Susceptibility of Eastern U.S. Habitats to Invasion of *Celastrus orbiculatus* (Oriental Bittersweet) Following Fire

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Abstract

Fire effects on invasive species are an important land management issue in areas subjected to prescribed fires as well as wildfires. These effects on invasive species can be manifested across life stages. The liana *Celastrus orbiculatus* (oriental bittersweet) is a widespread invader of eastern U.S. habitats including those where fire management is in practice. This study examined if prescribed fire makes these habitats more susceptible to invasion of *C. orbiculatus* by seed at Indiana Dunes National Lakeshore. Four treatments (control, litter removed, high and low intensity fire) were applied in six habitat types (sand savanna/woodland, sand prairie, moraine prairie, sand oak forest, beech-maple forest, and oak-hickory forest) and germinating seedlings were tracked over two growing seasons. Treatment did not have a great effect on the germination, survival, or biomass of *C. orbiculatus*. However, habitat type did influence these responses mostly in the first growing season. Moraine prairie, beech-maple forest, and oak-hickory forests had the greatest maximum percentage of germinants. Moraine prairie had significantly greater survival than oak forest and savanna habitats. Plots with intact litter, and the moraine prairie habitat had the tallest seedlings at germination, while tallest final heights and greatest aboveground biomass were highest in oak forest. Thus, fire and litter removal did not increase the susceptibility of these habitats to germination of *C. orbiculatus*. These results indicate that most eastern U.S. habitats are vulnerable to invasion by this species via seed regardless of the level or type of disturbance to the litter layer.

Keywords *Celastrus orbiculatus*, establishment, germination, invasive species, litter removal, post-burn environment

1. Introduction

The interaction between fire and invasive plants is highly complex. In some cases, fire helps to mitigate the effects of invasive species (Mandle *et al.*, 2011; Srinivasan *et al.*, 2012), while in other cases, fire can make habitats more vulnerable to invasion (D'Antonio and Vitousek, 1992; Pauchard *et al.*, 2008). Prescribed fire is a common technique in a variety of habitats used to decrease fuels and promote biodiversity (Hutchinson *et al.*, 2005). In a given situation, it is difficult to predict which way fire will push an ecosystem in terms of invasion (Mandle *et al.*, 2011). For land managers, the challenge is striking a balance between burning areas to reduce fuel and maintain habitats, and the potential to enhance the spread of invasive species.

Invasive species can be perturbed by fire due to seeds being incinerated, and aboveground growth being burned (Srinivasan *et al.*, 2012; Pavlovic and Leicht-Young, unpublished data). However, in some cases, following fire, established woody invasive (and native) plants respond to disturbance by vigorous resprouting (Bond and Midgley, 2003; Gurvich *et al.*, 2005; Hoffmann and Solbrig, 2003; Mandle *et al.*, 2011), as well as new recruitment from seeds (Behenna *et al.*, 2008; Glasgow and Matlack, 2007; Pauchard *et al.*, 2008). Germination of invasive plant species can benefit from the disturbance resulting from fire, resulting in the creation of "safe sites" (Fowler, 1988; McAlpine and Drake, 2003; Molofsky and Augspurger, 1992). Safe sites are locations or microsites suitable for the germination and establishment of plant species (Fowler, 1988; Harper *et al.*, 1961). Fire can establish safe sites for plant species through a variety of mechanisms including removal of litter (Bartuszevige *et al.*, 2007; Glasgow and Matlack, 2007), soil enhancement by nutrients (Glasgow and Matlack, 2007), stimulation of seeds (Behenna *et al.*, 2008; Todorovic *et al.*, 2010), and decreasing canopy cover (Elliott *et al.*, 1999).

In eastern forests, the effect of fire on invasive plant species has only recently been explored (but see: Emery *et al.*, 2011; Flory and Lewis, 2009; Glasgow and Matlack, 2007; Richburg *et al.*, 2004), as fire is often suppressed in these habitats (Nowacki and Abrams, 2008). However, where fire is still used for habitat maintenance or where wildfires still occur, little is known about how invasive plant species will respond. One prominent invader of eastern forests is the liana, *Celastrus orbiculatus* Thunb. (Celastraceae, oriental bittersweet). *Celastrus*

orbiculatus has the ability to change the successional trajectories of natural systems, through vigorous growth and blanketing of trees and ground vegetation (Fike and Niering, 1999). Lianas, both native and invasive, are notoriously challenging to control by any mechanism due to vigorous resprouting (Pavlovic et al. unpublished data; Gerwing, 2001; Schierenbeck *et al.*, 1994), and flexible growth habit (Putz and Holbrook, 1991).

Celastrus orbiculatus seedlings can survive and grow under a broad range of light levels (Bois *et al.*, 2012; Ellsworth *et al.*, 2004b; Leicht-Young *et al.*, 2007; Silveri *et al.*, 2001). Little is known, however, about the susceptibility of habitats to invasion from seed dispersal across gradients in light and soil chemistry. Whether fire creates safe sites via improving ground layer light and soil conditions that will increase the vulnerability of habitats to germination and establishment *C. orbiculatus* is unknown as well. *Celastrus orbiculatus* can be spread long distances via bird-dispersed seeds, and locally via passive dispersal, often in very great quantities (reported in Ellsworth et al. 2004a; 168 seeds/m^2), leading to germination of seedlings in high densities (107 seedlings/m^2; Ellsworth et al. 2004a). Thus, burned habitats adjacent to (Ellsworth *et al.*, 2004a), as well as longer distances away (LaFleur *et al.*, 2009; LaFleur *et al.*, 2007; Merow *et al.*, 2011) from infestations of *C. orbiculatus*, are susceptible to the introduction of new seeds following fire. To investigate the potential of fire to increase the susceptibility of eastern habitats to germination and establishment of *C. orbiculatus* seedlings via creation of safe sites, we examined burning and post fire effects on the germination, establishment, growth, and survival of this invasive species.

We used six common eastern habitat types and four experimental treatments to determine how fire may result in increased infiltration of these areas by seed of *C. orbiculatus*. We made two main predictions of how the treatments and habitats would influence germination of *C. orbiculatus*. (1) We predicted that treatments in which the litter was removed via fire or physical litter removal would have higher germination than treatments where litter was intact due to increased light availability and a reduced litter barrier to germination; (2) open, richer habitats (in terms of soil attributes) would have the greatest germination and survival of *C. orbiculatus*. Our research results will have practical applications for land managers to predict potential threats posed by *C. orbiculatus* in post-fire scenarios.

2. Materials and Methods

2.1. Seed collection

Seeds of *C. orbiculatus* were collected in February 2009 and 2010 from several (i.e., > 10 plants) throughout Indiana Dunes National Lakeshore (INDU) (41º38' N, 87º09' W) in northwest Indiana, USA, at the southern tip of Lake Michigan. Collection of the seeds in February assured that seeds received the proper cold stratification prior to sowing and most closely mimicked the natural process of seed dispersal (Ellsworth *et al.*, 2004a). Fruits were air-dried and seeds extracted from the fruits. Cleaned seeds were thoroughly mixed and placed in envelopes in the refrigerator before sowing.

2.2. Study sites

To test the extent to which fire makes different habitats susceptible to invasion by *C. orbiculatus*, we sought to examine how germination was affected across the two main soil types present at INDU, glacial moraine soils and sand dune soils. We sowed seeds in experimental plots in six habitat types, sand savanna/woodland (hereafter savanna), sand prairie, silt-loam prairie (moraine prairie), sand oak forest (oak forest), beech-maple forest (beech-maple), and oak-hickory forest (oak-hickory) in 12 randomized blocks. Savanna sites were dominated by *Quercus velutina* (black oak), had a litter layer dominated by oak litter, and were located among three sites. Sand prairie sites were C_4 grass dominated large openings in oak savanna matrix occurring at two sites. Sand oak forest was dominated by *Q. velutina* and occassional *Pinus strobus* (white pine), had oak and/or pine litter, had a canopy cover greater than 80% and was located at two sites. Moraine prairie sites were also dominated by C_4 grasses (*Andropogon gerardii*, *Panicum virgatum*, and *Sorghastrum nutans*) and forbs (e.g., *Solidago altissima*). Oak hickory was dominated by *Q. velutina*, *Q. alba*, *Carya ovata* and other mesophytic forest trees, had a mixture of oak and mesophytic litter, and were located on the forested moraine bluffs. Beech-maple forest plots were located at two sites, and were dominated by *Fagus grandiflora*, *Acer saccharum*, and other mesophytic forest trees, and had litter dominated by non-oak species. Thus, we had three parallel habitat types on moraine soils (moraine prairie, beech-maple, oak-hickory) and three on sandy soils (sand prairie, oak forest, savanna).

