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Response of wood nettle *(Laportea canadensis)* to Euro-American land-use in southeast Minnesota

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ABSTRACT

The legacy of post-settlement land-use is not always recognized in ecological studies, although it can have profound effects on the plant community and populations. This thesis employs historical documentation and current conditions to investigate the hypothesis that past human activity has produced differences in wood nettle density and population structure among maple-basswood forests in southeast Minnesota.

Both qualitative and quantitative vegetation surveys found that wood nettle density tends to be greater in stands that have experienced selective harvest, but forest structure provides more insight into the relationship between wood nettle and land-use. Wood nettle increases with decreasing density of sub-canopy trees (10 - 25 cm dbh). The current subcanopy layer is the dense woody re-growth that typically follows heavy selective harvest, clear-cut, and livestock grazing.. The woody re-growth appears to suppress wood nettle. Accelerated gap-phase succession follows mild selective harvest and from overstory disruption in old-growth stands and wool nettle appears to increase after these events. The life history traits of wood nettle and its relationship with tree canopy composition support this conclusion.

Variation in wood nettle population structure is primarily attributable to population density. The percent of sexually reproducing stems decreases with. increasing wood nettle density. Seed germination increases with the number of seed producing stems, but intra-specific competition reduces the number of germinants at high adult densities. Wood nettle stem height increases with inter- and intra-specific competition.

The number and proportion of sexually reproducing, seed-producing, and female stems increase with the density of the canopy layer (< 25 cm dbh). This study, however, fails to find a direct relationship between light availability and wood nettle reproduction.

The diversity and abundance of co-occurring summer forb, woody, and graminoid species are negatively correlated with increasing wood nettle density. The reduction of these species may occur through occupation of space or competition for light or other resources. The abundance and diversity of spring ephemeral and spring-reproducing species, with the exception of white trout-lily, are positively correlated with the previous year's wood nettle density. Wood nettle does not overlap phenologically with these species and may displace direct competitors.

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PREFACE

This thesis contains three chapters and nine appendices. In chapter 1, I use written histories, and both qualitative and quantitative vegetation surveys to examine the relationship between wood nettle colonization patterns and land-use. I use forest tree composition and structure, environmental variables (such as light and soil horizonation) and life history traits to support the results.

The structure of any plant population is a product of its current environment and the outcome of past demographic events. Chapter 2 attempts to detect the influence of land-use events in the reproductive structure of wood nettle populations through density effects, forest structure, and the time since last documented land-use event.

Chapter 3 examines wood nettle's relationship with other plant species. The abundance and diversity of both co-occurring summer species and the proceeding years spring species are compared with wood nettle density. The association and correlation with individual species are also included.

Appendices A through G summarize data for the sampled land-use parcels. Appendix H discusses the effects of deer browse. Appendix I presents data on phenology and compares population data between ,populations of wood nettle.

CHAPTER ONE

Colonization response of wood nettle *(Laportea canadensis)* to post-settlement land-use

Introduction

Broad-scale changes in natural ecosystems have been documented since the arrival of European settlers. Little is known, however, about the response of many plant species to human activity (Foster 1992). These uses of land can affect local plant populations by directly reducing the number of individuals, eliminating an entire population, or changing reproductive output (Bierzychudek 1982). Herbaceous species, in particular, are sensitive to environmental changes and often increase or decrease in abundance after a disruption of their habitat (Bratton 1994). This study examines the role of post-settlement land-use history in the distribution of an understory plant, wood nettle, in southeastern Minnesota.

Wood nettle *(Laportea canadensis* (L.) Wedd.) is a shade-tolerant herbaceous perennial that is common in mesic upland and floodplain forests in northeast North America. Natural community classification efforts and characterization studies have found the presence and abundance of wood nettle important for determining types of upland maple-basswood forests in Minnesota and Wisconsin (D. Wovcha 1999, *personal communication).* It was present in 90% of the maple-basswood forest stands sampled by Rogers (1981), and sugar maple was the only species to rival it in average percent cover. Kotar and Burger (1996) use wood nettle to define a variant of their Sugar Maple-Basswood/Blue Cohosh forest association of Wisconsin.

In some maple-basswood forests, wood nettle can spread throughout the understory, resulting in a dense monolayer that is 0.5 - 1.5 meters above the forest floor. There is a limited understanding of what factors lead to the plant's dominance in upland forest understories. Among the possible contributors are soil drainage (Srutek 1997), phosphorus and nitrogen concentrations, micro-topography (Bratton 1976), herbivore activity (Augustine 1997), and landuse activity. Within floodplain communities, wood nettle dominance is related to the flooding regime and drainage of the site (Curtis 1959, Menges 1983, and Menges and Waller 1983).

There are many reasons to suspect that human use has influenced the pattern of wood nettle colonization in upland maple-basswood forests. First, anecdotal speculation abounds from field ecologists in Minnesota, although the causal relationship is often contradictory. For example, Wovcha *et al.* (1995, p. 52) state that "unpleasant wood nettle often grows luxuriantly in the [maple-basswood] community on forest soils compacted or disrupted by grazing or forest vehicles." Augustine (1997), however, cites past livestock grazing as a possible cause of wood nettle reduction, even elimination, in forest stands. Canopy gaps, created through selective tree harvest or an individual's death, also seem to promote wood nettle growth.(Menges 1983, F.S. Harris 1998 *personal communication,* and Hoehne 1981).

Second, history of land-use has also been implicated in the distribution of other understory forbs (Rogers 1959, Harper 1963, Thomas *et al.* 1999, Motzkin *et al.* 1996). For example, plants with fur-dispersed seeds (burrs, hooks, or stickers), such as sweet cicely and white avens, increase after timber harvest or grazing (Wovcha *et al.* 1995). Terrestrial orchids often colonize patches of soil disrupted by human activity (Pavlovic 1994) and graminoid species increase after grazing (Smith and Cottam 1967).

Third, life history traits are important determinants of a plant's response to disturbance (McIntyre *et al.* 1995, Chambers 1995). Prach and Wade (1992) describe stinging nettle (a native . species in their European study area) as a species with a high "expansive ability." Wood nettle is in the same plant family and shares many of the characteristics they cite as important to expansive ability; both species are perennial, germinate without complicated dormancy mechanisms, can spread vegetatively, and are highly competitive species (Menges 1983). Menges and Waller (1983) conclude that wood nettle's competitive nature and plastic morphology contribute to its prominence on infrequently flooded elevations of floodplain forests in Wisconsin. Wood nettle's competitive traits, particularly its ability to reproduce both vegetatively and sexually, may contribute to its understory dominance in upland maple-basswood forests. Upon canopy closure, competitive plants, like wood nettle, are able to maintain stable populations through exclusion (Hughes and Fahey 1991).

This study employs historical documentation and current conditions to investigate the hypothesis that past human activity creates differences in wood nettle density among land-use parcels. In particular, I examine the role of timber harvest and livestock grazing as a filter or a promoter of wood nettle populations. I use random vegetation sampling to measure wood nettle density and use forest structure and composition to examine the effects of harvest intensity. Finally, I use wood nettle's response to time, soil horizonation, light, and its life history characteristics, to support the results of the vegetation surveys.

The maple-basswood forest of southeastern Minnesota is a highly fragmented community with. few, if any, undisturbed remnants. The Minnesota County Biological Survey estimates less than one percent of the pre-settlement maple-basswood forests remain in the Big Woods Ecosystem (Harris and Wovcha 1995). The remaining fragments have been altered by human activity, including livestock grazing, selective logging, and clear-cutting. Rapid development around the metropolitan area, and increasing public pressure for access to sensitive natural areas, threaten these remaining fragments. By studying the current distribution patterns of herbaceous species, like wood nettle, we can gain insight into the long-term response of ecological processes to land use (Risser 1987). This is of immediate conservation and management importance because understory plants are important ecologically as many birds, insects, and vertebrates rely on their biomass for food resources. The forest understory also is an important part of nutrient cycling; they store less nutrient capital, but the annual turnover in biomass is important (MacLean and Wein 1977). Finally, we need to understand community dynamics as the number and quality of natural communities continues to diminish.

Methods

Study Area

The Minnesota Department of Natural Resources defines a maple-basswood forest as one dominated by sugar maple and basswood trees with sprouted slippery elm, northern red oak, bur oak, and ash (Aaseng et al. 1993). Since fire and catastrophic blow-downs are rare in southeastern Minnesota, canopy gaps created by an individual tree's death are the principal regeneration niche in undisturbed stands. Other notable characteristics of maple-basswood forests include the presence of multi-aged sugar maple populations and spring ephemerals, a class of plants of that emerge, reproduce and sense before canopy closure (Minnesota Natural Heritage Program 1994). Since European settlement, disease and timber harvest preferences have reduced selected species, particularly American elm, butternut, and oaks.

Maple-basswood forests in central and southeastern Minnesota are often referred to as the Big Woods (Daubenmire 1936). At the time of settlement, Marshner (1974) estimates that the Big Woods covered approximately 16,900 km 2 (Grimm 1984). The Minnesota County Biological Survey estimated in 1995 that less than one percent of the pre-settlement maple-basswood forests remain in the Big Woods region of Minnesota (Harris and Wovcha 1995). Conversion to agriculture and urban uses is the primary reason for the loss.

To limit environmental variation, I restricted my study to upland forests in Nerstrand Big Woods State Park (NBWSP) in eastern Rice County, Minnesota (44° 20' N, 93° 06' W). With approximately 425 ha of forest cover, NBWSP contains one of the largest contiguous fragments of maple-basswood forest remaining in southeastern Minnesota. Before the park's founding in 1945, this area was a group of 147 ownership parcels, each with a different history of use (Mason 1994). Wood nettle density varies throughout the park, and the divergent land-use by individual owners provides an opportunity to test for differences among the parcels. Restricting my study to this area also helps controls for variation in historical documentation, current ownership and management, and geography, including the population density of white-tailed deer (a wood nettle herbivore), soil parent material and development, long-term climate, and short-term weather. Selection of this site does not address variation related to topography, such as soil horizonation, nutrient concentration, and drainage.

The Public Land Survey surveyed Rice County Minnesota in 1854, and settlement by Europeans quickly followed (Mason 1994). At the time of the public land survey, the area now occupied by NBWSP was a peninsula of maple-basswood forest that jutted into the surrounding prairie (Marshner 1974). As more European settlers arrived, the residents of the nearby city of Nerstrand divided the two forested sections (sec. 9 and 16) of Wheeling township (T 110N R19W) into parcels and distributed them among residents for resource use (Mason 1994): Figure 1.1 summarizes the parcel boundaries and their primary land-use.

NBWSP experiences a continental climate. In summer, the mean high temperature is 27 C and the mean low temperature is 20 C and during the winter months the average high , temperature. is -4 C and the mean low is -10 C (Midwest Climate Center 1999). The average yearly precipitation is 78.7 cm (Midwest Climate Center 1999). In 1998, several large storms passed through the park, resulting in the loss of many canopy-sized trees. Storms on May 17 and July 20 had the most severe winds, but the most significant event of 1998 occurred on the evening of June 26, when over 12 cm of rain fell: This event caused significant flooding and erosion in;. many parts of the park and the ground layer of vegetation was damaged by sheet erosion on the steeper slopes.

Maple-basswood forests. generally occur on fine textured soils, such as loam and silt-. loam, (Harper 1963), but they may develop on coarser soils if a water-confining layer underlies it. The area now occupied by NBWSP has been glaciated several times, but it was not glaciated during the last two events (Wisconsinan and Illinoian), and elements of the older erosional landscape are present in the park (MNDNR 1998). The topography of the park is varied as a result of the old erosional landscape, channels from glacial melt water, and continued development of rivulets leading to Prairie Creek. Most of the park is underlain with sedimentary bedrock and covered with a layer of loess, wind-blown silt from the peri-glacial region (MNDNR 1998).

The upland soils of NBWSP are transitional between broadleaf forests and prairie types, because of vegetation fluctuation along the prairie-forest border. Soils series in the park include Renova (a Typic Hapludalf), Vlasaty (a Glossaquic Hapludalf), Maxfield (a typic Haplaquoll), Kasson (an Aquollic Hapludalf), and Skyberg (an Udollic Epiaquaf) (United States 1975). These soils are loamy and well drained to poorly drained depending on the topography, which is steeply sloping to flat (Mason 1994).

Wood nettle genets have an unknown life span (Menges 1983) and response to disturbance events may be a protracted process. Short-term (2 years) observation can not fully establish the relationship between disturbance type and colonization patterns of wood nettle. A long-term experiment and monitoring project, while ideal for this type of study, was not possible for the timeframe of this project.

Survey methods

To determine if history is a factor in wood nettle colonization, this study uses three variables drawn from written parcel histories summarized by Mason (1994): type of land-use, timber sales, and time since the documented last land-use event. Although each parcel differs in the intensity and timing of use, five broad types of land-use emerge: selective tree harvest (called selective harvest here), complete harvest with no grazing (clear-cut), complete harvest followed by sheep grazing (sheep), complete harvest followed by cattle grazing (cattle), and cultivation (cultivation). The sale of timber to a commercial logging operation may have resulted in different disturbance intensity, which may lead to different wood nettle densities. Finally, if available, Mason (1994) records the period of the land-use event. In some cases, however, I estimated the time since the last documented land-use event using other written histories, such as the year of turnover to the state.

This study employs two different vegetation surveys: qualitative assessment and quantitative sampling. I conducted the qualitative assessment in 99 of the 147 original ownership parcels. The remaining 48 are not included because they are not forested, are intensively used for park facilities, or have extreme slopes. I randomly chose 33 of the 99 forested parcels for the quantitative sampling.

A professional survey crew marked the corners of each ownership parcel in the summer of 1997. In both vegetation surveys, I used a compass, map, and landmarks, such as trails, fences, and posts, to insure I remained in the proper parcel.

Qualitative vegetation survey

Qualitative assessment of wood nettle coverage occurred in August and early September 1997. I walked through each parcel several times and estimated the percent cover of wood nettle in each. I did not know the land-use history of the parcels while conducting this survey. A modified cover code for individual species was used to estimate the coverage of wood nettle (Muller-Dombois and Ellenberg 1974). I recorded six categories of coverage: 0%, 1-4%, 5-24%, 25-49%, 50-74%, and 75-100%. Only parcels that were assessed as completely devoid of wood nettles (after an extensive search) received 0% coverage. See Figure 1.2 for the distribution of wood nettle in the qualitatively surveyed parcels.

Quantitative vegetation survey

I selected the 33 parcels for quantitative random sampling by examining aerial photographs of the park (1938, 1940, 1958, 1964, and 1970) and satellite imagery from 1991. I grouped parcels with similar canopy densities and randomly chose three parcels from each of the twelve groups. A few groups contained only two parcels and, in these cases, I sampled both. See Figure 1.3 for locations of the sampled parcels and Appendix B for a brief summary of their history.

I randomly sampled the plant populations in the selected parcels between July 10 and August 15, 1998. 1 generated thirty sets of coordinate numbers .and determined qua drat location in the field using meter tapes and a compass. The origin of each coordinate system is at one of the professionally surveyed property corners. I eliminated quadrats from the survey if they occurred on a hiking trail or in the middle of a severe tree blow-down, resulting in 24 to 30 1-m2 quadrats surveyed for each parcel. In the 33 sampled parcels, I sampled 961 quadrats.

Within each quadrat, I measured the height in centimeters, and the reproductive status of each individual wood nettle stem. I also counted the number. of wood nettle germinants.

I identified and measured trees within a 127-cm radius of the quadrat center (5 m2). I counted and recorded the height of saplings shorter than 2 m and the diameter at breast height (dbh) for trees over 2 m tall. I used basal area (m2 ha) and tree density (trees ha) to describe the structure of each surveyed parcel,: I calculated these values for each species in a particular stratum and for the entire forest. I used the following strata categories: sapling (stems > 2 m tall, but < 10 cm dbh), sub-canopy (stems 10 - 25 cm dbh), and canopy (stems > 25 cm dbh) (Hutchinson and Vankat 1997). 1 also calculated basal area and tree density for all stems greater than 2 m for a summary description of the entire parcel. The data for saplings less than 2 m tall are reported in Chapter 3.

Light

Hemispherical photographs were taken at six randon-fly selected points in each parcel between June 27 and July 21, 1999. To limit variation among photographs, I worked between and 9:30 a.m. and 3:00 p.m. and on days with uniformly overcast skies and little wind. I used a Nikkormat camera with a Nikkor fisheye lens mounted on a tripod 1.1 meters from the forest floor. The camera top was oriented to north and the lens leveled before each shot. I used a red filter, maximum apenture, a shutter speed of 1/125 s, and Kodak TriX black and white 400 ASA film (Rich 1989, Becker *et al.* 1989, and Canham *et* al. 1994). Photos Inc., Minneapolis developed the film and scanned the negatives onto a Kodak PhotoCD. I analyzed digitized images with Solarcalc 6.0 (Macintosh), which calculated diffuse light (weighted percent canopy openness) and direct light [total daily photosynthetic photon flux density (PPFD) (mol m^{-2} day^{-2})] (Chazdon and Field 1987). The generated results are averaged for the entire parcel (Appendix C).

Soil

Soil descriptions to one meter or impermeable layer were taken with a 2.5-cm diameter probe at subjective locations within the 33 selected parcels. Selection of the probing location attempted to capture the average topographic condition of the parcel. If there was an abrupt change in topography, multiple points were probed. Description of the soil horizonation was recorded for each probe point. The distinction between the A horizon and E horizon was obscure, possibly because of earthworm activity, and depth to the B horizon is the only variable that could be clearly defined from the resulting descriptions.

Statistical analysis

I tested for data normalcy using a probability plot. The counts of wood nettle and its co-occurring species are integers, bounded by zero, with a large number of zero values. The data best fit a negative binomial distribution. This distribution and is similar to the Poisson distribution but has more dispersion around the value lambda (Long 1997). Analyses used negative binomial regressions and were done with the statistical package Stata 6.0, StataCorp1999).

Parcel means, wood nettle height, and proportion data are all relatively normal and can therefore be analyzed with ANOVA and normal simple linear regressions. I used SYSTAT (SPSS 1997) for ANOVA analyses and to generate summary statistics and cross-tabs.

I used Stata 6.0 for all normal regression analyses because this statistical package allows robust corrections for heteroscedasticity (StataCorp 1999). This correction could not be employed when the independent variable is categorical, such as land-use type. I used this program's cluster correction for analysis of time since the last land-use event for the quadrat data, to minimize the partially artificial variation among the parcels.

In reporting the results of the regression analyses, b corresponds to the slope of the line of best fit and S_b corresponds to the standard error of the slope. Unless otherwise reported, the results reported as significant have a P value less than 0.05.

Results

Qualitative survey

Table 1.1 provides the frequency of parcels with class of wood nettle coverage by landuse types. Note that selectively harvested parcels contain a wide range of wood nettle coverage, but all 29 parcels with coverage greater than 50% have a history of selective harvest. The only land-use type devoid of wood nettle is the single parcel with a cultivation history. It is not evaluated further.

Timber harvest by commercial logging did not influence the present coverage of wood, nettle. Parcel improvement through private management for red oak and basswood may have . increased wood nettle abundance (see canopy tree composition below), but gross categorization of harvest type does not reveal any significant patterns.

Quantitative vegetation surveys

When averaged to the parcel and compared by ANOVA, the mean number of wood nettle stems M72 does not vary significantly among the different landuse types. The number of parcel observations is smaller (33) than the number of quadrats (961) and the variance is higher so the differences are not significant.

	Selective harvest		**Clear-cut**		**Sheep**		**Cattle**
Mean wood nettle m^{-2}	7.46	=	3.6	=	3.34	=	0.58
Standard deviation	7.14				3		
Number of parcels	28		1		3		1

Wood nettle frequency (quadrats with wood nettle/total quadrats) also did not vary significantly with land-use type.

	Selective harvest		Clear-cut		Sheep		Cattle
Mean frequency	0.53	=	0.37	=	0.35	=	0.17
Standard deviation	0.35				0.19		
Number of parcels	28		1		3		1

If each individual 1-m2 quadrat is treated as a sample of past land-use, land-use is a significant factor in determining the density of wood nettle stems using dummy-variable negative binomial regressions where each land-use category is compared using dummy-variables.

The quadrats within areas of selective harvest contain significantly more wood nettle stems than those with clear-cut, sheep, or cattle histories. Quadrats within clear-cut areas are not different in number of wood nettle stems from those grazed by sheep, but are significantly greater than those grazed by cattle. Finally, clear-cut quadrats with a history of sheep grazing have more wood nettle stems than those with cattle grazing history.

	Selective harvest		Clear-cut		Sheep		Cattle
Wood nettle per quadrat	7.71	>	3.6	=	3.26	>	0.59
Standard deviation	10.84		8.45		6.74		2.08
Number of parcels	817		30		85		29

Time since the last documented land-use event

The mean number of wood nettle of 2 in each parcel is not related, by simple linear regression to the number of years since the last documented landuse event (b = 0.12; $Sb = 0.07$). Wood nettle frequency also increases with a greater time ($b = 0.008$; $Sb = 0.004$). If each individual quadrat represents a sample of past land-use, the number of wood nettle in each quadrat increases marginally with time since the last land-use event based on a simple negative binomial regression (b = 0.02; Sh = 0.01; $P < 0.10$).

