:63-69
- Drożdż, A. 1966. Food habits and food supply of rodents in the beech forest. *Acta Theriologica* 11:363-384.
- Dwyer, J.F., Nowak, D.J., Noble, M.H. 2003. Sustaining urban forests. *Journal of arboriculture* 29(1):49-55
- Elliott, K.J., Boring, L.R., Swank, W.T., Haines, B.R. 1997. Successional changes in plant species diversity and composition after clearcutting a southern Appalachian watershed. *Forest Ecology and Management* 92:67-85.
- Engstrom, A. 1948. Growing cottonwood from seed. *Journal of Forestry* 46(2):130-132.

- Eriksson, O., Ehrlén, J. 1992. Seed and microsite limitation of recruitment in plant populations. *Oecologia* 91:360-364.
- Everett, R.L., Meeuwig, R.O., Stevens, R. 1978. Deer mouse preference for seeds of commonly planted species, indigenous weed seed, and sacrifice food. *Journal of Range Management* 31:70-73.
- Fagan, M., Peart, D. 2004. Impact of the invasive shrub glossy buckthorn (*Rhamnus frangula* L.) on juvenile recruitment by canopy trees. *Forest Ecology and Management* 194:95-107.
- Feekes, W. 1936. De ontwikkeling van de natuurlijke vegetatie in de Wieringermeer-polder, de eerste groote droogmakerij van de Zuiderzee. *Nederlandsch Kruidkundig Archief* 46:1-294.
- Felfoldi, E. 1980. Seed Counts (Numbers of Seeds per Unit Weight). Technical Report Series, 32. Government of Victoria, Department of Agriculture.
- Fenner, M., Kitajima, K. 1999. Seed and seedling ecology. Pp. 589-611. In F.I. Pugnaire and F. Valladares (eds.) *Handbook of Functional Plant Ecology*. New York, NY: Marcel-Dekker.
- Food and Agriculture Organization of the United Nations. 1975. Forest Tree Seed Directory. Forest Service. 1974. Seeds of Woody Plants in the United States. Agriculture Handbook Number 450. Forest Service, U.S. Department of Agriculture, Washington, D.C.
- Fox, J., Weisberg, S. 2011. An {R} Companion to Applied Regression. Second Edition. Thousand Oaks CA: Sage.
- Frappier, B., Lee, T.D., Olson, K.F., Eckert, R.T. 2003. Small-scale invasion pattern, spread rate, and lag-phase behavior of *Rhamnus frangula* L. *Forest Ecology and Management* 186:1-6.
- Fredericksen, T.S. 1998. Impacts of logging and development on central Appalachian forests. *Natural Areas Journal* 18:175-178.
- Gaffin, S.R., Rosenzweig, C., Kong, A.Y.Y. 2012. Correspondence: adapting to climate change through urban green infrastructure. *Nature Climate Change* 2:704.
- Gill, R.M.A., Morgan, G. 2010. The effects of varying deer density on natural regeneration in woodlands in lowland Britain. *Forestry* 83(1):53-63.
- Grubb, P.J. 1977. Maintenance of species-richness in plant communities- importance of regeneration niche. *Biological Reviews* 52:107-145.

- Harper, J.L. 1977. Population biology of plants. New York, NY: Academic Press.
- Healy, W.M. 1997. Influence of deer on the structure and composition of oak forests in central Massachusetts. Pp. 246-266, *In* W.J. McShea, H.B. Underwood, and J.H. Rappole (Eds.). The Science of Overabundance: Deer Ecology and Population Management Smithsonian Institution Press, Washington, DC.
- Heneghan, L., Fatemi, F., Umek, L., Grady, K., Fagen, K., Workman, M. 2006. The invasive shrub European buckthorn (*Rhamnus cathartica* L.) alters soil properties in Midwestern US woodlands. *Applied Soil Ecology* 32(1):142-148.
- Henry, J.D., Swan, J.M.A. 1974. Reconstructing forest history from live and dead plant material-an approach to the study of forest succession in southwest New Hampshire. *Ecology* 55:772-783.
- Horsley, S.B., Stout, S.L., deCalesta, D.S. 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. *Journal of Applied Ecology* 13:98-118.
- Howe, H.F., Brown, J.S. 2000. Early consequences of rodent granivory on synthetic forb communities. *Ecological Applications* 10:917-924.
- Howe, H.F., Brown, J.S. 2001. The ghost of granivory past. *Ecology Letters* 4:371-378.
- Hubbell, S.P., Foster, R.B., O'Brien, S.T., Harms, K.E., Condit, R., Wechsler, B., Wright, S.J., de Lao, S.L. 1999. Light-gap disturbances, recruitment limitations, and tree diversity in a neotropical forest. *Science* 283:554-557.
- Hughes, R.F., Vitousek, P.M., Tunison, J.T. 1991. Effects of invasion by fire-enhancing C<sub>4</sub> grasses on native shrubs in Hawaii Volcanoes National Park. *Ecology* 72:743-746.
- Hulme, P.E. 1998. Post-dispersal seed predation: consequences for plant demography and evolution. *Perspectives in Plant Ecology, Evolution and Systematics* 1:32-46.
- Hulme, P.E., Benkman, C.W. 2002. Granivory. Pp. 132-154. *In* C.M. Herrera, O. Pellmyr (eds.) Plant-animal interactions: An evolutionary approach. Blackwell, Oxford.
- Inouye, R.S., Byers, G.S., Brown, J.H. 1980. Effects of predation and competition on survivorship, fecundity, and community structure of desert annuals. *Ecology* 61:1344-1351.
- Jameson, E.W. 1952. Food of deer mice, *Peromyscus maniculatus* and *P. boylei*, in the northern Sierra Nevada. *California Journal of Mammals* 33:50-60.