2.3. Experimental design

Blocks were selected in each area that lacked infestations of *C. orbiculatus* so that establishment of wild seedlings would be kept to a minimum. Most blocks were more than 30 m from each other when they occurred in the same habitat type and patch, except for one pair in one sand prairie location that were 8 m apart due to limited appropriate sites. Each block was 6 X 6 m with four 2 X 2 m nested treatment plots separated by 2 m buffer zones that were weed-whipped and raked prior to burning. Randomized treatments consisted of low intensity burn, high intensity burn, litter removal, and a control where litter remained intact (6 habitats X 12 blocks X 4 treatment plots = 288; fire treatments are explained in the section below).

Plots were established in late March 2009. We conducted the burns in the sand savanna, sand prairie, and moraine prairie in early April of 2009. With the rapid onset of the fire season and the closure of burning on April 15 at the Heron Rookery and Mnoke Prairie, we were unable to burn the oak hickory, oak forest, and beech maple plots in spring of 2009. Burns in the oak hickory, beech maple, and oak forest took place in the fall of 2009, when the leaf litter was dry, undecomposed, and flammable (Nowacki and Abrams, 2008).

In late April of 2009 and 2010 following the spring and fall burns, we added 25 seeds in each of the four treatment subplots within a randomly placed 25 cm x 25 cm plot. One seed was placed in each of 25 1 cm grid cells (5 x 5) created using a wooden frame for easier relocation of germinated seeds and the identification of any random "wildling" seedlings from outlying populations. Seeds were placed on top of the litter to simulate natural dispersal in the spring, when many of the fruits are finally removed or passively fall from the vines (Greenberg *et al.*, 2001). Seeds were added to the plots in spring because previous studies have shown that *C. orbiculatus* does not have a seed bank (Ellsworth *et al.*, 2004a; Van Clef and Stiles, 2001), thus seeds developed the previous fall are those that will germinate the following spring (Ellsworth *et al.*, 2004a). Seedlings were monitored monthly from May through the end of the growing season in September.

2.4. Fire treatments

To create the different fuel treatments, litter from the litter removal plot was placed on the high intensity plot to increase its fuel load. In the low intensity plots the fuel load was whatever ambient litter was present. On the day of the low-intensity and high-intensity burns, a 0.25 by 0.25 m litter sample was taken to assess fuel loads and moisture content. The sample was placed in a pre-weighed plastic bag and then reweighed. We then transferred the litter to a pre-weighed paper bag for drying at 70 ˚C for 12 hours. This litter biomass demonstrated that high intensity fuel loads were significantly greater than the low intensity fuel loads in the beech-maple, oak forest, oak-hickory, and moraine prairie habitats, but were not different in the savanna, and sand prairie ($F_{5,131}$ = 4.3 , P = 0.001).

Temperature sensitive paint tags deployed on a stake at (0, 0.15, 0.30, 0.46, 0.76, 1.07, 1.37 m) above the ground in each plot (Cole *et al.*, 1992). Temperature paints were 121 ºC, 149 ºC, 204 ºC, 260 ºC, 316 ºC, 371 ºC, 427 ºC, 482 ºC, 538 ºC, 649ºC. During the burns, rate of fire spread, flame height (minimum, maximum, and average), and wind speed and direction were recorded. The main differences in experimental burns was between the prairie fuels (savanna and prairies) and the forest fuels (oak-hickory, oak forest, and beech-maple), with the moraine prairie having the hottest and quickest burns. Mesic forests had significantly lower fire temperature maximums (397 ± 19°C) compared to prairies (453 ± 17°C) with oak forests being intermediate (423 ± 18°C; $F_{2,138}$ = 4.4, P = 0.013). Fire temperatures on the moraine were greater in the open habitats (501 ± 26°C) compared to the forested habitats (404 ± 22°C), but were lower on the sand dunes (400 ± 12°C) ($F_{1,136}$ = 4.4, P = 0.036). Rate of fire spread was 75% greater in the prairies than in the mesic and oak woods ($F_{2,130}$ = 25.5, P <0.001): prairie = 0.75 ± 0.07 m/minute, oak forests = 0.45 ± 0.02 m/minute, and mesic forest = 0.43 ± 0.01 m/minute. The greater rate in spread of burns in the prairies contributed to the significantly greater rate of spread in the open habitats compared to the forests ($F_{1,128}$ = 17, P < 0.001).

2.5. Plant/environmental measurements

Germinants were monitored monthly from May – September in 2009 – 2011. Number of live seedlings and height of plant from the ground to the apical meristem were measured. At the end of September 2010, we took the final height measurements of the plants for the year and then harvested the second year plants (moraine prairie, sand prairie, and savanna sites). We repeated

this harvest in September 2011 with the oak forest, beech-maple, and oak-hickory forest sites, so that both cohorts had the two full growing seasons. Plants were harvested at ground level as the roots in the ground were difficult to extract without breakage. The plants were dried in an oven for 24 hours at 70°C. Dried plants were weighed and aboveground biomass recorded.

During the course of the growing seasons, we collected additional environmental data on each of the four subplots. We took canopy photographs and calculated the percent openness over each treatment subplot using Gap Light Analyzer computer software (Frazer *et al.*, 1999). Finally, in each plot we collected samples of the upper 10 cm of soil prior to the fire treatments and sent them out for analysis. Samples were analyzed by A & L Great Lakes Laboratories, Inc. (FortWayne, IN) for percent organic matter, total phosphorous (ppm), potassium (% and ppm), magnesium (% and 198 ppm), calcium (% and ppm), pH, cation exchange capacity (CEC; 199 meq/100 g), nitrate (ppm), ammonium nitrogen (ppm) and the percentage of sand, silt and clay.

2.6. Statistical analyses

For the analysis, we took three main approaches: ANOVA, linear regression, and logistic regression. To examine the effect of the six habitats and four fire treatments, we used a full factorial two-way ANOVA. We ran the test twice: once for the first growing season, and once for the second growing season, as we expected that fire treatment effects would differ in the first year after treatment compared with the second year. The response variables that we used were 1) maximum percent germinants (square root transformation), 2) the proportion of plants surviving (excluding where there was no survival; square root transformation), 3) binomial survival response, 4) the amount of winter mortality, 5) mean height at germination (log (x +1) transformed), 6) final height at harvest (log (x + 1) transformed) and 7) final aboveground biomass of harvested seedlings.

Maximum percent germinants was the total cumulative number of seedlings germinated during the study in each subplot divided by 25. We used this value as opposed to percent germination to get a sense of how many seedlings were in the plots. We followed this measure up with the proportion of germinants surviving. This response enabled us to determine in plots where there was survival, if habitat or fire treatment influenced the proportion of seeds that survived. We calculated winter mortality by using the difference between the number of

seedlings observed in June of the second year and the number observed in August of the first year. The more negative the difference, the fewer plants survived the winter. Mean height at germination was examined in order to determine if litter or habitat affected the heights of the plants initially (we used the value for the first growing season in June). Final height at harvest (we used the value of the September heights) was analyzed to get a sense of how tall seedlings could get after two years. For final biomass, the ANOVA was unbalanced. However, upon using a random draw of 20 plants from the two highest groups (moraine prairie and oak-hickory) and using these values instead, we got the same results. All of these ANOVA tests were followed up with either Tukey's-b multiple comparisons test to examine differences between significant factors, or in the case of the final height, we used LSD pairwise comparisons. All of the ANOVA analyses were run in SPSS (SPSS Inc., 2003)

We ran simple linear regressions on the same response variables (maximum percentage of germinants, survival, winter mortality, mean height at germination, final height, and biomass) used in the ANOVA for year 1 and 2, using the soil chemistry and canopy openness (log transformation) as explanatory variables. We examined correlations to reduce soil chemistry variables that were highly correlated and results from principal components analysis (PCA) to identify the most important variables. To examine overall differences in soil chemistry and canopy openness in the habitats, we ran an ANOVA followed by Tukey's-b multiple comparisons on each of the soil and canopy openness values by habitat to determine if there were differences. We used square root of organic matter (sqrtOM), log of potassium (logK), square root of phosphorous (sqrtP), cation exchange capacity (CEC), pH, ammonium nitrogen (NH_4N), % sand, and % silt. To determine the best model, we ran stepAIC in R to reduce the number of variables (R version 2.15). We reported on the results of the final model.

