

BIOS 569: Practicum in Field Biology

The effects of shade tolerance, deer browsing, and seed predation on
forest regeneration on the UNDERC property

Regina McCormack

Advisor: Dr. Walter Carson

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Abstract

Studying sapling regeneration is integral to ecologists' understanding of forest ecology. The goal of this study was to determine if sapling regeneration is dependent on tolerance to shade, deer browsing, and seed predation. This study predicted that saplings of *Acer saccharum* and *Abies balsamea* would have high relative density and high relative dominance, that saplings of *Acer rubrum* and *Populus tremuloides* would have moderate relative density and moderate relative dominance, and that saplings of *Betula papyrifera* would have low relative density and low relative dominance. The observation demonstrated that *A. saccharum*, *A. balsamea*, and *A. rubrum* had high density and dominance and that both *P. tremuloides* and *B. papyrifera* had low density and dominance. The unexpected abundance of *A. rubrum* may be due to *A. rubrum*'s ability to grow in a variety of habitats and ability to germinate earlier than concurrent species. The unexpected low abundance of *P. tremuloides* is most likely due to its very low shade tolerance. The *P. tremuloides* population here may be approaching the natural end of its lifecycle. The low abundance may also be due to competition with *Corylus cornuta*, a shrub that shares *P. tremuloides*'s rooting zone. In general, species density and dominance were dependent on tolerance to shade, deer browsing, and seed predation.

Introduction

Studying sapling regeneration reveals important dynamics about forest ecology. As different tree species dominate the canopy, other forest species are affected. Trees provide habitats and food sources for many species. Predicting forest regeneration gives ecologists an opportunity to make long-term management decisions. When equipped with the knowledge about the differences in sapling regeneration among different species, ecologists may answer questions about the practices of logging and conservation and the study of ecology more comprehensively.

Like much of Michigan's western upper peninsula, the University of Notre Dame Environmental Research Center (UNDERC) forests were clear cut circa 1900 and selectively logged from 1950 to 1960 with the last recorded incidence of logging occurring in 1968 (Hsia and Francl 2006). Currently, the forests have had approximately 50 to 100 years to recover, resulting in forests of both early-successional and late-successional stages. This environment creates an ideal setting for studying forest regeneration.

The western upper peninsula of Michigan is made of three different forests, the late-successional deciduous forests, the early-successional deciduous forests, and the wet coniferous boreal forests (Dickmann and Leefers 2003). This study focused on sapling regeneration within the two deciduous forests. The typical species of the late-successional deciduous forests is *Acer saccharum* (-sugar maple). The species associated with *A. saccharum* in a late-successional deciduous forest include *Fagus spp.* (-beech), *Betula alleghaniensis* (-yellow birch), *Quercus rubra* (-red oak), *Tilia americana* (-

basswood), *Acer rubrum* (-red maple), *Tsuga canadensis* (-hemlock), *Pinus strobus* (-white pine), and *Picea glauca* (-white spruce) (Dickmann and Leefers 2003). The typical species of the early-successional forests are *Populus grandidentata* (-bigtooth aspen), and *Populus tremuloides* (-quaking aspen). The species associated with *Populus spp.* in an early-successional forest are *Betula papyrifera* (-paper birch), *Acer rubrum* (-red maple), *Abies balsamea* (-balsam fir), *Pinus resinosa* (-red pine), and *Pinus strobus* (-white pine) (Dickmann and Leefers 2003).

Species are typical of either early-successional or late-successional forests because they have different tolerances to environmental factors. Shade tolerance is the primary factor (Kobe et al. 1995, Barnes and Wagner 2007, Dickmann and Leefers 2003), although studies have shown that deer browsing is also a significant factor (Waller and Alverson 1997, Horsley et al. 2003, Long et al. 2007).

