Effects of deer herbivory, light availability and relative abundance of advanced regeneration on recruitment of *Aesculus glabra* in a deciduous, old-growth forest fragment

Jawad Hossain, Lindsay Hartwig, Sal Amjed, T’kyia Dean

School of Integrative Biology

University of Illinois

Urbana, IL 61801 USA

[jhossai2@illinois.edu](mailto:jhossai2@illinois.edu)

217-666-SATA

ABSTRACT

Recruitment of Ohio buckeyes, *Aesculus glabra,* in a forest differs depending on the biotic and abiotic conditions. In this study in Trelease woods, we examined whether deer herbivory, light availability and/or relative abundance of advanced regeneration explained changes in recruitment of Ohio buckeyes. If episodic deer browse affects size distribution of Ohio buckeye recruits, then there will be an abnormally lower number of recruits at size classes below the browse line. If availability of light explains differences in recruitment of Ohio Buckeyes, then the number and mean size of recruits will be greater at the forest edge than at the interior of the forest. If relative abundances of advanced regeneration among species, particularly Ohio buckeyes, explains future forest composition, then the future forest canopy will have more shade-tolerant species and less shade-intolerant species than the current composition. Our main assumptions were that Ohio buckeyes grow better in regions of high light, and that Ohio buckeyes are shade-tolerant species. Number and DBH of recruits were measured in 8 quadrats under canopy Ohio buckeyes, 8 quadrats away from the canopy trees, and 8 quadrats at the edge of the forest. Presence of episodic deer browse was supported. Mean size of the recruits was significantly greater at the edge than at the interior while the number of recruits was not significantly different. There were no Ohio buckeyes projected to be winners of the canopy however forest structure was found to be changing. The lack of Ohio buckeye in the future forest composition suggests that animal and soil communities that developed around the presence of the Ohio buckeye will face challenges in the future.

INTRODUCTION

Current and future forest structure may vary depending on changes in abiotic and biotic conditions. Forest structure that is not changing from one generation to next is said to be in equilibrium. Forests may be in equilibrium because canopy tree species are replaced by the same species over generations (Runkle 1981). Forests that are not in equilibrium experience changes in forest structure due to differences in recruitment through time (Parker et al. 1985). Recruitment refers to the trees and saplings that will take over as the current species composition undergoes mortality. Several biotic and abiotic factors affect recruitment (Pickett 1980). Biotic conditions include deer herbivory and relative abundance of advanced regeneration among species. Abiotic conditions include light availability in forest edge vs interior. Episodic recruitment may lead to an uneven distribution of recruits at each size class of trees while continual recruitment will lead to a more evenly spread size structure (Watson et al. 1997). Ability to predict future changes in forest structure may help us determine how animal and soil communities that depend on different tree species in the forest may be affected in the future.

*Odocoileus virginianus*, the white-tailed deer, has recently exploded in population and has had deleterious effects on the recruitment of certain species of trees in Trelease woods. Before Europeans conquered the Americas, the population of white-tailed deer in Illinois was relatively small and constant. Immediately after European settlement the deer faced an extreme threat in the form of unrestrained hunting and its population soon declined drastically (Waller and Alverson 1997). Hunting was restricted in the 1950s and since human agriculture was an abounding source of nutrition, deer populations quickly proliferated (Waller and Alverson 1997). This increase in deer has had an effect on the numbers of palatable forest tree species vs unpalatable species (Augustine and McNaughton 1998). Deer herbivory tends to be temporally intermittent, i.e. episodic, due to seasonal migration. Episodic herbivory will show on size distribution of the recruits of palatable species since deer tend to prefer recruits of certain heights more than others (Russel et al. 2001).

Forest structure is affected by the availability of light at different locations in a forest. Different species of trees in a forest have different light requirements for growth. Shade intolerant species require high levels of light to grow while shade tolerant species can grow well even in low light conditions (Oliveira et al. 2004). There is more light at the edge of the forest than in the interior (Esseen and Renhorn 1998). Light gaps in the interior exhibit similar conditions as the edge of a forest (Webster and Lorimer 2005). Light gaps are created when trees undergo mortality and fall, thus creating an opening where high levels of light can pour through. Large light gaps can occur when falling trees bring down more trees or the sudden increase in wind passage after the initial opening causes more trees to be unrooted (Webster and Lorimer 2005). Before colonization of the USA by Europeans, frequent forest fires set by Native Americans created big light gaps and allowed shade intolerant species like the Hickory and Oak to dominate Trelease woods (Rench et al. 2003). In the 200 years since, there has been no more intentional fires and shade tolerant species like the sugar maples have taken over (Rench et al. 2003).

Future composition of a forest canopy may vary depending on the relative abundances of advanced regeneration among species. Sub-canopy trees that have the ability to take over the canopy after canopy trees undergo mortality are the advanced regeneration (Cole and Lorimer 2005). Shade tolerant species generally have more advanced regeneration than shade intolerant species due to their ability to grow and thrive in the low light conditions of the sub-canopy (McLure et al. 2000). The advanced regeneration may take over the opening in the canopy by either growing vertically or expanding its lateral branches (Taylor and Lorimer 2003).