We ran two separate logistic regressions to look at both categorical (habitat type, fire treatment) and continuous effects (soil factors, canopy openness), on the binomial survival of seedlings at the end of the first and second years. We started with the same soil factors as the linear regression, and used step AIC in R to determine the best models.

3. Results

3.1. Habitats

When we examined the soil and canopy openness values for each of the habitats to see if there were differences, we found that the habitats did differ significantly in these environmental factors (Table 1). The main differences in soil composition were split between the plots that were on moraine soils (moraine prairie, beech-maple, and oak-hickory) vs. those on sandy soils (oak forest, savanna, and sand prairie), with the moraine soils being richer in soil nutrients. The moraine plots had significantly higher sqrtOM, NH_4N, and logK. Not surprisingly, the habitats with the significantly greatest canopy openness were the moraine prairie, sand prairie, and savanna (Table 1).

3.2. Maximum germinants

In general, germination of the seedlings occurred in the first growing season. There was mortality over the winter in all habitat types (Fig. 1; see transition from growing season 1 to 2). In the first growing season, the forested plots (especially beech-maple and oak forest) initially had a high number of germinants. This high number dropped off from a peak in June to the end of the first growing season in these plots (see discussion below). The more open plots showed a slower germination that later peaked a similar levels to the forest plots (Fig. 1).

For the categorical analysis of habitat and treatment effects on the maximum percent of germinants in each subplot, in the first year, only habitat had a significant effect on maximum percent germination, with the beach-maple, oak-hickory, and moraine prairie having the most germinants and the sand prairie and savanna having the fewest (Table 2, Fig 2). In the second year, there was a similar pattern, but the moraine prairie had the highest maximum percent of germinants and savanna, sand prairie, oak forest, and beech-maple had the lowest. Thus, the fire treatments did not have a significant effect on the maximum percent of germinants (Table 2).

For the regression analysis on maximum percentage of germinants in the first growing season, logK and sqrtOM were positively related to the square root of maximum germination, while in the second year, sqrtOM and canopy openness were significantly positively related to the square root of the max percent of germinants (Table 3).

3.3. Survival

When we examined what influenced the proportion survival of germinants where survival was greater than 0, we found similar patterns to the maximum number of germinants in both the ANOVA and regression analyses. For the ANOVA in the first years, only habitat had a significant effect (Table 2, Fig. 3). Tukey's-b multiple comparisons indicated that the moraine prairie had significantly greater survival than the oak forest and savanna habitats (Fig. 3). In the second year, neither habitat, nor treatment, nor the interaction was significant. The simple linear regression analysis for the first year had sqrtOM, CEC, and canopy openness with a significant positive effect on proportion surviving. The second year only had a significant positive effect of canopy openness (Table 3).

For winter mortality, ANOVA analysis indicated that there was a significant habitat x treatment interaction. Further investigation into this interaction through separate one-way ANOVAs for each habitat indicated that in the moraine prairie, the experimental fire treatment was significant ($F_{3,37} = 4.6$, Bonferroni corrected $p = 0.048$), and that the control, high and low fire intensity plots had significantly greater mortality over winter than the litter removed plots. The regression analysis indicated that % sand, logK, and sqrtOM were negatively related to winter mortality (Table 3).

Logistic regression analysis of binomial survival for year one again showed a positive relationship of logK and sqrtOM with survival. The second year only had a significant positive relationship with the logK (Table 4). Thus, these results were similar to both maximum percent of germinants and proportion survival.

3.4. Height

The height of seedlings at germination was significantly affected by habitat and treatment, but not the interaction (Table 2). Multiple comparisons indicated that the moraine prairie had the tallest seedlings at germination and these were significantly taller than those in the beech-maple forest, oak-hickory forest and oak savanna (Fig. 4A). In the only instance where treatment had a significant effect on oriental bittersweet response, the control treatment had significantly taller seedlings than the litter removed and fire treatment plots, and the low intensity fire plot had the shortest seedlings (Fig. 4B). In the linear regression analysis, logK had

a significantly positive effect on initial height at germination, while % silt and pH had slightly negative effects (Table 3).

Final height at the end of the second year of growth had significant main effects of habitat and treatment, but not the interaction (Table 2). LSD pairwise comparisons showed that the oak forest had the tallest plants at the end of the experiment, beech-maple, oak-hickory, sand prairie, and savanna were in the middle range, and moraine prairie had the shortest plants (Fig. 4A). For the treatments, the control and high intensity burns had the tallest plants and the litter removed and low intensity burns had the shortest plants (Fig. 4B). When we investigated this further, we saw that only in the savanna plot was the high intensity plants the tallest, which may have influenced the overall mean. In the linear regression, both % sand and logK negatively influenced final height, while sqrtP had a significantly positive effect (Table 3).

3.5. Biomass

Aboveground biomass of harvested seedlings was significantly affected by habitat, but not by fire treatment or the interaction between habitat and fire treatment (Table 2). Tukey's-b comparisons of habitats indicated that only the oak forest plants had significantly higher biomass than the other five habitats (Table 5). Regression analysis indicated that while % sand had a significant slightly negative effect on biomass, log(K) had a more strongly negative effect (Table 3).

4. Discussion

Overall, the experimental fire treatments and the litter removal treatment did not increase the probability of *C. orbiculatus* germination. Our study indicated that the type of habitat the seeds were introduced to had a greater influence on percent germination and survival than did the fire treatments or the removal of litter. We did not expect this result, as we predicted that the clearing of litter via fire or manual removal would promote germination of *C. orbiculatus* through creation of safe sites. We did see however, that the highest germination was in the moraine prairie plots that had the most canopy openness and the richest soils in terms of soil nutrients (Table 1). While the moraine prairie had the lowest litter biomass of all the habitats,

we suspect that this largely graminoid fuel was less compacted than oak leaf litter and provided better conditions for germination. Other open habitats such as the sand prairie did not exhibit as high germination rates. Our study is in contrast, however, with studies that looked at the relationship between fire and different invasive species which found increased levels of germination (Behenna *et al.*, 2008; Glasgow and Matlack, 2007; Maret and Wilson, 2000; Pauchard *et al.*, 2008).

4.1. Fire effects on germination

In many of the other studies, fire had a positive influence on germination of invasive species by removing the litter layer (Glasgow and Matlack, 2007), top killing other plants in competition (Pauchard *et al.*, 2008), and/or enhancing the soil with nutrients (Glasgow and Matlack, 2007). In a study by Glasgow and Matlack (2007), germination of *Rosa multiflora*, a similar woody invasive that also has bird dispersed seeds, was enhanced by the high intensity fire treatment. The high intensity treatment increased germination more than either the litter removal plot or a lime addition plot, indicating that the fire in some way enhanced the germination of this species, although the mechanism was unclear (Glasgow and Matlack, 2007). *Rosa multiflora* did germinate under all of the treatment conditions in some capacity. For *C. orbiculatus*, our evidence shows that the clearing of an area by fire or manual removal did not have an effect on the maximum number of germinants. Thus, it is likely that *C. orbiculatus* will not invade an area via germinating seeds more in an area burned by fire than any other natural area. *Celastrus orbiculatus* thus exhibits greater plasticity in terms of its ability to germinate across habitats and disturbance levels.

This result points to both positive and negative news for land managers. The positive is that burning a natural area will not result in an increased recruitment of *C. orbiculatus* from dispersed seeds. In fact, we conducted a small pilot experiment examining if seeds and fruit of *C. orbiculatus* could survive the temperatures of a prescribed fire. None of the seeds, from ground level up to 15.25 cm survived (Pavlovic and Leicht-Young, unpublished data). Thus, prescribed fires in the early spring would actually burn up much of the seeds that had fallen down or been dispersed over the winter and spring (Pavlovic and Leicht-Young, unpublished data). This is not surprising, as similar native species from Eastern deciduous forests are not

adapted to frequent fire (Emery *et al.*, 2011). In addition, *C. orbiculatus* seeds from the previous fall are the ones that germinate in the spring, and there is no real seedbank to germinate the following year (Ellsworth *et al.*, 2004a; Van Clef and Stiles, 2001). Other studies on invasive species have shown that using fire to burn up the surface layer seeds of invasive species could be an effective management technique (Srinivasan *et al.*, 2012), if the seeds do not have a long-lived seedbank, and burns were repeated. However, post-fire resprouting after top-kill of already established *C. orbiculatus* could lead to increased cover of this species (Pavlovic et al. unpublished manuscript). In addition, it is apparent that *C. orbiculatus* is capable of germinating across a very large range of habitats, even where the litter layer is intact and undisturbed; showing the great potential this species has for invading a range of habitats, regardless of the state of disturbance.

