Patterns of Woody Encroachment Establishment in a Restored Prairie Area

Andrea Colton

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Abstract

Tallgrass prairies require frequent disturbance from fire or grazing to avoid woody encroachment, but the natural disturbance regime has been disrupted across much of the range of tallgrass prairies. Many factors such as herbaceous plant biomass, diversity, herbivory, and nutrient changes in soils have been identified as potential enhancers or controls of woody seedlings coming into prairie areas, yet very few consistent patterns have been identified. Specifically, the relationship between initial plant diversity and competitive effects on woody species remains unclear. This study aims to test whether encroachment rates of woody species are reduced by deer herbivory or increasing herbaceous plant diversities in a restored prairie in Ames, Iowa. Oakridge Prairie is sectioned into eight plots (four allowing herbivory, four preventing herbivory) and each block has areas of low and high grass/forb diversity. Heights, species, and locations within diversity and herbivory treatments were recorded for all seedlings above 0.5 m within this prairie. Herbivory reduces woody seedling abundance and height, but we found no difference in seedling abundance between areas with low and high plant diversity. Together, this shows that herbivores strongly limit woody encroachment, but that high plant diversity does not prevent woody encroachment. Dispersal mode affects dispersal distance, with animal dispersed seeds traveling farther from their nearest conspecific than wind dispersed seeds.

Animals, likely birds, are dispersing seeds into prairies, leading to woody encroachment, and ultimately conversion of prairies to woodlands without periodic burning or more intense grazing.

Introduction

Tallgrass prairies are at less than 4% of their original range (Nature Conservancy). This reduction is largely due to anthropogenic utilization of the lands for urban and agricultural areas. The few prairie remnants and reconstructions that remain are threatened by a process known as woody encroachment. This process is a natural successional process that is characterized by woody species coming into and taking over an otherwise grass dominated habitat (Ratajczak et al., 2011), making it a potential concern for any landscape rich in grass species both across the United States and the world. Several studies look into encroachment in various habitat types, but very few look extensively at initial conditions (plant diversity, biomass, herbivory) that may increase or reduce encroachment into tallgrass prairie areas. While land managers in the state of Iowa have practices in place that address herbivory, few address the effects of herbaceous plant diversity or seed dispersal patterns on rates of woody encroachment. In order to address the current effectiveness of these factors as controls, we must first place their importance into a historical context.

One factor that has historically served as a natural control for encroachment in prairies is competition between grass and trees species (Iowa Association of Naturalists). It is well supported that woody species will eventually decrease surrounding herbaceous plant diversity once they are established (Ratajczak et al., 2012), yet few studies have looked into how initial prairie plant diversity and density may affect the rate of encroachment. Positive correlations have

been shown to occur between increasing grass biomass and grass-tree competition intensity, but the significance of these relationships has not yet been supported (Davis et al., 1998).

A prominent factor to the success of prairie plants to out-compete woody species is their suitability to natural disturbances such as fire and herbivory (Iowa Association of Naturalists). Historically, large mammals such as bison and elk were responsible for providing the herbivory needed to halt the establishment and recruitment of woody species; however, these mammals have been extirpated from the state creating the need to explore other herbivores as a control. Deer have been shown to reduce sapling abundance and height in forest areas (Levine et al., 2012). Additionally, they can enhance the spread of woody species by acting as frugivorous seed dispersers (Myers and Velland, 2004). Very few studies, however, look into these effects on open grassland habitats.

It is important to consider the roles of animals as dispersers and enhancers of woody encroachment. Both tree height and dispersal mode have been shown to be an important factor in seed dispersal distances, with seeds produced from taller tress and animal dispersed trees potentially travelling farther from adults (Thomson et al., 2011, Sorensen, 1986). This effect of animal dispersal mode on dispersal distances, however, applies to adhesive, rather than fruiting seeds (Sorensen, 1986). Significance between gut-passed seeds and longer distances specifically in comparison to wind dispersed seeds has not been fully supported.

This study aims to study how herbivory by deer, initial herbaceous plant diversity, and dispersal mode may aid in or prevent the establishment of woody encroachment specifically in a tall grass prairie system. By setting up treatment groups focusing on the presence of herbivory and differing surrounding plant diversities, we can shed light on the interactions and conditions

that reduce woody encroachment. In this study, we identify the ways herbivory and surrounding plant diversity may affect height and abundance of woody species present in an experimental restored prairie. We propose three hypotheses:

1. Herbivory will reduce the establishment and growth of woody species.
2. Surrounding herbaceous plant diversity will reduce the establishment and growth of woody species.
3. Dispersal distance of woody species will differ depending on the dispersal mode of their seeds (animal vs wind)