Deer have different preferences for different tree species. *A. balsamea* is not preferred by deer (Borgmann et al. 1999). In fact, *A. balsamea* is considered deer starvation food and only eaten when no other resources are available (Borgmann et al. 1999). Although browsed more commonly than *A. balsamea*, *A. saccharum* is also not preferred by deer (Long et al. 2007). *A. rubrum* and *B. papyrifera* are moderately browsed by deer (Nesom 2006a, Moore 2006). Both species' survival is adversely affected by deer browsing (Long et al. 2007, Krueger et al., unpublished data). *P. tremuloides* is highly preferred by deer; however, its shoots regenerate quickly, so deer browsing does not significantly inhibit regeneration (Dickmann and Leefers 2003).

Studies have also shown that seed predation by small mammals affects forest regeneration (Janzen 1970, Royo and Carson 2008). Like deer, small mammals also have preferences for seeds of different tree species. Small mammals are not known to prey on seeds of *A. balsamea* and *P. tremuloides* (USDA 2006, Nesom 2003). However, small mammals do prey on seeds of *A. saccharum*, *A. rubrum*, and *B. papyrifera*. Red squirrel, gray squirrel, and flying squirrel prey on seeds of *A. saccharum* (Nesom 2006b). Squirrels and chipmunks prey on seeds of *A. rubrum* (Nesom 2006a). Several species of birds and small mammals prey on the *B. papyrifera* buds, seeds, and catkins (Moore 2006). Royo and Carson suggest that small mammals prefer the larger seeds to smaller seeds (2008). This finding is indicative of the optimal foraging theory, which predicts that animals will choose prey that maximizes energy requirements (Molles 2008).

At UNDERC, certain environmental factors such as deer population, climate, and soil conditions are naturally controlled; however, species' responses to shade, deer browsing, and seed predation can be examined. The object of this study integrates these factors and applies them to five tree species on the UNDERC property. The hypothesis is that sapling regeneration is dependent on each species' tolerance to shade, deer browsing, and seed predation.

The five tree species sampled in this study are *A. saccharum*, *A. rubrum*, *A. balsamea*, *P. tremuloides*, and *B. papyrifera*. Species' tolerance to shade, deer browsing, and seed predation were given ranks, and these ranks were summed to determine predictions about sapling density and dominance (Table 1).

In this study, it was assumed, based on Royo and Carson (2008), that small mammals will prefer larger seeds to smaller seeds because they receive more nutrition per unit of foraging effort. Therefore, it was assumed that small mammals prefer *A. saccharum* seeds, which have the largest seeds, to *A. rubrum* seeds, which are smaller than *A. saccharum* seeds, to *B. papyrifera* seeds, which have the smallest seeds.

A. balsamea and *A. saccharum* are expected to be high in relative density and dominance, *A. rubrum* and *P. tremuloides* are expected to be moderate, and *B. papyrifera* is expected to be lowest in relative density and dominance.

Methods

The UNDERC property was surveyed for the five species of adult trees. Four replicates of each species, *A. balsamea*, *A. saccharum*, *A. rubrum*, *P. tremuloides*, and *B. papyrifera* were sampled in early-successional stands, and four replicates of each species were sampled in the late-successional stands. This amounted to 40 replicates, 20 in the early-successional stands, and 20 in the late-successional stands. The early-successional and late-successional stands within the UNDERC property were determined using an onsite ARC-GIS. The adults within each stand were at least 20 m from the road and at least 20 m from each other. The adults were selected haphazardly due to time constraints (Carson, W. P., personal communication).

Within a $25\pi \text{ m}^2$ area underneath each adult, saplings of all species were sampled for density and dominance data. Saplings, rather than seedlings, were sampled because sites in which saplings are abundant are predictable sites of where adults will grow

(Collins and Carson 2004). A sapling was defined as at least 160 cm tall and less than or equal to 10 cm diameter at breast height (dbh). Each sapling was identified and measured for dbh.

Results

Relative sapling density and sapling dominance were calculated per each adult tree and according to the following equations:

Density = the number of individuals of one species / the total number of individuals

Dominance = the basal area of individuals of one species / the total basal area of all individuals

(Curtis and McIntosh 1950, Stearns and Likens 2002).