Forest structure

Table 1.2 reports the relationship between tree strata and wood nettle density. In general, the density of wood nettle declines as the density and basal area of sub-canopy and sapling trees increase (Figures 1.4 through 1.6). The single parcel that was clear-cut and grazed by cattle has a very large density and basal area of sub-canopy trees (see discussion) and is an outlier. If this parcel is omitted from analysis, the mean number of wood nettle M-2 is still negatively related to sub-canopy density *(b = -0.01; Sb = 0*.004) and basal area (b = -0.47; Sn = 0.20).

Wood nettle frequency demonstrates a similar, but is only marginally significant, response to sub-canopy density and basal area (Table 1.3). This relationship, however, disappears when one removes the parcel with cattle grazing. Wood nettle frequency also decreases with increasing sapling basal area (Figure 1.7).

The tree species of each forest stratum does not influence the density-and frequency of wood nettle, with the exception of those strata containing red oak, basswood, ironwood, and green ash. I used simple linear regression on the four most common canopy, the two most common sub-canopy species, and the 5 most common sapling species. The mean number of wood nettles M-2 is negatively related to sapling-sized ironwood trees ha' *(b = -0*.009; *Sb = 0.003)* and positively correlated with sapling-sized green ash trees ha' *(b = 0.006; S6 = 0*.002) in simple linear regression. The mean wood nettle stems M-2 *(b = 0.18; Sb = 0.06)* and wood nettle frequency *(b = 0.01; Sb = 0*.003) increase with increasing basal area of canopy-sized red oaks. Wood nettle frequency increases with increasing basal area *(b* = 0.005; *Sb = 0*.002), and density *(b. = 0.001; Sb = 0*.0005) of canopy-sized basswood.

Light

The measured canopy light parameters are not correlated with wood nettle density and frequency. The basal area of forest strata, however, does significantly influence the availability of diffuse light to the understory (Table 1.4). Direct light (total daily photosynthetic photon flux density) cannot be attributed in these data to variation in forest structure. Direct light, however, decreases with time since the last documented land-use event *(b = -0*.29; *Sb = 0*.12), in a simple linear. regression.

Soil

An increase in the distance to the clay layer is accompanied in a simple linear regression, by an increase in the mean number of wood nettle *rri* 2 *(b* = 0.31; *Sb = 0*.13) and wood nettle frequency *(b = 0.01; Sb = 0.005).*

Discussion

This study offers compelling evidence that post-settlement land-use activities contribute to variation in wood nettle populations. Qualitative estimates offer evidence of persistence through an event and suggest that selective timber harvest may be the use most likely to result in a wood nettle dominated understory. While the quantitative vegetation survey results are somewhat ambiguous, forest structure suggests harvest intensity is essential to understanding the role of land-use in wood nettle colonization. Life history characteristics of wood nettle and its response to forest composition and old growth conditions support the results from the vegetation i surveys and structure analysis.

Environmental conditions not related to anthropogenic use, however, also influence wood nettle abundance and distribution. Figure 1.2 illustrates the general distribution of wood nettle in the areas qualitatively surveyed in 1997. One concern with an observational study, such as this one, is a failure to account for conditions before treatment. In this case, there are no known records of understory vegetation before the land-use activities occurred. Therefore, the absence of wood nettle in a parcel today may be the result of initial conditions or the land-use activity.

Persistence

Each disturbance event can act as a filter, removing species from the recovery pool (either standing biomass and/or from the seed bank). Once removed, seed dispersal or vegetative growth are the only means of recolonization. Unfortunately, this process may take a long time, as many understory forbs lack long-distance dispersal mechanisms and clonal spread is slow. If a propagule arrives at the stand, population establishment may be difficult because the time until first reproduction in some understory forbs is long (Bierzychudek 1982). Persistence through an event, therefore, is the principal determination of species presence after a disturbance event (Hughes and Fahey 1991, Jonsson and Esseen 1998).

Wood nettle in upland maple-basswood forests primarily relies on persistence to be present in a parcel after land-use. Its seeds lack a long-distance dispersal mechanism; seeds fall off the female flower structure, possibly in response to frost *(personal observation).* Furthermore, wood nettle seeds are relatively small and are unlikely to maintain a seed bank. The seeds do have the ability to float, but this is unlikely to contribute to long-distance dispersal in upland forests (Menges 1997, *personal communication).* Vegetative growth is its primary mode of wood nettle reproduction (Menges 1983), but even in continuous forest this method of species movement is slow (Matlack 1994).

Although several parcels lack wood nettle, only one type of land-use observed at NBWSP appears to filter out wood nettle. The act of cultivation disrupts the soil surface, destroys rootstocks, and disrupts seed banks. Only one formerly cultivated parcel is currently forested, however, and this is not sufficient for conclusive results.

The role of livestock grazing as a filter for wood nettle presence is a subject of much speculation. Wovcha *et al.* (1995) suggests grazing increases wood nettle populations and Augustine (1997) believes that grazing causes population decline. Qualitative results suggest livestock grazing neither eliminates wood nettle nor does it lead to wood nettle domination. Less than 25% of the currently forested parcels with a grazing history lack wood nettle and no grazed parcel has greater than 49% coverage.

Wood nettle resilience to livestock grazing is probably due to two factors: urticating hairs and reproductive flexibility. Although Augustine (1.997) demonstrates that white-tailed deer find wood nettle palatable, the unpleasant urticating hairs increase in density after a browse event and deter future consumption by vertebrates (Tuberville *et al.* 1996, Pollard and Briggs 1984). Species that are unpleasant to eat or poisonous often increase in abundance with livestock grazing. For example, European stinging nettle populations increase in abundance under heavy grazing pressure (Pullin and Gilbert 1989).

Reproductive flexibility, the facultative ability to produce seeds and the ability for vegetative growth is a reproductive strategy that is more likely to survive livestock grazing (Pettit *et al.* 1995). Wood nettle demonstrates reproductive flexibility by allocating reproductive energies in response to environmental conditions. Stems can produce male flowers, female flowers, vegetative growth, or a combination of these strategies (Menges 1990).

Gilliam *et al.* (1995) provides direct evidence of this plant's ability to respond to experimental clear-cuts. Marks (1942) also finds that wood nettle is among the plant species that remain in the understory after timber harvest. Timber harvesting, complete or selective, is not a filter to wood nettle presence in the forest understory. This study provides indirect evidence of wood nettle survival (assuming slow colonization): only four percent of the harvested parcels with no history of grazing do not have wood nettle.

Wood nettle and land-use type

The vegetation surveys fail to clearly distinguish differences among wood nettle population patterns within different land-use types. Results of the qualitative surveys suggest that selectively harvested parcels in some way encourage wood nettle growth; it is the only type of land-use to have coverage greater than 50% (Table 1.1). The extreme variation (0 to 100%) of wood nettle coverage, however, fails to demonstrate a clear directional response to selective harvest. This survey may also be biased because selectively harvested parcels are overrepresented in NBWSP.

If one uses the 1-m2 quadrats as representatives of land-use types, significant differences among wood nettle populations emerge. In this analysis, selectively harvested quadrats have more wood nettle stems than quadrats with a clear-cut history or a history of sheep grazing (no statistical difference between these). Quadrats with a history of cattle grazing have the lowest number of wood nettle.

These relationships, however, are ambiguous when one analyzes averages at the parcel level. The amount of variation inherent in summarizing wood nettle density for the entire parcel may overwhelm any variation due to the use and contribute to the difference between the results of these two levels of analysis.

This analysis also fails to distinguish variation from the intensity of the land-use, such as stocking rate. Selective harvest, in particular, is an ambiguous term that can apply to the removal of a few trees to a near-complete harvest. The current structure of the forest is a legacy of parcel history and the continuum of tree density and basal area is a record of harvest intensity and forest recovery.

Forest structure

Wood nettle is related to the density and basal area of the sub-canopy layer (trees 10 - 25 cm dbh) (Tables 1.2 and 1.3). As the density of this layer increases, the mean wood nettle m^{-2} and wood nettle frequency decrease. This relationship is related to post-settlement land-use activities in NBWSP; the types of land-use considered in this sample ceased at NBWSP between 12 to 63 (median 56) years prior to this survey when the current sub-canopy stratum was present as tree saplings.

Forest stands that undergo heavy selective or complete harvest typically experience dense tree re-growth once the logging activity has stopped (Harper 1963, Phillips and Shure 1990, Reader and Bricker 1992). Forest stands with grazing histories experience a similar response as livestock preferentially consume herbaceous species. Woody species are then released upon cessation of grazing activity (Belsky and Blumenthal 1997) and competition with woody regrowth limits the increase in forb frequency or prevents recolonization of some understory forbs (Meier et al. 1995, Reader and Bricker 1992). The present negative relationship between wood nettle and the current sapling layer (stems taller than 2 m, but less than 10 cm dbh) suggests continued competition between these forest components (Figures 1.6 and 1.7).

Stands with dense woody re-growth lack gap-phase succession, but mild selective harvest accelerates gap-phase succession by increasing the number of light gaps in the canopy (Meier *et al.* 1995, Thomas *et al.* 1999). Several studies have documented an increase in herbaceous plant diversity and reproduction in these gaps (e.g. Valverde and Silvertown 1998, Schmidt *et al.* 1996). Wood nettle appears to follow this pattern; Rogers (1959) found that wood nettle increased in stands with light harvest, but decreased again with heavier harvesting. Thompson (1979) documents the colonization of wood nettle along the edges of natural tree-fall pits.

Not all studies of forest gap creation and herbaceous growth agree with these findings. . For example, Jenkins and Parker's (1999) study of canopy openings and herbaceous species diversity failed to find shifts in species composition due to gap creation, particularly single tree openings. Whigham *et al.* (1993) concludes that canopy gaps are of little consequence in the long-term population dynamics of understory forbs. The relationship between canopy gaps and plant species is complex and depends on the characteristics of the species involved, age of gap, and other environmental conditions (Moore and Vankat 1986).

Canopy composition

The response of wood nettle to canopy composition also supports the conclusion that mild selective harvest promotes wood nettle growth. Wood nettle increases as the basal area of red oak and basswood increase. Red oak and basswood were commercially valuable species in the early twentieth century and were preferentially harvested from forests (Mason *1994).* Parcels that retained large individuals of these species likely experienced mild selective harvest as private owners thinned their forest to promote their growth for future harvest (Cushing *1999, personal communication).*

Intensive harvest could also lead to a greater quantity of basswood and red oak because both of these species re-sprout from the base. If this were the case, however, tree density, rather than basal area, would drive the relationship with wood nettle.

Canopy-sized red oaks also provide more light to the forest understory relative to other canopy species. They are among the last species to leaf-out in the spring, thus providing more light to wood nettle as it emerges in early summer. Furthermore, red oaks also have sparse crown architecture and allow for greater light transmission (particularly in the form of sunflecks) through its canopy (Canham *et* al. 1994). This is important for these parcels, where much of the light (21-72%) available at the forest floor are in the form of sunflecks *(unpublished data).* In contrast, sugar maple has a much thicker crown and prevents light from reaching the understory (Canham *et al.* 1994).

Old Growth

Mild selective harvest is similar to accelerated gap-phase succession, a process that defines old growth forests (Meier *et al.* 1995, Thomas *et al.* 1999). Large wood nettle populations are also found in maple-basswood forests that have experienced relatively little human activity since European settlement (Wovcha *et al.* 1995). Typically, old growth forests experience gap creation at a rate of 1 % area per year (Runkle 1982), but this can increase during a disease outbreak (Frelich and Reich *1995).* American elm was an important component of the maple-basswood until a Dutch elm disease *(Ceratocystds ulmi)* outbreak in the mid-twentieth century killed many adult trees (Grimm 1984) and wood nettle, like other herbaceous species, may have taken advantage of the resulting canopy gaps (Hughes and Cass 1997).

Light

If wood nettle responds to canopy gaps, one would expect understory light availability to be an important factor. Unfortunately, tests for differences between wood nettle and light, as evaluated by hemispherical photographs, failed to detect a relationship. This test, however, may not have been sensitive enough to detect a relationship. In this case, I averaged both the light data and the number of wood nettle m^{-2} to summarize parcel conditions, and I believe the variation within a parcel overwhelmed any possible relationships.

Other studies (Nicotra *et al.* 1999, Thomas *et al.* 1999) have found that averaged light conditions, as measured by hemispherical photographs, failed detect real differences in canopy conditions. Hemispherical photographs, therefore, are useful for comparison of point data, but not for comparing means of light availability.

This study did find relationships between canopy strata and the light environment. In general, as the density and abundance of the forest strata increased, the amount of diffuse and direct light detected decreased. Tree density is a relatively poor measure of the diffuse light available (there was no relationship between direct light and tree density). In contrast, there is a relatively strong relationship between the basal area of canopy strata and both diffuse and direct light (Table 1.4). Unfortunately, the mean number wood nettle stems m^{-2} and wood nettle frequency have few relationships with basal area, and therefore, one cannot infer an indirect relationship between wood nettle colonization and the current light environment.

Life history characteristics

The analysis of forest structure and composition suggest that mild selective harvest increases wood nettle abundance in the understory. The life history traits and growth form of wood nettle further support this hypothesis.

The life history characteristics are a critical part of understanding how a particular species responds to a disturbance event (Moloney and Levin 1996). Wood nettle is a competitive plant that has reproductive flexibility (Menges 1983). These qualities confer a superior ability to respond to canopy gaps created by mild selective harvest. It is also a light generalist species; that is, it does not specialize in either high light or low light environments (Menges and Waller 1983). Light generalist forbs are predicted to increase water intake, seedling establishment, sexual and vegetative reproduction, seed set, and survivorship in response to conditions created by an ideal canopy gap (Collins *et* al. 1985, p.233).

Wood nettle, like other species that ,reproduce sexually and asexually, can also respond quickly to the resources available after a disturbance event, increase in density, and exclude other species (Connell and Slatyer 1977, Callaghan *et al.* 1992). Vegetative growth, in particular, appears to benefit understory forbs after disturbance (Thomas *et al.* 1999, Whigham *et al.* 1993). For example, *Carex bigelowii* is opportunistic in ramet production and shifts resources among ramets to respond rapidly to newly available resources and increase in density (Callaghan 1976),..

Furthermore, understory plants categorized as competitive gain frequency in recently disturbed forests (Hughes and Fahey 1991). Competitive plants shift resource allocation to grow taller in high light situations and can out-compete co-occurring species. Wood nettle is such a plant; it responds to inter- and intra-specific competition by increasing in height .(Chapter 2, Menges 1983) and height also increases in canopy gaps (Menges 1987).

Wood nettle survival and forest recovery

The response of the herbaceous understory to an event can still be detected well after the canopy structure has recovered from logging (Thomas *et* al. 1999, Ehrenfeld and Schneider 1990). For example, Valverde and Silvertown (1997) found that the longevity of perennial stems was more important for the gap response of *Prirnula vulgaris.* The capacity for wood nettle to maintain or increase its population size during forest recovery is an important part of its response to timber harvest or grazing.

The number of wood nettles per quadrat increases weakly with time since the last documented land-use event. Direct and diffuse light also decreases with time since the last event, and one can infer that wood nettle maintains its populations as the parcel gets darker. Wood nettle frequency is also weakly correlated with the time since the last documented land-use event, which is expected because clonal plants become less patchy as the age of a forest stand increases (Whitford 1949, Meier *et al.* 1995).

The survival of established individual and genotypes, rather than sexual reproduction, is often more important to population growth (Damman and Cain 1998). Wood nettle life-history characteristics, particularly its ability for vegetative reproduction, allow it to survive in closed canopy situations. For example, vegetatively reproducing species can maintain dominance through competitive exclusion (Sebens and Thorne 1985, Connell and Slatyer 1977). Wood nettle appears to exclude other species through competition or occupation of space. In NBWSP, the number of co-occurring summer species decrease with wood nettle density (Chapter 3).

The architecture of wood nettle may also assist its survival in a closed forest. In a model of plant structure and adaptation, Givnish (1982) finds dimly lit forest understories favor plants with a single layer of leaves. Wood nettle has this type of structure; all of its leaves are in a whorl at the apex of the plant, which may explain its ability to persist in low light environments. Sakai's (1994) model of leaf phenology and photosynthesis predicts that late emerging forbs, like wood nettle, have a low photosynthetic capacity, which allow for efficient light use in shady conditions.

The ability for wood nettle to expand in closed canopy conditions may be particularly relevant in maple-basswood forests. This community is thought to be stable in space and time (Curtis 1959) because these forests have few widescale disturbance events, such as catastrophic blow-downs or fire. The lack of a large-scale disturbance event prevents recolonization of other species and may allow wood nettle to continue vegetative expansion unchecked.

Other environmental conditions

In addition to conditions related to past land-use, edaphic conditions act on plant populations and can influence their density and frequency in the forest understory (Motzkin *et al.* 1996). For example, wood nettle density and frequency is positively correlated with the depth to the clay layer (thickness of the A/E horizon[1]).

Although both species are found in moist environs, wood nettle and stinging nettle are not well adapted to anoxic conditions created by saturated soils (Menges 1983).

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[1] Many factors, including land use, contribute to the development of the soil. In NBWSP, topographic variation is considerable and is important for soil development. This study is not designed to consider the complicated relationship between wood nettle and soil. This example is simply illustrative of the myriad of other factors that are important for plant populations.

Furthermore, stinging nettle plants are most productive in areas with a deeper water table (Srutek 1997). In the sampled parcels, the distance to the clay layer ranged from 12 to.51 cm. Perhaps the parcels with the shorter distance to the water impounding (clay) layer have, at least temporarily, anoxic conditions (after a heavy rain or snowmelt) that reduce the survival or reproductive capacities of wood nettle. Additional research is needed to understand the relationship between wood nettle and soil drainage and topography.

Biological systems are complex entities and many other environmental factors contribute to the distribution of wood nettle. In addition to forest structure, wood nettle and other members of the family Urticaceae are known to respond to: soil organic matter, nitrogen, and phosphorus availability, flooding frequency, micro-topography, and floodplain elevation (Menges 1983, Bratton 1976, Hardin and Wistendahl 1983, Rorison 1968).

Variation in edaphic conditions, use intensity and frequency, stocking rate, harvest method, month of harvest, disease outbreaks, and weather events, such as severe storms or flooding, can influence the recovery trajectory from land-use and complicate results. Observational studies, like this one, cannot control for all of these factors and correlations are often weak. Nevertheless, this study reveals much about the relationship between land-use, wood nettle, and upland maple-basswood forests.

Conclusion

The legacy of human activity is not always recognized in ecological studies, although it can have profound effects on the plant community and populations. The results of this study demonstrate the importance of land-use history as a variable in the distribution and abundance of wood nettle, a common plant in upland maple-basswood forests.

Persistence is the first hurdle to presence in a forest stand after a land-use event. This study provides evidence that wood nettle persists through selective and complete timber harvest. Urticating hairs and reproductive flexibility assist wood nettle survival through livestock grazing.

The differences in wood nettle density and frequency among the sampled land-uses are somewhat ambiguous, but selective harvest generally allows for larger populations. The relationship between harvest intensity, as measured by sub-canopy density, and wood nettle colonization is clear. In this study, the sub-canopy layer represents the woody regeneration event that occurred after logging and grazing activity ceased. Dense woody re-growth typically follows heavy selective harvest, clear-cut, and livestock grazing events and this forest stratum appears to out-compete wood nettle. Mild selective harvest appears to increase wood nettle density and frequency through accelerated gap-phase succession.

Other results support the relationship between wood nettle and mild selective harvest. Several old growth forest stands also have high wood nettle density. They may have experienced accelerated gap-phase succession that results from an epidemic of Dutch elm's disease or another type of overstory disruption. The relationship between wood nettle and the basal area of canopy basswood and red oak trees also support this result. Basswood and red oak were commercially valuable species and mild selective harvest was a management tool to encourage their growth.

Wood nettle life history characteristics also support wood nettle's relationship to mild selective harvest. They are similar to other (idealized and actual) species that increase after gap creation and greater light availability. It is a light generalist and competitive plant that exhibits reproductive flexibility, including vegetative reproduction. These characteristics also allow wood nettle to maintain population size or continue to proliferate after conditions deteriorate. The positive relationship between wood nettle and time since the last documented land-use event underscores this ability.

Variation from environmental conditions can obscure relationships between a particular species and the land-use activity event. For example, the thickness of the A/E soil horizon is important to wood nettle growth.

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Figure 1.1 The land-use of the parcels at Nerstrand Big Woods State Park prior to the park's founding as documented by Mason (1994).