Methods

Study Site

The Oakridge prairie restoration within the city of Ames, Iowa was created in 2012 as part of a previous graduate student study focused on the establishment of plant communities in response to herbivory (Sullivan et al. 2016). The site is divided into eight blocks, each with a center containing seed additions of 51 plants species, four strips that have been covered in plastic tarps (allowing no natural dispersal and establishment of seeds), and remaining area within the block containing seed additions of 14 plant species. None of the additions included tree species. The blocks are 32x32 m^2 with the high diversity centers of 19.2m in diameter. Each of the strips measure 1.8x10m^2. Total areas are as follows: 662.47m^2 for low diversity, 289.53m^2 for high diversity, and 72m^2 for strips. Four of these sections have fences surrounding them to exclude herbivory (mainly by deer and voles) and four are open to herbivory.

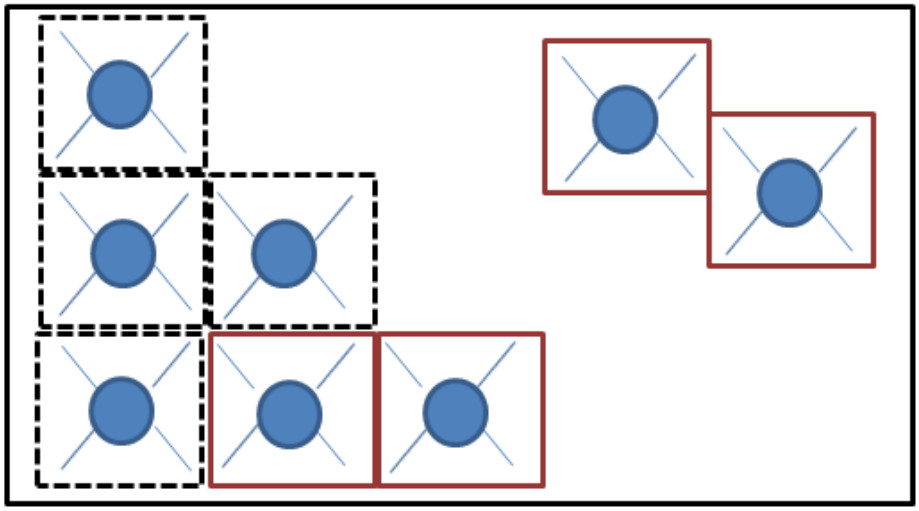

Figure 1. Study site layout. Dashed boxes allowed herbivory, boxes in red excluded herbivory. Blue circles represent 51 species seed addition diversity. Blue strips represent areas with no seed addition. All other space within the boxes represent 14 species seed addition diversity.

Tagging Trees

Transects were set up in each of the eight plots. Starting on one end of the plot, flagging posts were set up about 2-2.5 meters away from the end. This section was walked from south to north, the flagging posts were moved 2-2.5 meters over, and that section was walked from north to south. This pattern was repeated until the entire plot had been searched.

While walking the transects, we searched for tree and shrub seedlings only. Once a seedling was found, it was measured. Only seedlings with a height of 0.5 meters or higher were counted. In addition to this measurement, each tree was tagged with flagging tape and given a unique number and each species was identified. In order to gather evidence of seed caching underneath plastic strips marking no seed addition areas, it was noted if seedlings were within 15 cm of these strips.

GPS Data

The GPS coordinate of each seedling identified was recorded on a Trimble GeoXT. Additional points taken with the Trimble include the four posts outlining the eight plots and the ends of the no addition areas to distinguish between high and low diversity seed additions. This data was saved in the TerraSync program and uploaded to GPS Pathfinder to obtain a map of the seedlings. GPS data was also taken for conspecifics in the surrounding neighborhood to determine the minimum distance from seedlings in the prairie to their nearest conspecific.

Tree Identification

Tree species were keyed out using (Insert name of that book here). Trees that could not be keyed out in the field either had sample leaves taken or pictures taken to be identified at the Iowa State University Herbarium at a later time. The nearest conspecific individual for each species present was found in either the back tree line on the north side of the prairie or in the surrounding neighborhoods. All data collection occurred during Oct.-Nov of 2016.

Analysis

Generalized linear mixed effects models were used to test the differences of each parameter, with significance determined by 95% confidence intervals. If interactions between diversity treatment and herbivory were not significant, models were re-fit without the interaction.