4.2. Habitat effects on germination, growth, and survival

Celastrus orbiculatus is a species that exhibits a very high degree of plasticity throughout its life history. Established seedlings of this species area are able to survive and thrive at a very wide range of light and moisture conditions (Leicht-Young *et al.*, 2011; Leicht-Young *et al.*, 2007; Leicht and Silander, 2006). These seedlings can sit and wait in the understory for a long period of time, waiting for gaps to open in the overstory to ascend to the canopy, even in old growth forests (Pavlovic and Leicht-Young, 2011). As these plants get larger, they can grow in very high densities, which may in fact increase their chance of survival (Leicht-Young *et al.*, 2011). *Celastrus orbiculatus* can also grow in a shrub-like habit in open areas with no support, blanketing vegetation (Fike and Niering, 1999; Leicht-Young *et al.*, 2011).

The highest percentage of germinants was in the moraine prairie, beech-maple, and oak-hickory habitats. Over the course of the study (Fig. 1) it was the moraine prairie that sustained the greatest percent of germinants. This is likely because it both had full sun, and richer soils. High logK and logOM came out significant positive contributors to germination and survival in all of the regression analyses (Table 2). The openness of the moraine prairie also may have protected the seedlings from the damaging effects experienced in the beech-maple and oak forests where after high germination in June, there was substantial die-off both in our experimental plots as well as adjacent unrelated research plots (Fig. 1; Pavlovic and Leicht-

Young, pers. obs.). We feel this die-off was due to hot, humid, and wet weather in their first season of growth, 2010. In the shaded forest habitats, the humidity and moisture were even greater and could have caused the seedlings to dampen off.

Although *C. orbiculatus* can grow in open habitats with sandy soils (Leicht-Young and Pavlovic, 2012; Leicht-Young *et al.*, 2007), it prefers richer, moister habitats (Leicht-Young *et al.*, 2007; Pavlovic and Leicht-Young, 2011). There is also some evidence that *C. orbiculatus* may modify soil properties to make them richer, as its leaves are higher in potassium and calcium than native *Q. rubra* leaves (Leicht-Young *et al.*, 2009). Interestingly, in sandy habitats, there was no difference in the proportion of seedlings that survived compared with more mesic habitats (Fig. 3), even though there were fewer germinants overall. In the case of these habitats, once these plants germinated, they tended to survive, even at lower numbers. In another study that germinated *C. orbiculatus* across a range of light and moisture, there were no significant differences in percent germination across the locations used, or relationships between germination and light and moisture (Bois *et al.*, 2012).

After two years of growth, the final heights of *C. orbiculatus* were shortest in the moraine prairie and savanna and tallest in the oak forest; Fig. 4C). Thus, after the seedlings were initially taller in the moraine prairie (Fig. 4A), seedlings growing in forested habitats tended to be tallest at the end of two growing seasons. *Celastrus orbiculatus* seedlings under this greater canopy cover may be growing taller in order to reach additional light resources, as for lianas, reaching supports in the forest understory is critical to success. In the moraine prairie, because of the greater light availability, seedlings may take on more of a “shrub” habit vs. a vine habit, as active searching for light may not be as critical (Leicht-Young *et al.*, 2011).

Many other plant species, both invasive (Bartuszevige *et al.*, 2007) and native (Pavlovic and Grundel, 2009) benefit from disturbance of the litter creating appropriate safe sites. *Celastrus orbiculatus*, however, did not appear to benefit, nor to be negatively impacted by the disturbance treatments (fire, litter removal). Another study on temperate woody species in New Zealand indicated that germination of invasive species such as *Cytisus scoparius* were unaffected by presence of litter, but was more influenced by canopy openness. In the case of another species they examined, *Berberis darwinii*, litter in fact promoted its germination, along with that of two native species (McAlpine and Drake, 2003). Since *C. orbiculatus* does not germinate as well in dry, sandy habitats, the litter removal treatments probably exposed the seeds more to sun

and desiccation, thus not providing any enhancement of germination. Other studies have shown that *C. orbiculatus* is able to germinate successfully even with high amounts of litter. Ellworth et al. (2004a) experimentally determined that there was no significant difference between control and litter addition treatments except at the very highest amount of litter, which did depress germination significantly. In that study, *C. orbiculatus* showed a great degree of hypocotyl elongation through the leaf litter (up to 9 cm) to reach the surface. The drawback to this elongation is that less biomass is allocated to the cotyledons of seedlings that germinate under litter, which could prove detrimental to the survival of the seedlings (Ellsworth *et al.*, 2004a). We found that the control treatment (litter intact) had the tallest seedlings upon germination, supporting these experimental findings (Fig. 4). The habitat with the tallest seedlings, moraine prairie, also had the deepest litter as it was mostly comprised of deep layers of dead grasses (Leicht-Young and Pavlovic, pers. obs.). Thus, the *C. orbiculatus* seedlings in this habitat needed to grow taller to penetrate this thatch layer to reach sufficient light resources. The ability of this liana to make its way through many layers of litter gives it the capability to invade minimally disturbed habitats, and does not necessarily need a disturbance to release it to germinate.

5**. Conclusion**

The germination and survival of *C. orbiculatus* was not enhanced by prescribed fire. For both the maximum percentage of germinants and survival, experimental treatment had no significant effect, while habitat type did. Binomial survival was highest in habitats with high potassium and organic matter. *Celastrus orbiculatus* was able to germinate in both open and closed habitat types, and across a wide range of soils. Germinating seedlings were tallest in control plots, such that they were able to grow through an intact litter layer. While at the final harvest, the tallest plants were in forested habitats. Thus, disturbance of the litter by fire or mechanical mechanisms did not make these habitats more susceptible to germination of dispersed seeds of *C. orbiculatus*. The plastic nature of this invasive species enables it to germinate successfully across all conditions and it can threaten habitats with an intact litter layer.

Since *C. orbiculatus* lacks a seed bank, and its seeds are fire intolerant, prescribed fire with temparatures greater than 140º C (Pavlovic and Leicht-Young, unpublished data) in the

spring before the growing season, may actually aid control as the year's crop of seeds would be essentially eliminated. Otherwise habitat mediated by soil nutrients, not fire, appears to have most important influence on the successful establishment of oriental bittersweet. Thus, the main threat posed by *C. orbiculatus* in regards to prescribed fire is the effects on established plants (Pavlovic et al., unpublished manuscript). Land managers do need to be aware, however, that this invasive species is capable of germinating in locations with an undisturbed litter layer, and across a very wide range of habitats. Vigilance will be necessary to suppress the invasion of *C. orbiculatus* into high-quality habitats via bird dispersal. Additional studies on the interaction of fire and invasive species in Eastern habitats is important to using prescribed fire effectively to suppress invasion and enhance regeneration of desirable species.

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References

Bartuszevige, A.M., Hrenko, R.L., Gorchov, D.L., 2007. Effects of leaf litter on establishment, growth and survival of invasive plant seedlings in a deciduous forest. Am. Midl. Nat. 158, 472-477.

Behenna, M., Vetter, S., Fourie, S., 2008. Viability of alien and native seed banks after slash and burn: Effects of soil moisture, depth of burial and fuel load. S. Afr. J. Bot. 74, 454-462.

Bois, S.T., Ibáñez, I., Silander Jr., J.A., 2012. Colonization potential of three invasive species and their ecological analogs in New England; capitalizing on environmental stochasticity to understand seedling establishment and spread. Unpublished Manuscript.

Bond, W.J., Midgley, J.J., 2003. The evolutionary ecology of sprouting in woody plants. Int. J. Plant Sci. 164, S103-S114.