The relative sapling density and dominance were transformed using an arcsine transformation and then analyzed using a Kruskal-Wallis test, an ANOVA, and a Fisher's Least Significant Difference Test. After transformation, the data was not normally distributed, so the Kruskal-Wallis tests determined if the data was statistically significant. Because the Kruskal-Wallis tests showed statistical significance, an ANOVA and Fisher's test were used to determine the individual species' statistical differences.

The relative sapling densities were statistically different (Figure 1, Kruskal-Wallis $p < 0.001$, ANOVA $df=13$, $F=3.603$, $p < 0.001$). In the Fisher's test, *A. balsamea*, *A. rubrum*, and *A. saccharum* had higher densities than most other species, including *B. papyrifera* and *P. tremuloides*, but they did not have densities statistically different from each other (Table 2). *B. papyrifera* and *P. tremuloides* did not have densities statistically different from each other (Table 2). *Ostrya virginiana* (-hop-hornbeam) and *Fraxinus*

americana (-white ash) also had statistically higher densities than several species (Table 2).

The relative sapling dominances were also statistically different (Figure 2, Kruskal-Wallis $p < 0.001$, ANOVA $df=13$, $F=3.733$, $p < 0.001$). In the Fisher's test, *A. balsamea*, *A. rubrum*, and *A. saccharum* also had higher densities than most other species (Table 3). *A. balsamea* was statistically more dominant than *A. rubrum* but not *A. saccharum* (Table 3). *A. saccharum* and *A. rubrum* did not have statistically different dominance (Table 3). All three had higher dominance than *B. papyrifera* and *P. tremuloides* except for *A. rubrum*, which did not have a statistically higher dominance than *B. papyrifera* (Table 3). *O. virginiana* also had higher dominance than most other species (Table 3).

Species diversity and species richness were analyzed using a Kruskal-Wallis test because the data was not normally distributed. Species diversity and species richness did not statistically differ among the different adult trees. However, species diversity and species richness did differ between the early-successional stands and late-successional stands. The early-successional stands were more diverse than the late-successional stands (Figure 3, $df=1$, $H=4.655$, $p=0.031$). The early-successional stands had higher richness than the late-successional stands (Figure 4, $df=1$, $H=15.967$, $p < 0.001$).

Relative sapling density and sapling dominance when grouped by adult and by successional stand were not statistically different from each other. However, the ANOVA test of the adult *B. papyrifera* species appeared to be approaching significance. *F. americana* appears to be more dense and more dominant than other sapling species

when underneath *B. papyrifera* adults (relative density: Table 4, Kruskal-Wallis 0.054, ANOVA $df=11$, $F=2.071$, $p=0.076$; relative dominance: Table 5, Kruskal-Wallis 0.164, ANOVA $df=11$, $F=1.586$, $p=0.158$). Though this appears to be approaching significance, the data reports that this high abundance of *F. americana* occurred underneath only one of the adult *B. papyrifera* species. Therefore, this data should be considered with caution.

Discussion

Generally, the results from this study support the hypothesis that sapling regeneration is dependent on species' tolerance to shade, deer browsing, and seed predation. The relative density and relative dominance show that *A. balsamea*, *A. rubrum*, and *A. saccharum* are replacing themselves more readily than *B. papyrifera* and *P. tremuloides*. These results support the predictions made from the original hypothesis for *A. balsamea*, *A. saccharum*, and *B. papyrifera*. However, *A. rubrum* and *P. tremuloides* had relative densities and relative dominances different than expected based on their shade tolerance and susceptibility to deer browsing and seed predation.

In this study, *A. rubrum* is one of the more dense and dominant species, and it appears to have a high ranking in contrast to the expected moderate ranking. One explanation could be that *A. rubrum* is regenerating more readily on the UNDERC property due to its ability to flourish in a variety of environments. *A. rubrum* colonizes quickly in wet-mesic soils such as swamps and poorly drained sites, but *A. rubrum* can also survive in dry-mesic soils (Abrams 1998). Though the UNDERC property contains upland deciduous forests, several of these upland stands are in close proximity to wetland

sites (McCormack, R., personal observation). Therefore, *A. rubrum* on the UNDERC property benefits from this environmental variation.

