Intensive Selective Deer Browsing Favors Success of *Asimina triloba* (Paw Paw) a Native Tree Species

Intensive Selective Deer Browsing Favors Success of *Asimina triloba* (Paw paw) a Native Tree Species

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ABSTRACT: Although white-tailed deer (*Odocoileus virginianus* Zimmermann) are generalist herbivores, they can have significant effects on species composition and abundance of forest trees, especially when deer densities are high and most plant species are heavily browsed but a few are selectively avoided as browse. We evaluated effects of selective deer browsing on tree species abundance in an old-growth mesic/wet-mesic forest in central Illinois by repeated sampling of permanent study plots in 2003 and 2008 and relating changes in stem density between the two samples to the intensity of deer browsing of individual species. The study site has high deer density (75 deer km^2) during winter months, and initial observations indicated that paw paw (*Asimina triloba* (L.) Dunal) was strongly avoided as browse. Paw paw density increased in the seedling stratum between the two sample periods. However, nearly all other tree species declined in density; blue ash (*Fraxinus quadrangulata* Michx.) – a low-use browse species, had a small increase in seedling density. Tree species diversity decreased in the seedling stratum, but not in the sapling stratum, although sapling density declined for some species. The current trajectory of tree species growth and recruitment suggests that the development of a dense paw paw understory canopy will further decrease species diversity and reduce tree species recruitment. Based on the life history traits of paw paw, and high deer densities and selective browsing, this issue is of concern for current and future forest communities.

Index terms: Acer saccharum, Asimina triloba, deer herbivory, Odocoileus virginianus

INTRODUCTION

Even though white-tailed deer (*Odocoileus virginianus* Zimmermann) are generalist herbivores, they are a major factor affecting regeneration, species composition, and abundance of forest trees (Russell et al. 2001; Horsley et al. 2003; Côté et al. 2004; Aronson and Handel 2011). Deer browsing is an issue of particular concern when it promotes dense understories of avoided species that further inhibit other plant species (Stromayer and Warren 1997; de la Cretaz and Kelty 2002; Horsley et al. 2003; Rooney and Waller 2003; Goetsch 2011; Kain et al. 2011). We examined the relationship between the intensity of white-tailed deer herbivory and tree species abundance and diversity in a central Illinois old-growth forest subjected to intensive winter deer browsing. Notably, this forest site contains a large abundance of paw paw (*Asimina triloba* (L.) Dunal), a sub-canopy species, which is known to be well-defended against herbivory by plant chemical compounds (Zhao et al. 1992; Lewis et al. 1993; Zhao et al. 1994; He et al. 1997) and to experience little or no herbivory (Liang and Seagle 2002; Asnani et al. 2006).

Deer have high densities in Illinois at the present time and are considered to be a nuisance species in some locations. However, deer were virtually nonexistent in many parts of the state by the 1870s and were likely extirpated in Illinois by the end of the century due to intensive sport and commercial hunting pressure and destruction of deer habitat from large-scale land conversion to agricultural landscapes (Pietsch 1954). Recent high deer abundance in Illinois resulted from protective legislation that banned deer hunting in 1901, and federal and state sponsored deer reintroductions during the 1930s and 1940s. As a result, Illinois' deer population increased quickly and nuisance levels were reached in several counties by the mid-1950s, resulting in the lifting of the state-wide ban on deer hunting in 1957. Deer populations were still low to nonexistent in central Illinois at this time (Pietsch 1954); however, deer subsequently re-established themselves in the central Illinois region, and now are considered to have reached nuisance levels (Anderson 1997).

In central Illinois, vast tracts of agricultural cropland produce nearly limitless quantities of food throughout the year; however, these croplands supply only seasonal cover, which is created in the spring and then destroyed during the fall harvest. This seasonal cover creates the pattern of spring dispersal from and winter congregation in isolated forest fragments, which is peculiar to deer found in this type of habitat (Sparrow and Springer 1970; Nixon et al. 1991; Nixon and Hansen 1992). While these deer still obtain a substantial portion of their diet in agricultural fields, foraging on crop residues and winter wheat, browsing within forested areas is more intense during winter and early spring than during the summer (Nixon et al. 1991; Kelley 1994). This seasonal pattern of deer browsing pressure, combined with differential preferences for certain plant

species, has likely had substantial effects on the composition and abundance of tree species in the remaining forest fragments of central Illinois (Strole and Anderson 1992). High deer densities can prevent tree species regeneration and, thereby, alter forest successional patterns (Beals et al. 1960; Ross et al. 1970; Richards and Farnsworth 1971; Anderson and Loucks 1979; Marquis 1981; Horsley and Marquis 1983; Frelich and Lorimer 1985; Alverson et al. 1988; Russell et al. 2001; Rooney and Waller 2003). This phenomenon may be of particular concern in central Illinois, given the current high levels of deer abundance, and development of plant communities in the absence of deer for nearly a century (c. 1870 – 1960).

Focal Species

Paw paw trees reach a height of approximately 2.1 m after ten years of growth (Larimore et al. 2003), and reach a maximum height of approximately 10 m (pers. observ.); thus, they are understory trees and typically do not reach the forest canopy. Although paw paw has not been studied extensively, existing literature suggests that it is well-adapted to low-light conditions in the forest understory. Leaves of paw paw saplings possess photosynthetic properties that are similar to those of sugar maple (*Acer saccharum* Marsh.) (Slater 2011), a tree species which is considered to be highly shade-tolerant (Walters and Reich 2000). Furthermore, the clonal propagation of paw paw decreases the risk of mortality by allowing individual ramets to share resources with their parent plants (Hosaka et al. 2005; Hosaka et al. 2008). Given enough time, large colonies of paw paw are established, which intercept sufficient quantities of light to severely impede plant growth underneath their canopy (Cole and Weltzin 2005; Baumer and Runkle 2010).