Cole, K.L., Klick, K.F., Pavlovic, N.B., 1992. Fire temperature monitoring during experimental burns at Indiana Dunes National Lakeshore. Nat. Areas J. 12, 177-183.

D'Antonio, C.M., Vitousek, P.M., 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annu. Rev. Ecol. Syst. 23, 63-87.

Elliott, K.J., L. Hendrick, R., Major, A.E., Vose, J.M., Swank, W.T., 1999. Vegetation dynamics after a prescribed fire in the southern Appalachians. For. Ecol. Manag. 114, 199-213.

Ellsworth, J.W., Harrington, R.A., Fownes, J.H., 2004a. Seedling emergence, growth, and allocation of Oriental bittersweet: effects of seed input, seed bank, and forest floor litter. For. Ecol. Manag. 190, 255-264.

Ellsworth, J.W., Harrington, R.A., Fownes, J.H., 2004b. Survival, growth and gas exchange of *Celastrus orbiculatus* seedlings in sun and shade. Am. Midl. Nat. 151, 233-240.

Emery, S.M., Uwimbabazi, J., Flory, S.L., 2011. Fire intensity effects on seed germination of native and invasive Eastern deciduous forest understory plants. For. Ecol. Manag. 261, 1401-1408.

Fike, J., Niering, W.A., 1999. Four decades of old field vegetation development and the role of *Celastrus orbiculatus* in the northeastern United States. J. Veg. Sci. 10, 483-492.

Flory, S.L., Lewis, J., 2009. Nonchemical methods for managing Japanese stiltgrass (*Microstegium vimineum*). Invasive Plant Sci. Manag. 2, 301-308.

Fowler, N.L., 1988. What is a safe site?: Neighbor, litter, germination date, and patch effects. Ecology 69, 947-961.

Frazer, G.W., Canham, C.D., Lertzmann, K.P., 1999. Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true colour fisheye photographs, users manual and program documentation. In. Simon Fraser University and Institute of Ecosystem Studies, Burnaby, British Columbia, Canada and Millbrook, New York, USA. .

Gerwing, J.J., 2001. Testing liana cutting and controlled burning as silvicultural treatments for a logged forest in the eastern Amazon. J. Appl. Ecol. 38, 1264-1276.

Glasgow, L.S., Matlack, G.R., 2007. The effects of prescribed burning and canopy openness on establishment of two non-native plant species in a deciduous forest, southeast Ohio, USA. For. Ecol. Manag. 238, 319-329.

Greenberg, C.H., Smith, L.M., Levey, D.J., 2001. Fruit fate, seed germination and growth of an invasive vine - an experimental test of 'sit and wait' strategy. Biol. Invasions 3, 363-372.

Gurvich, D.E., Enrico, L., Cingolani, A.M., 2005. Linking plant functional traits with post-fire sprouting vigour in woody species in central Argentina. Austral. Ecol. 30, 868-875.

Harper, J.L., Clatworthy, J.N., McNaughton, I.H., Sagar, G.R., 1961. The evolution and ecology of closely related species living in the same area. Evolution 15, 209-227.

Hoffmann, W.A., Solbrig, O.T., 2003. The role of topkill in the differential response of savanna woody species to fire. For. Ecol. Manag. 180, 273-286.

Hutchinson, T.F., Boerner, R.E.J., Sutherland, S., Sutherland, E.K., Ortt, M., Iverson, L.R., 2005. Prescribed fire effects on the herbaceous layer of mixed-oak forests. Can. J. For. Res. 35, 877-890.

LaFleur, N., Rubega, M., Parent, J., 2009. Does frugivory by European starlings (*Sturnus vulgaris*) facilitate germination in invasive plants? J. Torrey Bot. Soc. 136, 332-341.

LaFleur, N.E., Rubega, M.A., Elphick, C.S., 2007. Invasive fruits, novel foods, and choice: An investigation of European Starling and American Robin frugivory. Wilson J. Ornithol. 119, 429-438.

Leicht-Young, S.A., Latimer, A.M., Silander, J.A., 2011. Lianas escape self-thinning: Experimental evidence of positive density dependence in temperate lianas *Celastrus orbiculatus* and *C. scandens*. Perspect. Plant Ecol. Evol. Syst. 13, 163-172.

Leicht-Young, S.A., O'Donnell, H., Latimer, A.M., Silander, J.A., 2009. Effects of an invasive plant species, *Celastrus orbiculatus*, on soil composition and processes. Am. Midl. Nat. 161, 219-231.

Leicht-Young, S.A., Pavlovic, N.B., 2012. Encroachment of oriental bittersweet into Pitcher's thistle habitat. Nat. Areas J. 32, 171-176.

Leicht-Young, S.A., Silander, J.A., Latimer, A.M., 2007. Comparative performance of invasive and native *Celastrus* species across environmental gradients. Oecologia 154, 273-282.

Leicht, S.A., Silander, J.A., 2006. Differential responses of invasive *Celastrus orbiculatus* (Celastraceae) and native *C. scandens* to changes in light quality Am. J. Bot. 93, 972-977.

Mandle, L., Bufford, J.L., Schmidt, I.B., Daehler, C.C., 2011. Woody exotic plant invasions and fire: reciprocal impacts and consequences for native ecosystems. Biol. Invasions 13, 1815-1827.

Maret, M.P., Wilson, M.V., 2000. Fire and seedling population dynamics in western Oregon prairies. J. Veg. Sci. 11, 307-314.

McAlpine, K.G., Drake, D.R., 2003. The effects of small-scale environmental heterogeneity on seed germination in experimental treefall gaps in New Zealand. Plant Ecol. 165, 207-215.

Merow, C., LaFleur, N., Silander, J.A., Wilson, A.M., Rubega, M., 2011. Developing dynamic mechanistic species distribution models: Predicting bird-mediated spread of invasive plants across northeastern North America. Am. Nat. 178, 30-43.

Molofsky, J., Augspurger, C.K., 1992. The effect of leaf litter on early seedling establishment in a tropical forest. Ecology 73, 68-77.

Nowacki, G.J., Abrams, M.D., 2008. The demise of fire and "mesophication" of forests in the eastern United States. Bioscience 58, 123-138.

Pauchard, A., Garcia, R.A., Pena, E., Gonzalez, C., Cavieres, L.A., Bustamante, R.O., 2008. Positive feedbacks between plant invasions and fire regimes: *Teline monspessulana* (L.) K. Koch (Fabaceae) in central Chile. Biol. Invasions 10, 547-553.

Pavlovic, N.B., Grundel, R., 2009. Reintroduction of wild lupine (*Lupinus perennis* L.) depends on variation in canopy, vegetation, and litter cover. Restor. Ecol. 17, 807-817.

Pavlovic, N.B., Leicht-Young, S.A., 2011. Are temperate mature forests buffered from invasive lianas? J. Torrey Bot. Soc. 138, 85-92.

Putz, F.E., Holbrook, N.M., 1991. Biomechanical studies of vines. In: Putz, F.E., Mooney, H.A. (Eds.), The Biology of Vines. Cambridge University Press, Cambridge, pp. 73-98.

Richburg, J.A., Patterson III, W.A., Ohman, M., 2004. Fire managment options for controlling woody invasive plants in the Northeastern and Mid-Atlantic US. In. University of Massechusetts, Department of Natural Resources Conservation, Amherst, MA, p. 59.

Schierenbeck, K.A., Mack, R.N., Sharitz, R.R., 1994. Effects of herbivory on growth and biomass allocation in native and introduced species of *Lonicera*. Ecology 75, 1661-1672.

Silveri, A., Dunwiddle, P.W., Michaels, H.J., 2001. Logging and edaphic factors in the invasion of an Asian woody vine in a mesic North American forest. Biol. Invasions 3, 379-389.

SPSS Inc., 2003. SPSS 12.0 for Windows.

Srinivasan, M.P., Kalita, R., Gurung, I.K., Bhattacharjee, S.K., Antony, P.M., Krishnan, S., Gleeson, S.K., 2012. Seedling germination success and survival of the invasive shrub Scotch broom (*Cytisus scoparius*) in response to fire and experimental clipping in the montane grasslands of the Nilgiris, south India. Acta Oecol. 38, 41-48.