Another reason could be that *A. rubrum* survives as both an early-successional and late-successional species because it grows quickly and is moderately shade tolerant (Abrams 1998). Therefore, *A. rubrum* can sustain itself well in both types of stands that were sampled. *A. rubrum* grows quickly because it reaches sexual maturity within 4 to 10 years, which is faster than most hardwood species (Abrams 1998). *A. rubrum* also grows quickly because it disseminates its seeds in the spring rather than in the fall, like most hardwood species (Abrams 1998). *A. rubrum* seeds do not need to overwinter before their first growing season, thus increasing the chance of germination before predation occurs (Abrams 1998). However, *A. rubrum* also employs seed banking, a fitness technique that may be a contributing factor to *A. rubrum*'s colonization of the eastern deciduous forests (Lambers and Clark 2005). When *A. rubrum* disseminate seeds late in the growing season, the seeds bank in the soil and lie dormant until the next growing season. This technique allows *A. rubrum* to avoid the higher mortality that is associated with late germination, which coincides with higher predation rates and detrimental weather conditions (Lambers and Clark 2005). These varying seed dissemination rates may be reasons as to why *A. rubrum* appears in relatively equal proportions with *A. saccharum* and *A. balsamea*. Both *A. saccharum* and *A. balsamea* disseminate their seeds in the fall. This suggests a new aspect to seed predation's effect on forest regeneration. Seed predation due to the optimal foraging theory may be only one of many ecological principles that affect forest regeneration. A future study could

test the hypothesis that early seed dissemination benefits tree survival when all other variables such as shade, deer browsing, and nutrient requirements are controlled.

In addition, *A. rubrum* was more dense than it was dominant. *A. rubrum*'s density was not statistically different from *A. saccharum* and *A. balsamea* (Table 2) but its dominance was statistically different from *A. balsamea* (Table 3). While *A. rubrum*'s life history traits such as early germination and ability to grow in a variety of environments may allow *A. rubrum* to establish more quickly than other species, it may not necessarily enable *A. rubrum* to gain dominance.

This study showed that *P. tremuloides* is one of the less dense and dominant species and is not statistically different from *B. papyrifera*. Therefore, *P. tremuloides* appears to have a low ranking in contrast to the expected moderate ranking. One explanation could be that *P. tremuloides* is regenerating less than expected because its low tolerance to shade eclipses its ability to tolerate deer browsing and its low seed predation rate. Another explanation could be that *P. tremuloides* in the UNDERC area is simply in the natural state of decline. The maximum age for *P. tremuloides* in the Great Lakes states is 50 to 60 years (Nesom 2003), and since the area was clear cut circa 1900 and subsequently logged until the 1960s (Hsia and Francl 2006), the *P. tremuloides* trees may be reaching their maximum lifespan.

Another reason may be competition with *Corlyus cornuta* (-beaked hazelnut), a common understory shrub of the Great Lakes region. The understory of the UNDERC property does contain *C. cornuta*, especially in the early-successional stands (McCormack, R., personal observation). *C. cornuta* and *P. tremuloides* both have

shallow root systems and thus occupy the same rooting zone (Mundell et al. 2007). Mundel et al. (2007) determined that aspen densities were significantly reduced in areas dominated by *C. cornuta*. They speculated that possible reasons included that the deeper roots of *P. tremuloides* are hormonally suppressed, that deeper roots take a longer time to reach the soil surface, and that deeper roots experience colder, and therefore inhibiting, conditions (Mundel et al. 2007). A future study could reproduce the Mundel et al. experiment in the UNDERC property and perhaps expand the experiment to include tolerance to shade, seed predation, and deer browsing.