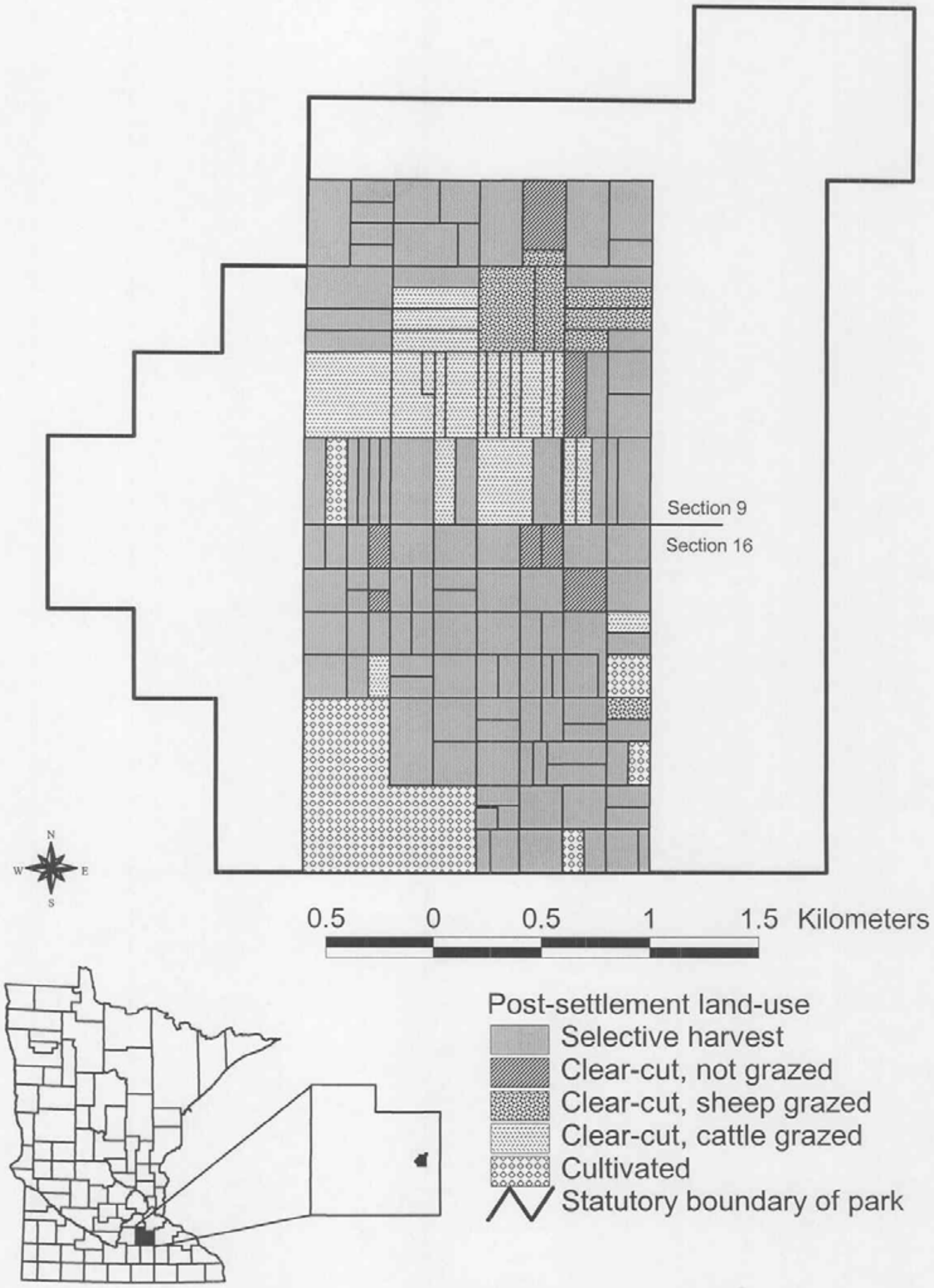
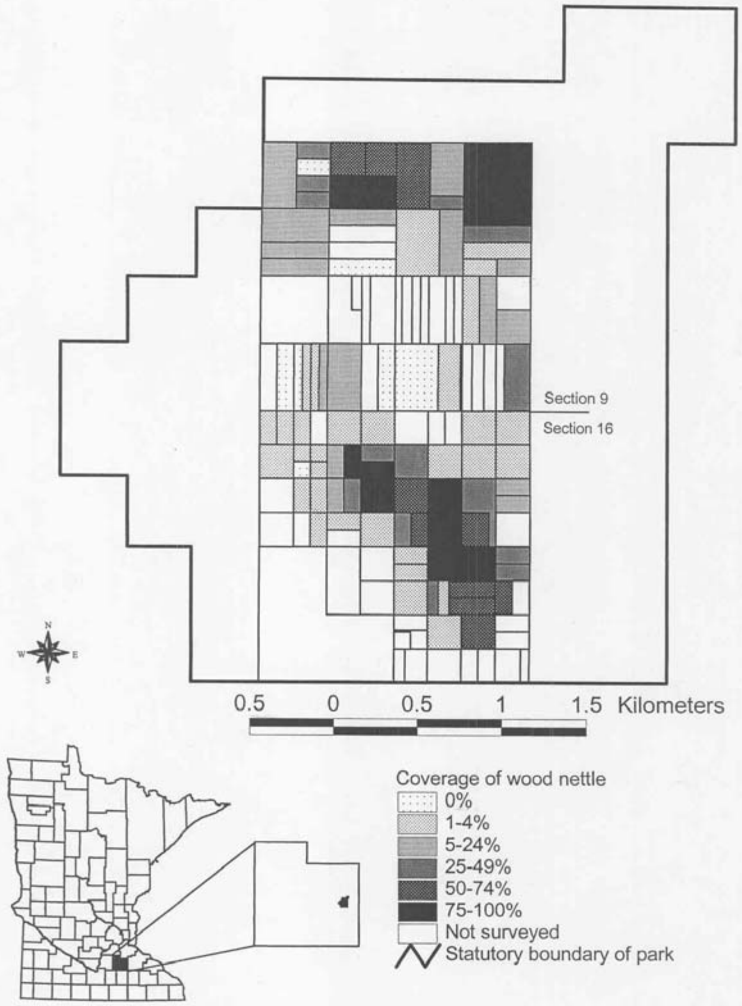


Figure 1.2 Wood nettle distribution in land-use parcels in Nerstrand Big Woods State Park drawn from data collected during qualitative survey in the summer of 1997.



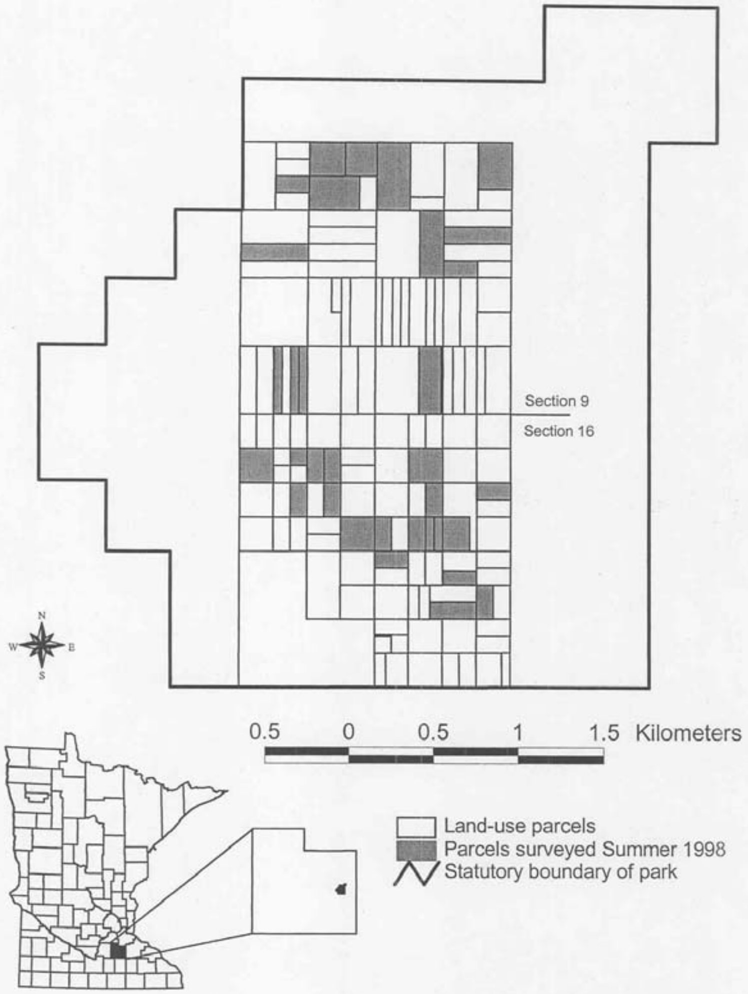


Figure 1.3 Land-use parcels of Nerstrand Big Woods State Park selected for quantitative survey in the summer of 1998.

Table 1. 1. Frequency of parcels with class of wood nettle coverage grouped by land-use type. Percent wood nettle coverage estimated by qualitative assessment of each parcel in the summer of 1997.

	Percent coverage						
	0%	**1-4 %**	**5-24 %**	**25-49 %**	**50-74 %**	**75-100 %**	**Total**
Selective timber harvest	3	25	15	9	11	18	81
Clear-cut, but not grazed	0	3	1	0	0	0	4
Clear-cut and sheep grazed	1	2	2	4	0	0	9
Clear-cut and cattle grazed	2	1	1	0	0	0	4
Cultivated	1	0	0	0	0	0	1
	7	31	19	13	11	18	99

Table 1.2. The relationship of wood nettle density (mean # stems rri 2) with increasing tree density (trees ha) and basal area (m2 ha) of forest strata using a simple negative binomial regression.

	# **Parcels**	**Density**		**Basal area**	
		slope	**Sb**	**slope**	**Sb**
Canopy (>25 cm dbh)	31	- 0.004	0.006	0.012	0.021
Sub-canopy (10 -25 cm dbh)	32	-0.010	* 0.004	-0.467	* 0.200
Sapling (> 2 m tall; < 10 cm dbh	31	-0.004	s 0.002	-0.680	* 0.274
Total trees (> 2 m tall)	32	-0.002	0.001	0.004	0.022

s P< 0.100; * P< 0.050

Table 1.3 The relationship of wood nettle frequency with increasing tree density (trees ha 1) and basal area (m2 ha-1) of forest strata using a simple negative binomial regression.

	# parcels	**Density**		**Basal area**		
		slope	**Sb**	**slope**		**Sb**
Canopy (>25 cm dbh)	31	0.0000	0.0003	0.002	s	0.001
Sub-canopy (10 -25 cm dbh)	32	-0.0003	0.0001	-0.016	s	0.009
Sapling (> 2 m tall; < 10 cm dbh	31	-0.0001	0.0001	-0.029	*	0.013
Total trees (> 2 m tall)	32	0.0000	0.0001	0.002		0.001

s $P< 0.100$; * $P< 0.050$

Table 1.4. The relationship between forest strata and diffuse light (percent weighted canopy openness) as measured by hemispherical photographs and analyzed with a simple linear regression.

	# **Parcels**	**Density**		**Basal area**		
		slope	**S**	**slope**		**S**
Canopy (>25 cm dbh)	31	-0.002	0.002	-0.009	*	0.004
Sub-canopy (10 -25 cm dbh)	32	-0.001	0.0006	-0.053	s	0.031
Sapling (> 2 m tall; < 10 cm dbh	31	-0.0005	0.0005	-0.109	*	0.036
Total trees (> 2 m tall)	32	-0.0005	0.0003	-0.010	*	0.004

s $P< 0.100$; * $P< 0.050$

CHAPTER TWO.

Wood nettle *(Laportea canadensis)* population structure in maple-basswood forests: Influences of past land-use and the current environment

Introduction

Each plant population has a defined history: an origin, maturity, and extinction (Wilmanns 1985). The ability of particular plant species and genotypes to achieve (or avoid, in the case of extinction) these milestones in population development lead to variation in stand and community composition. A disturbance event, natural or anthropogenic, can interact with a plant population at any point during population development and lead to greater variation in its population parameters. For example, if a disturbance event results in the destruction of biomass, certain plant species may face extinction at that site (Grime.1979)or an invasion window may offer another species the opportunity to become established (Johnstone 1986).

Disturbances also alter the availability of resources (White and Pickett 1985). For example, gap creation allows more light and precipitation to reach the forest understory below (Collins *et al.* 1985). Plant species respond to these resource changes by altering reproduction and growth patterns (Bazzaz 1996, Johnstone 1986). The population changes are often apparent long after the initial conditions are no longer detectable (Thomas *et al.* 1999). For example, wild geranium growth and rhizome weight increase in newly created canopy gaps. After gap closure, the greater storage tissue continues to support increased sexual reproduction in gap plants in comparison to those that remained under a closed canopy (Dahlem and Boerner 1987).

In chapter 1, I demonstrated wood nettle *(Laportea canadensis)* density and frequency in upland maple-basswood forests is a product of past land-use history. In particular, I found parcels with a dense sub-canopy layer had lower wood nettle density and frequency. A dense sub-canopy layer is an artifact of past heavy timber harvest and livestock grazing. Wood nettle increased in parcels with mild selective timber harvest. Other causes of accelerated gap-phase succession, such as Dutch elm disease, may also increase wood nettle, in the understory. I hypothesize that wood nettle life history characteristics, such as competitive ability, clonal growth, and facultative seed production, are responsible for its success in using resources available in canopy gaps. Many of these traits also assist in maintaining the population upon canopy closure.

The structure of any plant population is a product of its current environment and the outcome of past demographic events (Valverde and Silverstown 1997, Bullock *et al.* 1996, Gerber *et al.* 1997). If disturbance events have profound effects on population parameters, then land-use events should be detectable in the current population structure. Specifically, I expect that land-use will influence the reproductive structure of wood nettle populations through density effects, forest structure, and the time since last documented land-use event.

Population density is a regulator of reproduction (Bishir and Namkoong 1992, Klimes 1992). In general, sexual reproduction declines with increasing intra-specific density because resources for growth and reproduction become scarce (Harper 1977). I expect that in quadrats that have experienced an increase in wood nettle density, possibly because of land-use, the proportion[1] of flowering stems will be smaller. Seed-producing stems, in particular, will be reduced because of the cost of maternity. I also expect that recruitment from seed will decrease with an increase in con-specific density.

Current forest structure is a legacy of past disturbance events, such as land-use. The tree canopy intercepts light before it reaches the understory. As the forest understory becomes shady, resources available for reproduction also decline and one would again expect a reduction in the percentage of flowering stems (Kudph et al. 1999).

Time elapsed since the last documented land-use event will also influence wood nettle populations. Older plants tend to be larger and more productive, and an increase of hermaphroditic stems may indicate a maturing population. I expect that the proportion of hermaphroditic plants will increase with the age of the forest. Hermaphroditic stems are often larger than those with a single flower type and they are also more likely to support clonal offspring (Menges 1983).

Finally, I expect that variation in wood nettle stem height will also increase with the time since the last land-use event. Mature plant populations have greater size heterogeneity because time allows the accrual of age and size classes (Hutchings 1986).

Methods

Study species

Wood nettle is a perennial with an over-wintering rootstock in the family Urticaceae. In Nerstrand Big Woods State Park (NBWSP), the mean wood nettle stem height is 43 cm, but stems can reach 135 cm tall (Appendix I). Its morphology is plastic in response to environmental conditions (Menges 1983). Unless damaged, the stem is unbranched and the alternate leaves concentrate near the apex of the plant. Stinging hairs, a notable characteristic, are found on both stems and leaves.

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[1] The use of proportions are necessary because the number of flowering stems increase as the total number of wood nettle stems increases.

In his review of clonal plant reproductive strategies, Erikkson (1992) found that 30% of woodland clonal plant species recruit sexually and asexually simultaneously within the same population. Wood nettle conforms to this strategy. Sexual reproduction is in flowers generated from the leaf axils near the top of the plant. The plant is monoecious, but some individual stems produce flowers of only one sex. The reproductive status of an individual is not a genetic trait, but one that can vary from year to year in response to plant size and environment (Menges 1983). When an individual expresses both genders (a hermaphrodite), the male flowers emerge first (protandry) and develop among the leaves near the top of the plant. Female flowers emerge later in the summer and are borne on structures that extend above the stem and leaves. The timing of flowering and seed set can vary among and within populations (Menges 1983). . There are no published data for the pollen dispersal distance, the life span of an individual seed, stem, or genet, or the production of seeds in upland populations. The degree of self-compatibility is also unknown, although some other members of the family Urticaceae are self-compatible (Basset *et* al. 1977).

There is no obvious mechanism for dispersal; seeds appear to simply fall out of the fruit. Thompson (1979) includes wood nettle in a dispersal category with plants with a ballistic mechanism or no known mechanism for dispersal. I speculate that freezing might cause release of seed, because this behavior is known to occur in stinging nettle, another member of the family Urticaceae (Basset *et* al. 1977). Menges (1997, *personal communication)* believes that the seeds can float. This ability may contribute to long-distance dispersal in floodplains, but it probably results only in very localized upland dispersal.

Vegetative reproduction occurs through the production of rhizomes. Clonal ramets have a rhizome connection to the parental plant, which provides resources to the ramet and allows it to grow more rapidly than germinates. In floodplains, approximately 70 to 90% *of* wood nettle recruitment is from seeds; in uplands seed recruitment falls to 40% (Menges 1983). In Menges' sites (upland and floodplain), the percent reproducing in a single year, sexually or asexually, ranges from 7 to 40%:

Vegetative reproduction for wood nettle in undisturbed upland forests is relatively slow: a single ramet is produced every 4 to 5 years (Menges 1983). Most stems will support a single clonal offspring, only unusually large individuals will simultaneously have more than one ramet (Menges 1983). Rhizomes decompose after one or two years, but upland rhizomes may decay more rapidly (Menges 1983). Wood nettle's allocation to asexual structures is much lower than other shade-tolerant.understory species. It allocates only 6% of its mass to rhizomes, which is closer to the allocation of old-field species, such as Solidago (Menges 1987).

Twenty percent of stems that produce male flowers exclusively also support a clonal ramet and twenty-nine percent of hermaphroditic plants also support one or more clonal offspring (Menges 1983). Some stems fail to reproduce either sexually or vegetatively, and only 4.4 percent of non-flowering plants have clonal ramets (Menges 1983). Unusually large plants are capable of producing male flowers, female flowers, and ramets simultaneously.

Only five percent of stems that produce female flowers exclusively support clonal ramets (Menges 1983). Female reproduction appears to be a trade-off to clonal reproduction; female flowers generally fail to develop after a clonal year (Menges 1990).

In this study of wood nettle stems, I categorized stems as non-sexually reproducing, male, female, or hermaphroditic. I did not excavate any plants and cannot include asexual reproduction in the analysis. For the purpose of analysis, I grouped the flowering stems into two additional classes: sexually reproducing (all flowering stems) and seed-producing (female and hermaphroditic stems).

Study site

I restricted my study to upland forests in NBWSP in eastern Rice County, Minnesota (44° 20' N, 93° 06' W). NBWSP contains one of the largest contiguous fragments of maple-basswood forest in southern Minnesota. Before the park's founding in 1945, this area was a group of 147 ownership parcels, each with a different history of use (Mason 1994). Restricting my study to this area helps control for variation in historical documentation, current ownership and management, and geographical variation, including the population density of white-tailed deer (a wood nettle predator), glacial parent material, soils, long-term climate changes, and short-term weather patterns. Selection of this site does not address variation related to topography, such as soil horizonation, nutrient concentration, and drainage.

Quantitative vegetation surveys

I selected the 33 parcels for quantitative random sampling by examining aerial photographs of the park (1938, 1940, 1958, 1964, and 1970) and satellite imagery from 1991. 1 grouped parcels with similar canopy densities and randomly chose three parcels from each of twelve groups. A few groups contained only two parcels and in these cases, I sampled both parcels. See figure 1.2 for locations of the sampled parcels and appendix B for a brief summary of their history.

I randomly sampled the plant populations in the 33 ownership parcels between July 10 and August 15, 1998. I generated thirty sets of coordinate numbers and determined quadrat location in the field using meter tapes and a compass. The origin of the coordinate system is at one corner of the professionally surveyed parcel boundaries. I eliminated quadrats from the survey if they occurred on a hiking trail or in the middle of a severe tree blow-down, resulting in 24 to 30 1-m2 quadrats surveyed for each parcel. In the 33 sampled parcels, I sampled 961 quadrats.

Within each quadrat, I measured the height in centimeters and the reproductive status, of each individual wood nettle stem. I also counted the number of wood nettle germinants. I also noted the identity and number of stems all of other vascular plants in the quadrat. Since identification of genetic individuals is impossible without excavating, I counted each stem as an individual for all forbs (including wood nettle) and woody species (Czarnecka 1996). Defining an individual graminoid ramet was more difficult and I used a clump to represent an individual. .