Todorovic, S., Bozic, D., Simonovic, A., Filipovic, B., Dragicevic, M., Giba, Z., Grubisic, D., 2010. Interaction of fire-related cues in seed germination of the potentially invasive species *Paulownia tomentosa* Steud. Plant Species Biol. 25, 193-202.

Van Clef, M., Stiles, E.W., 2001. Seed longevity in three pairs of native and non-native congeners: Assessing invasive potential. Northeast. Nat. 8, 301-310.

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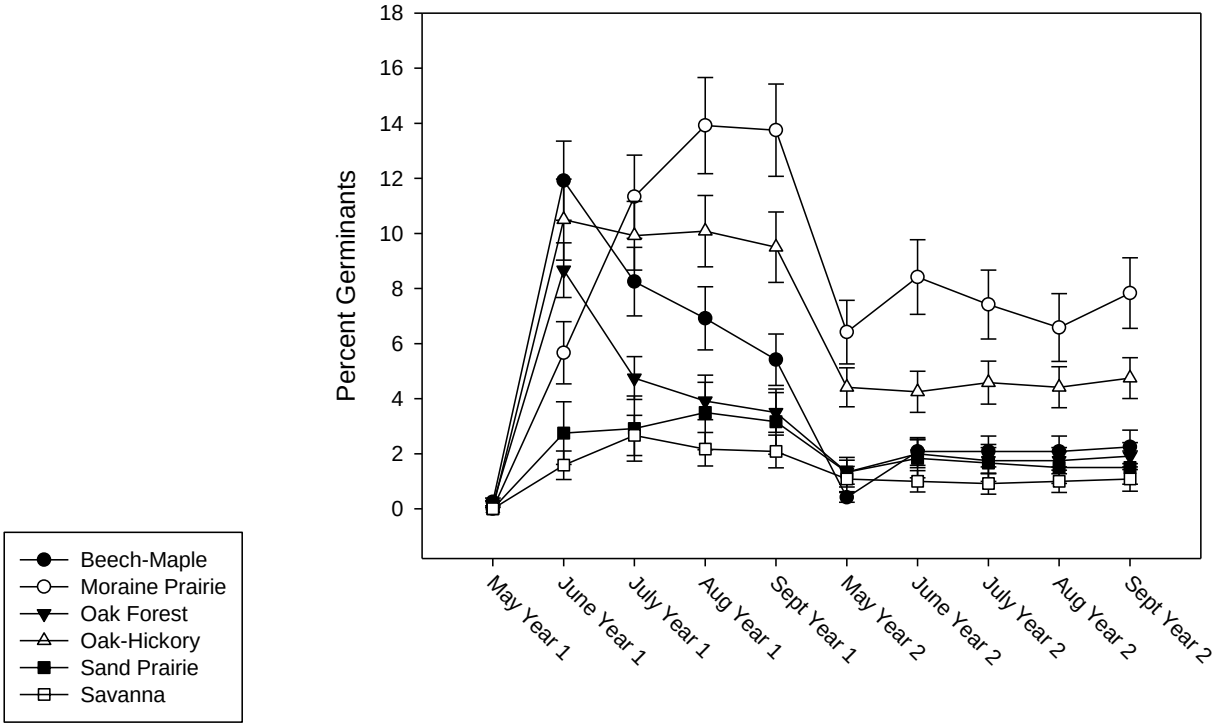

Fig. 1. Percent of germinants over the two growing seasons. Dots indicate the mean value ± the standard error.

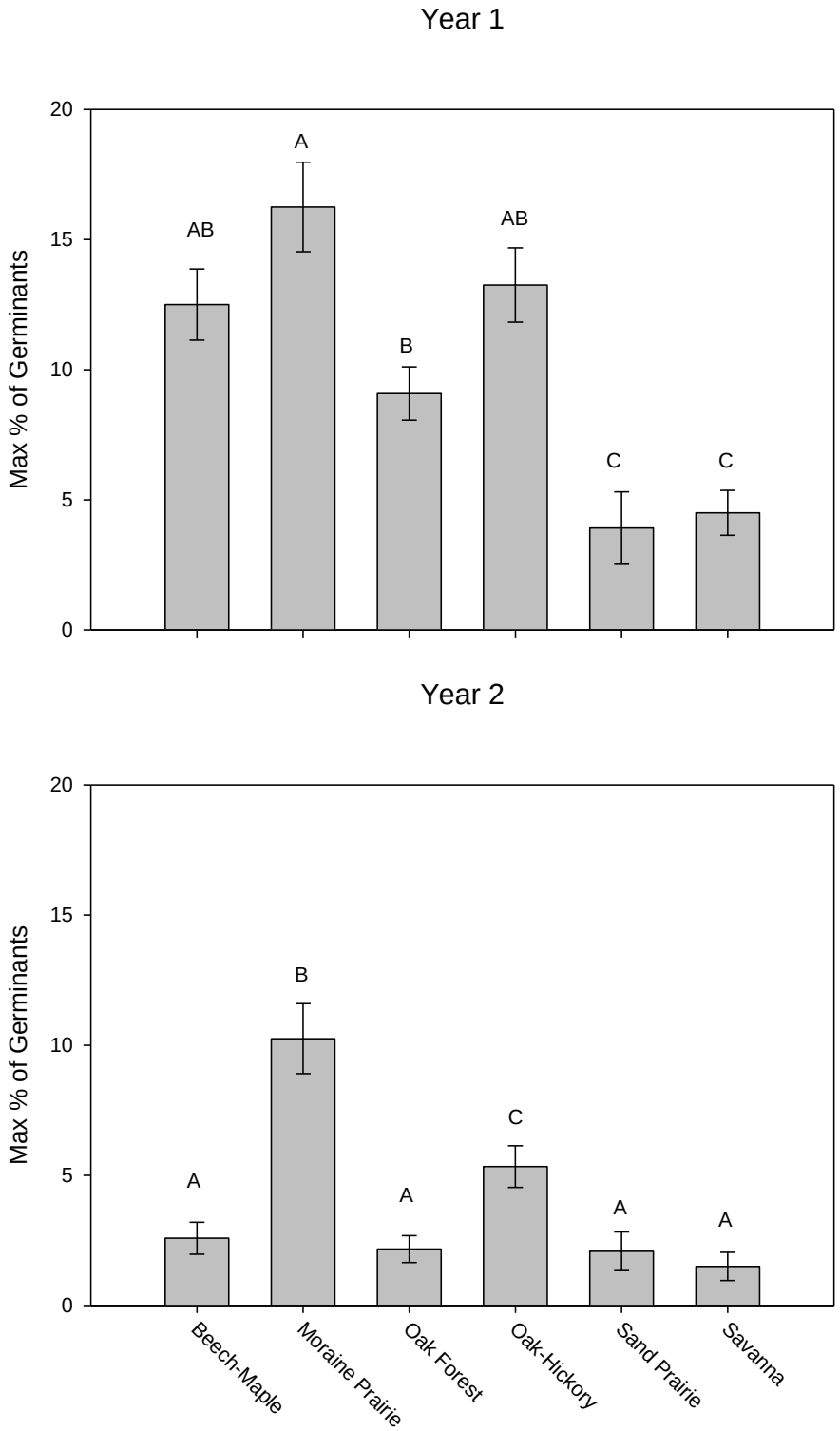

Fig. 2. Mean value ± standard error of the maximum percent of germinants by habitat for first (Year 1) and second (Year 2) growing seasons. Untransformed values were graphed for ease of interpretation. Different letters indicate significant differences at the $\alpha = 0.05$ level using ANOVA followed by Tukey's-b multiple comparisons.