Results

All species are more abundant in herbivore exclosure areas than in areas with herbivores. Species occurring in the highest abundances (with the exception of *Acer saccharinum*) are trees with fruiting seeds (animal dispersed), despite the fact they are occurring in areas where

herbivory is excluded (Figure 2). There was a significant difference between herbivory and abundance ($p = 0.000951$, $df = 13$, Fig 3) but not diversity and abundance ($p = 0.148752$, $df = 13$, Fig 3). There is a significant difference between both herbivory and height ($t = -2.909$, $df = 542$, Fig 4) and diversity and height ($t = -2.332$, $df = 542$, Fig 4). There is significance between dispersal distance and mode, with animal dispersed trees traveling farther from their nearest conspecific ($t = -13.79$, $df = 527$, Fig 5).

Discussion

We found that herbivory by deer, rabbits, and voles reduces the establishment and growth of woody species. There were fewer seedlings and lower average heights for seedlings located in open herbivory treatments than those in areas where herbivores were excluded. It is likely the majority of damage was inflicted by deer, indicating that herbivory by deer is limiting woody encroachment into prairie areas, which is supported by previous studies examining the effects of deer on woody seedlings (Levine et al., 2012).

Local herbaceous plant diversity did not significantly affect the establishment of woody species at 14 and 51 species seed addition treatment levels. Diversity did affect the growth, though not completely in line with our predictions. Seedlings are taller in high diversity treatments exposed to herbivores, than in the low diversity treatments or treatments without herbivores. These high diversity areas also have higher plant cover and biomass, therefore we hypothesize that the cover provides a “refuge” from herbivores that allows these seeds to establish and grow.

Relationships between plant diversity, biomass, and competition effects on surrounding woody species are complicated and sometimes contradictory. Grass competition has been shown

to suppress woody species growth of already established trees in savanna areas in Africa (Riginos, 2009), yet similar results have not been shown in oak-savanna or grassland habitats. Additionally, despite the fact that interspecific competition is a prevalent factor that can reduce competition in animal interactions (Bengtsson, 1989), it seems that this interaction is not an important role in plant communities. Furthermore, diversity of functional groups, rather than species, may produce stronger competition that could keep woody species down (Wardle and Barker 1997).

Animal dispersed seeds were dispersed farther from their nearest conspecific and putative parent tree, than wind dispersed species. A majority of the seedlings that produce fruit occurred in high abundances in herbivore exclosures, indicating that while deer have been shown to be effective dispersers (Myers and Vellend, 2004), birds may play a more important role of seed dispersal in this prairie. Interestingly, seed dispersal distance can be affected by frugivore size (Cousens et al, 2010), not only interspecifically, but also intraspecifically (Wotton and Kelly, 2012). Taking frugivore species and size into account, our results further indicate that in this system, the negative herbivory effects of deer may outweigh their potential roles as dispersers

These results provide helpful insight into establishment of woody species into pristine prairie areas. In particular, the effectiveness of herbivory by deer may prove to be beneficial in supplementing historic grazing conditions and decreasing the rates of woody encroachment despite the fact that they may also have a role in dispersing seeds (both native and invasive) into prairie areas (Van Auken, 2009). It may even be advantageous for grasses exposed to herbivory by deer, rather than bison, due to the difference in foraging behavior (Shipley, 1999). Bison, as grazers, may have a more negative effect on grasses (though they are ultimately adapted to

recover from this type of disturbance), than the browsing behavior of deer, which focuses on woody species.

In addition to studying foraging behavior effects on woody encroachment, plant interactions should be further studied in order to find solid relationships between diversity, biomass, and competition. Defining these interactions can provide valuable knowledge to both an understudied process and system. Woody encroachment has been shown to occur in grassland habitats across the world, yet few studies research the grassland habitats of North America and fewer yet research prairie systems. While encroachment is a natural process that has been occurring for decades, links between changing climate and vegetative response indicate that the encroachment problem will only grow in the next few years (Ratajczak et al., 2012). Understanding the processes that either enhance or reduce woody species coming into the once vast grasslands of the world is key to preserving the few expanses of prairie that remain and to ensuring the perseverance of a key feature to Iowa's landscape.