- Juenger, T., Bergelson, J. 2000. Factors limiting rosette recruitment in scarlet gilia, *Ipomopsis aggregata*: seed and disturbance limitation. *Oecologia* 123:358-363.
- Jutala, H.M., Grace, J.B. 2002. Effects of disturbance on germination and seedling establishment in a coastal prairie grassland: a test of the competitive release hypothesis. *Journal of Ecology* 90:291-302.
- Johnson, C.W., Baker, F.A., Johnson, W.S. 1990. Urban & community forestry, a guide to the interior Western United States. USDA Forest Service, Intermountain Region, Ogden, UT.
- Kelt, D.A., Brown, J.H., Heske, E.J., Marquet, P.A., Morton, S.R., Reid, J.R., Rogovin, K.A., Shenbrot, G. 1996. Community structure of desert small mammals: comparisons across four continents. *Ecology* 77:746-761.
- Keeley, J.E. 1977. Seed production, seed populations in soil, and seedling production after fire for two congeneric pairs of sprouting and nonsprouting chaparral shrubs. *Ecology* 58:820-829.
- Kimmins, J.P. 1987. Forest ecology. Macmillan Publishing Company, New York, 531.
- Klips, R.A., Sweeney, C.R., Gall, W.K. 1993. Vascular Plants of Tiff Nature Preserve. Unpublished Report, pp. 76.
- Kollmann, J., Goetze, D. 1998. Notes on seed traps interrestrial plant communities. *Flora*. 193:31-40.
- Leak, W.B., Graber, R.E. 1976. Seedling input, death, and growth in an uneven-aged northern hardwoods. *Canadian Journal of Forest Research* 6(3):368-374.
- Levine, J., Rees, M. 2002. Coexistence and relative abundance in annual plant assemblages: the roles of competition and colonization. *American Naturalist*. 160:452-467.
- Lobo, N. 2014. Conifer seed predation by terrestrial small mammals: A review of the patterns, implications, and limitations of top-down and bottom-up interactions. *Forest Ecology and management* 328:45-54.
- MacDougall, A.S., Wilson, S.D. 2007. Herbivory Limits Recruitment in an Old-Field Seed Addition Experiment. *Ecology* 88(5):1105-11.
- McKinney, M. 2008. Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosystems* 11:161-176.
- Merritt, J.F., Merritt, J.M. 1978. Population ecology and energy relationships of *Clethrionomys gapperi* in a Colorado subalpine forest. *Journal of Mammalogy*. 59:576-598.

- Michalak, J. 2011. Effects of habitat and landscape structure on Oregon white oak (*Quercus garryana*) regeneration across an urban gradient. *Northwest Science* 85:182-193.
- Moore, K.A. 2009. Fluctuating patch boundaries in a native annual forb: the roles of niche and dispersal limitation. *Ecology* 90:378-387.
- Muller-Landau, H.C., Wright, S.J., Calderon, O., Hubbell, S.P., Foster, R.B. 2002. Assessing recruitment limitation: concepts, methods and case-studies from a tropical forest. Pp. 35-53. In D.J. Levey, W.R. Silva, M. Galetti, (eds). *Seed Dispersal and Frugivory: Ecology, Evolution, and Conservation*, CAB International, Wallingford.
- Nathan, R., Muller-Landau, H.C. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution* 15:278-285.
- Nuttle, T., Royo, A.A., Adams, M.B., Carson, W.P. 2013. Historic disturbance regimes promote tree diversity only under low browsing regimes in eastern deciduous forest. *Ecological Monographs* 83(1):3-17.
- Oldfield, E.E., Warren, R.J., Felson, A.J., Bradford, M.A. 2013. Challenges and future directions in urban afforestation. *Journal of Applied Ecology* 50(5):1169-1177.
- Orrock, J.L., Levey, D.J., Danielson, B.J., Damshen, E.I. 2006. Seed predation, not seed dispersal, explains the landscape level abundance of an early-successional plant. *Journal of Ecology* 94:838-845.
- Overdyck, E., Clarkson, B.D. 2012. Seed rain and soil seed banks limit native regeneration within urban forest restoration plantings in Hamilton City, New Zealand. *New Zealand Journal of Ecology* 36:177-190.
- Pfister M., Wilson S.D. 2002. Root dynamics and spatial pattern in prairie and forest. *Ecology* 83:1199-203
- Pastor, J., Dewey, B., Naiman, R.J., McInnes, P.F., Cohen, Y. 1993. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. *Ecology* 74:467-480.
- Pataki, D.E., Carreiro, M.M., Cherrier, J., Grulke, N.E., Jennings, V., Pincetl, S., Pouyat, R.V., Whitlow, T.H., Zipperer, W.C. 2011. Coupling biogeochemical cycles in urban environments: ecosystem services, green solutions, and misconceptions. *Frontiers in Ecology and Environment* 9:27-36.

- Pennington, D.N., Hansel, J.R., Gorchov, D.L. 2010. Urbanization and riparian forest woody communities: diversity, composition, and structure within a metropolitan landscape. *Biological Conservation* 143:182-194.
- Peroni, P.A. 1994. Invasion of red maple (*Acer rubrum* L.) during old field succession in the North Carolina Piedmont: age structure of red maple in young pine stands. *Bulletin of the Torrey Botanical Club* 121:357-359.
- Peters, S.H., Macdonald, S.E., Boutin, S., Moses, R.A. 2004. Post dispersal seed predation of white spruce in cutblocks in the boreal mixedwoods: a short-term experimental study. *Canadian Journal of Forest Research* 34:907–915.
- Pickett, S.T.A., and P.S. White, editors. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, Orlando, Florida.
- Pincetl, S. 2010. Implementing municipal tree planting: Los Angeles million-tree initiative. *Environment Management* 45:227-238.
- Piqueray, J., Saad, L., Bizoux, J., Mahy, G. 2013. Why some species cannot colonise restored habitats? The effects of seed and microsite availability. *Journal for Nature Conservation* 21(4):189-197.
- Population Division of the Department of Economic and Social Affairs of the United Nations Secretariat. 2009. World Population Prospects: The 2008 Revision and World Urbanization Prospects: The 2009 Revision.
- Poulsen, J.R., Osenberg, C.W. Clark, C.J., Levey, D.J., Bolker, B.M. 2007. Plants as reef fish: fitting the functional form of seedling recruitment. *American Naturalist* 170(2):167-183
- Price, M.V., Jenkins, S.H. 1986. Rodents as seed consumers and dispersers. Pp. 191-235. In: Murray, D.R. (ed.), Seed Dispersal. Academic Press, Sydney, Australia.
- Primack, R.B., Miao, S.L. 1992. Dispersal Can Limit Local Plant Distribution. *Conservation Biology* 6(4):513-19.
- Pulliam, H.R. 2000. On the relationship between niche and distribution. *Ecology Letters* 3:349-361.
- R Development Core Team. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>.