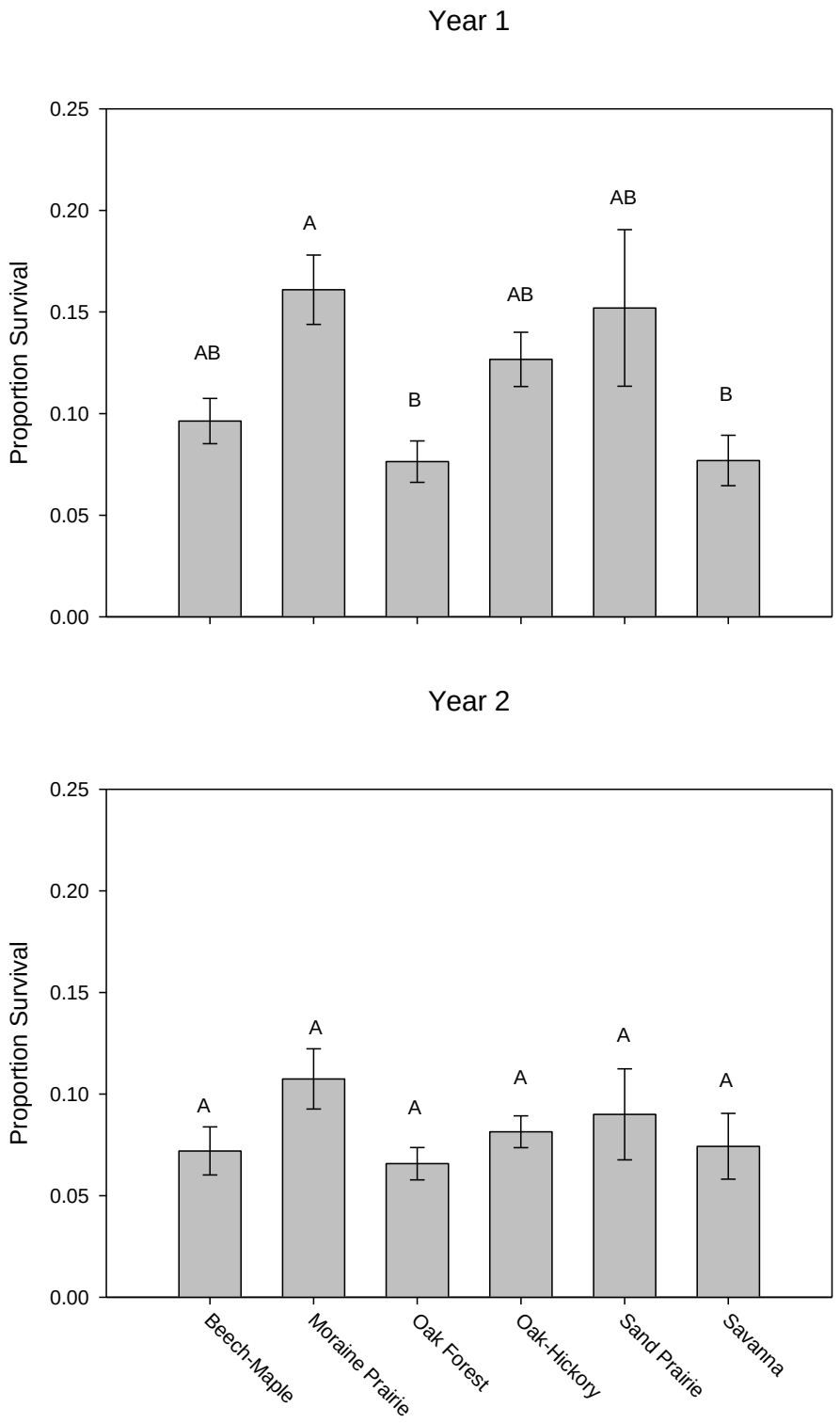

Fig. 3. Mean value ± standard error of the proportion of plants surviving (in plots only with surviving plants) by habitat for first (Year 1) and second (Year 2) growing seasons. Untransformed values were graphed for ease of interpretation. Different letters indicate significant differences at the $\alpha = 0.05$ level using ANOVA followed by Tukey's-b multiple comparisons.

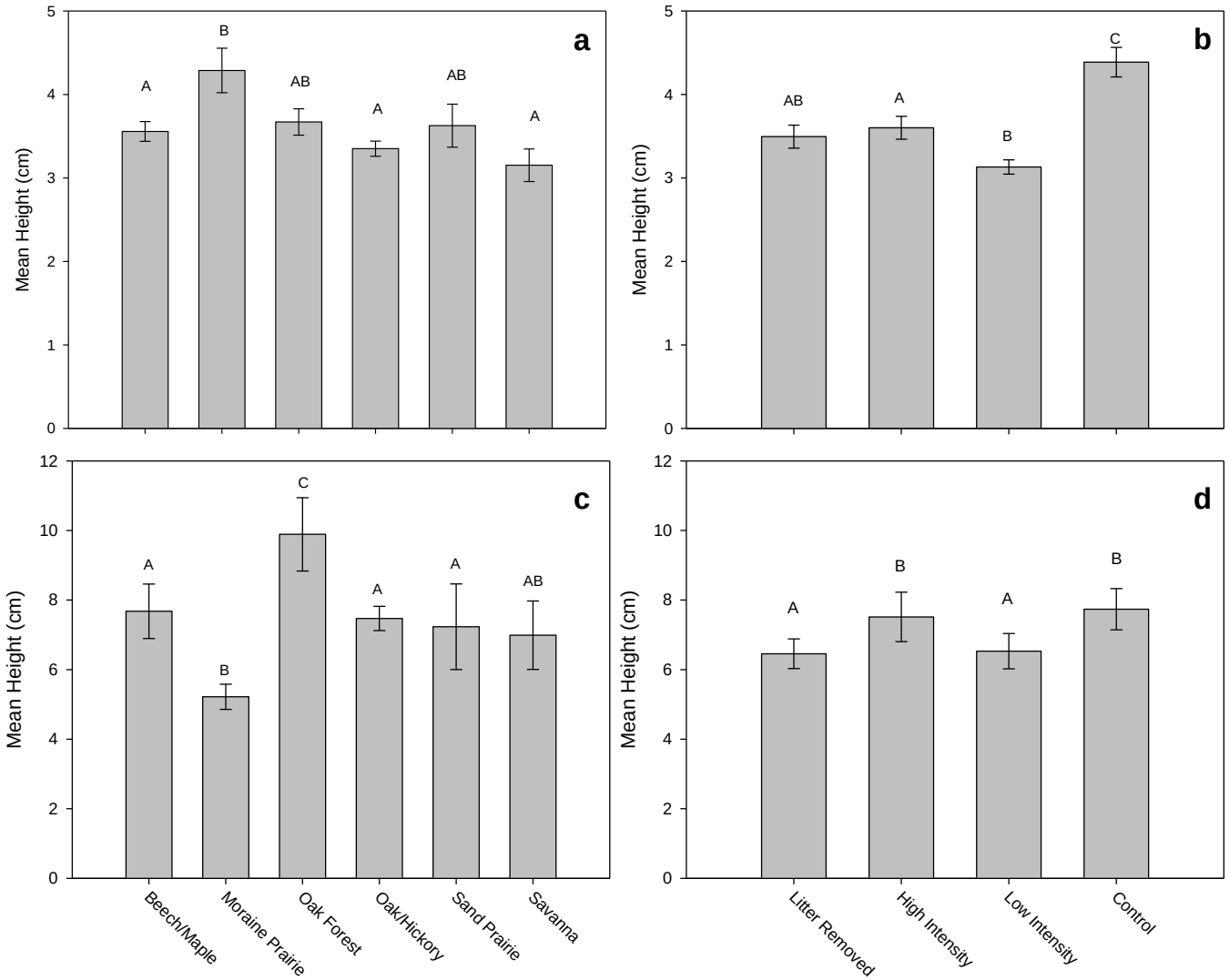

Fig. 4. Mean value ± standard error of the initial (June) heights in the first growing season and final (September) heights at the end of the second growing season of seedlings. Untransformed values are presented for ease of interpretation. a) June mean height vs. habitat; b) June mean height vs. treatment; c) September mean height vs. habitat; d) September mean height vs. treatment. Different letters indicate significant differences using at the $\alpha = 0.05$ level.

Table 1

Mean values ± standard error for the soil factors used in regression models. Different letters within a column indicate significant differences at the α = 0.05 level using ANOVA followed by Tukey's-b multiple comparisons.