Paw paw is the only species of the tropical plant family Annonaceae found in North American temperate forests. This plant family possesses a suite of biochemical defense mechanisms; however, studies have shown that acetogenins produced by paw paw are particularly potent defensive chemical compounds, which inhibit cellular respiration and confer negative, or lethal, effects even when consumed at low doses (Zhao et al. 1992; Lewis et al. 1993; Zhao et al. 1994; He et al. 1997).

Study Objectives

The objective of this study is to examine the influence of selective deer browsing on the regeneration success of paw paw and other native tree species. We posed two questions in this study: (1) Do white-tailed deer have a lower preference for paw paw as browse than other tree species? (2) Did deer herbivory influence changes in abundance of tree seedlings and saplings of paw paw and other species?

METHODS

Study Site

The 27-ha study site is located 35 km southwest of Bloomington, Illinois, within the 400- ha Funks Grove (40°21.2'N, 89°7.7'E). Species composition of the site is characteristic of central Illinois mesic/wet-mesic forests (Adams and Anderson 1980): sapling and seedling strata at this site are currently dominated by sugar maple and paw paw, and sugar maple is the dominant species in the tree stratum (Smith 2004).

Funks Grove has been affected by high densities of white-tail deer during the winter months for several years. As an example, during the winter of 2007 – 2008, an aerial deer survey in the Funks Grove area estimated a density of > 75 deer km^{-2} (Pers. comm. with E. Smith, Illinois Department of Natural Resources, Springfield, 2008), whereas historic deer density was likely 4 – 8 deer km^{-2} (McCabe and McCabe 1997). The increased abundance of paw paw tracks the local increase in deer abundance. Using counts of annual deer-vehicle collisions (1980 – 2003) on state owned or maintained roads and deer harvested during the firearm season (1970 – 2008) as surrogates for population surveys, deer are estimated to have increased 500% during the 1980s and by another 50% – 75% between 1990 and the early 2000s in McLean County (IDNR 2011; Shelton 2011). In an area adjacent to our Funks Grove study site, paw paw seedlings and saplings (combined) increased from 400 to 975 stems ha^{-1} between 1977 and 2011. In contrast, sugar maple reached its highest density of 2085 stems ha^{-1} (seedlings and saplings combined) in 1984, but this number declined to 875 stems ha^{-1} in 2011, and all of the stems were saplings. For five vegetation samples taken during

this time period (1977, 1984, 1994, 2005, and 2011) there was a significant positive correlation ($R^2 = 0.848$, $P = 0.0264$, df = 4) between paw paw stem density and deer killed by fire arms in McLean County in the same five years (paw paw stem density = combined seedlings and saplings ha^{-1}, natural log transformed, R.C. Anderson, unpubl. data).

Deer exclosures were not available for this study in Funks Grove, and because of high deer density, neither were regional reference forests without deer herbivory. Consequently, we examined variation in intensity of deer browsing on seedlings of all tree species and related this variation to changes in seedling and sapling abundances using repeated sampling of permanent study plots. We used this information to determine how variation in deer browsing intensity among species may be shaping the tree species community at this site and the extent to which paw paw is being avoided as a browse species.

Sampling Design

Sampling points ($n = 105$) were located using a stratified random technique (Krebs 1999) within the 27-ha study site (Smith 2004); a 50 × 50 m grid system was established and sampling points were emplaced at 1-m increments (0 – 9 m, first number) to the east or west (even or odd, second number) using a list of two-digit randomly generated numbers. At each sampling point, measurements of tree diameters at breast height [dbh (diameter 1.5 m above ground level)], and stem counts of saplings and seedlings were taken by species in circular, nested quadrats (Krebs 1999) with areas of 0.07, 0.02, and 0.007 ha, respectively. Individuals of tree species were placed into one of three categories: (1) Trees: stems > 9.0 cm dbh, (2) Saplings: stems ≤ 9.0 cm but ≥ 1.0 cm dbh, and (3) Seedlings: stems < 1.0 cm dbh but > 20 cm tall. Seedlings and saplings were each further subdivided into three size classes. Seedling size classes were: (1) > 20 cm tall, but stem diameter ≤ 0.5 cm at 20 cm height; (2) stem diameter > 0.5 cm at 20 cm height, but less than 1.5 m tall; (3) height greater than 1.5 m, but stems ≤ 1 cm dbh. Sapling size classes were: (4) 1.0 cm < stem ≤ 3.5 cm dbh; (5) 3.5 cm < stem ≤ 6.0 cm dbh; and (6) 6.0 cm < stem ≤ 9.0 cm dbh. Sampling occurred during the summer months of

2003 (Smith 2004) and again in 2008. In addition, during the 2008 sampling period, seedlings were recorded as being browsed or not browsed by deer.

Statistical Analysis

Change in density of tree species abundance (stems ha^{-1}) across size classes (seedlings, saplings, and trees at 10-cm dbh intervals) was examined by constructing structural diagrams (diameter size class distribution) by species. Separate structural diagrams contrasting the 2003 and 2008 sampling periods were generated for the six most abundant tree species, and less common species were grouped together into a single "others" category. To determine if there was a significant difference in tree species diversity between the 2003 and 2008 samples, Shannon-Wiener indices (H') and evenness (J) (Magurran 1988) were calculated separately for tree seedlings (Size Classes 1, 2 and 3 combined) and tree saplings (Size Class 4). These are the size classes where most of the deer browsing occurred and where deer-browsing effects on sapling recruitment would be most apparent between the two samples (Strole and Anderson 1992). To determine the effect of paw paw on seedling diversity, paired t-tests were used to test for statistically significant differences in Shannon-Wiener indices, with and without paw paw being included in the sample. This analysis was conducted between the 2003 and 2008 samples and within each year separately. Alpha values were corrected for multiple comparisons using a sequential Bonferroni correction; all three comparisons with significant

results met the requirement for the most conservative correction (α < 0.05/5).