Another observation to discuss is the high relative density and high relative dominance of *A. saccharum*. *A. saccharum* was predicted to have high density and dominance even though the prediction sum for *A. saccharum* is 9 out of 12, a prediction rank that could be considered “moderate” on this scale from 3 to 12 (Table 1). *A. saccharum* was given a prediction rank of “high” because *A. saccharum* is the typical dominant canopy species of northern deciduous forests (Dickmann and Leefers 2003). Ecologists note *A. saccharum* for its exceptional shade tolerance and attribute its widespread distribution to this characteristic (Barnes and Wagner 2004). In this study, *A. saccharum* is statistically more dense and dominant than several other species yet not statistically more dense than *A. balsamea* and *A. rubrum*, thus suggesting that *A. saccharum*'s shade tolerance and tolerance to deer browsing are greater contributing factors than its tolerance to seed predation.

Another interesting aspect of this study is the relative density and dominance of *F. americana* saplings. The density of *F. americana* saplings appeared to be approaching

significance especially underneath *B. papyrifera* adults (Table 4, 5). This finding is of particular interest in light of the destruction of ash trees by the emerald ash borer. These results suggest that *F. americana* and perhaps other ash species may have a tendency to grow underneath the early-successional species *B. papyrifera*. If true, this correlation may affect forest regeneration in the future as the emerald ash borer population spreads westward. As the early-successional *B. papyrifera* naturally declines, *F. americana* will take its place. When the emerald ash borer attacks these ash trees, large gaps within the canopy may appear. More early-successional species may colonize, thus perpetuating early-successional stands more readily than in the absence of the emerald ash borer. This study included sampling of eight *B. papyrifera* trees, and only one of the *B. papyrifera* trees contained this high abundance of *F. americana* saplings. Further replication is needed to determine if this prediction is statistically accurate.

The greater diversity (Figure 3, $df=1$, $H=4.655$, $p=0.031$) and greater richness (Figure 4, $df=1$, $H=15.967$, $p<0.001$) in the early-successional stands also supports the hypothesis that sapling regeneration is dependent on shade tolerance, deer browsing, and seed predation. The early-successional stands cast relatively less shade than the late-successional stands so shade tolerance is not yet a significant factor. Provided that deer browsing, seed predation, and nutrient requirements are not prohibitive, saplings of any shade tolerance can grow in the early-successional understory.

In conclusion, sapling regeneration is dependent on shade tolerance, deer browsing, and seed predation. Studying these interactions and other contributing factors

such as seasonal seedling germination and understory competition more closely may yield both interesting and useful knowledge about forest ecology.

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Table 1. A model was developed to predict relative density and dominance. Shade tolerance was ranked from 1 to 5 with 1 as very intolerant. Browsing tolerance was ranked as 1 for intolerant and 2 for tolerant. Seed predation was ranked 1 to 5 with 1 as high predation. These ranks were summed to produce a prediction sum ranging from 3 to 12, with 12 being the prediction of the highest density and dominance. Though these rankings assisted in quantifying the predictions, other species traits were also considered. Thus, the rankings are subject to interpretation as in the case of *A. saccharum*. Though the prediction sum for *A. saccharum* is 9 out of 12, a prediction rank that could be considered “moderate” on this scale, *A. saccharum* was expected to have high density and dominance because it is the typical dominant canopy species of northern deciduous forests (Dickmann and Leefer 2003). Ecologists note *A. saccharum* for its exceptional shade tolerance and attribute its widespread distribution to this characteristic (Barnes and Wagner 2004).

Tree	Shade Tolerance*	Shade Tolerance Rank	Deer Preference and Browsing Tolerance	Browsing Tolerance Rank	Seed Predation	Seed Predation Rank	Prediction of Relative Density and Relative Dominance	Prediction Sum
<i>A. balsamea</i>	Very tolerant	5	Low, tolerant	2	Low	5	High	12
<i>A. saccharum</i>	Very tolerant	5	Low, tolerant	2	Moderate/High	2	High	9
<i>A. rubrum</i>	Tolerant	4	Moderate, intolerant	1	Moderate	3	Moderate	8
<i>B. papyrifera</i>	Very intolerant	1	Moderate, intolerant	1	Low/Moderate	4	Low	6
<i>P. tremuloides</i>	Very intolerant	1	High, tolerant	2	Low	5	Moderate	8

*Shade tolerance rankings (Barnes and Wagner 2004).