I identified and measured trees within a 127-cm radius of the quadrat center (5 m2). I recorded the height of tree seedlings and saplings shorter than 2 meters and the diameter at breast height (dbh) for trees over 2 meters tall. I used basal area (m2 ha-) and density (trees ha-) to describe the structure of each surveyed parcel. I.calculated these values for each species in a particular stratum and for the entire forest, in the following strata categories: sapling (stems > 2 m tall, but < 10 cm dbh), sub-canopy (10 - 25 cm dbh), and canopy (stems > 25 cm dbh) (Hutchinson and Vankat 1997). I also calculated basal area and density for stems > 10 cm dbh for a description of the total canopy and for all stems greater than 2, m for a summary description of the entire parcel. I do not include saplings less than 2 m tall in this chapter (see Chapter 3).

Statistical analysis

I tested for data normalcy using a probability plot. The counts of wood nettle and its co-occurring species are integers, bounded by zero, with a large number of zero values. The data best fit a negative binomial distribution. This distribution is similar to the Poisson distribution but has more dispersion around the value lambda (Long 1997). Analysis was by negative binomial regression, using the statistical package Stata 6.0 (StataCorp 1999). Averages, height, and proportion data (at the parcel level) are all relatively normal and, therefore, can be analyzed with simple linear and multiple regressions.

I used Stata 6.0 for all normal regression analyses because this statistical package allows robust corrections for heteroscedasticity (StataCorp 1999). I used SYSTAT (SPSS 1997) for ANOVA analyses and to generate summary statistics and cross-tabs. In reporting the results of the regression analyses, b corresponds to the slope of the line of best fit and *Sb* corresponds to the standard error of the slope. Unless otherwise reported, the results reported as significant have a P value less than 0.050.

I tested the relationship between reproductive response to forest structure and time since the last land-use event in two ways. First, I compared these parameters with percent of stems in each reproductive class using a simple linear regression. Second, I compared the number of individuals in each reproductive class using multiple regression with forest structure and time, using the total number of wood nettle m^2 as a control variable.

Unless otherwise specified, only adult stems are used in analyses.

Results

Land-use history and reproductive expression

At NBWSP, I encountered four land-uses during random sampling: selective tree harvest, complete harvest with no grazing (called clear-cut here), complete harvest followed by sheep grazing (sheen), complete harvest followed by cattle grazing (cattle), and cultivation. There are no consistent differences in mean wood nettle reproduction in parcels with different historical land-uses using ANOVA (Table 2.1).

If one considers each individual 1-m2 quadrat as a sampling unit, past land-use is a factor in determining the number of wood nettle stems in each reproductive class (Table 2.2) using dummy-variable negative binomial regressions where each land-use category is compared using dummy-variables.

Wood nettle density

The number of stems in each reproductive class increases as the total number of adults increases. The percent of stems that are non-sexually reproducing increase with the density of adult wood nettle stems within a quadrat and the percent of stems that are sexually reproducing, seed-producing, and female decrease with adult wood nettle stems (Table 2.3).

Germinants

Germinants have an interesting relationship to adult wood nettle density. The number of germinants in a quadrat is positively related to the number of stems *($b = 0.25$; $Sb = 0.021$)* and has a negative relationship to the number of stems squared *($b = -0.003$; $Sb = 0.0003$)* in a multiple negative binomial regression. This parabolic relationship demonstrates that germinants are most abundant at moderate wood nettle densities (Figure 2.1).

When the total number of adult wood nettle is controlled for as an independent variable in multiple regression, germinants are positively correlated with the number of sexually reproducing, seed producing, female, and hermaphroditic stems (Table 2.4). Germinants are negatively related to the number of non-reproducing stems and are not related to the number of male stems.

Forest structure

Although both statistical tests (using the percent and number of each reproductive class) show similar trends, the latter method yielded results that are more significant (Table 2.5). In .. both cases, the density (trees ha') of the canopy layer (stems > 25 cm dbh) is somewhat important to the reproductive make-up of the wood nettle population. The density of all other canopy strata were not correlated with wood nettle reproductive class. In the previous chapter; .I reported that the sub-canopy layer was the most important stratum for the development of large wood nettle populations.

The basal area (m2 ha-) of the canopy strata is not related to any reproductive class, except for female stems, which increase with increasing canopy basal area ($b = 0.002$; $Sb = 0.001$).

Time since the last documented land use event

The proportion and number of sexually reproducing, seed-producing, and hermaphroditic stems in a quadrat increase and the proportion arid number of males decrease with the number of years since the last land-use event (Table 2.6). The number of female stems in a quadrat increases with the time since land-use, but the proportion of female stems is unrelated to the years since the last documented land-use event.

Height

The variation in height, as measured by the difference between the tallest and shortest wood nettle stems in each quadrat, increases with the total number of wood nettle stems *(b* = 2.36; *Sb* = 0.102) using a simple linear regression. The difference between the tallest and shortest also increases with time since last land-use event *(b* = 0.39; *Sb = 0*.067) using a simple linear regression.

I used two tests to examine the response of wood nettle height to inter- and intra-specific competition. First, I performed multiple regression with mean wood nettle height in a quadrat as the dependent variable and total wood nettle stems and total co-occurring stems as independent variables. The mean height of wood nettle adults increases with both inter- *(b* = 1.37; *Sb = 0*.086) and intra-specific *(b* = 0.12; *Sb = 0*.037) competition. Second, I replaced total co-occurring stems with co-occurring forb stems. Again, mean wood nettle height was positively related to increases with both inter- *(b* = 1.37; *Sb = 0*.082) and intra-specific *(b = 0*.24; *Sb = 0*.049) competition.

Discussion

The reproductive structure of plant populations results from current stand conditions and past demographic events (Cipollini *et al.* 1993, Bullock *et al.* 1996, Gerber *et al.* 1997). Land-use appears to indirectly influence the population structure of wood nettle through intra-specific density, canopy structure, and the passage of time.

Land-use history and reproductive expression

The relationship between the number of wood nettle stems in each reproductive class and previous land-use is similar to that of the number of total wood nettle stems. These results demonstrate the relative importance of current stem density on the number of reproductive stems, rather than a clear response to past land-use (see discussion below for male stems).

Reproduction and intra-specific density

At high intra-specific densities, plants devote scarce resources to survival rather than to reproduction (Harper 1977). At NBWSP, wood nettle conforms to this strategy. The proportion of stems that sexually reproduce, produce seeds, or are female decrease with higher total stem densities (Table 2.3).

The percent of non-sexually reproducing stems increases with total wood nettle density. These stems may represent clonal offspring, or immature independent stems, but without excavation, one cannot make conclusions about identity. Menges (1990) found no relationship between allocation to clonal reproduction and density.

Germination

The local (in 1-m2) supply of seeds appears to be important for recruitment. Assuming this years reproductive distribution is similar to last year, the number of germinants increase with the number seed producing stems (Table 2.4). Wood nettle germinants increase with adult density because the number of seed producing stems also increases with stem density. Intraspecific competition, however, overwhelms seedling survival at higher adult densities (Figure 2.1).

Forest structure and reproduction

Regardless of the method used to control for total adult wood nettle density, the tree density of the canopy layer is somewhat important for wood nettle reproduction. It is generally expected that as resources decline, plant species devote less effort to reproduction. The results of this part of the study do not follow this pattern. The number and proportion of sexually reproducing, seed-producing, and female stems increase with the density of the canopy layer. If canopy density reduces the availability of light to the understory light availability, than a decrease of resources causes an increase in sexual reproduction, seed production, and female flowering.

The use of hemispherical photographs failed to characterize the light environment of the forests at NBWSP in a useful way (Chapter 1), but the availability of light is, without question, important to wood nettle growth and reproduction (Menges 1983). There is a single instance where one can forge an indirect relationship between light availability and reproduction. The number of female stems increases with the canopy basal area. Diffuse light (weighted canopy openness) decreases with the basal area of the canopy (Chapter 1, Table 1.4).

In wood nettle, the increase in female stems with decreasing light availability may be particularly important. Female wood nettle stems are generally shorter than other stem types and only five percent support clonal offspring (Menges 1983). The relative inexpense of producing a female stem may account for its increase in proportion when light availability is low. It may be at wood nettle's advantage to increase seed production in shady stands. Seed production is a means of genetic recombination and can enhance species' survival under deteriorating conditions (Eriksson 1986, Matlack 1994). Even in species with short dispersal distances, seeds are a means of escape to an area with better growing conditions.

Time since the last documented land-use event and reproduction

As expected, the proportion of hermaphroditic stems increases with time since the last documented land-use event. Size and reproductive development can be a substitute for age in plant populations, where aging mechanisms are not apparent. Hermaphroditic stems develop both male and female flowers, tend to be taller, and have more clonal offspring than exclusively male or female stems (Menges 1983).

Although it was not expected, the proportion of seed-producing, and sexually reproducing stems also increases, and the proportion of male stems decreases, with the time since the last documented land-use event. The ability to produce seeds may be a function of plant age or the light environment of older forests.

Mature plant populations have greater variation in size structure (Wiener 1988). This characteristic promotes survivorship and fecundity in monocultures and, therefore, is important for the maintenance of large populations (Hutchings 1986). For example, the stability of monocultures of *Allium ursinum* in Germany is dependent, in part, on the distribution of multipleage classes within a population (Ernst 1979). Wood nettle populations at NBWSP increase size variation with increasing con-specific density and with time since the last land-use event. Size variation may allow wood nettle to maintain or expand in closed canopy conditions. Menges (1983) also found an increase in stem height variation in dense wood nettle populations.

Height and competition

Competitive plants grow taller when faced with inter-specific competition (Grime 1985). The height of wood nettle stems increases with intra- and inter-specific competition and, therefore, is considered competitive. Taller stems insure greater access to light, a limiting resource in forest understories. Menges (1987) found that this increase in height comes at the expense of structural support; taller stems weigh less per unit length than shorter stems.

The mean height of wood nettle stems in a parcel was not related to forest structure or the measured light resources. Menges (1987) found that the height of wood nettle stems is positively related to percent open sky. At first, these results appear to contradict. However, unlike Menges, I do not have light measurements for each of my quadrats and cannot make direct comparisons between wood nettle height and the local light environment.

Male stems

The quantity and proportion of male stems relate to few environmental factors. I hypothesize that there is a trade-off between exclusive male flower production and male flower production and vegetative growth. Male flowers are relatively inexpensive to produce and twenty percent of male wood nettle stems support clonal ramets (Menges 1983). Therefore, when resources are scarce wood nettle will tend to invest in exclusively male stems. When resource availability is greater, wood nettle stems can invest in both asexual reproduction and male flower production. Because I did not measure the number of clonal ramets, I cannot test this hypothesis:

Problems and improvements for this study

Some of the conclusions of this study are weak and contradictory because the demography of understory plants is affected by stochastic variation in the environment (De, Ridder and Dhondt 1992, Gerber *et al.* 1997). Non-linear variation in environmental conditions, the plastic qualities of the study organism, and lack of genetic identification contribute to the difficulty of drawing conclusions.

Year to year variation in weather can change population parameters, such as seedling recruitment, and can bias conclusions from observations in a single year (Eriksson 1989, Bierzcheduk 1982). For example, *Asarum canadense* showed great. year to year variation in ramet density in early successional habitats (Damman and Cain 1998), and Whigham *et al.* (1993) found that short-term observations of population parameters failed to predict patch dynamics. Longitudinal monitoring of wood nettle populations is required to uncover patterns in plant demography and future population trajectories.

Furthermore, qualities, such as morphological plasticity and facultative seed production, that allow wood nettle to respond rapidly to newly available resources also contribute to the difficulty of relating past land-use to current reproductive structure. Menges (1983) also had a hard time detecting which environmental variables were important to reproductive biomass allocation in upland forests. Point measurements of environmental data and technological advancements in collection techniques will improve understanding of allocation and growth.

Finally, although it is often necessary to restrict a population study to stern census, it is difficult to derive anything about the genet structure and asexual reproduction (Harper 1977). A complete understanding of wood nettle populations in upland forest understories will require data on the structure of both the genet and ramet populations, rather than stem counts. Examination of land-use effects can be improved by measuring the extent of individual genets, the rate of clonal expansion, and the degree of relatedness of clones within a parcel understory.

Conclusion

Three sets of results illustrate the indirect effect of past land-use on the reproductive structure of wood nettle populations. First, the density of wood nettle stems is an important influence on its population's reproductive structure. In chapter 1, I found that mild selective timber harvest contributed to the development of dense wood nettle populations. Therefore, landuse influences the percent of sexually reproducing stems because it is negatively correlated with adult density because the resources available to each stem is limited. Density of germinants is also related to the density of adult wood nettle stems. At low adult densities, the local supply of seeds limits the number of germinants. High adult densities limit germination and growth through intra-specific competition.

Second, the density of the overstory canopy is an important predictor of the number of female stems in the forest understory. In general, reproduction declines with decreasing resource availability, but in this case, the opposite trend is observed. For wood nettle, exclusive female stems may be a relatively inexpensive means of reproduction and may provide the plant a means of escape from deteriorating conditions.

Third, time since the last documented land-use event increases the number of hermaphroditic stems. These stems are large and likely represent a mature, well-developed population. The proportion of female, seed-producing, and sexually reproducing stems also increases, and the proportion of male stems decreases, with the time since the last documented land-use event. The ability to produce seeds may be a function of plant age or the light environment of older forests.

The number and percent of male stems are not related to any measured biological or environmental variable. The relative inexpense of male flower production and a trade-off with vegetative growth probably contributes to the lack of a distribution pattern.

Stem height variation within a quadrat increases with intra-specific density and time since land-use. Size-variation lends stability to plant populations and helps monocultures maintain dominance through continued recruitment of individual stems into the reproductive classes. The height of wood nettle stems increases with inter- and intra-specific competition. Taller plants are better able to compete for light, which is limiting in the forest understory.

The limitations of this study suggest methods that may be useful for future studies of plant populations in the forest understory. For example, point measurements of environmental variables, rather than data generalized by stand conditions, may yield stronger correlations with reproductive status. Longitudinal observations will distinguish the role of weather from population trends driven by density and time. Finally, genetic description will also contribute to an understanding of wood nettle response to changes in environmental conditions.

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Table 2.1. A comparison of the mean number of reproductive stems of wood nettle stems in parcels with different land-use histories using ANOVA.

	Selectively Harvest		Clear-cut		Sheep		Cattle
Total adult stems (mean)	7.46	=	3.60	=	3.34	=	0.59
Total adult stems (standard deviation)	7.15				3.01		
Non-sexually reproducing (mean)	5.79	=	3.20	=	2.82	=	0.45
Non-sexually reproducing (standard deviation)	5.63				2.44		
Sexually reproducing (mean) .	1.67	=	0.40	=	0.52	=	0.03
Sexually reproducing (standard deviation)	1.64				0.60		
Male (mean)	0.50	=	0.23	=	0.18	=	0.03
Male (standard deviation)	0.58				0.23		
Seed-producing (mean)	1.17	=	0.17	=	0.34	=	0.13
Seed-producing (standard deviation)	1.19				0.37		
Female (mean)	0.32	=	0.03	=	0.06	n.a.*	
Female (standard deviation)	0.38				0.05		
Hermaphroditic (mean)	0.84	=	0.13	=	0.28	=	0.1
Hermaphroditic (standard deviation)	0.87				0.35		
Germinants (mean)	7.57	=	0.13	=	1.13	=	0.35
Germinants (standard deviation)	9.49				0.95		
Number of parcels	28		1		3		1

* There are no female stems in quadrats that have been grazed by cattle.

Table 2.2. A comparison of the number of reproductive stems of wood nettle stems in quadrats with different land-use histories using dummy-variable negative binomial regressions, where each land-use category is compared using dummy-variables.

	Selectively Harvest		**Clear-cut**		**Sheep**		**Cattle**
Total adult stems (mean)	7.7	>	3.6	=	3.3	>	0.06
Total adult stems (standard deviation)	10.84		8.45		6.74		2.08
Non-sexually reproducing (mean)	5.99	=	3.2	=	2.75	>	0.45
Non-sexually reproducing (standard deviation)	8.87		7.97		5.92		1.38
Sexually reproducing (mean)	1.72	>	0.4	=	0.51	>	0.03
Sexually reproducing (standard deviation)	2.73		0.89		1.28		0.19
Male (mean)	0.52	=	0.23	=	0.18	=	0.03
Male (standard deviation)	1.2		0.68		0.64		0.19
Seed-producing (mean)	1.2	>	0.17	=	0.33	=	0.1
Seed-producing (standard deviation)	2.12		0.63		0.86		0.56
Female (mean)	0.33	>	0.03	=	0.06	n.a.*	
Female (standard deviation)	0.83		0.18		0.24		
Hermaphroditic (mean)	0.87	>	0.13	=	0.27	=	0.1
Hermaphroditic (standard deviation)	1.65		0.51		0.76		0.56
Germinants (mean)	7.65	>	0.13	=	1.12	=	0.35
Germinants (standard deviation)	16.62		0.51		3.4		1.68
Number of quadrats	817		30		85		29

* There are no female stems in quadrats that have been grazed by cattle.

Table 2.3. The relationship between wood nettle density and the proportion of stems in each reproductive class within a quadrat, analyzed by a simple linear regression.

	Wood nettle density	
	slope	**Sb**
Non-sexually reproducing	0.002	* 0.0008
Sexually reproducing	-0.002	* 0.0008
Male	-0.0002	0.0004
Seed-producing	-0.002	* 0.0007
Female	-0.0008	0.0004
Hermaphroditic	-0.0007	0.0006

* $P < 0.050$

Table 2.4. The relationship between wood nettle germinant density and the number of reproductive stems, analyzed by multiple negative binomial regression with the total number of wood nettle stems as a control variable.

	Germinants		
	slope		**Sb**
Non-sexually reproducing	-0.134	*	0.05
Sexually reproducing	0.136	*	0.05
Male	0.090		0.11
Seed-producing	0.125	*	0.05
Female	0.200	*	0.10
Hermaphroditic	0.117	*	0.06

* $P < 0.050$

Table 2.5. The relationship between increasing canopy (trees > 25 cm dbh) density (trees ha^{-1} of trees > 25 cm dbh) and the proportion and number of stems in each reproductive class. I used simple linear regression to analyze the proportion data. I used multiple regression to compare the number of stem in each reproductive class with canopy density, using the total number of wood nettle stems as a control variable.

	Proportion		**Number**	
	slope	**Sb**	**slope**	**Sb**
Non-sexually reproducing	-0.0001	0.0001	-0.001	* 0.0004
Sexually reproducing	0.0002	0.0001	0.001	* 0.0004
Male	0.0000	0.0000	0.000	0.0001
Seed-producing	0.0001	0.0001	0.001	* 0.0004
Female	0.0001	*0.0001	0.001	* 0.0002
Hermaphroditc	0.0000	0.0000	0.000	0.0004

* $P < 0.050$

Table 2.6. The relationship between the years since the last documented land-use event and the proportion and number of stems in each reproductive class. I used simple linear regression to analyze the proportion data. I used multiple negative binomial regression to compare the number of stem in each reproductive class with canopy density, using the total number of wood nettle stems as a control variable.

	Proportion		**Number**	
	slope	**L**	**slope**	**Sb**
Non-sexually reproducing	-0.002	0.0009	0.013	* 0.003
Sexually reproducing	0.002	0.0009	0.025	* 0.005
Male	-0.001	* 0.0006	-0.005	0.005
Seed-producing	0.003	* 0.0009	0.038	* 0.007
Female	0.001	0.0006	0.043	* 0.011
Hermaphroditc	0.003	* 0.0006	0.036	* 0.006

$P < 0.050$

CHAPTER THREE

Consequences of wood nettle *(Laportea canadensis)* density for the diversity and structure of maple-basswood forests

Introduction

A single aggressive exotic or native herbaceous plant species can have detrimental affects on the cover, abundance, and diversity of other local species (Hutchinson and Vankat 1997, Kolb *et al.* 1990, Davison and Forman 1982, Hurst and John 1999, Iida and Nakashizuku 1995). For example, the invasion of the exotic grass *Brachypodium pinnatum* reduced forb species diversity in English chalk grasslands (Hurst and John 1999). Davison and Forman (1982) found that mayapple is negatively correlated with other understory species.

Many of these aggressive species are able to respond to localized disturbance events, such as a canopy gap, by forming dense mono-specific patches (George and Bazzaz 1999a). These mono-specific patches may exclude other species through the occupation of space or use of resources (Johnstone 1986, Connell and Slatyer 1977). Furthermore, these exclusionary patches can persist indefinitely (Connell and Slayter 1977) and continue to erode the abundance and diversity of co-occurring species (Davison and Forman 1982).

In chapter one, I demonstrated that wood nettle increases with accelerated gap-phase succession associated with mild selective timber harvest in upland maple-basswood forests. This species, I propose, takes advantage of the greater light in canopy gaps and expands through vegetative growth and seedling recruitment. This reproductive strategy also helps wood nettle maintain dominance, and possibly allows for continued expansion, after the canopy closes.

The possible interaction between wood nettle and other members of the upland forest understory has not been directly examined. Menges and Waller (1983 p. 455) noted that higher floodplain elevations dominated by wood nettle "were often rich in species." Conversely, stinging nettle, another member of the family Urticaceae, out-competes other plant species on European floodplains and meadows (Srutek 1993, Al-Mufti *et al.* 1977).