The intensity of deer browsing and change in abundance of tree species within the seedling category were also examined. Blue ash (*Fraxinus quadrangulata*) was the only species, other than paw paw, that increased within the seedling stratum between the 2003 and 2008 samples. We used a χ^2 test to determine if the proportions of blue ash and all other species combined were significantly different between the two years of the study, as a percentage of the total number of seedling stems sampled (2003 + 2008). A greater proportion of the total stems sampled (2003 + 2008) in 2008 than in 2003 would indicate an increase in seedling stems between the two samples. Paw paw exhibited virtually no signs of deer browsing (we recorded 7 of 464 stems with broken tips, which were conservatively recorded as browsed), and was, therefore, excluded from this analysis. All other tree species, except paw paw, were combined to achieve an adequate sample size for the χ^2.

Several parameters were operationally defined: (1) Relative Use (RU), (2) Relative Abundance (RA), (3) Relative Change in Seedling Abundance, and (4) Percentage of Seedlings Not Browsed (see Table 1), and then evaluated with linear regression. To evaluate the intensity of deer browsing on individual tree species, linear regression analysis of Relative Use (RU) and Relative Abundance (RA) was conducted for seedlings (Size Class 1 – 3 combined)

(Strole and Anderson 1992). The effect of deer browsing on seedling abundance was examined by performing a regression analysis of Relative Change in Seedling Abundance (ΔSA) between 2003 and 2008 and Percentage of Seedlings Not Browsed (% N.B.); ΔSA was calculated by subtracting the number of stems in a size class in 2003 from the stems in the same size class in 2008 and expressing this difference as a percentage of the stems in the size class in 2003 (Table 1).

RESULTS

Changes in Stem Density in Size Classes

Between the 2003 and 2008 sampling periods, the largest increase of paw paw occurred in the seedling class, from 329 to 616 stems ha^{-1}. Within the sapling class and the only tree size class in which paw paw occurred (9.0 – 19.9 cm dbh), abundance was relatively stable between sampling periods. Paw paw decreased from 276 to 254 saplings ha^{-1}, and increased from 7 to 12 trees ha^{-1} in these two size classes, respectively (Figure 1). However, the other tree species combined decreased in the seedling and sapling size classes and density of these species in the smallest tree size class was nearly the same in 2003 and 2008 (Figure 1). The only taxon that had an increase in stems in the seedling class, other than paw paw, was blue ash. Most species decreased between 2003 and 2008 in proportion to their abundance in 2003 (Figure 2). The proportions of total

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Table 1. Calculation of variables used in regression analysis: RU = Relative Use, RA = Relative Abundance, ΔSA = Relative Change in Seedling Abundance (ΔSA) between 2003 and 2008, N.B. = Percent of Stems not Browsed.

$$RU = \frac{\text{Number of stems of a species browsed}}{\text{Number of stems of all species browsed}} \times 100$$

$$RA = \frac{\text{Number of stems of a species}}{\text{Number of stems of all species}} \times 100$$

$$\Delta SA = \frac{\text{Number of seedlings in a size class in 2008} - \text{Number of seedlings in 2003}}{\text{Number of seedling in 2003}} \times 100$$

$$\% \text{ N.B.} = \frac{\text{Number of seedlings not browsed in 2008}}{\text{Number of not browsed plus browsed seedlings in 2008}} \times 100$$

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seedling stems sampled in 2003 and 2008 for blue ash and all other species combined (excluding paw paw) were significantly different (χ^2 = 13.35, df = 1, P < 0.047). For blue ash, the proportions were 0.414 and 0.585 in 2003 and 2008, respectively; and for all other species combined, the proportions were 0.593 and 0.407 for the same years, respectively.

Density of stems in dbh size classes larger than the first tree class (9.0 – 19.9 cm dbh) was nearly identical in 2003 and 2008 when data for all taxa other than paw paw were combined (Figure 3). The six leading taxa, sugar maple, oaks species (*Quercus* spp.), elm species (*Ulmus* spp.), blue ash, other ash species [green ash (*Fraxinus pennsylvanica* Marsh.) and white ash (*F. americana* L.)], and hackberry (*Celtis occidentalis* L.) had similar stem densities in 2003 and 2008 in all tree dbh size classes. However, hackberry had a slight increase in density in the first two dbh size classes in 2008. Oak species [bur oak (*Quercus macrocarpa* Michx.), red oak (*Quercus rubra* [Michx] Farw.), and chinquapin oak (*Quercus muhlenbergii* Englem.)]

had their greatest density of stems in the larger size classes (stems greater than 60 cm dbh), although there was an increase in oak seedlings and a decline in saplings between 2003 and 2008 (Figure 3).

Diversity in the Seedling and Sapling Strata

Diversity (H') of tree species within the seedling stratum significantly decreased (t = 6.766, df = 1,341, P < 0.0001) between 2003 and 2008, at H' = 1.81 and H' = 1.40, respectively (Table 2). Evenness (J) also decreased (J = 0.71 and 0.53 in 2003 and 2008, respectively), reflecting the increased relative density (Rel. Den.) of paw paw between the 2003 (Rel. Den. = 40%) and 2008 (Rel. Den. = 62%) samples. Species richness (S) was nearly the same in 2003 (S = 13) and 2008 (S = 14). Therefore, change in evenness, resulting from the increase in paw paw and decreases in most other species, was responsible for the decline in diversity (H'). When paw paw was excluded from the diversity (H') calculations within each year separately, diversity increased compared to when paw paw was included for the 2008 sample (t = 11.097, df = 970, P < 0.0001) but not the 2003 sample (t = 1.614, df = 883, P < 0.100) (Table 2). However, there was no statistically significant change in diversity (t = 0.327, df = 555, P = 0.743) between 2003 and 2008 with paw paw excluded, because in 2008 most tree species other than paw paw had decreased in proportion to their abundance in 2003 as previously noted (Figure 2).