Table 2. The p-values of the Fisher's test for sapling relative density. The density of the sapling species in the left-most column were compared with the density of the sapling species in the top row to assess if the densities were statistically different. The asterisks indicate statistically significant p-values.

	A. balsamea	A. rubrum	A. saccharum	A. sanguinea	B. alleghaniensis	B. papyrifera	F. americana	F. nigra	O. virginiana	P. glauca	P. mariana	P. serotina	P. tremuloides
A. rubrum	0.379	--	--	--	--	--	--	--	--	--	--	--	--
A. saccharum	0.354	0.999	--	--	--	--	--	--	--	--	--	--	--
Amelanchier sanguinea (-service berry)	0.004*	0.033*	0.029*	--	--	--	--	--	--	--	--	--	--
B. alleghaniensis	0.108	0.244	0.239	0.793	--	--	--	--	--	--	--	--	--
B. papyrifera	0.001*	0.012*	0.010*	0.672	0.566	--	--	--	--	--	--	--	--
F. americana	0.399	0.869	0.865	0.088	0.325	0.038*	--	--	--	--	--	--	--
Fraxinus nigra (-black ash)	0.048*	0.159	0.152	0.734	0.982	0.481	0.252	--	--	--	--	--	--
O. virginiana	0.405	0.139	0.127	0.002*	0.0516	0.001*	0.169	0.020*	--	--	--	--	--
P. glauca	<0.001*	0.005*	0.004*	0.599	0.517	0.943	0.022*	0.421	<0.001*	--	--	--	--
Picea mariana (-black spruce)	0.074	0.127	0.125	0.528	0.463	0.673	0.155	0.431	0.044*	0.694	--	--	--
Prunus serotina (-black cherry)	0.001*	0.009*	0.008*	0.619	0.529	0.943	0.032*	0.442	<0.001*	0.997	0.699	--	--
P. tremuloides	0.004*	0.046*	0.039*	0.684	0.993	0.391	0.135	0.984	0.002*	0.313	0.411	0.348	--
Prunus virginiana (-choke cherry)	0.164	0.303	0.299	0.865	0.963	0.659	0.372	0.944	0.088	0.618	0.511	0.625	0.949

Table 3. The p-values of the Fisher's test for sapling relative dominance. The dominance of the sapling species in the left-most column were compared with the dominance of the sapling species in the top row to assess if the densities were statistically different. The asterisks indicate statistically significant p-values.

	A. balsamea	A. rubrum	A. saccharum	A. sanguinea	B. alleghaniensis	B. papyrifera	F. americana	F. nigra	O. virginiana	P. glauca	P. mariana	P. serotina	P. tremuloides
A. rubrum	0.049*	--	--	--	--	--	--	--	--	--	--	--	--
A. saccharum	0.200	0.465	--	--	--	--	--	--	--	--	--	--	--
A. sanguinea	0.001*	0.055*	0.013*	--	--	--	--	--	--	--	--	--	--
B. alleghaniensis	0.150	0.628	0.395	0.454	--	--	--	--	--	--	--	--	--
B. papyrifera	0.003*	0.119	0.036*	0.818	0.574	--	--	--	--	--	--	--	--
F. americana	0.095	0.871	0.464	0.128	0.725	0.217	--	--	--	--	--	--	--
F. nigra	0.032*	0.349	0.162	0.553	0.817	0.708	0.470	--	--	--	--	--	--
O. virginiana	0.478	0.026*	0.092	0.000*	0.084	0.002*	0.046*	0.017*	--	--	--	--	--
P. glauca	0.000*	0.025*	0.004*	0.834	0.361	0.661	0.075	0.430	<0.001*	--	--	--	--
P. mariana	0.090	0.259	0.177	0.740	0.457	0.660	0.300	0.529	0.059*	0.812	--	--	--
P. serotina	0.024*	0.387	0.162	0.410	0.907	0.565	0.531	0.880	0.013*	0.295	0.467	--	--
P. tremuloides	<0.001*	0.024*	0.003*	0.987	0.422	0.788	0.086	0.511	<0.001*	0.827	0.740	0.355	--
P. virginiana	0.051*	0.246	0.143	0.945	0.538	0.829	0.309	0.638	0.029*	0.952	0.808	0.548	0.95

Table 4. The p-values of the Fisher's test for sapling relative density underneath *B. papyrifera* adults. The density of the sapling species in the left-most column were compared with the density of the sapling species in the top row to assess if the densities were statistically different. This contained no statistically significant p-values.