The following chapter explores the consequences of wood nettle domination by examining three different components of the forest community (1) the abundance and diversity of co-occurring species, (2) the abundance and diversity of vernal forbs, and (3) the composition and structure of the seedling layer.

I hypothesize that upland populations of wood nettle will reduce the local abundance of co-occurring forb, graminoid, and woody species. Wood nettle is taller than many other understory forbs in maple-basswood forests and is, therefore, considered a competitive plant (Menges 1983). Light is an important resource in closed forest understory and taller plants prevent shorter species from obtaining this resource. High nutrient demands of wood nettle may also prevent the local establishment of other individuals.

The decline in the abundance of co-occurring species within a quadrat will eventually erode diversity through localized extinction as chance events eliminate sparse species. Therefore, I predict that quadrat diversity will also be lower with increasing wood nettle stems. Total parcel diversity, as measured by species richness, should also be lower in parcels with increasing wood nettle density.

Conversely, I expect that the abundance of wood nettle will enhance the number of vernal species present in quadrats. The phenology of vernal forbs does not conflict with wood nettle and, therefore, these species do not compete for light (Menges 1983). Furthermore, wood nettle, a late emerging species, may competitively exclude summer species that emerge earlier and overlap phenologically with the vernal species. This effective removal of co-occurring species will increase the light available to vernal species and promote their growth and reproduction (Meier *et al.* 1995). Quadrat and parcel diversity of vernal species may also be higher in areas dominated by wood nettle, as chance events are less likely to cause the local extinction of abundant species.

While I expect the above hypotheses to apply to the understory community in general, individual species have different habitat requirements and will be affected by wood nettle differently. Two other studies of upland and floodplain communities in Wisconsin document relationships between wood nettle and individual plant species (Menges 1983, Smith and Cottam 1967) (Table 3.5), and I will use individual species data to replicate these results and establish other relationships at Nerstrand Big Wood State Park (NBWSP).

Finally, variation in the herbaceous understory creates variation in litter cover, moisture holding capability, and light availability which, in turn, influences tree germination and growth. For example, tree germination and seedling growth are differentially affected by *Osmunda claytoniana* and *Dennstaedtia punctilobula* clones (George and Bazzaz 1999a). Light availability is a particularly strong influence on seedling growth (Pacala *et al.* 1994). Therefore, I hypothesize that wood nettle will exclude shade intolerant tree seedlings, which may skew the future canopy composition toward shade-tolerant species.

This study is correlative and does not test for the causal mechanisms behind the proposed relationships. Longitudinal monitoring and experimentation are necessary to determine the longterm effects of wood nettle on upland maple-basswood forests in central Minnesota.

Methods

Study-site

Nerstrand Big Woods State Park (44° 20' N, 93° 06' W) is one of the largest contiguous fragments of maple-basswood forests in southeastern Minnesota (425 ha). Nerstrand is well suited for this type of study because before the park's founding in 1945, this area was a group of 147 ownership parcels, each with a different history of use (Mason 1994). NBWSP has relatively consistent historical documentation, and current ownership and management. Environmental variation due to geography is also limited, including the population density of white-tailed deer (a wood nettle herbivore), soil parent material, long-term climate, and short-term weather. Selection of this site does not address variation related to topography, such as soil horizonation, nutrient concentration, and drainage.

Summer survey

I selected the 33 parcels for quantitative random sampling by examining aerial photographs of the park (1938, 1940, 1958, 1964, and 1970) and satellite imagery from 1991, I grouped parcels with similar canopy densities and randomly chose three parcels from each of the twelve groups. A few groups contained only two parcels and in these cases, I sampled both parcels. See Figure 1.2 for locations of the sampled parcels and Appendix B for a brief summary of their history.

I randomly sampled the plant populations in the selected ownership parcels between July 10 and August 15, 1998. I generated thirty sets of coordinate numbers and determined quadrat location in the field using meter tapes and a compass. The origin of each coordinate system is at the corner professionally surveyed parcel boundaries. I eliminated quadrats from the survey if they occurred on a hiking trail or in the middle of a severe tree blowdown, resulting in 24 to 30 1-m2 quadrats surveyed for each parcel in the summer of 1998.

Within each quadrat, I measured the height in centimeters and the reproductive status of each individual wood nettle stem. I also noted the identity and number of stems of all other vascular plants in the quadrat. Since identification of genetic individuals is impossible without excavation or genetic testing, I counted each stem as an individual for all forb (including wood nettle) and woody species (Czarnecka 1996). Defining an individual graminoid ramet was more difficult and, therefore, I used a clump to represent an individual.

I sampled 961 quadrats during the summer of 1998. In addition to individual species, I grouped co-occurring species into three categories for analysis: summer-reproducing forb, graminoid, and woody. Spring reproducing species also occur in the summer plots, but were not compared with wood nettle density. I compared both the number of stems and the number of species with the number of wood nettle stems in each quadrat using a simple negative binomial regression. To test whether a relationship is the result of wood nettle and not general competition, I also compared quadrat diversity to the total number of stems (including wood nettle and spring-reproducing forbs) also using a simple negative binomial regression.

Spring survey

I sampled vernal forb species at NBWSP between April 16 and May 1, 1999. The deterioration of some of ephemeral species from the early onset of warm temperatures resulted in the sampling of only 29 of the 33 selected parcels (Figure 3.1, Appendix B). I randomly sampled vernal forbs by relocating the same quadrats sampled in the summer 1998. To insure that the same quadrats were sampled, I used the same coordinate system and relocated six flags planted in selected quadrats during the summer of 1998. I eliminated quadrats from the spring survey if I was uncertain of their location. This resulted in 22 to 30 1-m2 quadrats surveyed for each parcel for a total of 786 quadrats.

The species encountered during the vernal forb survey include three categories: true ephemerals, spring-reproducing species, and summer-reproducing species. True ephemerals emerge, reproduce, and decompose above ground before canopy renewal. In NBWSP, I categorized those species that appeared in spring sampling, but were absent during the summer sampling period, as true ephemerals. Spring-reproducing species reproduce before the tree canopy closes, but the aboveground structures are present throughout most of the summer. I used flowering times (Newcomb 1977) and personal experience to categorize spring-reproducing species.

The summer-reproducing species that were present during the spring sampling period appeared as basal rosettes, primary structures, or germinants. This category of plant reproduces after the canopy closes and includes wood nettle. Since emergence of summer-reproducing species occurs throughout the spring sampling period, they were not included in the spring analysis. See Appendix A for a list of the species identified in NBWSP, their scientific names, and their classification as ephemeral, spring, or summer-reproducing species in this study.

I compared the number and diversity of both ephemeral and spring-reproducing forb species with the number of wood nettle present in the plot in 1998 using a simple negative binomial regression. I also compared quadrat diversity with the total number of forb stems from the 1998 summer plots to determine if the results can be attributed to wood nettle or are an artifact of competition with summer species in general.

Individual species

In this study, the relationship between individual species and wood nettle is analyzed in two ways: association and correlation. Mutual presence is the basis for species associations and analysis the identifies species that require similar or divergent environmental conditions. To determine associations with wood nettle, I used a chi-square analysis with data reflecting species presence or absence in each quadrat. Correlations examine the relationship between the number of wood nettle and the abundance of a particular species. I used simple negative binomial regression to test if wood nettle enhances or inhibits the abundance of each species.

Tree seedlings and saplings

During the 1998 summer survey, I identified and measured trees within a 127-cm,radius of the quadrat center (5-m2). I recorded the height of seedlings and saplings shorter than 2 meters and the diameter at breast height (dbh) for trees over 2 meters tall. In this chapter, I examine the interaction between wood nettle and trees below 2 meters (see chapters 1 and 2 for a discussion of forest structure)..

I stratified tree seedlings under two meters into four categories: 0-25, 26-50, 51-75.and 76-100; and tree saplings into two categories: 101-150, and 150-200 cm. The low number of seedlings of species other than sugar maple in each category necessitated collapsing these data into a single category. I used simple linear regression to determine if wood nettle stems reduce the number of sugar maple and other woody stems in each height category.

Statistical methods

I tested for data normalcy using a probability plot. The counts of wood nettle and its co-occurring species are integers; bounded by zero, with a large number of zero values. The data best fit a negative binomial distribution. This data distribution is not normal and is similar to the Poisson distribution, but with more dispersion around the value lambda (Long 1997). Analyses of this type of data requires the use of a negative binomial regression, which were conducted using the statistical package Stata 6.0 (StataCorp1999). I used Stata 6.0 for all normal regression, analyses because this statistical package allows robust corrections for heteroscedasticity.

The categorical nature of the land-use data prevented using this variable as a covariate in regression analysis. To account for possible interaction with use, I repeated these analyses for only parcels with a history of selective harvest and the results were nearly identical. The results reported include all types of land-use. Only adult stems of wood nettle are used in these analyses.

Species richness, or the diversity of the entire parcel, is estimated by counting the number of species found in all of the quadrats in a parcel. I expended no extra effort to document additional species. Only forb and total species richness were compared using a simple linear regression with the mean number of wood nettle stems *rri* 2.

In reporting the results of the regression analyses, *b* corresponds to the slope of the line of best fit and *Sh* corresponds to the standard error of the slope. Unless otherwise reported, the results reported as significant have a P value less than 0.05.

Results

Summer sampling

The number of summer-reproducing forb, woody, and graminoid co-occurring stems decline with increasing wood nettle density in a quadrat (Table 3.1). Likewise, summer reproducing forb, graminoid, and woody diversity decline with wood nettle abundance. The loss of co-occurring summer-reproducing forb species diversity can be attributed to stems of wood nettle, rather than the presence of a general competing herbaceous stem (Table 3.1). The relationship between wood nettle and graminoid and woody diversity is less clear; the number of these species also decrease with an increase in the number of total forb stems.

The mean number of wood nettle stems ni 2 does not influence the richness of forb species in a parcel *(b = -0.194; Sb = 0.*122), but total species richness declines as the mean number of wood nettle stems increase *(b = -0.*646; *Sh = 0.*167).

Spring sampling

The number of ephemeral stems is lower in quadrats with a greater number of wood nettle (Table 3.2). If one removes the number of white trout lily stems, however, the number of ephemeral stems significantly increases with increasing wood nettle density. White trout lily is negatively associated with wood nettle *(b = -0.*026; *Sb = 0.*005) and may have hundreds of individuals in a single square meter (Figure 3.2). The number of white trout lily plants overwhelms the number of other species in the plot and can skew the relationship between ephemerals in general and wood nettle. In contrast, toothwort is the next abundant ephemeral and has a maximum of 100 plants in a quadrat.

The quadrat diversity of ephemeral species increases with the number of wood nettle stems (Figure 3.2). The increase of ephemeral species can be attributed to the presence of wood nettle, because the number of ephemeral species is not related to an increase of total summer forb stems (including wood nettle).

The number of spring-reproducing species in each quadrat also increases with wood nettle. The relative importance of wood nettle is less clear in the case of spring-reproducing forb species. The diversity of spring-reproducing species also increases with total summer forb stems (Table 3.2).

The species richness of ephemeral species did not change with the mean number of wood nettle rri Z *(b* = 0.014; *Sb = 0*.038). The species richness of ephemeral species did not change with the mean number of wood nettle rri 2 *(b* = 0.072; *Sb = 0*.053). Therefore, parcels with higher densities of wood nettle (mean # stems M-2) do not have more species than those with low densities of wood nettle.

Individual species

I sampled 961 quadrats in the summer of 1998. Four hundred and eighty-eight (488) quadrats had wood nettle in 488 quadrats and 473 quadrats had none. Table 3.3 reports results for the summer-reproducing species that were significantly associated with wood nettle. Other summer-reproducing species either were too sparse for analysis or had no significant relationship with wood nettle.

I sampled 786 quadrats in the spring of 1999. Four hundred eight (408) quadrats had wood nettle during the summer months and 378 had none. Table 3.4 reports results for the spring species that were significantly associated with wood nettle. Other spring species were either too sparse for analysis or had no significant relationship with wood nettle.

Tree seedlings and saplings

All woody stems (sugar maple and others) in classes less than 150 cm tall decrease with increasing wood nettle density (Table 3.6).

Discussion

Wood nettle appears to respond to localized disturbance events, such as a canopy gap, by forming dense patches (Connell and Slayter 1977, George and Bazzaz 1999a). These large patches of wood nettle influences local populations of plant species, possibly through competition for light. In general, the abundance of wood nettle is negatively correlated with the diversity and abundance of co-occurring summer-reproducing forb, woody, and graminoid species in a quadrat. Wood nettle density positively correlates with the diversity and abundance of ephemeral and spring forb species in quadrats.

Summer species

The abundance of summer-reproducing forbs, woody, and graminoid species decreases with wood nettle abundance. Wood nettle may be excluding individuals of other species through the occupation of space or through competition for resources. The presence of dense forb layer prevents the invasion of new individuals or species (Collins et al. 1984).

The diversity of these species also declines with increasing wood nettle. Conversely, the diversity of summer-reproducing forbs, increases with the total number of forb stems. This implies that it is wood nettle, rather than general forb competition, that is responsible for the loss of species.

Wood nettle's light gathering structure and its nutrient requirements may contribute to its ability to reduce co-occurring plant diversity and abundance. Wood nettle is a competitive plant (Menges and Waller 1983), and it grows taller in quadrats with increased inter-specific competition (Chapter 2). Height affords the ability to collect more light and shade individuals below. Wood nettle also concentrates its leaves near its apex, which allows for efficient light absorption, but also blocks light transmission to other, shorter species (Givnish 1982).

Wood nettle, like other members of the family Urticaceae, requires relatively high amounts of nitrogen and phosphorous (Rorison 1968). Wood nettle may locally deplete nutrient supplies and depress other species.

Although wood nettle reduces the diversity and abundance of forb species within a quadrat, forb species richness (parcel diversity) is not related to the mean number of wood nettle M'2 . Therefore, while wood nettle colonization may cause the localized decline of forb species, it does not reduce diversity of the entire parcel. Local reduction, however, may eventually lead to species loss within the parcel. The frequency of individual plant species declines with increasing wood nettle density, and these species become more vulnerable to chance events that could eliminate a species from the parcel. This is particularly important as the parcel ages, since wood nettle colonization increases with time since the last documented land-use event (Chapter 1).

It is possible that the conditions that brought about the increase in wood nettle stems coincidentally caused the reduction in co-occurring plant species. The co-occurring species may be more susceptible to mild selective harvest, but Reader and Bricker (1992) found damage due to the mechanical action of partial canopy removal has only a minor negative impact on understory summer forbs. Furthermore, species diversity often increase as canopy gaps, created by selective timber harvest, allow for more heterogeneity in the forest understory (Valverde and Silvertown 1998, Stone and Wolfe 1996). Jenkins and Parker (1999), however, failed to find shifts in forb species composition due to gap creation, particularly single tree openings.

Spring species

The number. of ephemeral stems (with the exception of white trout lily) increases as the number of wood nettle in the previous year increases. The diversity of all vernal species within a. quadrat also increases with wood nettle.

Vernal forbs meet most of their energy needs before wood nettle interferes with light transmission from the tree canopy. Therefore, wood nettle is not directly competing with ephemeral or spring-reproducing species for light. Ephemeral forb species senesce before the . overstory canopy closes in late May. Wood nettle emerges between April 27 and May 11, but does not reach full expansion until July (Appendix I, Bratton 1976). Likewise, spring-reproducing forb species reproduce and gain most of their biomass before wood nettle fully expands.

Wood nettle may also depress other summer species that may directly compete with ephemeral and spring-reproducing forb species. Other summer species emerge and expand earlier than wood nettle and may interfere with light absorption by vernal.forb species. Thus, by displacing early emerging summer species, wood nettle is effectively increasing light resources to vernal species and extending their growing season. For example, Hughes (1992) found white trout lily, an ephemeral, increased in abundance after removal of summer species in the same quadrat.

Furthermore, nutrient dynamics may favor the relationship between wood nettle and ephemeral species. Herbaceous vegetation is a small portion of a forest's biomass, but it has a significant influence on. nutrient dynamics and competitive interactions (Gilliam and Turrel 1993). Wood nettle leaves decompose rapidly in the spring *(personal observation)* and may be an early source of nutrients for ephemeral and spring-reproducing forb species growth and reproduction. Ephemerals release nutrients as they decay, and these nutrients are immediately available to summer species (Peterson and Rolfe 1982). Wood nettle may benefit from this flush of nutrients as it emerges and grows.

Finally, wood nettle may also serve to protect species vulnerable to extirpation from harvest. There are two species are harvested from Minnesota's maple-basswood forest[1]: wild leek, an ephemeral, and American ginseng, a state protected spring-reproducing species. The presence of wild leek is not related to wood nettle, but its abundance increases in quadrats with wood nettle (Table 3.4).

The presence of American ginseng has not been reported in the park since 1947 (Minnesota Department of Natural Resources 1998). I did not encounter enough American ginseng plants for analysis, but I did find several individuals under wood nettle canopies. Wood nettle, therefore, may afford American ginseng further protection because its leaf structure effectively hides the plants below. The stinging hairs may also discourage harvesters from entering a stand.

The mean number of wood nettle stems m^{-2} in each parcel does not relate to the richness of ephemeral and spring-reproducing forb species. The greater diversity and abundance of species in quadrats with wood nettle presence, however, may prevent species loss over time.

Despite the strong correlation, the relationship between wood nettle and ephemeral species may be coincidental, as past land-use may be responsible for the positive relationship. Both wood nettle and vernal herbaceous plants respond to past selective harvest in the same way. Both require canopy gaps for reproduction and their presence is enhanced in partially logged stands (Meier et al. 1995, Hughes and Fahey 1991). Heavy disturbance, such as clear-cutting, lowers vernal herbaceous species diversity (Duffy and Meier 1992) and suppresses wood nettle through competition with woody re-growth (Chapter 1).

Individual species

Species may be negatively related if they actively compete for resources, or if they have divergent ecological requirements (Smith and Cottam 1967). The correlation and association of species can vary among sites (Hurst and John 1999), therefore the relationships found at NBWSP may not necessarily be found in other areas. This study supports many findings of previous studies, disagrees with one, and is inconclusive for several established relationships (Table 3.5).

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[1] Both species are protected from harvest within the park and other managed areas.

Wood nettle is positively associated with the following ephemeral species: spring beauty, toothwort, false rue anemone, and Dutchman's breeches (Table 3.4). All of these species, except Dutchman's breeches, also increase in abundance with wood nettle. White trout lily is negatively related to wood nettle, and it is the only ephemeral species in NBWSP to decline in abundance with wood nettle (Figure 3.2). This negative relationship exists presumably because they have different moisture needs (Smith and Cottam 1967).

Wild blue phlox, wild ginger, touch-me-not germinants (but not adults of this annual species), and Virginia water-leaf are the only non-ephemeral species that increase in abundance as wood nettle increases.

I found the presence of two year-old 2 sugar maple seedlings to be positively associated with wood nettle presence, but the number of seedlings and seedlings below 100 cm are uncorrelated to the abundance of wood nettle.

Tree seedlings and saplings

Differences in seedling mortality among tree species determine future forest structure, composition, and community dynamics (Kobe *et al.* 1995). Environmental conditions created by the herbaceous understory can create these differences and favor particular tree species.(George and Bazzaz 1999a, 1999b, Clinton and Voss 1996). For example, understory grass and fern stems reduce light levels and retard the growth of red oak and white pine seedlings (Kolb *et al.* 1990).

Wood nettle is a general barrier to seedling growth and does not appear to favor a particular species. There is a negative relationship between wood nettle and the presence and abundance of all tree species in NBWSP (Table 3.3). Lindsey *et al.* (1961) and Wheeler and Knapp (1978) document exclusion of shade intolerant species by wood nettle. In NBWSP, there is apparent no skew towards shade-tolerant species under wood nettle. Sugar maple is the most shade tolerant species in maple-basswood forests (Hett and Louck 1970).

The negative relationship between wood nettle and the seedling layer dissolves with the taller saplings (Table 3.6). Many shade tolerant species, including sugar maple, can persist in the understory for many years (Hubbell and Foster 1986). The layer of saplings greater than 150 cm may represent a multi-aged congregation of individuals that grew through the wood nettle canopy.

'Sugar maple is a masting species (Curtis 1959) and current year germination was minimal.

Its capacity to reduce the number of seedlings may perpetuate wood nettle in the forest understory. Competition from woody species may slow wood nettle growth (Chapter 1), but if established patches prevent the establishment of woody species, wood nettle can continue unchecked by woody competition.

Diversity and management

Biodiversity is important for community function; it maintains the integrity of thermodynamics and the movement of energy and materials through the community (Folke et al. 1996, Angermeier and Karr 1994). Furthermore, a variety of component species allows natural communities to resist change during a disturbance event and reinforces ecosystem resilience, and the ability to recover from disturbance (Halpern 1988). Maintaining current diversity is among the goals of the forest management plan of NBWSP (Minnesota Department of Natural Resources 1998).

