St. Olaf College

Local Ecology Research Papers

Herbivory by *Odocoileus viginianus* alters species composition in a Minnesota forest restoration by suppressing *Quercus macrocarpa* density.”

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2018

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Field Ecology
December 12, 2018
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Abstract

Maple Basswood forests once covered a large portion of the Minnesota landscape, but much of this forest has since been replaced with intensive corn and soybean agriculture (Minnesota DNR, 2006). Today, there is increasing interest in efforts to restore this ecosystem for purposes of ecosystem services and biodiversity preservation. A wide variety of factors are important for determining the success of a restoration effort, but herbivory by deer (*Odocoileus* virginianus) has been shown to significantly impact the presence of invasive species (Averill, et. al, 2018), as well as tree size and recruitment on a species-specific basis (Côte et al. 2004 and Tanentzap et al. 2011). I examined the effect of exposure to deer herbivory on tree community composition, density and size two ongoing forest restorations in Northfield, Minnesota. I found that exposure to deer herbivory did not affect the sizes of trees or species diversity, but did suppress bur oak (*Quercus macrocarpa*) density. This is consistent with bur oak responses to herbivory previously seen as far afield as Sweden (Leonardsson et al. 2015) as well as here in Northfield (Rand 2009). This suggests that restoration efforts seeking to promote bur oak could benefit from strategies to mitigate the impact of herbivory, potentially ranging from fencing or tree tubes to the inclusion of alternative species more palatable to herbivores.

Keywords

Forest restoration, bur oak, *Quercus macrocarpa*, herbivory, *Odocoileus virginianus*

Introduction

Increased interest in forest and prairie restoration in southern Minnesota has developed out of recognition of the substantial impact of human behavior, especially intensive agriculture, on ecosystem diversity and function. Restorations are often undertaken with the goal of using a piece of land to support a greater presence of native species that align with distributions and diversity of plants and animals in Minnesota before European settlement, with the idea that restored communities should be self-sustaining without human inputs (Hobbs et al. 2007). Human land-use practices and management of wildlife through hunting are important for the success of a restoration, in terms of maintaining biodiversity or achieving a specific ecological character. The impact of herbivores, especially white-tailed deer is one important piece influencing successional processes. In the face of changing climate, people engaged in developing hunting regulations, in establishing restored forest, and making plans for decades in the future can benefit from a better understanding of the way that forest restorations from seed develop over time, and the way that herbivores influence this development.

The potential for large herbivores to impact forest composition is well known. One famous example of the importance of herbivory is the long-term study on Isle Royale in Lake Superior. Four moose exclosures built in the 1940's relieved the pressure of moose herbivory on the aspens and birch, and under these conditions, the deciduous trees dominated the forest (Krefting 1974). Outside of the exclosures herbivory selected against the aspen and birch, making spruce dominant and resulting variety of other cascading effects on the landscape. For example, the nutrient cycling in the soil was dramatically impacted - nitrogen availability within the exclosures was as much as 50% higher than in areas exposed to moose herbivory (Pastor 1993). While the boreal forests of northern Minnesota are not directly comparable to those of the southern half of the state, this highlights the powerful influence that herbivores have on successional processes. Clearly under the right conditions, and with enough time, large herbivores can have a substantial long-term impact on the composition of forest communities.

More specifically to southern Minnesota, and ongoing restoration efforts in Northfield, there is substantial evidence supporting the importance of herbivory in deciduous dominated forests. Deer browsing in the northeastern United States has been found to reduce native community diversity and promote several invasive including garlic mustard (*Alliaria petiolate*), Japanese stiltgrass (*Microstegium vimineum*) (Averill, et. al, 2018), which suggests that deer herbivory may be detrimental to restorations that aim to promote high species diversity. Similarly, in Sweden, forest succession after a thinning disturbance favored the regeneration of oak if herbivore exclosures were used, while exposure to herbivory favored competing understory species (Leondardsson 2015). In other instances, the impact of herbivory on forest management efforts have been less successful. In Ontario, Canada, high deer densities of (55 per km^2) resulted in losses in recruitment of trees to the canopy and these rates did not recover after deer populations were substantially reduced (Tanzentzap, et al. 2011). They argue that deer impact in this manner has the potential to alter landscapes, and some modeling even suggests that deer mediated forest composition can persist for hundreds of years (Frelich 1985). In the light of these findings, the potential for these dramatic impacts are of special importance for forest restorations and efforts at conservation translocation, which necessarily operate at similarly long timeframes.