	A. balsamea	A. rubrum	A. saccharum	A. sanguinea	B. alleghaniensis	B. papyrifera	F. americana	F. nigra	O. virginiana	P. glauca	P. serotina
A. rubrum	0.138	--	--	--	--	--	--	--	--	--	--
A. saccharum	0.933	0.245	--	--	--	--	--	--	--	--	--
A. sanguinea	0.089	0.594	0.350	--	--	--	--	--	--	--	--
B. alleghaniensis	0.352	0.488	0.244	0.737	--	--	--	--	--	--	--
B. papyrifera	0.095	0.706	0.461	0.724	0.552	--	--	--	--	--	--
F. americana	0.459	0.025	0.220	0.082	0.212	0.073	--	--	--	--	--
F. nigra	0.247	0.553	0.309	0.896	0.858	0.676	0.157	--	--	--	--
O. virginiana	0.525	0.343	0.099	0.292	0.626	0.231	0.291	0.482	--	--	--
P. glauca	0.172	0.615	0.370	0.949	0.729	0.802	0.116	0.866	0.366	--	--
P. serotina	0.052	0.650	0.406	0.827	0.608	0.861	0.058	0.758	0.200	0.909	--
P. tremuloides	0.123	0.470	0.225	0.564	0.947	0.406	0.126	0.766	0.504	0.608	0.405

Table 5. The p-values of the Fisher's test for sapling relative dominance underneath *B. papyrifera* adults. The dominance of the sapling species in the left-most column were compared with the dominance of the sapling species in the top row to assess if the densities were statistically different. The asterisks indicate statistically significant p-values.

	A. balsamea	A. rubrum	A. saccharum	A. sanguinea	B. alleghaniensis	B. papyrifera	F. americana	F. nigra	O. virginiana	P. glauca	P. serotina
A. rubrum	0.550	--	--	--	--	--	--	--	--	--	--
A. saccharum	0.673	0.935	--	--	--	--	--	--	--	--	--
A. sanguinea	0.025*	0.071	0.085	--	--	--	--	--	--	--	--
B. alleghaniensis	0.144	0.261	0.264	0.793	--	--	--	--	--	--	--
B. papyrifera	0.398	0.610	0.593	0.412	0.626	--	--	--	--	--	--
F. americana	0.396	0.255	0.302	0.029*	0.086	0.206	--	--	--	--	--
F. nigra	0.170	0.300	0.301	0.730	0.943	0.677	0.099	--	--	--	--
O. virginiana	0.279	0.579	0.570	0.210	0.467	0.894	0.158	0.522	--	--	--
P. glauca	0.349	0.548	0.535	0.459	0.677	0.944	0.183	0.730	0.826	--	--
P. serotina	0.395	0.688	0.665	0.225	0.458	0.855	0.200	0.509	0.939	0.792	--
P. tremuloides	0.007*	0.040*	0.061	0.812	0.911	0.460	0.024	0.838	0.195	0.517	0.223