- Radvanyi, A. 1970. Small mammals and regeneration of white spruce forests in western Alberta. *Ecology* 51:1102-1105.
- Rankin, W. T., Pickett, S.T.A. 1989. Time of establishment of red maple (*Acer rubrum*) in early oldfield succession. *Bulletin of the Torrey Botanical Club* 116:182-186.
- Rawlinson, H., Dickinson, N., Nolan, P., Putwain, P. 2004. Woodland establishment on closed old-style landfill sites in NW England. *Forest Ecology and Management* 202:265-280.
- Reichman, O.J. 1979. Desert granivore foraging and its impact on seed densities and distributions. *Ecology* 60:1085-1092.
- Ribbens, E.R., Silander, J.A., Pacala, S.W. 1994. Seedling recruitment in forests: calibrating models to predict patterns of tree seedling dispersion. *Ecology* 75(6):1794-1806.
- Robinson, G.R., Handel, S.N. 1993. Forest restoration on a closed landfill – rapid addition of new species by bird dispersal. *Conservation Biology* 7:271-278.
- Robinson, G.R., Handel, S.N. 2000. Directing spatial patterns of recruitment during an experimental urban woodland reclamation. *Ecological Applications* 10:174-188.
- Robinson, G.R., Handel, S.N., Schmalhofer, V.R. 1992. Survival, reproduction, and recruitment of woody plants after 14 years on a reforested landfill. *Environmental Management* 16:265-271.
- Rooney, T. P., Solheim, S.L., Waller, D.M. 2002. Factors affecting the regeneration of northern white cedar in lowland forests of the Upper Great Lakes region, U.S.A. *Forest Ecology and Management* 163:119-130.
- Roughgarden, J., Iwasa, Y. 1986. Dynamics of a metapopulation with space-limited subpopulations. *Theoretical Population Biology* 29:235-261
- Runkle, J.R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. *Ecology* 63(5):1533-1546.
- Salk, T.T., Frelich, L.E., Sugita, S., Calcote, R., Ferrari, J.B., Montgomery, R.A. 2011. Poor recruitment is changing the structure and species composition of an old-growth hemlock-hardwood forest. *Forest Ecology and Management*. 261:1998-2006.
- Schupp, E.W., Fuentes, M. 1995. Spatial patterns of seed dispersal and the unification of plant population ecology. *Ecoscience* 2:267-275.
- Schupp, E.W., Muller, T., Russo, S.E. 2002. Dispersal limitation and the origin and maintenance of species-rich tropical forests. *Seed dispersal and frugivory: ecology,*

- evolution and conservation*. D.J. Levey, W.R. Silva, and M. Galetti, eds. CAB International, Wallingford.
- Shen, W.J., Jianguo, W., Grimm, N.B., Hope, D. 2008. Effects of urbanization-induced environmental changes on ecosystem functioning in the Phoenix metropolitan region, USA. *Ecosystems* 11:138-155.
- Shimano, K. 2000. A power function for forest structure and regeneration pattern of pioneer and climax species in patch mosaic forests. *Plant Ecology* 146:207-220.
- Thompson, K., Grime, J.P. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *Journal of Ecology* 67:893-921.
- Sivy, K.J., Ostojia, S.M., Schupp, S.M., Durham, S. 2011. Effects of rodent species, seed species, and predator cues on seed. *Acta Oecologica* 37:321-328.
- Spiering, D. 2009. Tifft Nature Preserve Management Plan: February.
- Stromayer, K.A.K., Warren, R.J. 1997. Are overabundant deer herds in the eastern United States creating alternate stable states in forest plant communities? *Wildlife Society Bulletin*. 25(2):227-234.
- Sullivan, J.J., Meurk, C., Whaley, K.J., Simcock, R. 2009. Restoring native ecosystems in urban Auckland: urban soils, isolation, and weeds as impediments to forest establishment. *New Zealand Journal of Ecology* 33:60-71.
- Sullivan, T.P., Sullivan, D.S. 1982. The use of alternative foods to reduce lodgepole pine seed predation by small mammals. *Journal of Applied Ecology* 19:33-45.
- Svenning, J.C., Wright, S.J. 2005. Seed limitation in a Panamanian forest. *Journal of Ecology* 93:853-862.
- Tilman, D. 1987. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* 78(1):81-92.
- Tilman, D. 2004. Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion and community assembly. *Proceedings of the National Academy of Sciences USA* 101:10854-10861.
- Trammell, T.L.E., Carreiro, M.M. 2011. Vegetation composition and structure of woody plant communities along urban interstate corridors in Louisville, KY, USA. *Urban Ecosystems* 14:501-524.