The abundance of paw paw in the sapling class remained relatively stable between 2003 and 2008. No significant change in diversity (t = 0.62, df = 1100, corrected P = 0.535) was observed among (Class 4) saplings between the 2003 and 2008 samples (H' = 1.17 and 1.21, J = 0.51 and 0.47, S = 10 and 13 in 2003 and 2008, respectively); however, the stem density (all taxa combined) in this size class decreased from 330 to 260 total stems.

Intensity of Browsing All Species Combined

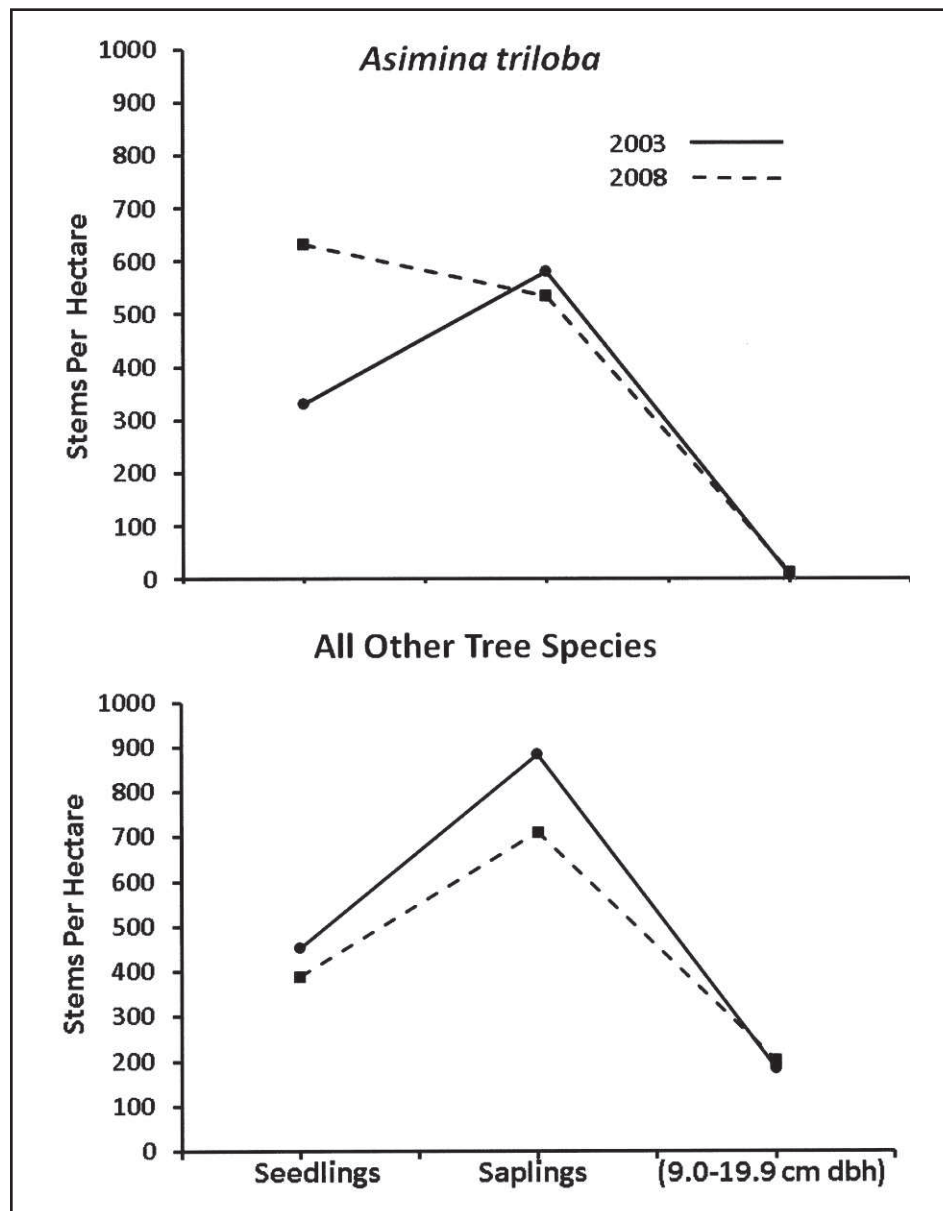The pecentage of the total number of seedling stems sampled that were browsed