Here at St. Olaf, ongoing restorations of oak savannah and maple basswood forest are in progress, with the hope that they will benefit native species and avoid harboring harmful invasive species. All of these areas are exposed to herbivory by local populations of white-tailed deer (*Odocoileus virginianus*). This study focuses specifically on two fields which were restored from intensive agricultural use in 2005 and 2009 respectively, allowing for a rudimentary chronosequence comparing changes over time. Herbivore exclosures were built at the start of these restoration efforts, allowing for comparisons between exposed and unexposed patches. Research by a previous student, Rebecca Rand, found that bur oak (*Quercus macrocarpa*) that were exposed to herbivory were smaller than those in one of these exclosures in the 2005 area (Rand 2009), which suggests that browsing had an effect even fairly early on. That study, however, did not include a comparison of restorations at different ages, and different places in the successional process.

In the light of the impact that deer were having on the restorations in Northfield ten years ago, it seems likely that the effect of deer will have been magnified over time. Considering the progress of these restorations generally, I hypothesize that (1) the density, size and diversity of species will differ between the older and newer sites. Further, that (2) exposure to herbivory by deer will alter the species diversity, density and size of the trees present and that(3) soil characteristics in terms of organic matter is similar between all four plots, unaffected by either the age of the forest, or the presence or absence of herbivory.

Materials and Methods

In order to examine my hypotheses regarding the impact of herbivory and forest restoration, I compared two ongoing forest restoration plots in the St. Olaf Natural Lands. One of the two plots was restored from seed in 2005, and the other in 2009, and this four-year period that elapsed between their planting allows them to function as a simple chronosequence. Both include two 10 square meter herbivore exclosures which were established at the same time as the seeding of these areas. I sampled one of these 10x10m exclosures in each restoration zone, as well as an identically sized, nearby plot which was exposed to herbivory. The direction and distance of the exposed plot from the exclosure was chosen using a random number generator to avoid sampling bias. All four plots were divided into four smaller quadrants which aided both in accurately sampling trees, as well as in conducting statistical analysis. Measurements of diameter at breast height (DBH) was used to assess tree size. I counted all trees present in each quadrant and identified them by species, categorizing them as seedlings (shorter than 0.5m), saplings (taller than 0.5m but with DBH < 2.5 cm) or as maturing trees with a DBH ≥ 2.5cm (hereafter referred to as "maturing trees"). The actual DBH measurement was also recorded in addition to species for these maturing trees.

In order to assess differences in moisture, organic matter and bulk density, three soil samples were taken from each of the four sites. Samples were weighed initially while still wet, and then again after drying an oven at 105°C for 48 hours in order to calculate soil moisture content. Percent moisture by weight was calculated by comparing the wet and dry weights of the soil. Organic matter content was calculated by burning off the organic material in a muffle furnace. First 4.5 to 9.0 grams of each dried sample through a 2mm sieve. These were weighed, heated to 500°C for four hours, and weighed again. Percent organic matter was calculated by comparing the sample weight before and after the organic matter was burned off. Bulk density was calculated by dividing the dry weight of the soil by the volume of each sample, 188 cm^3.

Statistical analysis of the data was done using Microsoft Excel (version 16.19), R (version 3.5.1), Rstudio (version 1.1.495) and R Commander (version 2.5-1). Excel was used to add totals of species and DBH values, as well as to calculate standard deviations and generate figures. In addition, I used Excel to calculate Shannon and Simpson diversity indices, to do a pairwise comparison of Ds values between plots, and test that comparison for statistical significance. All other key relationships were tested for statistical significance using ANOVAs generated using R Commander.

Results

A total of 951 trees were measured across all four sites. In total at the older restoration, there were 227 seedlings, 321 saplings, and 155 maturing trees, and the newer restoration plots there were 46 seedlings, 186 saplings and 16 maturing trees. Of the 12 species present, red oak (*Qurecus rubra*), bur oak (*Quercus macrocarpa*), green ash (*Fraxinus pennsylvanica*) and siberian elm (*Ulmus pumila*) were most common (Table 1) There were not significant differences in the Shannon or Simpson indices between the two treatment plots within each site, however there was significantly less diversity at older sites as opposed to the more recent restoration (Table 2)**.**

The densities of trees at the old and new restorations, when including all individuals of all species, were not significantly different (Table 3). Additionally, no significant differences were found between all four plots for either seedlings or saplings of all species combined. For maturing trees with a DBH $\geq$ 2.5 cm, there were significantly higher combined densities (for all species) at the older restoration started in 2005 (Table 4). Examining this more closely, at the older plots there were no significant differences between seedling or sapling density, regardless of herbivory exposure. There were, however, significantly higher densities of maturing trees when the plot was protected from herbivory (Table 5). Comparing the two most common species, red and bur oak, there were no significant difference between exposed and unexposed red oak densities at the older sites (Table 6) but bur oak density at the 2009 site was significantly higher when protected from deer herbivory (Table 7).