- Turnbull, L.A., Crawley, M.J., Rees, M. 2000. Are populations seed-limited? A review of seed sowing experiments. *Oikos* 88:225-238.
- Tyler, C.M., Davis, F.W., Mahall, B.E. 2008. The relative importance of factors affecting age-specific seedling survival of two co-occurring oak species in southern California. *Forest Ecology and Management* 255:3063-3074.
- United Nations. 2014. Revision of the World Urbanization Prospects.
- Van der Meijden, E. Klinkhamer, P.G., De Jong, T.J., Van Wijk, C.A.M. 1992. Meta-population dynamics of biennial plants - how to exploit temporary habitats. *Acta Botanica Neerlandica* 41:249-70.
- Vander Wall, S.B. 1992. Establishment of Jeffrey pine seedlings from animal caches. *Western Journal of Applied Forestry* 7:14-20
- Verheyen, K., Hermy, M. 2004. Recruitment and Growth of Herb-Layer Species with Different Colonizing Capacities in Ancient and Recent Forests. *Journal of Vegetation Science* 15(1):125-34.
- Wang, B., Chen, J., 2009. Seed size, more than nutrient or tannin content, affects seed caching behavior of a common genus of Old World rodents. *Ecology* 90:3023-3032.
- Wania, A., Kühn, I., Klotz, S. 2006. Plant richness patterns in agricultural and urban landscapes in Central Germany – spatial gradients of species richness. *Landscape and Urban Planning* 75:97-110.
- Warren II, R.J., Bahn, V., Bradford, M.A. 2012. The interaction between propagule pressure, habitat suitability and density-dependent reproduction in species invasion. *Oikos* 121(6):874-881.
- Warren II, R. J., Bradford, M.A. 2011. The shape of things to come: woodland herb niche contraction begins during recruitment in mesic forest microhabitat. *Proceedings of the Royal Society of London: Biological Sciences* 278:1390-1398.
- Warren II, R.J., Rossell, I.M., Moorehead, K.K. 2004. Colonization and establishment of red maple (*Acer rubrum*) in a Southern Appalachian wetland. *Wetlands* 24(2):364–374.
- Webster, C.R., Jenkins, M.A., Rock, J.H. 2005. Long-term response of spring flora to chronic herbivory and deer exclusion in Great Smoky Mountains National Park, USA. *Biological Conservation* 125:297-307.

- Wiersum, K.F. 1995. 200 years of sustainability in forestry: lessons from history. *Journal of Environmental Management* 19(3):321-329.
- White, M.A. 2012. Long-term effects of deer browsing: composition, structure, and productivity in a northeastern Minnesota old-growth forest. *Forest Ecology and Management* 269:222-228.
- Yodzis, P. 1978. Competition for Space and the Structure of Ecological Communities. Springer-Verlag, New York.
- Zeiter, M., Stampfli, A., Newberry, D.M. 2006. Recruitment Limitation Constrains Local Species Richness and Productivity in Dry Grasslands. *Ecology* 87(4):942-951.
- Zobel, M., Otsus, M., Liira, J., Moora, M., Mols, I. 2000. Is smallscale species richness limited by seed availability or microsite availability? *Ecology* 81:3274-3282.

Table 1. Weight differences between seeds and seedlings of study species. Values in parentheses denote standard errors.

Table 1

<b>Species</b>	<b>Grasslands</b>	<b>Woodlands</b>
<i>Populus deltoides</i>	87 (55.16)	623 (65.17)
<i>Rhus typhina</i>	0	1
<i>Rhamnus cathartica</i>	0	2 (1.37)
<i>Cornus</i> spp.	0	0.5 (0.5)

Table 2. Species and abundance of seed composition in seed traps per plot for each habitat.

Values in parentheses denote standard errors.

Table 2

<b>Species</b>	<b>Seed mass (g)</b>	<b>Seedling mass (g)</b>
<i>Populus deltoides</i>	0.007 (0.001)	0.076 (0.013)
<i>Acer saccharum</i>	0.071 (0.005)	0.203 (0.044)
<i>Pinus strobus</i>	0.017 (0.004)	0.563 (0.029)



Table 3. Abiotic and biomass differences between habitats. Values in parentheses denote standard errors.

Table 3

	<b>Grasslands</b>	<b>Woodlands</b>
<b>Photosynthetically active radiation (%)</b>	97.03 (0.58)	46.04 (0.53)
<b>Soil moisture (%)</b>	18.21 (0.31)	46.75 (0.91)
<b>Soil temperature (°C)</b>	17.53 (0.18)	17.08 (0.20)
<b>Herbaceous layer biomass (g/m<sup>2</sup>)</b>	807.20 (19.88)	78.52 (7.60)
<b>Overstory woody basal area (m<sup>2</sup>/ha)</b>	2.22 (1.76)	21.52 (2.80)
<b>Understory woody basal area (m<sup>2</sup>/ha)</b>	0.16 (0.08)	0.68 (0.08)

Figure 1. Habitat suitability experiment grids for overstory species recruitment with Burning (plot burned with propane torch) and Herbivore exclusion (plot surrounded by PVC frame covered in nylon bird netting) treatments. Tree seeds were experimentally planted: *Populus deltoides* (Pd), *Acer saccharum* (As), *Pinus strobus* (Ps). Placement of treatments and seed species were randomized. Study site was Tifft Nature Preserve in Buffalo, NY.