Figure 1. Structure diagrams showing the changes in stems density for paw paw (*Asimina triloba*) and other tree species combined within the Funks Grove study site for the size classes in which paw paw occurred (seedling, sapling, and first tree size class).
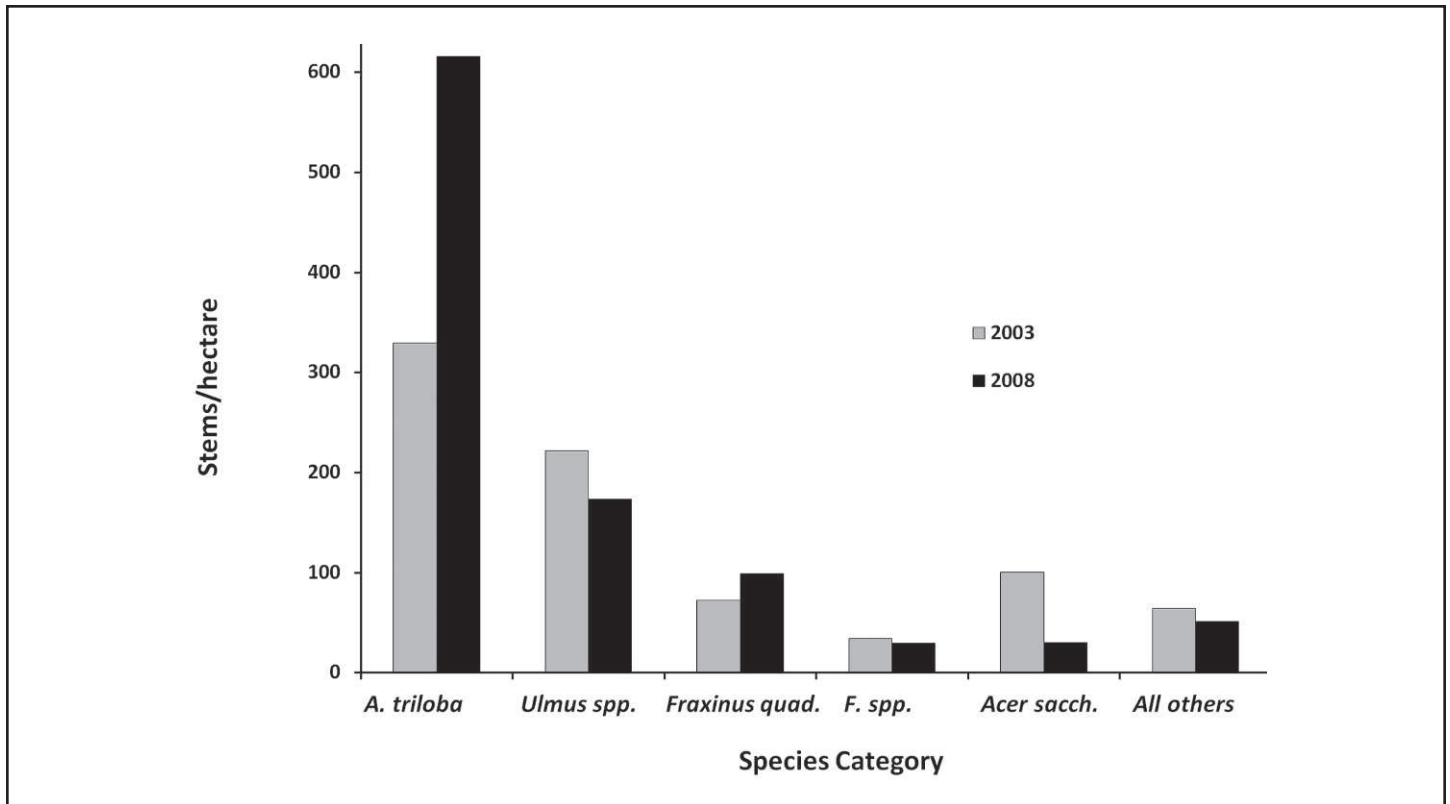
Figure 2. Seedlings per hectare of tree species containing ≥ 4 stems in 2003 or 2008. Blue ash (*Fraxinus quadrangulata* Michx.), a low-use browse species, is the only taxon other than paw paw that demonstrated an increase between sampling periods.

in 2008, including paw paw, was 28.1%. However, if paw paw was omitted from the data the percentage of stems browsed for the remaining taxa was 62.5%. The percentage of seedling stems browsed for individual taxa ranged from 1.5% for paw paw to 83.3% and 84.0% for hackberry and elm species, repectively.

Selective Browsing by White-tailed Deer

Analysis of species preferences and deer browsing patterns, with paw paw included in the data, showed there was not a significant relationship between relative use and relative abundance (RU vs. RA, P = 0.8933, adj. R^2 = -0.003, df = 7). Paw paw is strongly avoided by deer, and the percent of total stems browsed was only 1.5% (7 of 464 total stems sampled were browsed) (Figure 4A). However, seedlings of the other tree species were generally browsed in proportion to their relative abundances as indicated by the regression analysis (RU vs. RA, P < 0.0001, R^2 = 0.956, df =

6) with paw paw excluded. Blue ash was the only species whose relative use was substantially below the fitted regression line (Figure 4B). Sample points occurring above the line indicate species that are browsed more than would be predicted by their abundance, and points below the line indicate species that are browsed less than predicted by their abundance. These results suggest that browsing is sufficiently intense so that the correlation between relative use and relative abundance is being driven towards 1.0, which occurs when stems of all species are completely browsed regardless of their preferences by deer, and relative use and relative abundance are the same. Removal of blue ash from the data set increased the R^2- value of the regression to 0.989 (df = 5, P < 0.0001), consistent with the high browsing pressures experienced by the remaining species.