A comparison of the size (DBH) of all trees between the older and newer restoration revealed that the older trees were larger by a significant margin (Table 8). At both the older (Table 9) and newer site (Table 10) restoration, there was no significant difference in the DBH of all species whether or not they were exposed to herbivory.

The soils present in all four plots were very similar. There was no significant difference in soil moisture (Table 11) or in bulk density (Table 12) between any of the plots, however, there was a significantly lower proportion of organic matter in the soil of the older restoration which was exposed to herbivory (Table 13).

Discussion

The decreased species diversity at the older restoration site and increased size suggests that, as hypothesized, species composition does change as restoration progresses over time, confirming my first hypothesis. However, although older restorations were less diverse than more recent restorations, there was no statistically significant difference between exposed and unexposed plots at the same age. This suggests that deer herbivory has not resulted in a change in species diversity over time, and that these changes were instead driven by factors other than herbivory.

Deer herbivory has indeed had an effect on the community of tree species over time, confirming my second hypothesis. Although exposure to herbivory did not affect either the species diversity or the size of the trees, it did have an impact on the long-term species density. The nine-year-old plots are identical regardless of exposure to browsing, but at the older exposed site, bur oak density was suppressed. The difference in impact on the longer running restoration suggests that either the impact of herbivory takes an extended period of time to accumulate. Alternatively, it is possible that deer herbivory exerted a stronger selective pressure early in the growth of the 2005 restoration, and that this pressure decreased before 2009.

In any case, impacts on oaks as a result of deer herbivory are consistent with the findings of previous studies. Rebecca Rand, a student who previously examined the impact of herbivory on forest restoration at St. Olaf found that exposure to herbivory significantly suppressed the height of bur oak (Rand 2009). While density and height are not directly connected, perhaps these shorter oaks were less competitive and were selected against. Furthermore, the greater prevalence of bur oak within the exclosures is consistent with the findings that herbivore exclosures promoted oak regeneration after disturbance in Sweden (Leonardson, et. al, 2015). With respect to soil, little can be concluded from the lower organic matter content observed for the exposed plot at the 2009 site, as no baseline values for organic matter over time are available. Nonetheless, it suggests the possibility that there may be a more complex interaction occurring between deer and bur oak, potentially even resulting in a cascading effect all the way to soil quality, such as the moose – mediated decrease in nutrient levels on Isle Royale in Michigan.

Responsive management that takes into account the stress of herbivory for bur oak trees in an effort to promote oak regeneration could take a variety of forms. One cost effective option may be planting additional species, such as black cherry (*Prunus serotine*), which are preferred by deer. This shifts herbivory pressure way from the heavily impacted bur oak, ultimately allowing for more successful growth (Burney 2018). Alternatively, intentionally managed herbivory, perhaps by goats, could be used to restore ecosystems like oak savanna, as some evidence suggests that deer can aid this transition (Côté 2004).

Before jumping to too many conclusions however, there are several important sources of error in this study. One of the most important is the very small sample size and lack of replication. Because the plots are only $10m^2$, it is easy for the entire plot to be dominated by a single clump of trees, failing to account for the heterogeneity present in the site. Additionally, a high level of heterogeneity and lack of consistent control over the initial seeding process for restoration (Larson, Nelson 2018) may have contributed to differences in species composition. Another important source of error is potentially the differences in edge effects between the two restoration sites. The older site is surrounded for fairly large distances by similar early successional forest, while in contrast, the newer site is very close to a mature maple – basswood forest fragment. This may have been especially important if this forest fragment includes mature siberian elms, or green ash, which were present in large numbers in the newer restoration but not the old.