Figure 1

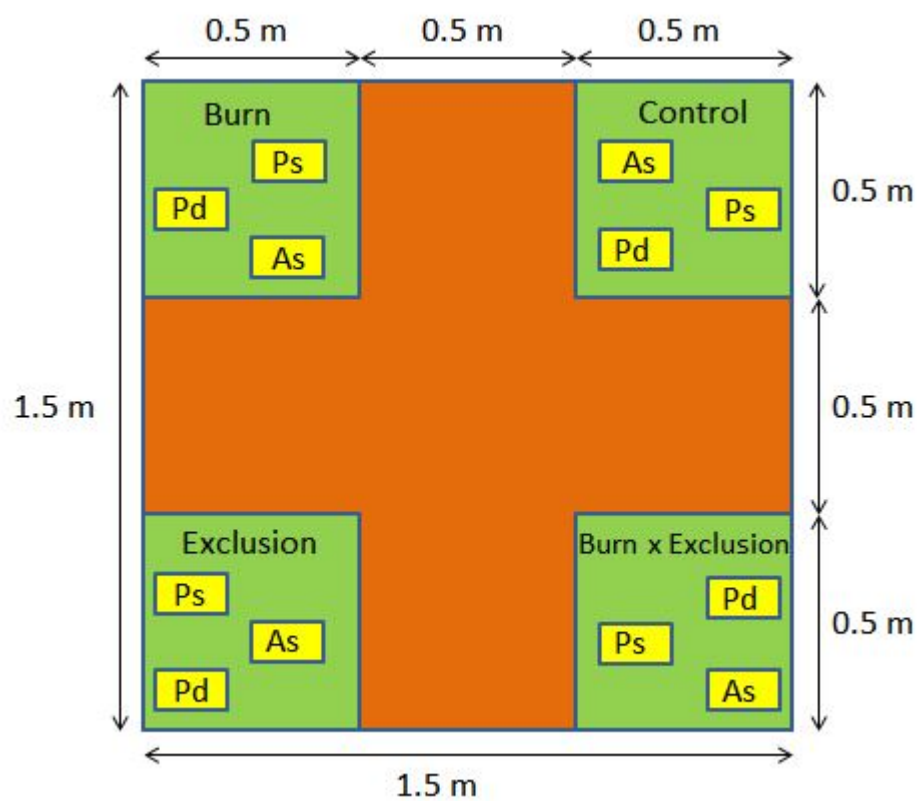


Figure 2. Canopy size class distribution of all canopy species (.25 ha) for (a) Tifft Nature Preserve (Buffalo, NY) and (b) a theoretical, self-sustaining temperate, deciduous forest (Shimano (2000)). (Note: y-axes differ.) Sustainable forests should have diameter at breast height (DBH) class distribution curves with a right-skewed, inverse-J pattern (Figure 2b) [Kimmens 1987; Shimano 2000], indicating future canopy replacement by seedlings and saplings.

Figure 2

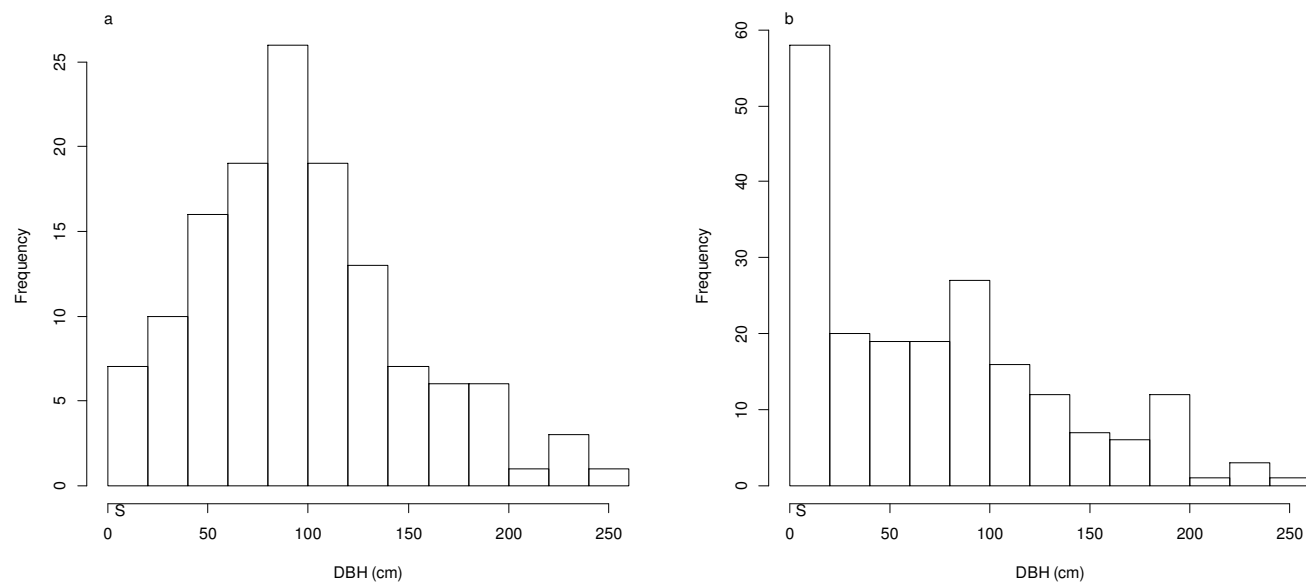


Figure 3. Interaction plot of the effect on mean ( $\pm$  SE) proportional germination of *Acer saccharum*, *Pinus strobus*, and *Populus deltoides* by habitat at Tifft Nature Preserve (Buffalo, NY). Habitat influenced germination for *P. strobus* but did not have an effect on the other two species.