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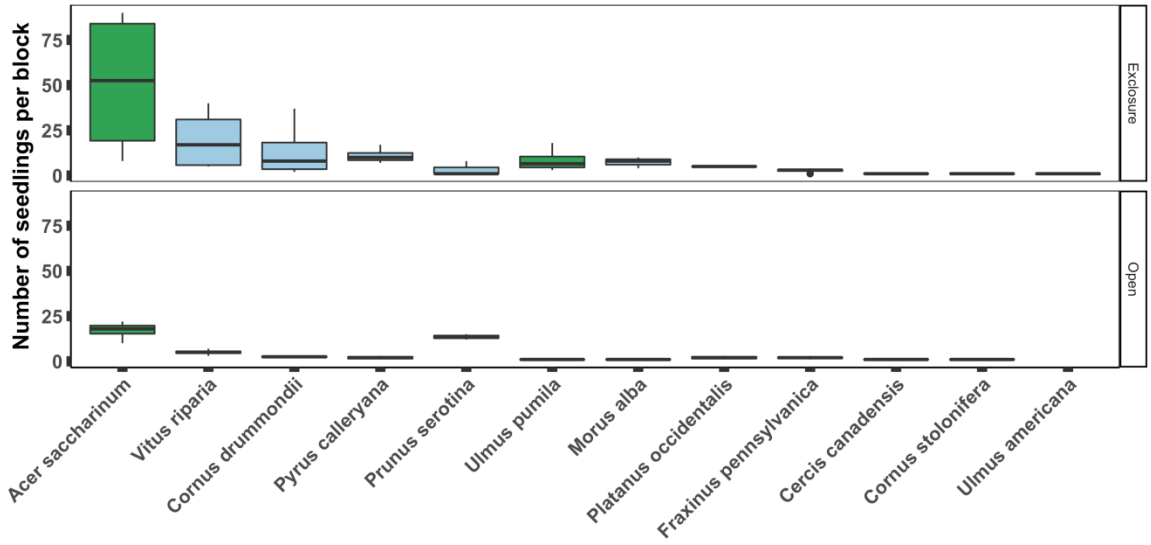

Figure 2. Abundances in exclosure and open herbivory split by species in the prairie. Green represents animal dispersal modes and blue represents wind dispersal.

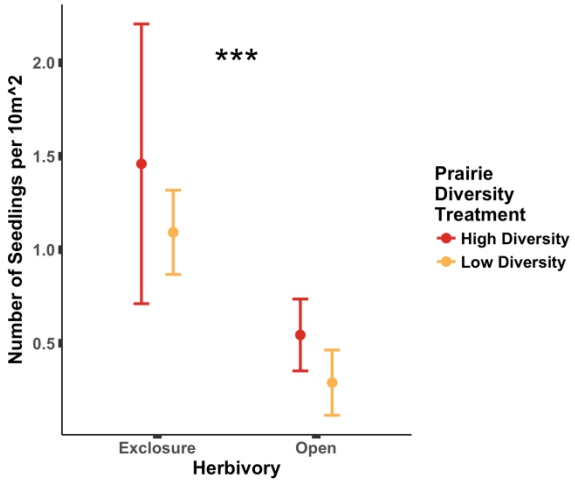

Figure 3. Differences in abundance between herbivory and diversity treatments.

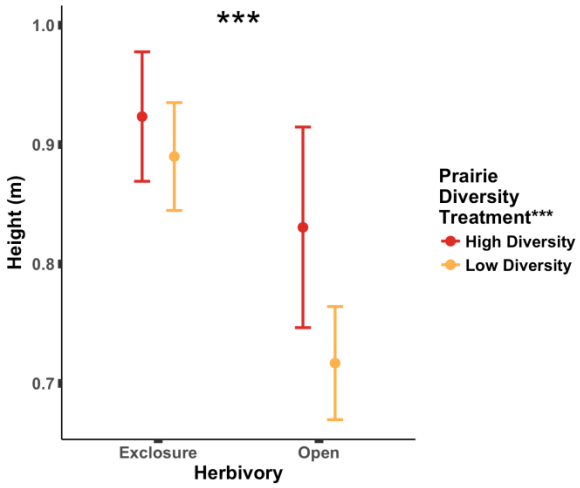

Figure 4. Height differences between herbivory and diversity treatments

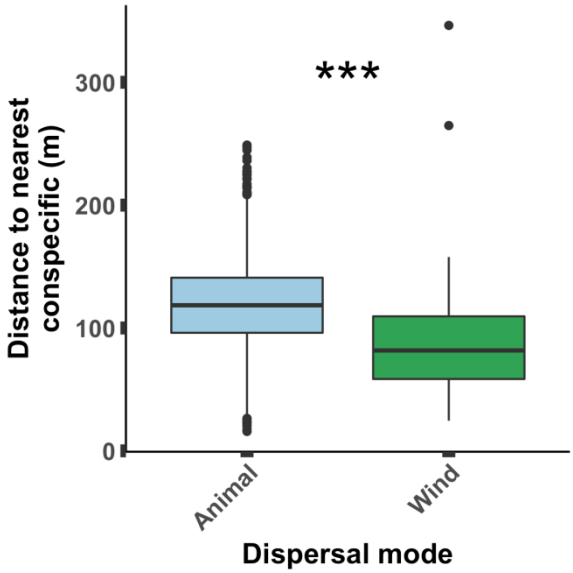

Figure 5. Difference in dispersal distance between animal (blue) and wind dispersed seeds (green)