Conclusion

Here at St. Olaf, understanding the impact of deer herbivory on forest restoration is important in order to more successfully manage the return of historical species and plan for the future of these forests. More broadly, based upon this information, others engaged in similar forest restoration projects can act in order to protect bur oak seedlings from deer herbivory, if one of their goals is to promote bur oak regeneration. Additionally, with knowledge of this interaction, other strategies for mitigating deer herbivory can be explored. Thinking more broadly, as appreciation for the ecosystem services provided by forests increases in the face of climate change, information about reestablishing stable forests and understanding influences on their development will become all the more important. Many restorations set out with the aim of supporting native species in distributions similar to their historical range, and with the goal of self-sustaining communities (Hobbs et al, 2007). In the light of this interaction between deer herbivory and oaks, restoration efforts that are prioritizing the return of bur oak to their historical range could utilize fencing, tubes or other strategies to allow this species greater success.

Acknowledgements

This study was made possible through the support St. Olaf College Biology department, which provided measurement equipment and data analysis tools, as well as the natural lands endowment for supporting the ongoing restoration work. Nicolaas Nelson provided invaluable insight into the fine variations present in these restoration areas. Professor Kathleen Shea, the current Curator of the Natural Lands, provided invaluable aid in understanding the natural history of the Big Woods, developing the experimental design, and also with statistical analysis. I also want to recognize Professor Emeritus Eugene Bakko, a former Curator of the Natural Lands for his work in organizing and planting the restoration and building the herbivore exclosures which make this work possible.

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Tables and Figures

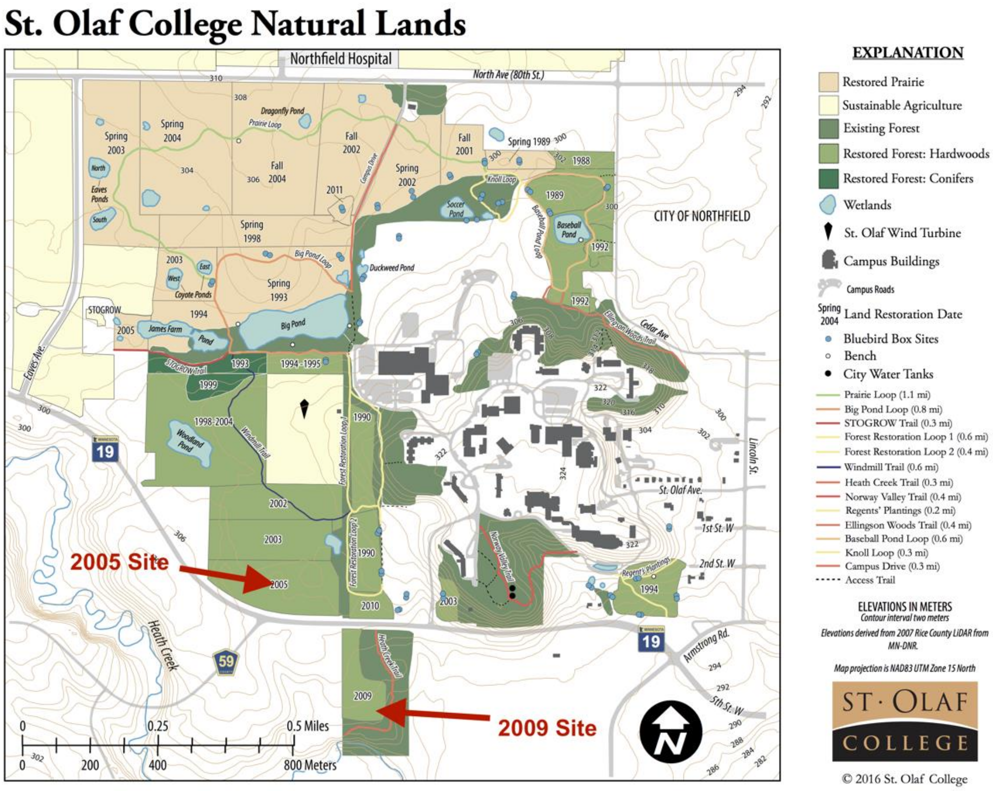

Figure 1: Map of the St. Olaf College Natural Lands
The locations of study sites are marked within the 2005 and 2009 forest restoration plots. The plots exposed to herbivory are a short distance (3~5m) north of the herbivore exclosures.

Table 1: The number of individuals of each species observed in each plot.