Figure 3

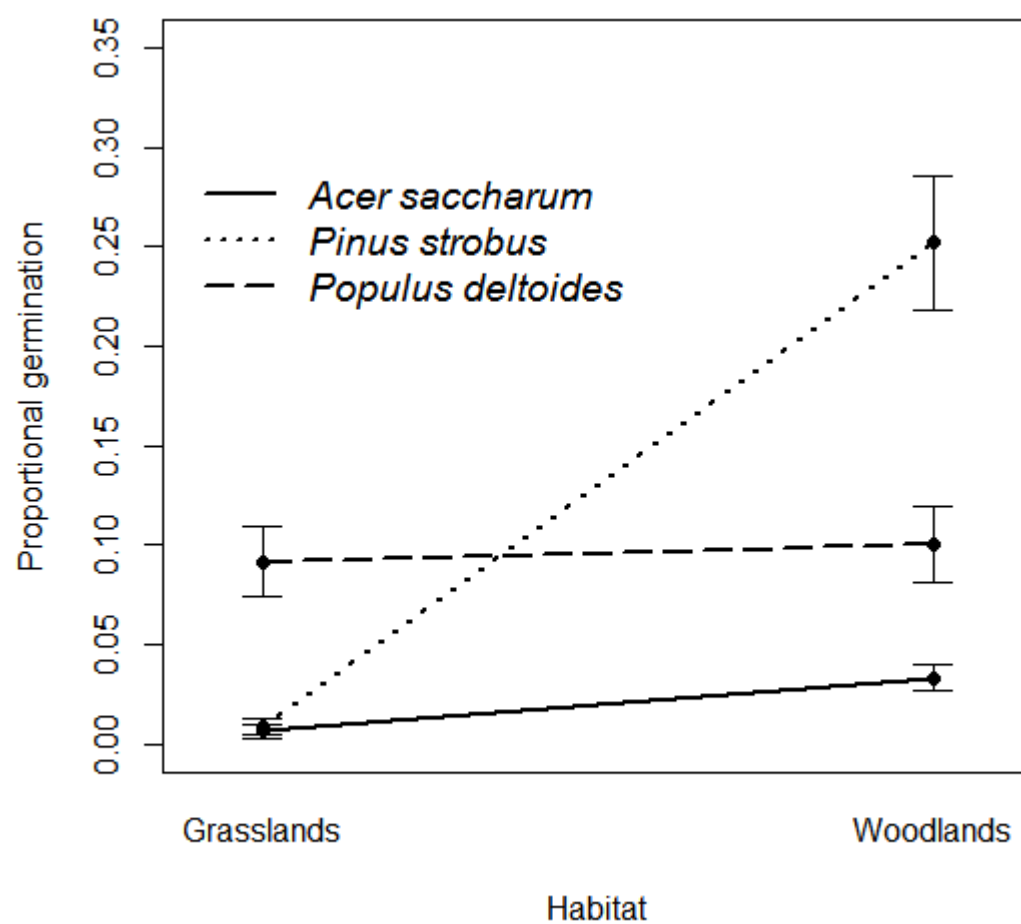




Figure 4. Interaction plot of the effect on mean ( $\pm$  SE) proportional germination of *Acer saccharum*, *Pinus strobus*, and *Populus deltoides* by treatment at Tiff Nature Preserve (Buffalo, NY). *Acer saccharum* and *P. strobus* increased germination only under exclusion treatment. *Populus deltoides* increased germination under burn treatment and burn + exclusion treatment.

Figure 4

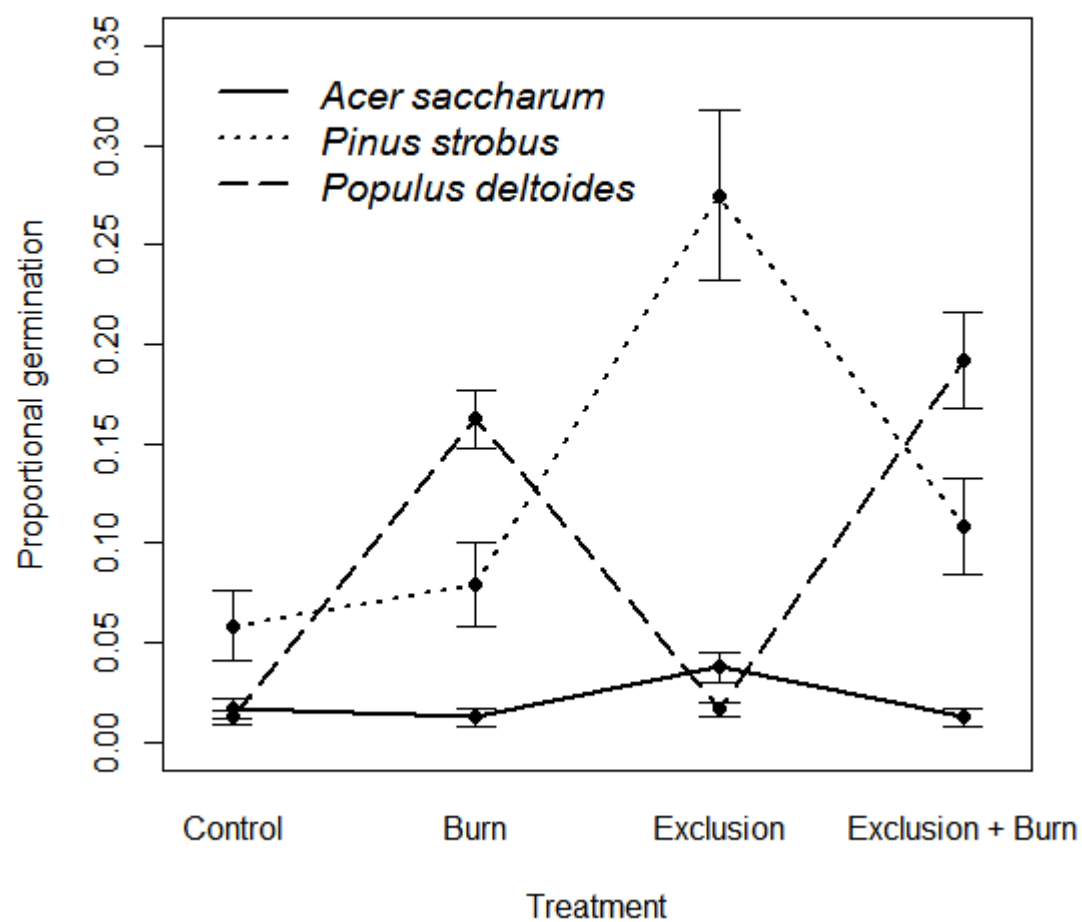


Figure 5. Interaction plot of the effect on mean ( $\pm$  SE) proportional germination of treatments by habitat at Tifft Nature Preserve (Buffalo, NY). Germination under exclusion and burn treatments, and control was higher in the woodlands than in the grasslands.