Regression analysis of relative ΔSA and % N.B., the independent variable, showed a significant positive relationship between

the two variables (P < 0.0260, adj. R^2 = 0.3273, df = 15), suggesting that changes in species abundances are related to deer browsing patterns (Figure 5). Between sampling periods, paw paw increased in all three seedling size classes; blue ash increased in size class two, but showed little change in the other two size classes between sampled years. Elm species had an increase in the smallest size classes but declined in Size Classes 2 and 3 between 2003 and 2008. Oak species had an increase in the first size class between 2003 and 2008, but was not present in the two larger seedling classes in 2008. All other species by size class combinations exhibited a decrease in abundance between the two samples. Sugar maple had a high percentage of stems not browsed in Size Class 1, but it had fewer stems in all seedling size classes in 2008 than 2003, as indicated by the negative relative change for sugar maple in Size Classes 1 and 3. Seedling Size Class 2 is not shown in Figure 5 for sugar maple because there were no seedlings in
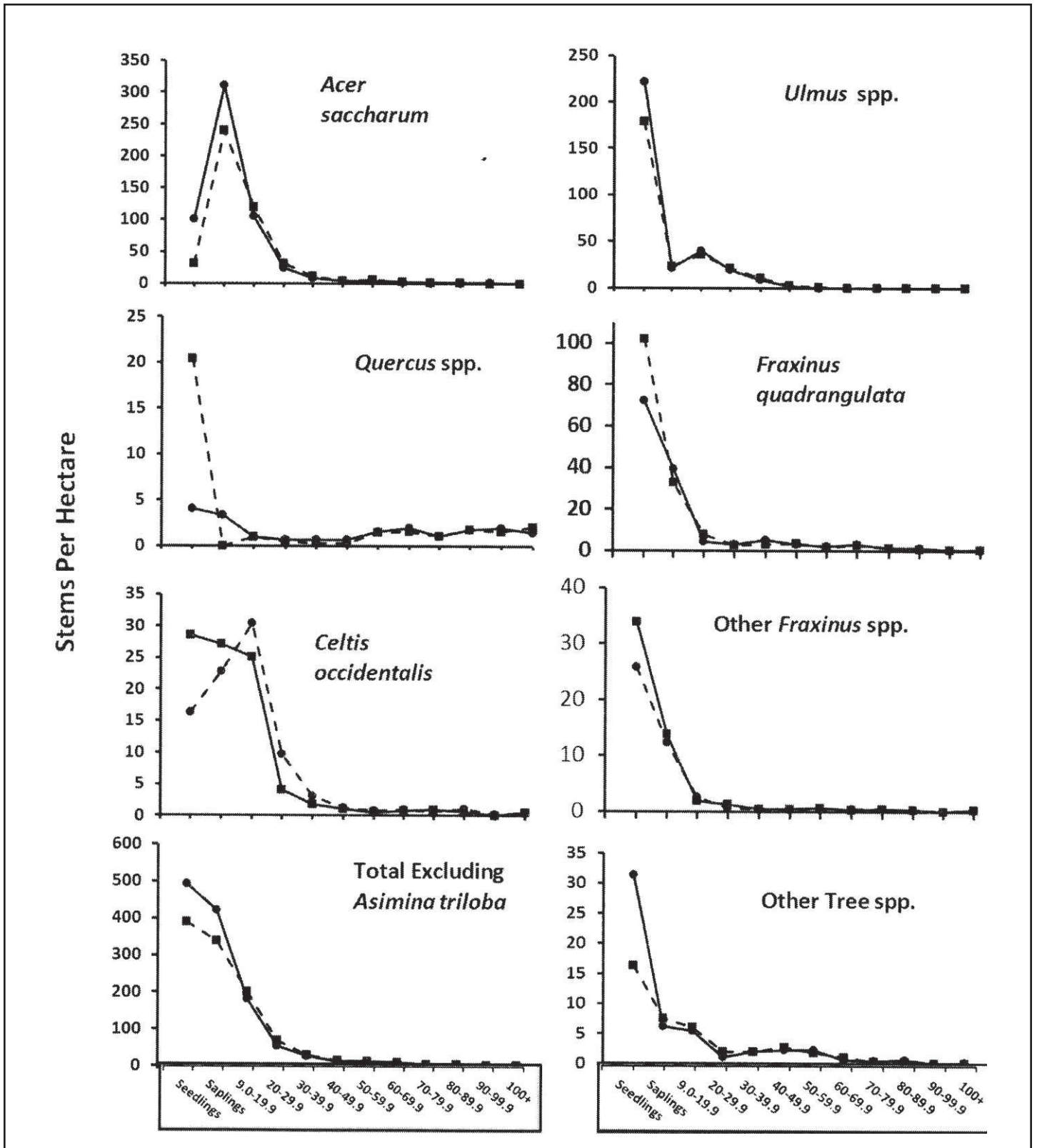
Figure 3. Structure diagrams showing size class distribution of prominent tree taxa located within the Funks Grove study site. Solid lines and dashed lines indicate 2003 and 2008 data, respectively.

Table 2. Shannon-Weiner Diversity Index (H'), Species Richness (S), and Evenness (J) for Seedlings all Classes combined in 2003 and 2008.

Variable	H'	S	J
All Tree Seedlings			
Year			
2003	1.81	13	0.71
2008	1.40	14	0.53
Excluding Paw paw			
Year			
2003	1.90	12	0.77
2008	1.92	13	0.75

this class in 2008 and percent of stems not browsed could not be calculated.

DISCUSSION

Examination of early-successional communities have demonstrated that deer browsing may create alternate stable states in forest communities by promoting the formation of dense understories of herbaceous plants (Horsley and Marquis 1983; Stromayer and Warren 1997; Augustine et al. 1998). These understory communities typically have low species diversity and are dominated by a single species, which limits the growth of other plant species; furthermore, these communities are often highly resistant to change once established (Royo and Carson 2006). Additionally, Rooney and Waller (2003) found that deer browsing can reduce the time for late successional species to dominate the tree canopy. The current trajectory of tree species growth and recruitment at our study site suggests a similar outcome (i.e., an alternate stable state system or accelerated progression toward a late-successional community composition with a dense understory of paw paw, which reduces tree species diversity, is likely to occur at locations with suitable growth conditions where paw paw has become established).