Relative Sapling Density

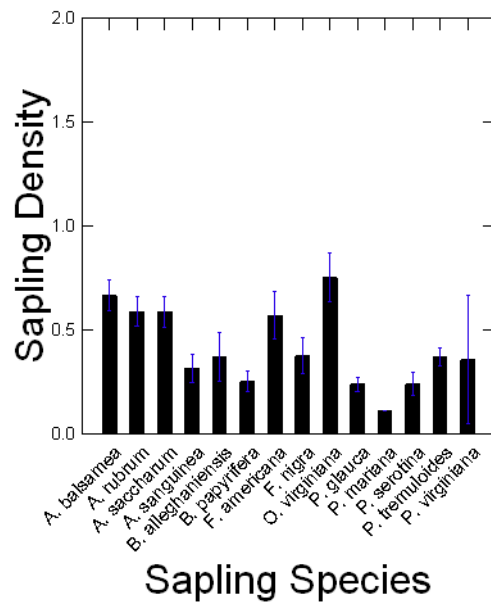


Figure 1. Relative sapling density underneath all adult species (Kruskal-Wallis $p < 0.001$, ANOVA $df=13$, $F=3.603$, $p < 0.001$).

Relative Sapling Dominance

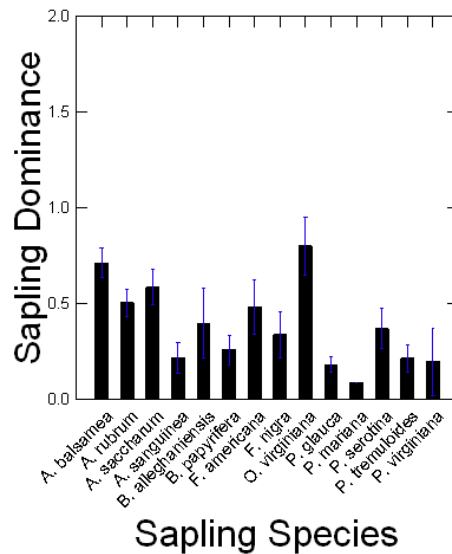


Figure 2. Relative sapling dominance underneath all adult species (Kruskal-Wallis $p < 0.001$, ANOVA $df=13$, $F=3.733$, $p < 0.001$).

Species Diversity

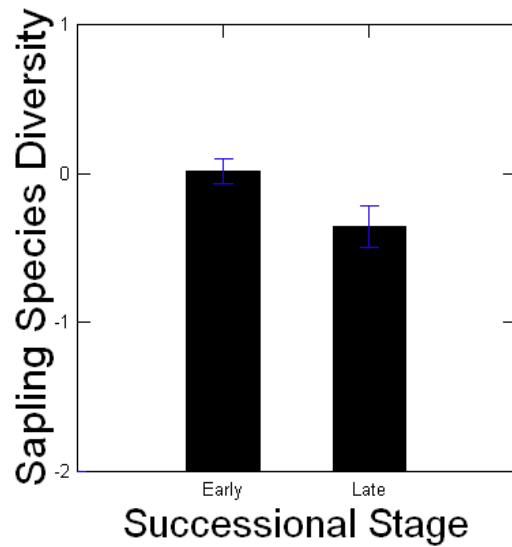


Figure 3. Species diversity of saplings within early-successional and late-successional forests ($df=1$, $H=4.655$, $p=0.031$).

Species Richness

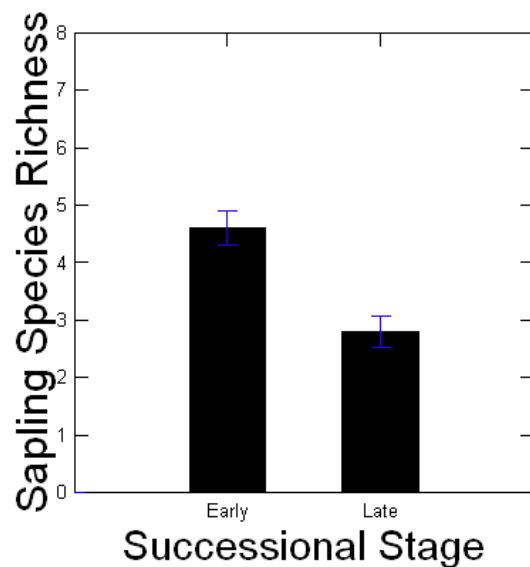


Figure 4. Species richness of saplings with early-successional and late-successional forests ($df=1$, $H=15.967$, $p<0.001$).