This study’s objective was to determine if episodic deer browse, light availability and relative abundance of advanced regeneration affects recruitment of Ohio buckeyes. If episodic deer browse affects size distribution of Ohio buckeye recruits, then there will be abnormally lower number of recruits at size classes below the browse line. If availability of light limits recruitment of Ohio Buckeyes, then the number and mean size of recruits at the forest edge will be greater than that in the interior of the forest. If future forest structure depends on the relative abundances of advanced regeneration among species, particularly Ohio buckeyes, then the future forest canopy will have more shade-tolerant species and less shade-intolerant species than the current composition. One assumption was that deer prefer to browse recruits below the maximum height they can reach, the browse line. It was also assumed that Ohio buckeyes grow better in regions of high light, and that Ohio buckeyes are shade-tolerant species that have greater advanced regeneration than shade intolerant species.

METHODS

*Study site*

This study was conducted in Trelease woods, an old growth forest fragment located 5 km northeast of Urbana in Champaign County, Illinois, USA (40°13’, 88°14’W). This 26.8 hectare fragment contains high-quality upland mesic forest and is flat with elevation differences less than 5 m. Before colonization of the USA by Europeans, Trelease woods was dominated mostly by oak and hickory, in part due to frequent forest fires set by Native Americans. In the 200 years since colonization, intentional fires have stopped and shade tolerant species like the sugar maples have started to dominate. In 1922, this forest had 37 woody species, 6 liana species, and 134 herb species. American elm and sugar maple used to dominate. Between 1925 and the 1970s, there was a sharp increase in the number of sugar maple trees and a corresponding decrease in elms. This was due to the widespread deaths of the elms around the 1950s from Dutch elm disease (a fungal disease that causes phloem necrosis). The elms were almost eliminated and the sugar maples thrived. In 2005, unpublished data collected by J. Edginton showed that the forest had become very dominated by sugar maple while the Ohio buckeye, basswood, and hackberry were also very prominent. Ohio buckeyes, *Aesculus glabra,* can be described as shade tolerant since it can grow well in shady forests by undergoing early leaf out and taking advantage of the abundant light before canopy trees sprout leaves.

*Experimental design*

8 canopy Ohio buckeye trees were chosen and the projected canopy winners were determined. Number and DBH of recruits in 8.5m by 8.5m quadrats under and 17m away from each canopy tree were measured. The quadrats were specified at the time of measurement using 4 flags placed 6m away diagonally from the center. Each recruit at and below the DBH class of 3cm were determined for damage (damaged or not damaged). Number and DBH of recruits were also recorded at eight quadrats (8m by 2m) at the north edge of Trelease woods.

*Statistical tests*

The number of Ohio buckeye recruits under vs away from the canopy trees were tested by a paired t-test. The number and DBH of Ohio buckeye recruits at the interior vs at the edge of the forest were tested by two t-tests. The species composition of the current vs future canopy was tested by X^2 test for independence.

RESULTS

The number of Ohio buckeye recruits increased from the 1cm DBH class interval to the 3cm class interval. There was then an almost exponential decrease in the number of recruits towards larger DBH class intervals. 85% of recruits with DBH below 3cm, the browse line, were found to be damaged. The density of recruits in the away quadrats did not significantly differ from the density of recruits in the under quadrats (paired t-test, P>0.05) (Fig.2). Seven of the eight parent trees studied had greater recruitment in the away vs under quadrats while the last one had an extremely high recruitment in the under quadrat as compared to its away quadrat. Density of recruits at the edge vs the interior of the forest was not significantly different (t-test P>0.05) (Fig. 3a) while the DBH of the recruits were significantly greater at the edge than at the interior (t-test P<0.05) (Fig. 3b). Species composition of the canopy differed significantly depending on the time period (current vs. future) (t-test p<0.05) (Fig.4). Ohio buckeye had no projected canopy winners while sugar maple dominated the projected future canopy composition with basswood coming second.

DISCUSSION

The number of Ohio buckeye recruits in the 1cm and 2cm DBH class intervals were less than that in the 3cm class and the proportion of damaged recruits at or below the browse line (3cm) was 85%. This supports our prediction that episodic deer foraging will lead to an uneven distribution of DBH of recruits and that the deer foraging height determines the proportion of recruits damaged. Ohio buckeyes produce large numbers of recruits at smaller size classes but competition and other resource limiting factors reduce the number of recruits that grow and reach larger size classes (Terborgh et al. 2008). Deer tend to feed on palatable species that are below a certain height and are easier to reach so the number of recruits below the browse line are reduced in the presence of episodic deer herbivory (Augustine and McNaughton 1998). Continual deer herbivory would have shown a more even spread of DBH of recruits since recruitment would be affected at all seasons and thus very low numbers of recruits would survive herbivory to make it to larger size classes.