Habitat	sqrt (OM)	sqrt (P)	log (K)	NH4N	% sand	% silt	log (canopy openness)
Beech/Maple	2.19 ± 0.04[a]	3.45 ± 0.1[ab]	1.77 ± 0.02[a]	14.58 ± 0.34[a]	47.58 ± 1.66[a]	36.50 ± 1.06[a]	0.96 ± 0.01[a]
Oak/Hickory	2.08 ± 0.02[b]	3.98 ± 0.09[cd]	2.07 ± 0.01[b]	12.42 ± 0.25[b]	26.58 ± 1.89[b]	49.50 ± 1.22[b]	1.01 ± 0.01[b]
Oak Forest	1.28 ± 0.02[c]	3.62 ± 0.08[abc]	1.37 ± 0.00[c]	7.25 ± 0.34[c]	90.83 ± 0.11[c]	5.92 ± 0.19[c]	0.98 ± 0.01[ab]
Moraine Prairie	1.68 ± 0.02[d]	4.02 ± 0.04[d]	2.05 ± 0.01[b]	10.42 ± 0.26[d]	50.92 ± 0.67[a]	32.67 ± 0.71[d]	1.95 ± 0.00[c]
Sand Prairie	1.10 ± 0.02[e]	3.35 ± 0.12[a]	1.41 ± 0.01[d]	7.33 ± 0.18[c]	93.50 ± 0.25[c]	4.50 ± 0.25[c]	1.55 ± 0.01[d]
Savanna	1.05 ± 0.01[e]	3.79 ± 0.13[bcd]	1.46 ± 0.01[e]	7.42 ± 0.19[c]	93.83 ± 0.1[c]	4.17 ± 0.10[c]	1.37 ± 0.02[e]

Table 2
ANOVA table for response variables. Sqrt (Max % Germination) = the square root transformed maximum % germinants), sqrt (Proportion Survival) = the square root transformed proportion surviving plants in plots where there was survival, winter mortality = the difference in surviving plants from August of the first growing season to June of the second growing season. Year 1 and year 2 = the first and second growing seasons, respectively.

Response Variable	SS	df	MS	F	P-value
sqrt (Max % Germinants)					
Year 1					
Corrected Model	355.58	23	15.46	5.58	< 0.0001
Intercept	1768.75	1	1768.75	638.21	< 0.0001
Habitat	283.64	5	56.73	20.47	< 0.0001
Treatment	10.80	3	3.60	1.30	0.28
Habitat x Treatment	61.14	15	4.08	1.47	0.12
Error	731.66	264	2.77		
Total	2856.00	288			
Year 2					
Corrected Model	207.32	23	9.01	4.65	< 0.0001
Intercept	429.32	1	429.32	221.64	< 0.0001
Habitat	177.86	5	35.57	18.36	< 0.0001
Treatment	6.75	3	2.25	1.16	0.33
Habitat x Treatment	22.71	15	1.51	0.78	0.70
Error	511.36	264	1.94		
Total	1148	288			
sqrt (Proportion Survival)					
Year 1					
Corrected Model	0.59	23	0.03	2.15	<0.01
Intercept	10.73	1	10.73	905.22	< 0.0001
Habitat	0.26	5	0.05	4.46	< 0.001
Treatment	0.07	3	0.02	2.07	0.11
Habitat x Treatment	0.20	15	0.01	1.13	0.33
Error	1.48	125	0.01		
Total	17.96	149			
Year 2					
Corrected Model	0.21	23	0.01	1.15	0.32
Intercept	4.81	1	4.81	608.66	< 0.0001
Habitat	0.04	5	0.01	1.04	0.40
Treatment	0.03	3	0.01	1.09	0.36
Habitat x Treatment	0.13	15	0.01	1.06	0.41
Error	0.66	83	0.01		
Total	9.28	107			

Winter Mortality					
Corrected Model	118.45	23	5.15	1.69	0.34
Intercept	272.29	1	272.29	89.59	< 0.0001
Habitat	27.81	5	5.56	1.83	0.11
Treatment	4.32	3	1.44	0.47	0.7
Habitat x Treatment	81.29	15	5.42	1.78	0.04
Error	410.32	135	3.04		
Total	925	159			
Log (Initial Height + 1) (cm)					
Corrected Model	0.44	23	0.02	3.93	<0.0001
Intercept	41.098	1	41.098	8520.98	<0.0001
Habitat	0.08	5	0.02	3.35	0.007
Treatment	0.19	3	0.06	12.84	<0.0001
Habitat x Treatment	0.09	15	0.01	1.22	0.27
Error	0.62	128	0.01		
Total	67.07	152			
Log (Final Height + 1) (cm)					
Corrected Model	1.14	23	0.05	3.3	< 0.0001
Intercept	52.81	1	52.81	3522.17	< 0.0001
Habitat	0.73	5	0.15	9.73	< 0.0001
Treatment	0.21	3	0.07	4.58	0.01
Habitat x Treatment	0.27	15	0.02	1.21	0.28
Error	1.24	83	0.01		
Total	84.93	107			
sqrt (Biomass (g))					
Corrected Model	0.43	23	0.02	2.16	<0.01
Intercept	2.25	1	2.25	258.83	< 0.0001
Habitat	0.32	5	0.06	7.46	< 0.0001
Treatment	0.02	3	0.01	0.65	0.58
Habitat x Treatment	0.16	15	0.01	1.22	0.27
Error	0.72	83	0.01		
Total	4.4	107			

Table 3
Simple linear regression results using step AIC. For abbreviations of response variables, see explanation in Table 1.

Response Variable	Coefficient	Estimate	Std. Error	t-value	p
sqrt (Max % Germination)					
Year 1	Intercept	-4.86	1.82	-2.67	< 0.01
	% sand	0.02	0.01	1.92	0.06
	log (K)	2.49	0.67	3.72	< 0.001
	NH4N	-0.07	0.04	-1.80	0.07
	sqrt (OM)	1.71	0.37	4.68	< 0.001
Year 2	Intercept	-3.18	0.52	-6.17	< 0.001
	log (K)	1.41	0.43	3.27	0.001
	sqrt (OM)	0.44	0.28	1.55	0.12
	log (canopy openness)	1.03	0.28	3.67	< 0.001
sqrt (Proportion Survival)					
Year 1	Intercept	-0.07	0.11	-0.62	0.53
	% sand	0.00	0.00	1.82	0.07
	sqrt (OM)	0.06	0.03	2.02	0.05
	CEC	0.02	0.01	2.41	0.02
	log (canopy openness)	0.10	0.02	4.33	< 0.001
Year 2	Intercept	0.20	0.05	3.71	< 0.001
	NH4N	0.00	0.00	-1.65	0.10
	sqrt (OM)	0.04	0.03	1.70	0.10
	log (canopy openness)	0.04	0.02	2.16	0.03
Winter Mortality					
	Intercept	6.49	2.33	2.79	< 0.01
	% sand	-0.03	0.01	-2.86	< 0.01
	log (K)	-1.80	0.85	-2.11	0.04
	sqrt (OM)	-1.77	0.43	-4.13	< 0.001
Initial germination height log(Height +1)					
	Intercept	0.68	0.08	8.11	< 0.001
	% silt	-0.001	0.00	-2.23	0.03
	log (K)	0.11	0.04	2.47	0.01
	pH	-0.03	0.15	-1.99	0.05
Final height log(Height+1)					
	Intercept	2.10	0.18	11.42	< 0.001
	% sand	-0.004	0.00	-5.55	< 0.001
	log (K)	-0.61	0.09	-6.91	< 0.001
	sqrt (P)	0.05	0.02	2.86	< 0.01
sqrt (Biomass (g))					
	Intercept	0.75	0.15	5.16	< 0.001

% sand	-0.00	0.00	-2.79	< 0.01
log (K)	-0.23	0.06	-3.93	< 0.001
NH4N	0.00	0.00	-1.54	0.13

Table 4
Logistic regression results from binomial survival values.

Response Variable	Coefficient	Estimate	Std. Error	z value	p
Binomial Survival					
Year 1	Intercept	-5.04	0.83	-6.06	< 0.0001
	log (K)	2.61	0.65	4.03	< 0.0001
	sqrt (OM)	1.17	0.46	2.55	0.011
	CEC	-0.17	0.09	-1.93	0.05
Year 2					
	Intercept	-8.67	2.38	-3.64	< 0.001
	% sand	0.02	0.01	1.66	0.10
	log (K)	3.52	0.88	3.98	< 0.0001
	sqrt (OM)	0.58	0.40	1.43	0.15

Table 5
Mean biomass (g) ± standard error.

Habitat	N	Mean
Beech/Maple	28	0.028 ± 0.006[a]
Moraine Prairie	95	0.022 ± 0.002[a]
Oak/Hickory	59	0.041 ± 0.011[a]
Sand Prairie	26	0.025 ± 0.004[a]
Oak Savanna	5	0.041 ± 0.018[a]
Oak Forest	22	0.135 ± 0.037[b]