The intermediate disturbance hypothesis postulates that communities with infrequent disturbance will gradually lose species diversity through competition with a few aggressive species (Roberts and Gilliam 1995, Hobbs and Huenneke 1992). Maple-basswood forests are often considered stable in time and space because they generally lack large-scale disturbance events (Struik and Curtis 1962). The intermediate disturbance model predicts that maple-basswood forests should become dominated by a few species. Therefore, the observed pattern of wood nettle domination of the understory of maple-basswood forests may be part of the ecosystem's function. The understory of maple-basswood forests may tolerate patches of a dominant species, relying on nearby populations for diversity maintenance and future re-establishment. Fragmentation, however, prevents re-colonization by isolating source populations (Matlack 1994).

Recreational use of public parks causes slow erosion of structural and compositional diversity (Drayton and Primack 1996, Marion and Cole 1996, Adkison and Jackson 1996). To conserve summer species diversity and promote the growth of tree species within NBWSP and other managed areas with wood nettle, management should try to reduce or prevent actions that may lead to increased wood nettle reproduction and vegetative growth. For example, creation of canopy gaps by selective tree removal, for trail creation or maintenance, should be avoided in areas with wood nettle. Management should also limit fragmentation to allow for recolonization.

Removal of wood nettle is not recommended because wood nettle is a native species and its role within maple-basswood forests is largely unknown. For example, wood nettle may enhance vernal species diversity and its presence may slow the potential loss of these species to recreation and fragmentation.

Conclusion

This correlative study found a negative relationship between wood nettle and the diversity and abundance of co-occurring summer species: summer reproducing forb, woody, and graminoid. The reduction of these species may be through occupation of space or competition. Wood nettle's leaf structure and height prevent light transmission to plants below, but competition for nutrients may also be important. Summer-reproducing forb species richness is not related to the mean number of wood nettle stems m 2, but erosion of parcel diversity may occur as chance events remove more sparsely distributed species.

Diversity and abundance of spring-reproducing and ephemeral (minus white trout lily) species increase with the previous year's wood nettle abundance. This positive relationship may be directly related to wood nettle's presence, but may also be an artifact of conditions that promote both types of species. Wood nettle does not overlap phenologically with these species and may displace direct competitors. Furthermore, the timing of nutrient release as each group decays may enhance the other species growth.

The number of tree seedlings and saplings under 150 cm decline with increasing wood nettle density. This reduction appears to affect all species, regardless of shade tolerance. Wood nettle presence does not appear shift the composition of the future overstory to sugar maple. By excluding seedlings and preventing competition, wood nettle may be perpetuating favorable conditions for its own growth.

Clearly, wood nettle is an important component of forests in the Big Woods Ecoregion of Minnesota. Many of the remaining forests in this region have large populations of wood nettle and understanding the role of wood nettle is critical for conservation and restoration efforts. Long-term monitoring and experimentation are needed to understand the causation of the presented relationships between wood nettle and other species in the forest understory.

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Table 3.1 The relationship between species abundance and diversity and wood nettle density as analyzed by a simple negative binomial regression. To test whether a relationship is the result of wood nettle and not general competition, I also compared quadrat diversity to the total number of forb stems (including wood nettle and spring-reproducing forbs).

	Wood nettle							**Total summer forb**		
	# parcels	**Abundance**			**Diversity**			**Diversity**		
		slope		**Sb**	**slope**		**Sb**	**slope**		**Sb**
Summer-reproducing forb species	961	-0.027	*	0.004	-0.012	*	0.003	0.021	*	0.002
Graminoid species	961	-0.035	*	0.015	-0.042	*	0.008	-0.005	*	0.004
Woody species	961	-0.026	*	0.003	-0.021	*	0.002	-0.011	*	0.001

* $P < 0.050$

Table 3.2 The relationship between 1998 wood nettle density and the diversity and abundance of spring forb species as analyzed by a simple negative binomial regression. To test whether a relationship is the result of wood nettle and not general competition, I also compared quadrat diversity to the total number of stems (including wood nettle and spring-reproducing forb species in 1998).

		Wood nettle						**Total summer forbs**		
	# parcels	**Abundance**			**Diversity**			**Diversity**		
		slope		**Sb**	**slope**		**Sb**	**slope**		**Sb**
Ephemeral species (total)	786	-0.015	*	0.003	0.007	*	0.002	0.002		0.001
Ephemeral species w/out white trout lily	786	0.021	*	0.005	0.015	*	0.003	0.005		0.002
Spring-reproducing species	786	0.011	*	0.003	0.006	*	0.002	0.007	*	0.001

* $P < 0.050$

Table 3.3. Plant species encountered during the 1998 summer random survey with a significant relationship to wood nettle. To test for associations I used a chi-square analysis with data reflecting species presence or absence in each quadrat. The value is the Pearson Chi-square value. Correlation examines the relationship between the abundance of wood nettle and each species and I used simple negative binomial regression for analysis.

Summer forb and graminoid species	**Association (XZ)**			**Correlation**		
	relationship		**value**	**slope**		**Sb**
Ranunculus sp.	+	*	4.45	-0.015		0.012
Osmorhiza sp.	+	*	4.76	-0.005		0.012
Athyrium fclix femina	+	*	13.07	-0.031	*	0.012
Impatiens sp. (germinants, spring *1999)*	+	*	33.67	0.033	*	0.009
Impatiens sp. (adults)	+	*	11.35	-0.012		0.013
Cryptotaenia canadensis	+	*	11.1	0.007		0.015
Sanicula sp.	+	*	24.63	0.013		0.010
Circaea lutetiana	0		0.067	-0.019	*	0.007
Adiantum pedatum	-	*	4.34	-0.080	*	0.020
Aralia nudicaulis	-	*	10.2	-0.083	*	0.036
Amphicarpaea bracteata	-	*	34.35	-0.184	*	0.038
Solidago flexicaulis	-	*	10.75	-0.103	*	0.029
Desmodium glutinosum	-	*	46.44	-0.224	*	0.044
Carex sp.	-	*	33	-0.162	0.057	

Woody species	**Association *(XZ)***			**Correlation**		
	relationship		**value**	**slope**		**Sb**
2 year old *Acer saccharum* seedlings	+	*	33.84	0.003		0.006
Total *Acer saccharum*	-	*	0.44	-0.011	*	0.005
Fraxinus nigra	0		0.005	-0.018	*	0.005
Parthenocissus sp.	0		1.48	-0.029	*	0.010
Vitis riparia	0		0.413	-0.093	*	0.040
Rhus radicans	-	*	6.85	-0.129		0.081
Ostrya virginiana	-	*	51.04.	-0.126	*	0.024
Quercus alba group	-	*	7.95	-0.208	*	0.062
Quercus rubra group	-	*	6.79	-0.053	*	0.023
Tilia americana	-	*	9.33	-0.042	*	0.014
Fraxinus pennsylvanica	-	*	85.12	-0.068	*	0.018
Carya cordiformis	-	*	24.79	-0.04	*	0.008
Zanthoxylum americanum	-	*	7.57	-0.136	*	0.053
Prunus sp.	-	*	18.42	-0.074	*	0.014
Ribes sp.	-	*	9.68	-0.027	*	0.012

***** $P < 0.050$**

Table 3.4. Plant species encountered during the 1999 spring random survey with a significant relationship to wood nettle. To test for associations I used a chi-square analysis with data reflecting species presence or absence in each quadrat. The value is the Pearson Chi-square value. Correlation examines the relationship between the abundance of wood nettle and each species and I used single negative binomial regression for analysis.

Ephemeral species	**Association (X2)**			**Correlation**		
	relationship		**value**	**slope**		**Sb**
Claytonia virginica	+	*	6.8	0.128	*	0.031
Cardamine concatentata	+	*	26.13	0.034	*	0.01
Isopyrum biternatum	+	*	12.42	0.079	*	0.015
Dicentra cucullaria	+	*	7.13	-0.021		0.023
Allium triccocum	0		2.22	0.032	*	0.016
Erythronium albidum	0		2.18	-0.026	*	0.005

Spring-reproducing species	**Association (X2)**			**Correlation**		
	relationship		**value**	**slope**		**Sb**
Phlox divaricata	+	*	15.54	0.094	*	0.018
Hydrophyllum virginianum	+	*	47.3	0.015	*	0.005
Asarum canadense	+	*	6.51	0.036	*	0.015
Uvularia grandiflora	+	*	6.62	0.004		0.014
Trillium sp.	+	*	15	0.003		0.011
Viola sp.	+	*	5.63	0.005		0.004
Anemone quinquefolia	-	*	6.21	-0.021	*	0.008
Thalictrum dioicum	-	*	14.01	-0.04	*	0.01

* P < 0.050

Table 3.5 A comparison of the relationships between understory species and wood nettle documented by other studies in Wisconsin and the results from this study.

	Wisconsin	**NBWSP upland populations**	
Species	**Studies**	**Association**	**Correlation**
Agreement			
Osmorhiza sp.	+ 1	+	n.s.
Impatiens sp.	+ 1	+	n.s.
Ranunculus sp.	+ 2	+	n.s.
Cryptotaenia canadensis	+ 2	+	n.s.
Phlox divaricata	+ 2	+	+
Cardamine concatentata	+ 1	+	+
Hydrophyllum virginianum	+ 1	+	+
Circaea lutetiana	- 1	*n.s.*	-
Parthenocissus sp.	- 1	n.s.	-
Carex sp.	- 2	-	n. s.
Erythronium albidum	- 1	n.s.	-
Disagreement			
Claytonia virginica	- 1	+	+
Inconclusive			
Galium aparine	+ 2 / - 1	n. s.	n.s.
Viola sp.	+ 2 / 0 1	+	n.s.
Not enough NBWSP data			
Onoclea sensibilis	+ 2		
Dioscorea villosa	+ 2		
Sambucus sp.	+ 2		
Smilax sp.	+ 2		

1 Smith and Cottam (1967) Upland
2 Menges (1983) Floodplain

Table 3.6 The relationship between tree seedling (0 - 100 cm) and sapling (101 -200 cm) abundance in each height stratum and wood nettle abundance using simple linear regression.

	# parcels	**Sugar maple**			**Other tree seedlings**		
Height (cm)		**slope**		**Sb**	**slope**		**Sb**
0-25	911	-0.014	*	0.002	-0.062	*	0.005
26-50	911	-0.018	*	0.003	-0.047	*	0.004
51-75	911	-0.005	*	0.001	-0.019	*	0.003
76-100	911	-0.003	*	0.001	-0.011	*	0.002
101-150	911	-0.002	*	0.001	-0.005	*	0.002
151-200	911	-0.001		0.0002	-0.001		0.001

APPENDIX A. Scientific names of plant species encountered at Nerstrand Big Woods State Park. Nomenclature follows Gleason and Cronquist (1991).

	Latin Name	Common Name
Ephemeral species		
	Allium triccocum	Wild leek
	Claytonia virginica	Spring beauty
	Cardamine concatentata	Toothwort
	Dicentra cucullaria	Dutchman's breeches
	Erythronium albidum	White trout lily
	Galium aparine	Cleavers
	Isopyrum biternatum	False rue anemone
Spring forb species		
	Allium canadense	Wild onion
	Anemone quinquefolia	Wood anemone
	Arisaema triphyllum	Jack-in-the-pulpit
	Asarum canadense	Wild ginger
	Caulophyllum thalictroides	Blue cohosh
	Galearis spectabilis	Showy orchid
	Geranium maculatum	Wild geranium
	Geum canadense	White avens
	Hepatica acutiloba	Cut-leaved liverwort
	Hydrophyllum virginianum	Virginia water-leaf
	Maianthemum canadense	Mayflower
	Phlox divaricata	Wild blue phlox
	Podophyllum peltatum	Mayapple
	Polygonatum biflorum	Solomon's seal
	Ranunculus abortivus	Aborted buttercup
	Sanguinaria canadense	Bloodroot
	Smilacina racemosa	False Solomon's seal
	Thalictrum dioicum	Early meadow rue
	Trillium sp.	Trillium species
	Uvularia grandiflora	Large-flowered bellwort
	Viola pubescens	Downy violet
	Viola sp.	Violet species
	Zizia aurea	Golden Alexanders
Summer-reproducing forb species		
	Actaea rubra	Red baneberry
	Adinatum pedatum	Maidenhair fern
	Agrimonia cf. striata	Woodland agrimony
	Amphicarpaea bracteata	Hog peanut
	Aquilegia canadensis	Wild columbine
	Aralia nudicaulis	Wild sarsaparilla
	Aralia racemosa	Spikenard
	Aster sp.	Aster species
	Athyrium filix *femina*	Lady fern
	Botrychium virginianum	Rattlesnake fern
	Chenopodium sp.	Lamb's quarters
	Circaea lutetiana	Enchanter's nightshade
	Cryptotaenia canadensis	Honewort
	Desmodium glutinosum	Pointed-leaved tickfoil
	Dioscorea villosa	Wild yam
	Dryopteris sp.	Wood fern
	Erigeron sp.	Fleabane

Eupatorium purpureum	Purple boneset
Galium cocinnum	Shining bedstraw
Galium sp.	Bedstraw species

Appendix A continued

Latin Name	**Common Name**
Galium triflorum	Sweet-scented bedstraw
Impatiens sp.	Touch-me-not
Laportea canadensis	Wood nettle
Matteuccia struthiopteris	Ostrich fern
Monotropa uniflora	Indian pipe
Onoclea sensibilis	Sensitive fern
Orchidaceae	Orchid species
Osmorhiza sp.	Sweet cicely
Osmunda claytoniana	Interrupted fern
Panax quinquefolia	American ginseng
Pastinaca sativa	Wild parsnip
Phryma leptostachya	Lopseed
Pilea pumila	Clearweed
Plantago major	Common plantain
Polygonum amphibium	Smartweed
Pteridium aquilinum	Bracken fern
Ranunculus sp.	Buttercup species
Rudbeckia laciniata	Goldenglow
Sanicula sp.	Snakeroot
Smilax sp.	Green briarers
Solidago flexicaulis	Zigzag goldenrod
Taraxacum officinale	Dandelion
Urtica dioica	Stinging nettle

Graminoid species

Carex sp.	Sedge species
Elymus hystrix	Bottle-brush grass
Oryzopsis asperifolia	Mountain-rice grass

Woody species

Acer negundo	Boxelder
Acer rubrum	Red maple
Acer saccharum	Sugar maple
Carya cordiformis	Yellow-bud hickory
Celtis occidentalis	Hackberry
Cornus sp.	Dogwood species
Crataegus sp.	Hawthorne species
Fraxinus nigra	Black ash
Fraxinus pennsylvanica	Green ash
Juglans cinerea	Butternut
Lonicera sp.,	Honeysuckle species
Menispermum canadense	Moonseed
Ostrya virginiana	Ironwood
Parthenocissus sp.	Virginia creeper
Populus deltoides	Cottonwood
Populus trernuloides	Aspen
Prunus sp.	Cherry species
Quercus alba group	White oak group
Quercus rubra group	Red oak group

Quercus sp.	Oak species
Rhamnus cathartica	European buckthorn
Rhus radicans	Poison Ivy
Ribes sp.	Gooseberry species
Rubus sp.	Raspberry

Appendix A continued

Latin Name	**Common Name**
Sambucus sp.	Elderberry species
Tilia americana	Basswood
Ulmus sp.	Elm species
Vitis riparia	Wild grape
Zanthoxylum americanum	Prickly ash

APPENDIX B. Summary of wooded parcels at Nerstrand Big Woods State Park qualitatively assessed in 1997 for wood nettle coverage.

	Section	Parcel	General land-use history	Year of last use	Commercial harvest	Wood nettle coverage
*	9	1	Selectively harvested	1964	No	5
	9	2	Selectively harvested ,	1968	No	5
	9	3	Selectively harvested	1959	Yes	2
*	9	4	Selectively harvested	1957	Yes	4
	9	5	Clear-cut, sheep grazing	1945	Yes	3
	9	6	Selectively harvested	1958	No	5
	9	7	Selectively harvested	1959	No	5
*	9	8	Clear-cut, sheep grazing	1951	Yes	3
	9	9	Clear-cut, sheep grazing	1945	Yes	1
	9	10	Selectively harvested	1962	No	2
*	9	11	Clear-cut, sheep grazing	1945	Yes	1
*	9	12	Clear-cut, sheep grazing	1945	Yes	3
	9	12.5	Clear-cut, sheep grazing	1938	Yes	2
	9	13	Clear-cut, sheep grazing	1938	No	2
	9	13.5	Clear-cut, sheep grazing	1945	No	0
	9	21	Clear-cut	1940	No	1
	9	22	Selectively harvested	1943	No	2
	9	24	Selectively harvested	1942	No	2
	9	25	Selectively harvested	1944	No	3
*	9	31	Selectively harvested	1940	No	1
	9	32	Clear-cut, cattle grazing	1940	Yes	0
	9	33	Selectively harvested	1954	Yes	0
	9	35	Selectively harvested	1977	Yes	2
*	9	36	Selectively harvested	1969	No	2
*	9	37	Selectively harvested	1969	NO	1
	9	38	Selectively harvested	1954	No	1
*	9	39	Selectively harvested	1968	No	0
	9	40	Cultivated	1972	No	0
	9	47	Clear-cut, cattle grazing	1952	Yes	0
	9	50	Selectively harvested	1935	No	2
	9	51	Selectively harvested	1977	No	5
*	9	52	Selectively harvested	1974	No	4
+	9	53	Selectively harvested	1958	No	4
+	9	54	Selectively harvested	1958	No	5
	9	55	Selectively harvested	1979	No	4
	9	55.5	Selectively harvested	1979	No	2
+	9	56	Selectively harvested	1986	No	3
	9	57	Selectively harvested	1977	No	0
	9	58	Selectively harvested	1988	No	3
	9	59	Selectively harvested	1972	No	2
	9	60	Selectively harvested	1988	Yes	2
+	9	61	Selectively harvested	1979	No	2
	9	62	Selectively harvested	1972	No	2

+ Parcels randomly sampled summer 1998 only

* Parcels randomly sampled summer 1998 and spring 1999

Coverage categories: 5 = >75%; 4= 50-74%; 3= 25-49%; 2= 5-24%; 1= 1-4%; 0= no wood nettle

Appendix B continued.

	Section	Parcel	General land-use history	Year of lastuse	Commercial harvest	Wood nettle coverage
*	16	19	Selectively harvested	1942	No	5
*	16	20	Selectively harvested	1942	No	5
*	16	21	Selectively harvested	1948	No	4
	16	22.5	Clear-cut, sheep grazing	1940	Yes	3
	16	23	Selectively harvested	1940	No	1
	16	24	Selectively harvested	1942	No	1
	16	26	Selectively harvested	1942	No	1
	16	27	Selectively harvested	1942	No	1
	16	28	Selectively harvested	1972	No	1
*	16	29	Selectively harvested	1942	No	1
*	16	30	Clear-cut	1940	No	2
	16	30.5	Selectively harvested	1939	No	1
	16	31	Selectively harvested	1942	No	1
*	16	31.5	Selectively harvested	1942	No	1
	16	32	Clear-cut	1937	No	1
*	16	33	Selectively harvested	1942	No	2
*	16	34	Selectively harvested	1942	No	5
	16	35	Selectively harvested	1954	Yes	3
	16	36	Selectively harvested	1942	No	5
	16	37	Selectively harvested	1954	Yes	5
*	16	38	Selectively harvested		No	3
	16	38.5	Selectively harvested	1942	No	1
*	16	39	Selectively harvested	1942	No	1
	16	40	Selectively harvested	1942	No	1
	16	44.5	Clear-cut, cattle grazing	1955	Yes	1
	16	45	Selectively harvested	1954	Yes	1
*	16	46	Selectively harvested	1942	No	1
	16	47	Selectively harvested	1942	No	3
*	16	48	Selectively harvested	1942	No	5
	16	49	Selectively harvested	1942	No	5
	16	50	Selectively harvested	1954	Yes	5
	16	51	Selectively harvested	1942	No	5
	16	52	Selectively harvested	1942	No	1
	16	53	Selectively harvested	1942	No	1
*	16	54	Selectively harvested	1942	No	4
	16	55	Selectively harvested	1942	No	4
*	16	56	Selectively harvested	1935	No	4
	16	60	Selectively harvested	1940	No	4
	16	61	Selectively harvested	1942	No	1

APPENDIX C. Environmental data from random surveys, Summer 1998.