Species	Old Exposed	Old Enclosed	New Exposed	New Enclosed
Red Oak	18	52	55	70
Bur Oak	4	31	73	67
Bitternut Hickory	1	9	6	16
Amur Maple	2	0	8	9
Bigtooth Aspen	1	0	1	0
Green Ash	15	37	1	2
Siberian Elm	26	14	0	0
Boxelder	5	18	0	0
American Elm	8	4	0	0
Buckthorn	0	1	162	0
White Pine	0	1	0	0
Basswood	1	0	0	0

Table 2: The species richness, as well as Shannon and Simpson diversity indices calculated from the species totals in Table 1. Diversity is significantly higher ($p < 0.05$) at the new site in comparison with the older restoration, but there is no difference between the exposed and enclosed plots at each site.

	New Exposed	New Enclosed	Old Exposed	Old Enclosed
Richness	10	9	7	5
Shannon (H')	0.788	0.767	0.520	0.508
Simpson (Ds)	0.806	0.802	0.631	0.642
Variance of Ds	0.00050	0.00020	0.00040	0.00039

Table 3: An ANOVA comparison of the densities of all species at all age classes between the older and the more recent restorations. $p = 0.227$, $df = 2$, $F = 1.59$

Plot	Mean density per ha	Standard deviation	# of sub-plots
New	62000	44300	8
Old	117000	115000	8

Table 4: An ANOVA comparison of the combined density of all species of maturing trees to the restoration plot. $p = 1.19e{-6}$, $df = 3$, $F = 42.2$

Plot	Mean density per ha	Standard deviation	# of sub-plots
New EN	2500	3000	4
New EX	5500	5507	4
Old EN	46000	10700	4
Old EX	29000	2580	4

Table 5: An ANOVA comparing the combined density of maturing trees of all species between exposed and unexposed plots at the older site. $p = 0.0212$, $df = 1$, $F = 9.53$

Plot	Mean density per ha	Standard deviation	# of sub-plots
Old EN	46000	10700	4
Old EX	29000	2580	4

Table 6: An ANOVA comparing the combined density of maturing trees of all species between exposed and unexposed plots at the newer site. $p = 0.0212$, $df = 1$, $F = 9.53$

Plot	Mean density of red oak per ha	Standard deviation	# of sub-plots
Old EN	19000	4163	4
Old EX	21000	3464	4

Table 7: An ANOVA comparing the combined density of maturing bur oak between exposed and unexposed plots at the newer. p = 0.00439, df = 1, F = 19.7

Plot	Mean density of bur oak per ha	Standard deviation	# of sub-plots
Old EN	24000	7480	4
Old EX	5000	4160	4

Table 8: An ANOVA comparing the DBH of all species at all age classes between the new and old restoration sites. p = 0.0.001, df = 1, F = 11.7

Plot	Mean DBH (cm) of all species	Standard deviation	# of individuals
New	2.9	0.3	16
Old	3.8	1.1	58

Table 9: An ANOVA comparing the DBH of all species with respect to their exposure to herbivory at the older restoration site. p = 0.548, df = 1, F = 0.363

Plot	Mean DBH (cm)	Standard deviation	# of individuals
Old EN	4.3	1.8	94
Old EX	4.7	4.5	60

Table 10: An ANOVA comparing the DBH of all species with respect to their exposure to herbivory at the more recent restoration site. p = 0.00439, df = 1, F = 19.7

Plot	Mean DBH (cm)	Standard deviation	# of individuals
New EN	2.8	0.3	5
New EX	2.9	0.4	11

Table 11: An ANOVA comparing the percent of moisture in the soil by mass at each site. p = 0.281, df = 3, F = 1.525

Plot	Mean % moisture	Standard deviation	# of samples
New EN	18.10	1.30	3
New EX	21.90	4.71	3
Old EN	20.76	1.87	3
Old EX	18.25	0.399	3

Table 12: An ANOVA comparing the soil bulk density between sites. p = 0.281, df = 3, F = 0.121

Plot	Mean bulk density	Standard deviation	# of samples
New EN	0.303	0.0046	3
New EX	0.291	0.0717	3
Old EN	0.290	0.0324	3
Old EX	0.284	0.0286	3

Table 13: An ANOVA comparing the percent of the soil which is organic matter i by mass for each site. p = 0.0123, df = 3, F = 7.066

Plot	Mean % organic matter	Standard deviation	# of samples
New EN	4.43	0.942	3
New EX	5.17	0.281	3
Old EN	4.13	0.456	3
Old EX	3.16	0.102	3