Preference of deer for particular heights was supported by a prior study with *Cervus elaphus,* or the red deer,and *Salix caprea* (Renaud et al. 2003). In the study, 12 tamed *Cervus elaphus* of similar heightswere offered fresh branches of *Salix caprea* at several height ranges and it was found that the deer preferred the *Salix caprea* that were at around their shoulder heights. Several studies (Witt and Webster 2010; Russel et al. 2000; Waller and Alverson 1997) also support that herbivory by *Odocoileus viginianus* will have an impact on the variation in recruitment at different size classes. However, there was no consistency in which size classes were preferred by the *Odocoileus viginianus.*

Size of Ohio buckeye recruits was significantly greater at the edge of the forest than at the interior while numbers of recruits were not significantly different. This only partially supports our hypothesis that light availability affects number and mean size of recruits. There was only one outlier datum where number of recruits was exceedingly high at the interior of the forest and this is very likely the cause for the overlapping error bars and the lack of significance of the numbers of recruits at the interior vs the edge. One reason for this outlier datum might be that the measurement that corresponds to this datum was carried out close to a light gap where large amounts of light pour in and conditions are similar to the edge of the forest. Based on our assumption that there is more light available at the edge of the forest than at the interior, Ohio buckeye recruits at the edge can photosynthesize and produce more food for growth, thus explaining the differences in size of recruits at the edge vs interior of the forest.

In a study in the Brazilian Atlantic forest (Oliveira 2004) it was found that the mean number of trees at the forest edge was significantly greater than at the interior. This does not support our results that number of recruits at the edge vs the interior was not significant however if we ignored our outlier datum there is good correspondence. In another study in Amazonian rainforest fragments (Laurance et al. 2006), the mean size of trees in the edge forest plots decreased significantly compared to the interior plots. This contradicts our findings that the mean size of Ohio buckeye recruits was significantly greater at the edge. A potential explanation for this contradiction might be that the conditions, like wind strength, at the edge of Trelease wood might be very different from the conditions at the edges of the Amazonian rainforests. Another potential explanation might be that Ohio buckeyes are not as shade-tolerant as we thought as a prior study (Augspurger 2008) that determined senescence of Ohio buckeyes in shaded environments found that only 7% of the plants were alive after 2 years if kept in complete shade.

Our prediction that a greater proportion of Ohio buckeyes will be projected to be winners of the canopy than the current proportion was not supported, however there was significant support for a dynamic forest structure. Ohio buckeyes did not have any advanced regeneration unlike other shade-tolerant species like the sugar maples. Ohio buckeyes might not be as shade-tolerant as we assumed it to be. Our results that Ohio buckeyes usually had more recruitment at the edge than at the interior seem to support this statement. It might also be that Ohio buckeyes are more likely to be damaged by deer herbivory than other shade tolerant species like the sugar maples and thus the damaged Ohio buckeyes are very easily outcompeted.

A prior study (Henderson et al. 1993) in Trelease woods supported our findings that Ohio buckeye recruits were more concentrated at the edges of the forest. It also found that there were few saplings and trees of Ohio buckeyes in Trelease woods while there were large numbers of saplings and trees of sugar maples, and hence seems to support our finding that there were large amounts of advanced regeneration for the sugar maple but no advanced regeneration for the Ohio buckeyes. In a study in a Tsuga canadensis forest (Anderson and Loucks 1979) of the effects of the white tailed deer on the structure and composition of the forest, it was found that sugar maples outcompeted hemlock when heavy deer browse affected both species. This supports our explanation that Ohio buckeyes might be outcompeted by the sugar maples even though both are shade tolerant and are affected by heavy deer browse.

One limitation was that we only determined projected winners at canopies that are currently occupied by Ohio buckeyes and so density dependent foraging by predators meant that there were few recruits underneath the canopy that could compete to become the advanced regeneration. Our assumptions did not take into account the possibility that other natural enemies may also be affecting recruitment of Ohio buckeyes. Another limitation was that when comparing recruitment at the edge vs interior, we used measurements made at only one edge of the forest and for the interior we only used measurements made under canopy Ohio buckeye trees. A future study should use measurements of number and DBH of recruits at several randomly placed quadrats in the interior of the forest as well as at all edges of the forest. Care should be taken to mark down any measurements made at light gaps where conditions are similar to the edges of the forest. Data for the advanced regeneration at canopies occupied by several different species should be used in determining the relative abundance of advanced regeneration of Ohio buckeyes.

Episodic deer herbivory affects recruitment of Ohio buckeyes and the relative abundance of advanced regeneration of Ohio buckeyes affects forest structure. This study clearly showed that episodic deer herbivory can explain the size distribution of Ohio buckeye recruits. There is evidence that light availability leads to changes in recruitment of Ohio buckeyes however it is only partially supported. This study also showed that forest structure can be explained by the relative abundances of advanced regeneration among tree species. It is not yet clear why the Ohio buckeyes have no advanced regeneration in the forest but the lack of Ohio buckeyes in the future canopy will likely have important consequences on the animals that feed on Ohio buckeye seeds and saplings as well as the soil communities that developed around the presence of Ohio buckeyes.

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Fig 1. Number of Ohio buckeye recruits present at each DBH class

Fig 2. Difference in density (per m2) of recruits under and away from each canopy tree

(a)

(b)

Fig 3. Average density (or number of recruits per m2) and average DBH of recruits at the interior vs edge

Figure 4. Number of individuals of each species of tree in the current vs future canopy