Figure 5

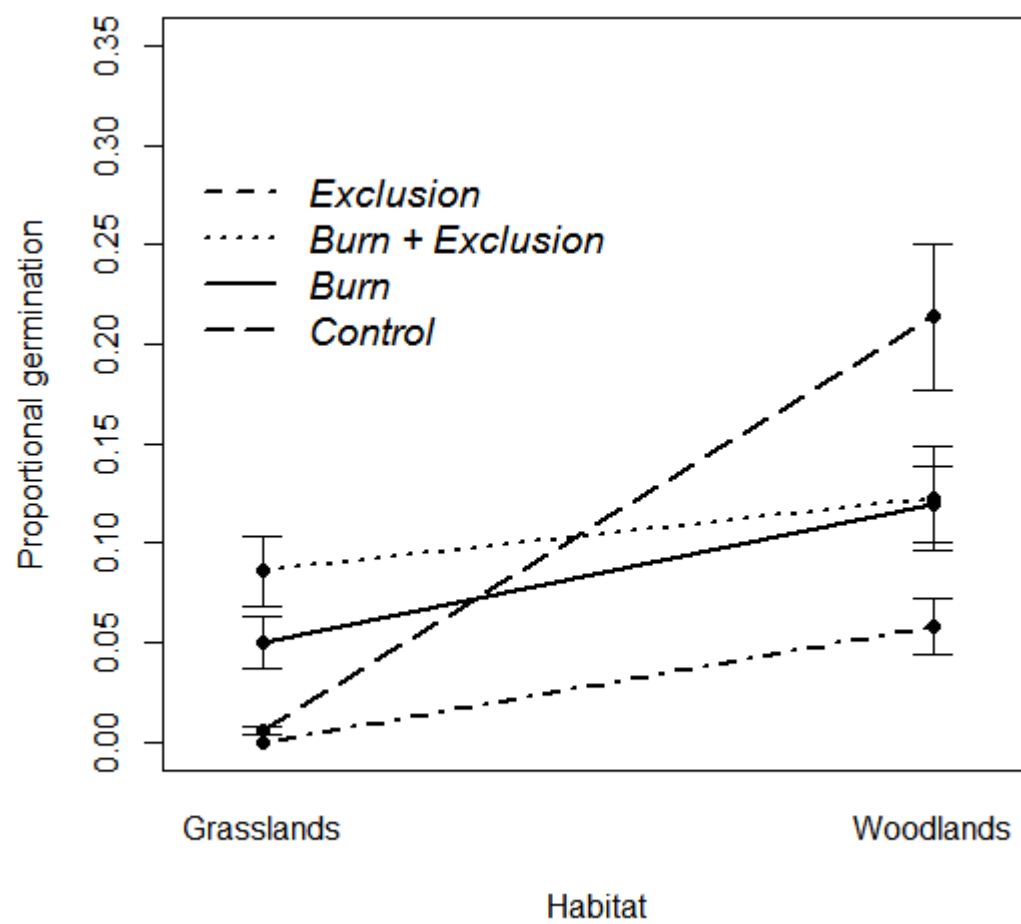


Figure 6. Scatterplot of proportional germination by plot vegetation biomass (g) at Tifft Nature Preserve (Buffalo, NY). Proportional germination is negatively correlated with biomass (*coeff.* = -0.006, *SE* = 0.002, *t-value* = -3.364, *p-value* < 0.001).

Figure 6

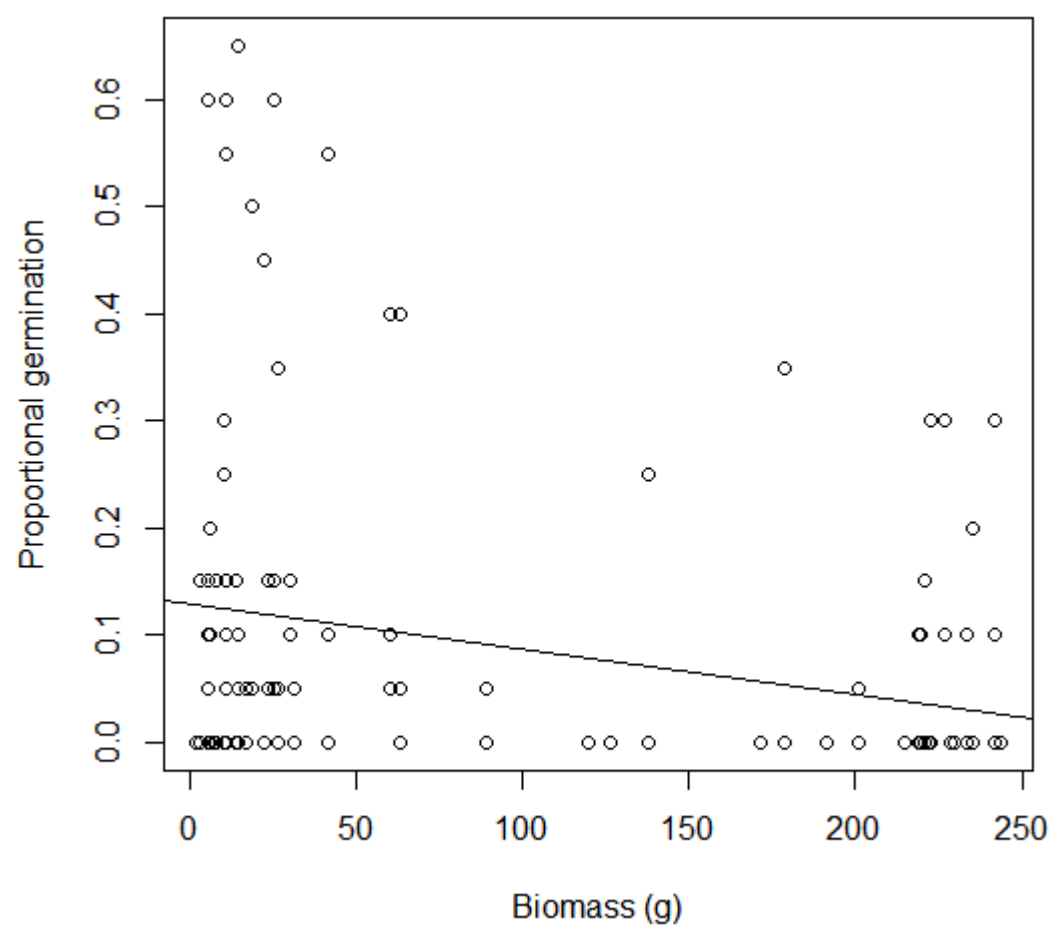


Figure 7. Mean ( $\pm$ SE) proportional seedling survival by species at Tifft Nature Preserve (Buffalo, NY). *Acer saccharum* had a higher survival rate than *P. deltoides*, though there was no significant difference between the *P. strobus* and *A. saccharum* or *P. strobus* and *P. deltoides*. Responses that are not significantly different share the same letter.