Deer browsing does not negatively affect paw paw, while intense browsing is eliminating other species from the seedling stratum, reducing its diversity, and may eventually prevent recruitment of these species to larger size classes. Our data comparing tree density over a 5-year period did not indicate that deer browsing has reduced recruitment into the tree stratum at the present time; however, a lag in the decline of stems in the sapling and the smaller tree size classes following intense browsing of seedlings is not unexpected. Recruitment of sugar maple into the overstory can take an average of 110 to 125 years in undisturbed forests (Canham 1985) with individuals often persisting as seedlings for 10 – 40 years (Marks and Gardescu 1998). Loss of overstory trees reduces competition for resources and increases light availability, which has been shown to cause large increases in the abundance of paw paw (Shotola et al. 1992) and other species of shade-tolerant trees (Canham 1985, 1988; Marks and Gardescu 1998). However, the decline in seedlings we found between the 2003 and 2008 samples suggests that continued deer browsing will largely eliminate these
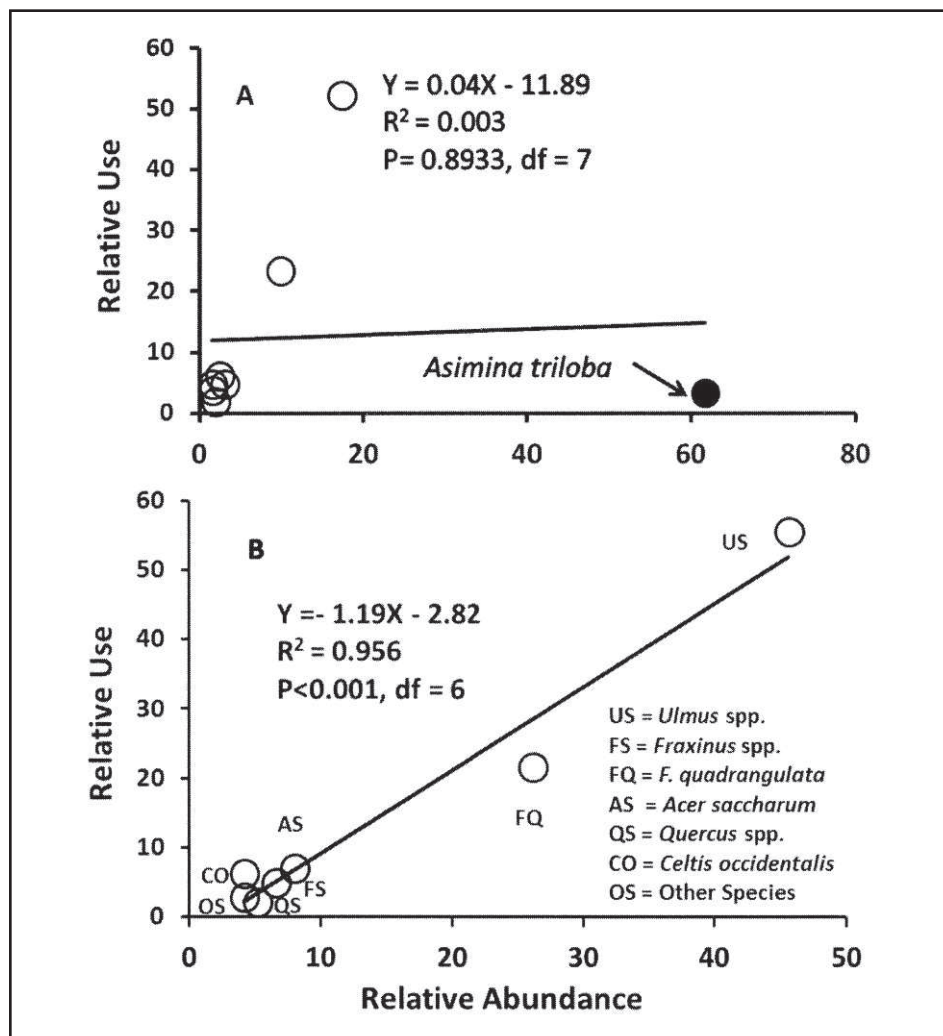
Figure 4. The relationship between relative use as deer browse and relative abundance of tree species seedlings excluding paw paw. Panel (A) has data for all species and (B) omits paw paw, which shows the results of the regression analysis of relative use and relative abundance.
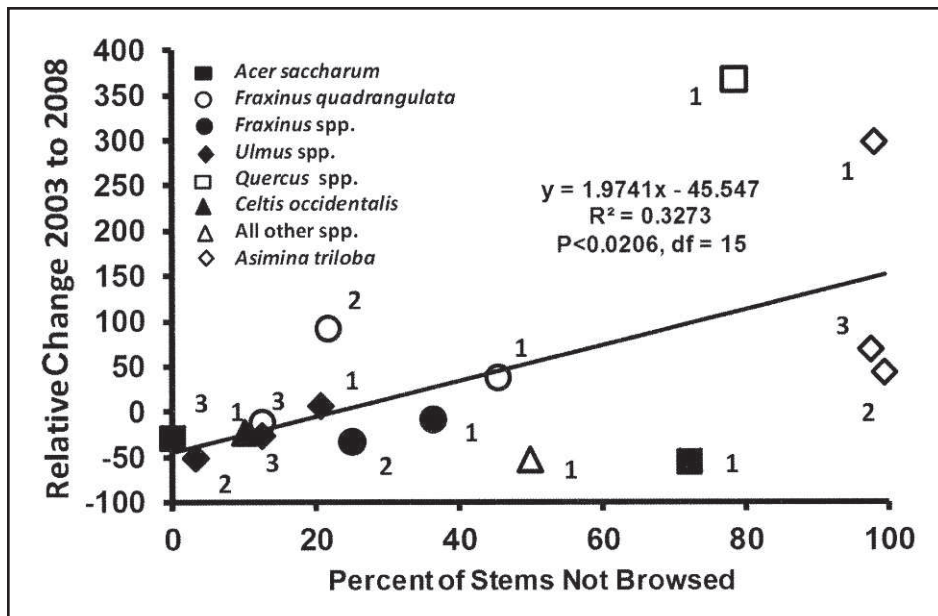
Figure 5. Relationship between percent change in seedling abundance (ΔSA) between 2003 and 2008 and browsing intensity (% of seedlings not browsed) for tree species by size class.

other species from the seedling stratum and promote dense understory canopies of paw paw, which will restrict replacement of overstory trees as they are lost from canopy positions.