Section	Parcel	General land-use history	Area (ha)	A/E soil horizon thickness	Years since disturbance	Weighted canopy openness (%)	Total daily photosynthetic photon flux density (mol nit day')
9	1	Selective Harvest	6	42	34	6.02	2.28
9	4	Selective Harvest	8	22	41	2.42	0.79
9	8	Clear-cut, sheep grazing	4	47	3.19	1.21	
9	11	Clear-cut, sheep grazing	2	53	4.18	1.63	
9	12	Clear-cut, sheep grazing	4.5	34	53	2.99	2.87
9	31	Selective Harvest	4	21	58	2.80	1.09
9	36	Selective Harvest	1.2	20	29	4.15	1.78
9	37	Selective Harvest	1.2	30	29	4.48	1.65
9	39	Selective Harvest	1.2	15.5	30	3.37	1.30
9	52	Selective Harvest	4	23	24	2.42	0.94
9	53	Selective Harvest	4	38	40	3.76	1.41
9	54	Selective Harvest	6	35	40	5.60	1.57
9	56	Selective Harvest	1.5	38	12	5.35	2.47
9	61	Selective Harvest	6	12	19		
16	7	Selective Harvest	4	18	44	1.13	0.34
16	10	Clear-cut, cattle grazing	2	29	27	1.63	0.54
16	13	Selective Harvest	2	25	56-	0.93	0.44
16	16	Selective Harvest	2	26	56	2.92	0.80
16	18	Selective Harvest	2	24	56	3.92	1.81
16	19	Selective Harvest	1	26	56	3.24	1.51
16	20	Selective Harvest	1	25	56	3.24	1.38
16	21	Selective Harvest	1.25	26	50	2.38	0.86
16	29	Selective Harvest	4		56		
16	30	Clear-cut	2	25	58	2.78	1.10
16	31.5	Selective Harvest	1	28	56	0.48	0.19
16	33	Selective Harvest	2	21	56	0.55	0.20
16	34	Selective Harvest	2	48	56	2.49	1.03
16	38	Selective Harvest	2	26		2.49	0.99
16	39	Selective Harvest	2	24	56	1.28	0.69
16	46	Selective Harvest	4	32	56	3.09	0.91
16	48	Selective Harvest	1	51	56	3.91	1.63
16	54	Selective Harvest	4.5	30	56	2.83	0.73
16	6	Selective Harvest	2	20	63	0.92	0.54

APPENDIX D. Structural summary data from random surveys, Summer 1998

		Canopy (>25 cm dbh)			Sub-canopy (10-25 cm dbh)			Total canopy (>l0cm dbh)			Sapling layer (>2 m, <10cm dbh) .			Total stand (> 2m)		
Section	Parcel	# species	BA	Tree ha'	# species	BA	Tree ha'	# species	BA	Tree ha'	# species	BA	Tree ha'	# species	BA	Tree ha'
			(n f2 ha-')				(ni 2 ha')			On Z ha')					(m 2 ha')	
		(ni 2 ha')														
9	1	1	26.20	200.0	0	0.00	0.0	1	26.20	200.0	1	0.16	66.7	2	26.35	266.7
9	4	0	0.00	0.0	1	3.02	160.0	2	110.98	560.0	1	0.23	80.0	3	111.20	640.0
9	8	2	30.86	296.3	3	10.04	518.5	4	40.32	814.8	2	1.40	370.4	6	41.72	1185.2
9	11	2	22.55	206.9	3	7.67	344.8	5	30.22	620.7	2	1.70	896.6	6	31.92	1517.2.
9	12	3	77.16	206.9	4	9.79	551.7	6	86.95	896.6	4	1.87	827.6	8	88.82	1724.1
9	31	2	13.24	250.0	0	0.00	0.0	2	13.24	250.0	6	1.80	1250.0	6	15.05	1500.0
9	36	1	3.82	66.7	0	0.00	0.0	1	3.82	66.7	3	1.-03	533.3	3	4.85	600.0
9	39	2	62.75	466.7	2	7.70	333.3	3	70.45	800.0	5	1.36	666.7	6	71.81	1466.7
9	52	3	82.28	333.3	5	8.92	533.3	5	91.73	866.7	6	3.17	2400.0	6	94.90	3266.7
9	53	3	81.22	333.3	3	8.32	466.7	5	89.54	800.0	4	1.80	800.0	6	91.35	1600.0
9	54	0	0.00	0.0	3	6.80	285.7	3	6.80	285.7	4	3.10	1428.6	5	9.90	1714.3
9	56	5	58.12	600.0	2	5.95	333.3	5	64.08	933.3	5	1.47	1466.7	6	65.54	2400.0
9	61	3	29.46	250.0	3	5.00	333.3	5	34.47	583.3	5	1.43	1583.3	8	35.90	2166.7
16	7	4	28.50	533.3	3	14.80	466.7	4	51.70	1200.0	4	2.74	1000.0	7	54.44	2200.0
16	10	1	26.54	69.0	5	25.83	1241.4	6	52.37	1310.3	5	4.22	1655.2	7	56.59	2965.5
16	13	5	223.56	800.0	2	3.06	133.3	5	226.62	933.3	4	1.47	1133.3	6	228.09	2066.7
16	16	1	12.32	66.7	1	2.85	133.3	2	15.17	200.0	2	0.32	266.7	3	15.48	466.7
16	18	2	72.24	266.7	0	0.00	0.0	2	72.24	266.7	2	0.87	600.0	3	73.11	866.7
16	19	3	137.48	413.8	1	3.12	69.0	3	140.60	482.8	1	0.22	206.9	3	140.82	689.7
16	20	2	36.90	266.7	3	7.87	266.7	4	44.76	600.0	2	1.62	466.7	4	46.38	466.7
16	21	4	64.04	275.9	1	0.54	69.0	4	64.58	413.8	1	1.94	1241.4	4	66.52	1655.2
16	29	3	40.68	416.7	1	2.25	250.0	3	42.93	666.7	2	0.34	250.0	5	43.27	916.7
16	30	3	28.37	333.3	2	5.54	200.0	4	36.45	533.3	2	0.03	200.0	6	36.47	733.3
16	31.5	3	152.06	600.0	2	6.23	266.7	3	158.29	866.7	5	1.06	1400.0	6 .	159.36	2266.7
16	33	2	33.02	133.3	2	5.13	266.7	3	38.15	400.0	3	0.20	1333.3	5	38.35	1733.3
16	34	1	0.01	66.7	0	0.00	0.0	1	0.01	66.7	1	0.01	133.3	2	0.02	266.7
16	38	2	16.72	142.9	0	0.00	0.0	2	12.93	357.0	4	0.58	357.1	5	13.51	3785.7
16	39	2	15.58	142.9	1	0.68	71.4	2	16.26	214.3	1	16.26	500.0	3	32.51	714.3
46	46	4	61.87	357.1	2	2.40	142.9	5	64.27	500.0	3	2.13	1285.7	6	66.40	1785.7
16	48	2	55.04	413.8	1	1.92	137.9	2	56.96	551.7	2	0.74	1034.5	3	57.70	1586.2
16	54	4	59.52	400.0	2	10.13	480.0	5	69.65	880.0	4	0.34	880.0	7	69.99	1760.0
16	56	2	66.32	518.5	3	10.63	518.5	3	76.95	1037.0	3	1.09	1185.2	3	78.04	2222.2

APPENDIX E Wood nettle summary data from random surveys, Summer 1998

			Mean number of wood nettle stems m^{-2}							Wood nettle
Section	**Parcel**	**General land-use history**	**Total Nettles**	**Non-reproductive**	**Reproductive**	**Male**	**Female**	**Hermaphroditic**	**Seedling**	**frequency**
9	1	Selective Harvest	21.53	16.63	4.90	2.67	0.50	1.73	5.03	0.80
9	4	Selective Harvest	9.32	7.12	2.20	1.04	0.20	0.96	30.88	0.84
9	8	Clear-cut, sheep grazing	6.81	5.63	1.19	0.44	0.07	0.67	1.67	0.52
9	11	Clear-cut, sheep grazing	1.62	1.59	0.03	0.03	0.00	0.00	0.03	0.14
9	12	Clear-cut, sheep grazing	1.59	1.24	0.34	0.07	0.10	0.17	1.69	0.38
9	31	Selective Harvest	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
9	36	Selective Harvest	0.37	0.30	0.07	0.03	0.00	0.03	0.00	0.13
9	37	Selective Harvest	0.42	0.39	0.03	0.00	0.03	0.00	0.45	0.12
9	39	Selective Harvest	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
9	52	Selective Harvest	7.53	6.53	1.00	0.67	0.03	0.30	6.00	0.73
9	53	Selective Harvest	7.10	5.13	1.77	0.83	0.27	0.70	2.27	0.50
9	54	Selective Harvest	5.96	5.07	0.89	0.36	0.21	0.32	5.50	0.57
9	56	Selective Harvest	3.63	2.53	1.10	0.37	0.17	0.57	0.00	0.33
9	61	Selective Harvest	0.29	0.25	0.04	0.00	0.04	0.00	0.33	0.13
16	7	Selective Harvest	0.47	0.33	0.13	0.00	0.07	0.07	1.60	0.10
16	10	Clear-cut, cattle grazing	0.59	0.45	0.03	0.03	0.00	0.10	0.34	0.17
16	13	Selective Harvest	9.47	6.93	2.53	0.73	0.87	0.93	17.73	0.83
16	16	Selective Harvest	6.53	5.13	1.40	0.43	0.23	0.73	2.33	0.57
16	18	Selective Harvest	16.33	13.53	2.80	0.77	0.33	1.70	11.90	0.97
16	19	Selective Harvest	13.97	11.14	2.83	0.59	0.59	1.66	13.03	0.86
16	20	Selective Harvest	13.41	10.48	2.93	0.70	0.70	1.54	10.35	0.87
16	21	Selective Harvest	20.52	16.62	3.90	0.72	0.62	2.55	16.55	0.93
16	29	Selective Harvest	0.08	0.04	0.04	0.00	0.00	0.04	0.00	0.04
16	30	Clear-cut	3.60	3.20	0.40	0.23	0.03	0.13	0.13	0.37
16	31.5	Selective Harvest	1.87	1.80	0.07	0.03	0.03	0.00	0.00	0.33
16	33	Selective Harvest	7.57	5.67	1.90	0.47	0.53	0.90	14.83	0.80
16	34	Selective Harvest	22.90	18.03	4.87	1.53	0.77	2.57	35.80	0.97
16	38	Selective Harvest	12.04	10.29	1.75	0.46	0.25	1.04	10.86	0.61
16	39	Selective Harvest	0.57	0.43	0.14	0.04	0.00	0.11	0.00	0.25
16	46	Selective Harvest	0.39	0.29	0.11	0.00	0.04	0.07	0.21	0.11
16	48	Selective Harvest	11.21	7.10	4.10	0.62	1.62	1.86	11.72	1.00
16	54	Selective Harvest	2.28	1.48	0.80	0.16	0.12	0.52	0.00	0.48
16	56	Selective Harvest	13.22	8.81	4.41	0.89	0.78	2.74	14.52	0.93

APPENDIX F Species summary data from random surveys, Summer 1998

				Mean number of stems m^{-2}				Mean number of species m^{-2}				Species richness (stand)	
Section	Parcel	General land-use history	# of plots	Summer forb	Woody	Graminoid	Total	Summer forb	Woody	Graminoid	Total	Total	Summer forb
9	1	Selective Harvest	30	6.20	4.53	1.17	11.90	2.83	1.13	0.37	4.33	26	17
9	4	Selective Harvest	25	15.40	7.72	0.28	23.40	5.76	2.88	0.28	8.92	48	32
9	8	Clear-cut, sheep grazing	27	17.81	4.26	0.78	22.85	6.19	1.96	0.44	8.59	45	30
9	11	Clear-cut, sheep grazing	29	16.66	11.62	0.55	28.83	6.17	4.55	0.38	11.10	61	34
9	12	Clear-cut, sheep grazing	29	16.59	10.76	0.31	27.66	6.24	4.17	0.24	10.66	57	35
9	31	Selective Harvest	24	19.46	8.58	4.21	32.25	4.83	3.58	0.58	9.00	54	30
9	36	Selective Harvest	30	15.03	15.27	0.87	31.17	4.30	3.90	0.43	8.63	53	29
9	37	Selective Harvest	33	28.03	9.33	4.09	41.45	6.45	2.82	0.58	9.85	60	39
9	39	Selective Harvest	30	18.57	9.10	1.80	29.47	5.00	4.17	0.60	9.77	58	30
9	52	Selective Harvest	30	21.10	7.57	0.43	29.10	5.80	2.77	0.17	8.73	54	35
9	53	Selective Harvest	30	22.47	10.20	0.63	33.30	6.40	3.47	0.33	10.20	60	36
9	54	Selective Harvest	28	16.82	6.32	0.21	23.36	4.82	2.29	0.14	7.25	45	27
9	56	Selective Harvest	30	17.97	10.57	1.93	30.47	4.87	3.60	0.70	9.17	49	28
9	61	Selective Harvest	24	18.96	14.08	1.21	34.25	5.67	4.96	0.58	11.21	53	29
16	7	Selective Harvest	30	17.37	11.73	0.97	30.07	4.83	3.53	0.47	8.83	45	26
16	10	Clear-cut, cattle grazing	29	13.93	9.79	2.76	26.48	4.66	3.28	0.79	8.72	45	25
16	13	Selective Harvest	30	16.73	14.30	1.63	32.67	4.70	3.10	0.30	8.10	46	28
16	16	Selective Harvest	30	16.30	9.80	0.53	26.63	3.77	2.67	0.20	6.63	36	21
16	18	Selective Harvest	30	14.10	9.70	0.17	23.97	4.13	2.70	0.07	6.90	35	21
16	19	Selective Harvest	29	15.24	12.24	0.10	27.59	3.79	2.72	0.10	6.62	41	26
16	20	Selective Harvest	30	14.48	9.50	0.37	24.35	4.26	2.15	0.17	6.59	46	28
16	21	Selective Harvest	29	17.76	4.24	0.76	22.76	4.38	1.59	0.24	6.21	41	25
16	29	Selective Harvest	24	9.75	18.58	2.25	30.58	3.67	5.38	0.67	9.71	45	20
16	30	Clear-cut	30	15.67	11.47	0.83	27.97	3.60	3.23	0.30	7.13	44	24
16	31.5	Selective Harvest	30	18.97	10.50	0.83	30.30	5.63	3.73	0.40	9.77	47	27
16	33	Selective Harvest	30	17.37	13.37	0.97	31.70	5.43	3.27	0.20	8.90	37	23
16	34	Selective Harvest	30	11.50	7.77	1.93	21.20	4.10	2.03	0.23	6.37	41	27
16	38	Selective Harvest	28	19.25	16.29	0.50	36.04	5.96	4.14	0.36	10.46	52	32
16	39	Selective Harvest	28	16.57	19.68	3.14	39.39	4.29	4.32	0.43	9.04	47	27
16	46	Selective Harvest	28	16.61	10.93	0.43	27.96	3.57	3.89	0.29	7.75	44	23
16	48	Selective Harvest	29	24.79	10.48	1.21	36.48	6.52	2.83	0.45	9.79	45	29
16	54	Selective Harvest	25	13.36	14.60	0.32	28.28	4.60	3.40	0.28	8.28	46	28
16	56	Selective Harvest	27	14.78	10.52	0.85	26.15	4.59	2.78	0.26	7.63	48	29

APPENDIX G Forb species summary data from random surveys, Spring 1999.

				Mean number of stems m^{-2}			Mean number of species m^{-2}			Species richness (stand)		
Section	**Parcel**	**General land-use History**	**# of Plots**	**Ephemeral**	**Spring**	**Total**	**Ephemeral**	**Spring**	**Total**	**Ephemeral**	**Spring**	**Total**
9	1	Selective Harvest	28	68.07	8.50	84.71	3.04	2.07	6.39	8	11	22
9	4	Selective Harvest	25	36.16	13.44	61.16	1.92	3.00	6.60	5	11	22
9	8	Clear-cut, sheep grazing	27	44.37	9.33	60.78	2.81	2.63	6.85	8	11	25
9	11	Clear-cut, sheep grazing	28	120.89	6.07	129.21	2.18	1.75	4.93	6	8	20
9	12	Clear-cut, sheep grazing	27	44.67	14.96	72.74	2.30	3.04	7.48	5	13	27
9	31	Selective Harvest	22	46.64	10.82	59.18	1.50	3.09	5.09	4	12	22
9	36	Selective Harvest	29	68.83	10.14	81.66	1.52	2.48	4.59	5	13	24
9	37	Selective Harvest	29	75.24	12.24	89.72	1.24	2.28	3.90	3	11	19
9	39	Selective Harvest	29	88.72	12.45	101.76	1.38	1.83	3.31	3	9	14
9	52	Selective Harvest	29	50.90	11.90	77.59	1.69	2.38	6.34	4	12	27
16	7	Selective Harvest	27	108.22	9.63	119.96	1.52	1.70	3.70	5	9	16
16	10	Clear-cut, cattle grazing	27	32.74	8.37	43.78	1.15	1.56	3.37	3	7	16
16	13	Selective Harvest	22	55.14	11.36	67.32	1.32	2.36	4.09	2	9	14
16	16	Selective Harvest	30	29.87	11.83	42.90	1.23	2.20	3.77	4	9	18
16	18	Selective Harvest	30	39.33	19.73	60.30	1.33	2.87	4.47	2	10	16
16	19	Selective Harvest	29	42.24	16.14	60.00	1.72	2.83	5.14	4	11	21
16	20	Selective Harvest	27	49.15	13.15	64.59	1.59	2.15	4.07	4	11	18
16	21	Selective Harvest	30	29.97	17.20	51.50	1.17	2.90	5.03	3	14	24
16	29	Selective Harvest	25	112.68	5.00	117.84	1.64	1.84	3.52	5	9	15
16	30	Clear-cut	30	55.80	7.67	63.90	1.53	1.87	3.70	5	10	19
16	31.5	Selective Harvest	29	49.41	20.03	69.86	1.72	3.21	5.21	5	13	20
16	33	Selective Harvest	29	33.45	12.62	46.52	1.55	2.52	4.31	4	10	16
16	34	Selective Harvest	30	31.80	7.27	39.57	1.77	2.10	4.13	5	11	19
16	38	Selective Harvest	27	52.33	18.07	72.33	2.56	3.26	6.44	6	13	25
16	39	Selective Harvest	28	87.04	7.18	94.29	2.00	1.82	3.89	5	7	14
16	46	Selective Harvest	28	44.86	10.54	55.39	1.46	2.46	3.93	4	12	16
16	48	Selective Harvest	30	50.67	22.97	77.43	1.93	3.70	6.80	5	13	25
16	54	Selective Harvest	24	57.33	15.79	73.54	1.42	3.63	5.29	4	15	22
16	56	Selective Harvest	28	54.21	18.32	74.86	1.50	3.79	6.18	4	13	24

APPENDIX H

Wood nettle population regulation and white-tailed deer

Introduction

A recent study on deer browse on herbaceous species in maple-basswood forests found that white-tailed deer *(Odocoileus virginianus)* preferentially chooses wood nettle stems as a summer food source (Augustine 1997). The present study attempts to replicate Augustine' (1997) results through intensive sampling of several populations within one of Augustine's low deer density study sites. (Nerstrand Big Woods State Park).

Furthermore, Augustine (1997), by using a theoretical predator/prey model, claimed that white-tailed deer pose a severe limitation to wood nettle growth and proliferation. A brief review of the literature on reproduction and defense mechanisms in wood nettle and stinging nettle casts doubt on this conclusion.

Methods

I randomly sampled the plant populations in the selected 33 ownership parcels between July 10 and August 15, 1998. 1 generated thirty sets of coordinate numbers and determined quadrat location in the field using meter tapes and a compass. The origin of each coordinate system is at one of the professionally surveyed property corners. I eliminated quadrats from the survey if they occurred on a hiking trail, resulting in 24 to 30 1-m2 quadrats surveyed for each parcel. In the 33 sampled parcels, I sampled 961 quadrats.

Within each quadrat, I measured the height in centimeters, the reproductive status, and possible deer browse history of each individual wood nettle stem. If a stem is browsed or brokenoff it will re-grow and branch from the injury point (Menges 1983, Augustine 1997). 1 assumed all injuries to be caused by browse because other types seemed rare. I did not attempt to estimate the age of the injury.

Augustine's (1997) study examines many stands with varying deer densities and uses deer density as a factor in analysis. My study examined many wood nettle populations within a single "low deer-density" site. I assume deer density is constant throughout the entire park and can eliminate this factor from analysis.

Results

In Nerstrand Big Woods State Park (NBWSP), white-tailed deer browsed zero to 100 percent of stems in each quadrat with wood nettle. In each parcel, the percent of wood nettle stems browsed by white-tailed deer varied between zero to 37.5 percent.

Augustine (1997) found that, when analyzed at the parcel level, deer browse showed a steeply saturating type II functional response to wood nettle availability. That is, deer eat a greater proportion of available wood nettle stems when wood nettle is sparse. This indicates that although understory forbs are a relatively small part of a deer's diet, they preferentially feed on wood nettle by seeking it out, even when it is rare (Augustine 1997). Both my stand and quadrat data support this conclusion (Figures H.1 and H.2).

Discussion

Land-use, disturbance activities, and environmental conditions created the initial wood nettle populations earlier in the twentieth century when white-tailed deer populations in Minnesota were very low. Conservation efforts and favorable landscape configurations have allowed deer populations to increase in some areas and browse has become a more important factor in forest understories (Stromayer and Warren 1997).

Augustine (1997) employed the Noy-Meir (1975) model of alternative stable states, which finds that four initial combinations of predator and prey population sizes lead to two sizes of plant population. In low predator/high prey and low predator/low prey conditions, the herbivore does not regulate plant populations. In high predator/high prey conditions, the effect of herbivore is not enough to overwhelm the number of prey and regulate them. Only in the high predator/very low prey condition do herbivores regulate plant populations.