Figure 7

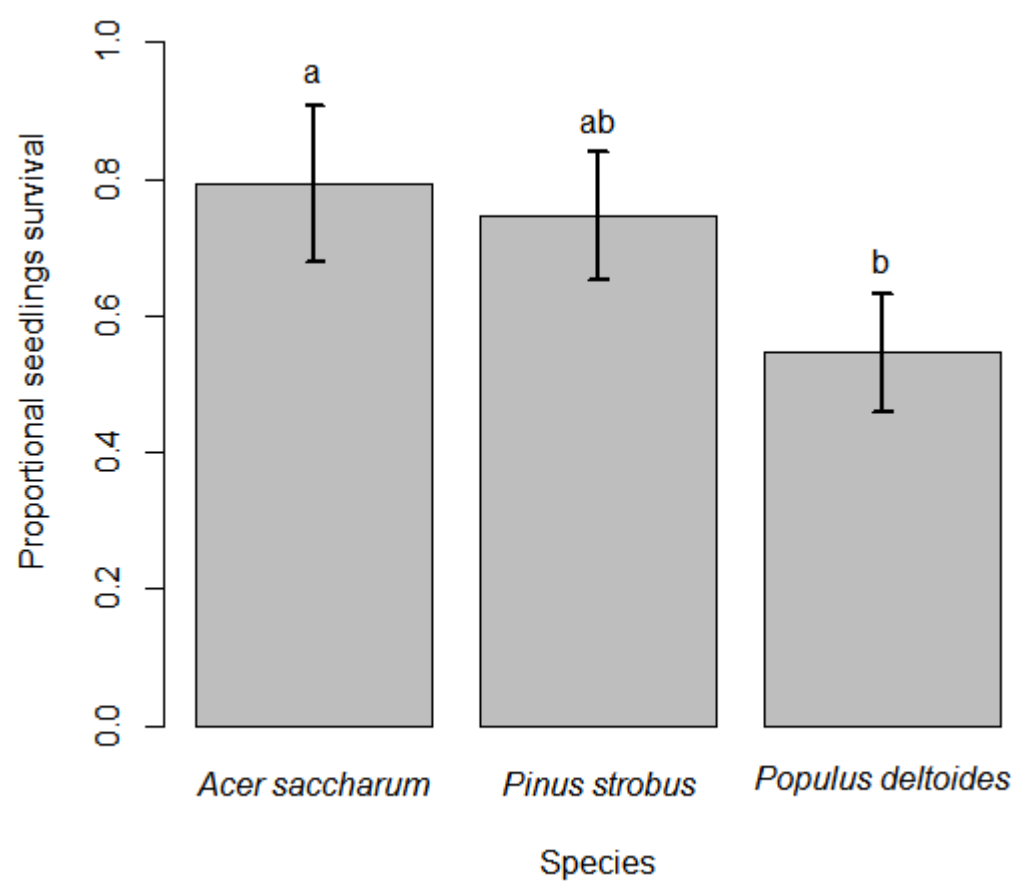




Figure 8. Mean ( $\pm$ SE) proportional seedling survival by treatment at Tifft Nature Preserve (Buffalo, NY). The burn + exclusion treatment and exclusion treatment yielded higher survival rates than burn treatment, but control was not significantly different from any other treatment. Responses that are not significantly different share the same letter.

Figure 8

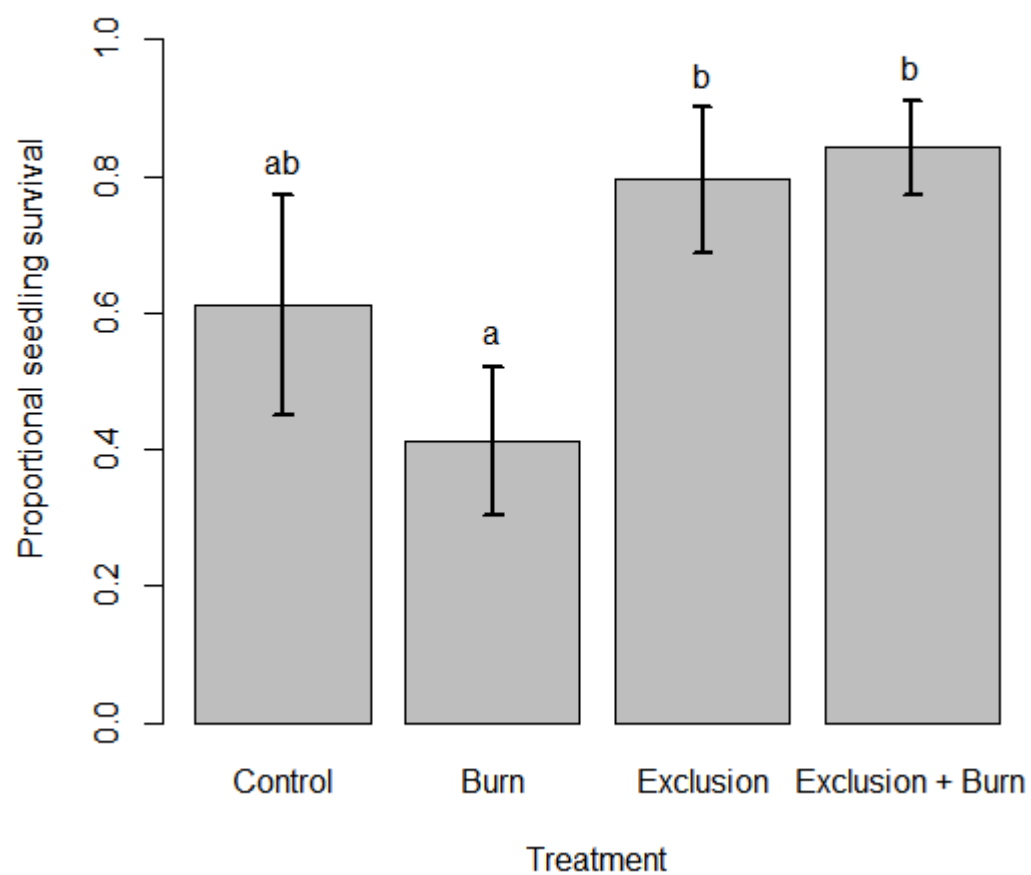


Figure 9. Effect of woody basal area ( $\text{cm}^2/\text{ha}$ ) on number of seeds per seed trap at Tifft Nature Preserve (Buffalo, NY). Number of seeds per trap increased significantly with woody basal area up to  $4.3 \text{ cm}^2/\text{ha}$  and decreased significantly after  $4.3 \text{ cm}^2/\text{ha}$ .

Figure 9.