Our data show that oak species are currently abundant in the largest tree size classes, but have low abundances of seedlings and saplings, which is typical of shade-intolerant tree species in forests dominated by sugar maple, a shade-tolerant mesophytic species (Adams and Anderson 1980; Nowacki and Abrams 2008). On our study site, oak species had a relatively high abundance of Size Class 1 seedlings in 2008, but these seedlings likely resulted from seeds that germinated in the fall (white oak group) but grew little until the following spring, or germinated during the spring (black oak group) before we sampled (Smallwood et al. 2010). Thus, they were unavailable as deer browse during the winter before we sampled in 2008. Similarly, sugar maple had a high percentage (72%) of stems not browsed in Size Class 1. Most of these stems were barely 20 cm tall and were probably too small during the winter prior to our 2008 sample to be noticed by browsing deer. The seedlings in Size Class 1 for both of these species were likely browsed by deer in the winter following our sampling.

The percentage of seedling stems browsed in our study (28.1% and 62.4% if paw paw is excluded from the sample) is notably higher than an area of southeastern Ohio with a deer density of 6 deer km^{-2} where 13.8% to 16.7% of stems (10 cm – 1.5 m tall) were browsed (Apsley and McCarthy 2004). Currently, paw paw and blue ash are the only species which appear to be browsed to a degree that allows seedlings to reach sizes above the "browse line" at our study site. This result alone indicates that deer are altering the trajectory of forest succession at this site.

Under a condition of lower deer densities than we had on our study site, it is likely that paw paw would increase in the forest understory, but sugar maple probably would not experience a decline in seedling abundance as we report for our study site between 2003 and 2008 (71 to 31 stems ha^{-1}, a 56% decline). This conclusion is supported by the findings of a study conducted in an old-growth forest dominated by sugar maple in southwestern Illinois (Union County) where deer browsing was not an issue of concern at the time (pers. comm. on October 10, 2012, with Clark Ashby, 2012 Emeritus professor, Plant Science Department, Southern Illinois University, Carbondale); paw paw stems less than 35 cm tall increased 54% and

sugar maple increased 302% between 1967 and 1983, while other tree species [except red elm (*Ulmus rubra* Muhl.)] experienced a decline in stems less than 35 cm tall (Shotola et al. 1992). The authors concluded that the dense understory of paw paw and sugar maple will limit regeneration of shade-intolerant and moderately shade-intolerant species, but sugar maple will continue its dominance in the forest (Shotola et al. 1992). In contrast, our results indicate negative effects of intensive deer browsing on tree regeneration of shade-tolerant (sugar maple) and shade-intolerant tree species.

Historically, paw paw was limited to wet areas, because its abundance is diminished by fire. Frequent or intense burns, which were common on upland mesic sites dominated by shade-intolerant, fire-resistant oaks and hickories (*Carya* spp.), caused local reductions of paw paw (Larimore et al. 2003; Holzmueller et al. 2009). Currently, paw paw is still largely restricted to moist, shady environments (Adams and Anderson 1980; Anderson and Mitsch 2003), at least within the northern portion of the species' range (Lagrange and Tramer 1985). However, a sharp reduction in frequency of fire disturbance following European settlement (Abrams 1992; Nowacki and Abrams 2008) has resulted in a decline of shade-intolerant, preferred-browse species (*Quercus* spp.) (Strole and Anderson 1992) and increased abundances of fire-sensitive, shade-tolerant tree species (Adams and Anderson 1980; Hartnett and Krofta 1989; Nowacki and Abrams 2008). As oak-hickory forests on mesic sites become increasingly dominated by sugar maple and undergo mesophication – a positive feedback process, where shade-tolerant species increase canopy closure (reducing irradiance, temperature, and wind movement at ground level) and produce leaf litter with low flammability (Nowacki and Abrams 2008) – these forests become wetter and less likely to burn. These conditions favor shade-tolerant, fire-sensitive species (Weaver and Ashby 1971; Schlesinger 1976, 1989; Anderson and Adams 1978; Weaver and Robertson 1981; Shotola et al. 1992; Nowacki and Abrams 2008), which promotes further mesophication, and may effectively extend the species' range of paw paw (Larimore

et al. 2003). These changing conditions coupled with high deer densities, which reduce seedling abundance of most species, increase the likelihood that paw paw may eventually dominate forest understories over a widespread area. Thus, its spread and establishment may become an issue of concern for existing and future forest communities.

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Mitchell A. Slater currently works for the U.S.D.A. Forest Service as a Biological Science Technician at the research station in Grand Rapids, MN, U.S.A. The work presented here was conducted for his M.S. thesis at Illinois State University.

Roger C. Anderson is an Emeritus Distinguished Professor in the School of Biological Sciences at Illinois State University. He has published 140 articles on the ecology of forests, prairies, savannas, and invasive species, and is a co-editor of Barrens, Savannas, and Rock Outcrop Plant Communities of North America, Cambridge University Press.

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