Although some assumptions of the theoretical model are violated', Augustine's (1997) application of the model provides convincing evidence that high whitetailed deer populations do regulate low wood nettle populations. However, the application of theoretical predator/prey models, such as the Lotka-Volterra and Noy-Meir models, assumes a stable plant population and overlooks factors that cause variation in plant populations (Crawley 1988). Inter- and intraspecific competition, variation in nutrient supply, and canopy heterogeneity are environmental conditions that also contribute to differences in population growth rates and this can affect the impact of herbivory on a population. For example, Bastrenta *et* al. (1995) found differences in environmental conditions, rather than herbivore variation, caused differences in *Anthyllis* vuleraria population growth.

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[1] For example, the Noy-Meir (1975) theoretical model is based on a simple system with one herbivore predator and one plant prey species. Augustine (1997) justifies the violation of this assumption because wood nettle is a small part of the summer diet of white-tailed deer.

Most importantly, wood nettle has a defense mechanism that may influence the rate of its consumption of deer. Augustine's (1997) fails to explore this complication in the antagonistic relationship between wood nettle and white-tailed deer.

Wood nettle is in the family Urticacae, which is characterized by urticating hairs, or stinging trichomes. The chemicals present in wood nettle's urticting hairs are histamine, acetylcholine, and 5-hydroxytryptamine (5-HT) (Hardin and Arena 1969). Several studies of wood nettle and stinging nettle found that the defensive hairs do not inhibit invertebrate 2 herbivory and are, therefore, likely to deter vertebrate herbivores (Tuberville et al. 1996).

After vertebrate herbivore damage to stem and leaf tissue, nettle species typically increase hair density on regrowth (Pullin and Gilbert 1989, Mutikainen and Wells 1995). The increase in density deters further consumption by mammals (Pollard and Briggs 1984). Populations under heavy grazing pressure exhibit higher number of stinging trichomes, but it is unclear whether individuals retain the defense over time (Pullin and Gilbert 1989). Qualitatively, I have observed that some populations have many more hairs than others do, possibly indicating a longer history of deer browse pressure.

Augustine's (1997) data offer some support for this hypothesis. Only one study site qualified as a high deer/low nettle stand, and transplants were necessary there to conduct exelosure experiments. In this stand, the unprotected transplants had much lower rate of increase than protected transplants. He does not identify the source population of the transplants, but presumably, they are from a less-well defended population. One of the two small nontransplant populations showed no differences between the protected and unprotected treatments and the other had only a slight increase in the growth rate of protected treatment. The resident populations may have experienced many years of browse and developed more stinging hairs, which deters deer browse.

Augustine (1997) finds that plants in unprotected treatments are less likely to reproduce sexually. There is a trade-off between sexual reproduction and urticating hair production because both activities require resources (Mutikainen and Walls 1995). This trade-off may insure greater long-term survival for wood nettle in a particular forest. Since clonal genets can live for many years, simple survival of established individuals is an important contribution to demographic stability (Bishir and Namkoong 1992, Damman and Cain 1998).

There may also be differences in defense among the reproductive classes. For example, the increase in the number of urticating hairs is greater in female stinging nettle plants, presumably because these plants invest more in reproduction and have more to lose if browsed (Mutikainen et al. 1994). This may be particularly important as seeds ripen, I have noticed that deer do not eat female flowers with developed (black) seeds. Instead, they eat all the plant's leaves and leave a naked stalk with a flower head on it.

Conclusion

Herbivory studies often examine population regulation through herbivore preference and population dynamics without consideration of plant population dynamics driven by environmental variation and competition (Crawley 1988). Wood nettle, furthermore, possesses a defense mechanism that may deter vertebrate herbivores and influence palatability among populations (Pullin and Gilbert 1989, Mutikainen and Wells 1995, Pollard and Briggs 1984). The alternate stable-states and population regulation described by Augustine (1997) are too simplistic and do not fully describe the dynamics of wood nettle in forest understories.

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[2] In NBWSP, invertebrate herbivores of wood nettle include slugs, least one stinkbug species *(Euschistus sp.),* and possibly a gall-producing fly.

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Figure H.1. Percent wood nettle stems browsed by white-tailed deer within each quadrat in the summer of 1998.

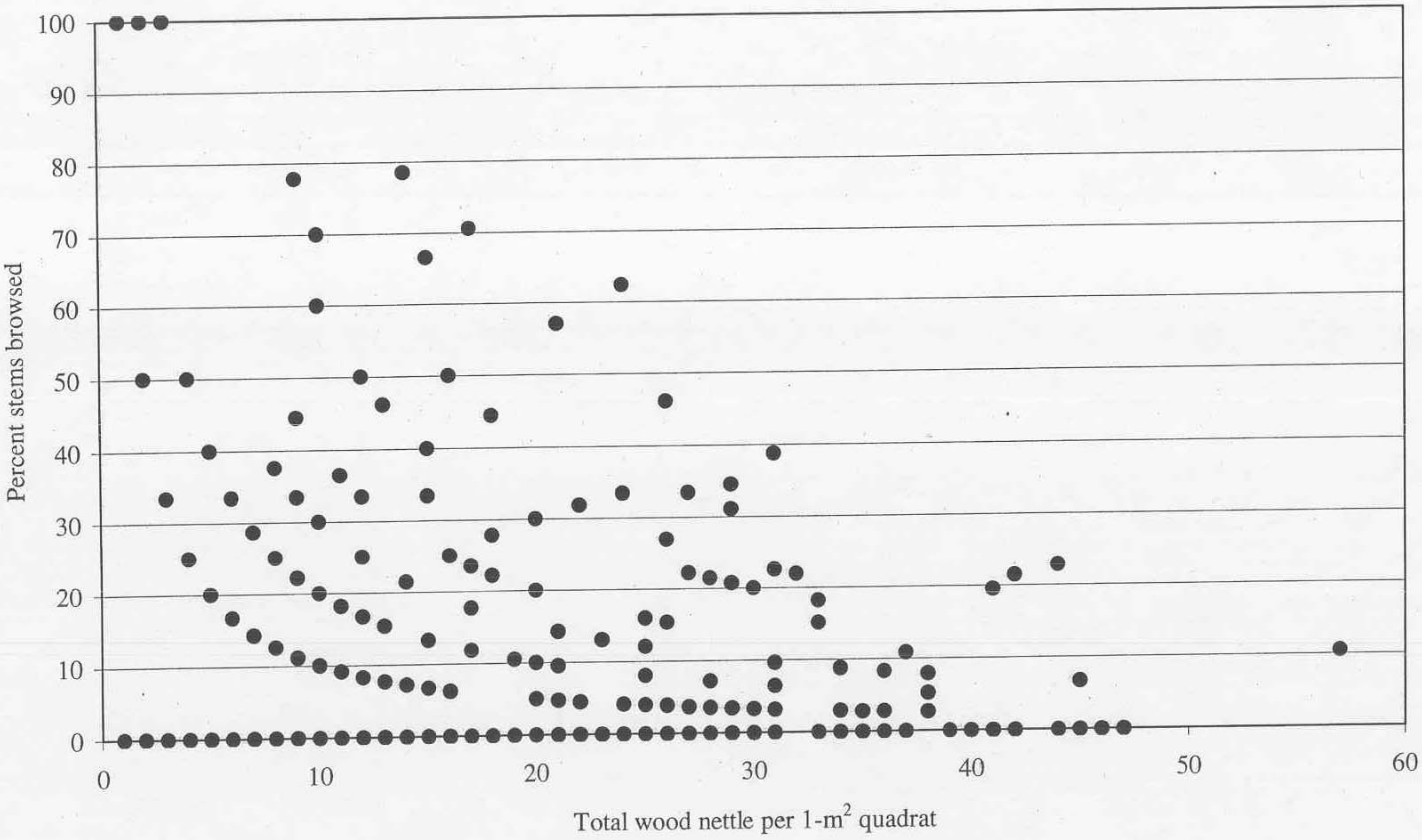
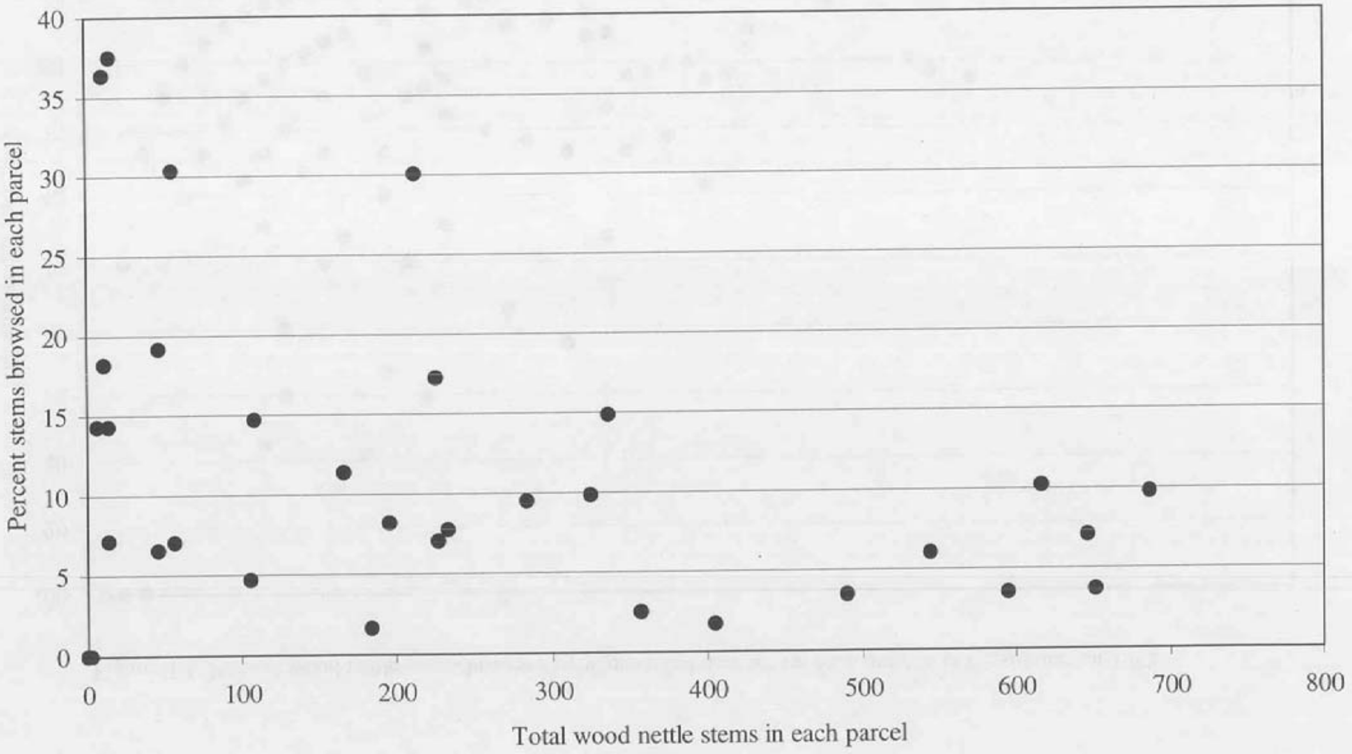


Figure H.2 Percent wood nettle stems browsed by white-tailed deer in each parcel in the summer of 1998



APPENDIX I

Phenology and other characteristics of wood nettle in southeast Minnesota

There is a general scarcity of information on the life history characteristics and demographic parameters of understory plants (Bierzychudek 1982). These characteristics describe how individual plant species interact with their environment, respond to disturbance events, and compete with other organisms. This data deficiency retards research, conservation, and restoration efforts. For example, proper preserve design should account for the dispersal of seeds within the boundaries.

This appendix reports demographic parameters measured from wood nettle populations in southeast Minnesota. In his 1983 study of wood nettle biomass allocation, Menges measured many parameters, including reproductive effort, phenology, and height ranges for each reproductive strategy, but these characteristics can vary throughout a species' geographic range.

Methods

Study sites

The permanent phenology plots, pilot surveys, and the random surveys are from wood nettle populations in upland forests in Nerstrand Big Woods State Park (NBWSP) in eastern Rice County, Minnesota (44° 20' N, 93° 06' W). I also randomly sampled in two isolated forest stands (Taylor's and Diamond Creek Woods) in Elm Creek Park Reserve, Hennepin County, Minnesota (44° 11' N 93° 29' W) selected for their "old-growth" status, high density of wood nettle populations, and history of vegetation surveys (Daubenmire 1936, Bray 1956, Rogers 1981, and Augustine 1997).

Permanent phenology plots

In April of 1997, I randomly established four transects in a single, selectively harvested, land-use parcel (section 9, parcel 1) to become familiar with the reproductive biology, phenology, and survival of wood nettle. Along each 40-m transect I randomly placed 10 1-m2 quadrats and marked each plot corner with a plastic flag. One week after establishment, two plots could not be relocated, resulting in 38 sampled quadrats.

I conducted a census of wood nettle seedlings and adult wood nettle stems, on April 27, 1997. I continued this census weekly from May 11 to July 27 and every 2 weeks From July 27 to

September 7, 1997. I noted gender expression on the wood nettle plants between June 29 through September 7.

Random surveys

I randomly sampled the plant populations in the selected 33 ownership parcels between July 10 and August 15, 1998. I generated thirty sets of coordinate numbers and determined quadrat location in the field using meter tapes and a compass. The origin of each coordinate system is at one of the professionally surveyed property corners. I eliminated quadrats from the survey if they occurred on a hiking trail, resulting in 24 to 30 1-m2 quadrats surveyed for each parcel. In the 33 sampled parcels, I sampled a total of 961 quadrats.

I randomly sampled the forest understory in Taylor's and Diamond Creek Woods in Hennepin County on August 4, 1998. For each survey, I generated thirty sets of coordinate numbers and determined plot location in the field using meter tapes and a compass. I estimated the location of origin of the coordinate system at one corner of the stand. I eliminated plots from the survey if they occurred in the middle of a severe tree blow-down, resulting in 26 and 30 1-m2 quadrats surveyed in the two stands.

Within each quadrat, I measured the height in centimeters, the reproductive status, and possible deer browse history of each individual wood nettle stem. I also counted the number of wood nettle seedlings.

Results and Discussion

Phenological Data

In 1997, wood nettle stems began to emerge between April 27 and May 11, reaching peak numbers on June 29. Ninety-three percent (93%) of stems emerge by June 1. Eighty-two percent (82%) of the stems survive until September 7. Wood nettle seedlings emerged before May 18 and reach their peak at June 8. The greatest seedling mortality occurs in July. Three percent (3%) of the seedlings survive until September 7 (Figure I.1).

Menges (1983) also roughly established phenological events for wood nettle populations in western Wisconsin. He found that germination begins in late May. Seedling survival is 50% before June 3 and 25-40% thereafter. The greatest seedling mortality occurs in July. Upland sites experience 80% seedling mortality. Seventy percent (70%) of clonal ramets emerge before June 3 (Menges 1983).

At NBWSP, exclusively male flowers emerge and decline before June 29. As the number of exclusively male flowers decreases, the number of hermaphroditic stems rises due to the development of female flowers on the previously male stems. The number of hermaphroditic stems peak on August 10. Exclusively female stems begin to emerge on July 20 and increase their numbers as the remains of male flowers fall off stems (Figure I.2). I used these data to determine when to time the random surveys.

Overall sexual expression and size

At NBWSP, wood nettle stems range between 4 and 135 cm and mean 43 cm in height. The mean height of the sexually reproducing stems is 68 cm. In the Hennepin County stands, wood nettle stems range between 4 and 173 cm and mean 45 cm in height. The mean height of the sexually reproducing stems is 83 cm. See Table I.1 for ranges and means of stem height for each reproductive class. In Menges' (1983) Wisconsin stands, the mean reproductive stem is 40 cm tall, male and female stems mean 80 cm tall and hermaphroditic stems are at least 60 cm tall and mean 97 cm. In his upland stands the male and hermaphroditic plants mean 10 cm taller than female stems.

The table below compares the percent of stems in each reproductive class among Menges' (1983) Wisconsin populations and populations in NBWSP and in Hennepin County, Minnesota.

	Wisconsin	**NBWSP**	**Hennepin County**
Percent non-sexually reproducing stems	64.7	78.1	80.1
Percent male stems	9.2	6.7	2.8
Percent female stems	1.7	4.2	4.7
Percent hermaphroditic stems	24.4	11	12.4

Wood nettle expansion

Rogers (1981) surveyed Taylor's Woods, an old growth stand in Hennepin County, in 1978 and found 39% wood nettle coverage. Twenty years later, I surveyed the same stand with different techniques and found a mean of 20.92 wood nettle stems of 2 and 77% frequency. I would estimate coverage of wood nettle between 70 and 80%. It appears that wood nettle is expanding in this stand.

Like Menges' work, this study only provides a single snapshot of wood nettle populations and is subject to the criticism applicable to any study of plant populations with only a few years of study. Year to year variations in weather conditions, in particular, can obscure other processes at work in the forest understory. Unfortunately, long-term population data are not available for wood nettle or any other species at Nerstrand Big Woods State Park, except for the federally endangered and Minnesota endemic dwarf trout lily *(Erythronium propullans)*.

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Figure I.1. Total number of wood nettle adult stems and seedlings taken from 38 permanent phenology plots at Nerstrand Big Woods State Park. The census occurred weekly between May 11 and July 27 and bi-weekly until September 7, 1997.

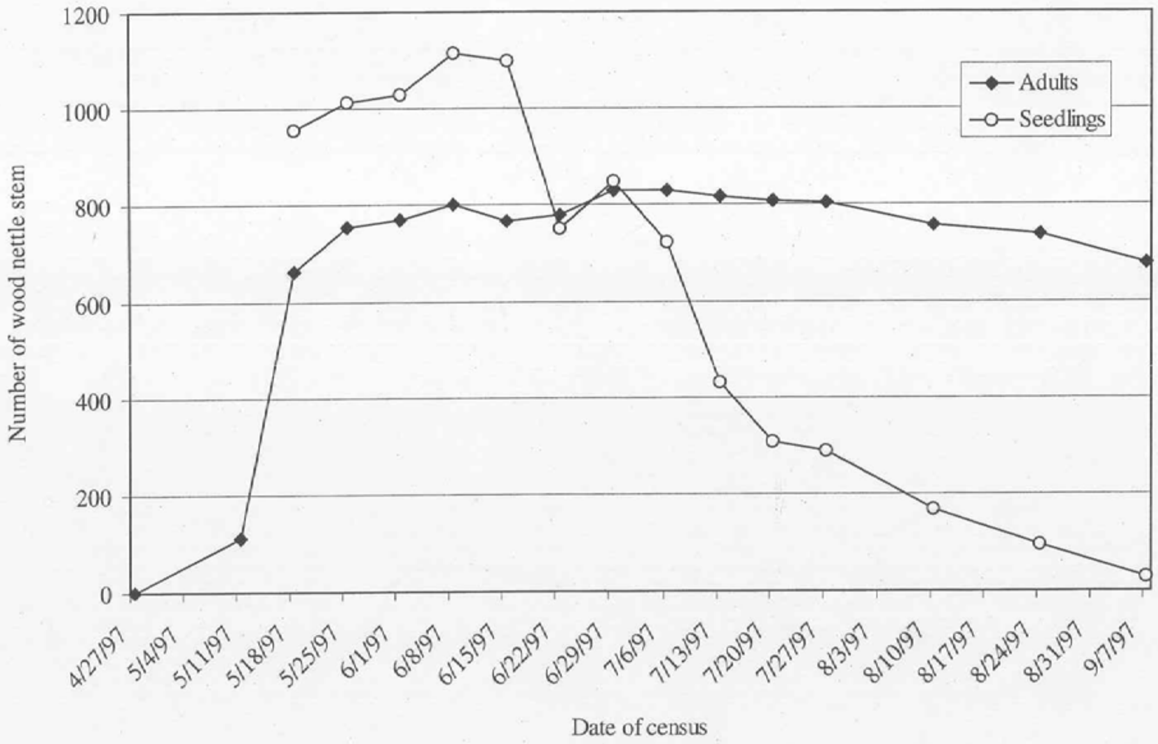

Table I.1 The height in centimeters of each wood nettle reproductive class at NBWSP and in two selected Hennepin County forest stands drawn from random surveys of both areas in July and August 1998.

	Nerstrand Big Woods State Park				**Hennepin County Stands**			
	Non-flowering	**Male**	**Female**	**Hermaphroditic**	**Non-flowering**	**Male**	**Female**	**Hermaphroditic**
Minimum height (cm)	4	21	20	15	4	53	17	23
Maximum height (cm)	120	125	100	135	120	174	145	173
Mean height (cm)	36	69	56	71	35	80	70	89
Median height (cm)	33	67	56	70	32	73	76	90

Figure I.2. Phenology of wood nettle flower development taken from 38 permanent plots at Nerstrand Big Woods State Park. The census occurred weekly between June 29 and July 27 and bi-weekly until September 7, 1997.