

**Effects of Autumn Olive (*Elaeagnus umbellata* Thunb.) Density on
the Growth of Mature White Oak Trees (*Quercus alba* L.)**

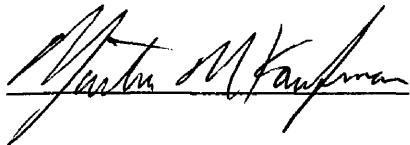
Marija R. Andrijonas

**Thesis submitted to the Faculty of the University of Michigan-Flint
in partial fulfillment of the requirements for the degree of
Master of Science in Biology
2011**

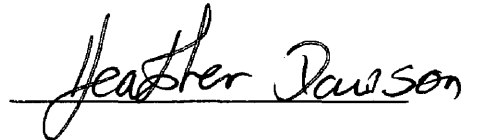
Approved By:



**Tracy L. Wacker
Committee Chairperson
Biology Department**



**Dr. Martin M. Kaufman
Committee Member
Earth and Resource Science Department**



**Dr. Heather Dawson
Committee Member
Biology Department**



**Dr. Joseph Susic
Program Director
Biology Department**

Dedication

This work is dedicated to my grandfather Viktoras Andrijonas and my father Antanas Andrijonas, who lived in harmony with their native forest and its inhabitants.

Abstract

Invasive alien plants threaten forest ecosystems by employing numerous survival strategies including nitrogen fixation. Autumn olive (*Elaeagnus umbellata* L.), in association with the symbiont *Frankia*, may alter forest soil chemistry, species composition and diversity and increase vegetative growth. This study examined the effects of autumn olive density on mature white oak (*Quercus alba* L.) growth in a second growth Michigan forest. Three forest plots were selected showing increasing gradation of autumn olive density. White oak height, stem diameter, annual radial growth, leaf nitrogen content and leaf area were measured. Soil profiles were analyzed, focusing on nitrogen concentrations. Tree seedlings and saplings were also sampled in each plot. Oaks grew significantly more per year and had significantly larger leaves in the high density and intermediate plots compared to the control plot. Tree juvenile abundance was highest in the control, whereas juvenile diversity was lowest in the high density plot. Chronic autumn olive nitrogen deposition may be increasing white oak vegetative growth and inhibiting juvenile tree growth.

Acknowledgments

I thank my major advisor and mentor Tracy L. Wacker, committee members Heather Dawson PhD, Martin Kaufman PhD, the Department of Biology at the University of Michigan-Flint for providing financial support, the Lapeer State Game Area DNR for providing experimental areas, research assistants Dennis J. Riley, Pat Schierup, Eva Newman, Donovan Tipett, statistician Thomas Wilke and historian Joe Leonardi.

Table of Contents

	Page number
List of Tables.....	vi
List of Figures.....	vii
Introduction.....	1
Materials and Methods.....	7
Results.....	11
Discussion.....	20
Conclusion.....	27
Works Cited.....	29
Appendix A.....	37
B.....	38
C.....	41

List of Tables

Table 1. Autumn olive characteristics compared by plot

Table 2. Comparisons of mean and standard deviation between plots for leaf area, leaf nitrogen, stem diameter, trunk height and annual ring diameter.

Table 3. Tree juvenile mean frequencies across plots.

List of Figures

- Figure 1. Map of Lapeer State Game Area
- Figure 2. Photograph showing Plot A
- Figure 3. Comparison of mean soil nitrate concentrations.
- Figure 4. Comparison of mean soil ammonium concentrations.
- Figure 5. Comparison of soil ammonium to soil nitrate concentrations.
- Figure 6. Comparison of mean leaf area.
- Figure 7. Comparison of mean annual radial growth.
- Figure 8. Dominance-diversity curve for plots A, B and C.

Introduction

Within the past several decades there has been an increasing global focus on environmental sustainability, particularly for forests (Chornesky et al. 2005). Forests comprise one third of the planet's land masses, are centers for biodiversity, release oxygen and store carbon, produce billions of dollars of forest products and are valued for their aesthetics and recreation opportunities. However, forests are becoming major casualties of civilization. The anthropogenic war on forests (Vitousek et al. 1997a) is being fought at its borders by hundreds of foreigners: invasive alien plants. These invasive alien species (IAS) have been arriving by the thousands (Vitousek and Walker 1989; Pimentel et al. 2000) since the Age of Exploration began. In modern times, especially in the last thirty years, with increased global trade and improved transportation, exotic plants are being introduced into native ecosystems at an alarming rate. Their human transporters hope to beautify their landscape, improve agriculture (Funk et al. 1979), attract game, stabilize and enrich soils (Brenner 1979) and simply surround themselves with a familiar landscape. Others arrived by accident, often hidden in imported crop seed (Czarapata 2005).

Invasive alien species exert severe negative influences in their newly colonized habitats (Mooney 2005; Mack et al. 2000; Pimentel et al. 2000; Vitousek et al. 1997a). These impacts manifest themselves in global ecological and economical losses (Pimentel et al. 2000; Vitousek 1994). Before the year 2000, the United States spent approximately

\$137 billion dollars per year ameliorating environmental damage caused by all introduced organisms (Pimentel et al. 2000). Invasive species cause problems for farmers. Annual losses due to crop and pasture weeds reach \$24 billion dollars and an additional 8 billion is spent on management (Pimentel et al. 2000). The ecological impacts are no less staggering. For example, garlic mustard (*Alliaria petiolata*), introduced in the 1850s is aggressively spreading at the rate of 6400 square kilometers per year (Nuzzo 1999). With its arsenal of cyanide compounds (Cipollini and Gruner 2007) garlic mustard decreases mycorrhizal populations and inhibits forest tree seedling growth (Stinson et al. 2006). Many invasive shrubs such as the buckthorns (*Rhamnus cathartica*, *Rhamnus frangula*) and the honeysuckles (*Lonicera* spp.) spread rapidly, aided by fruit eating birds, and form thick hedges (Mortensen 2002). Another invasive plant, Oriental bittersweet (*Celastrus orbiculatus*) shades out forest spring ephemerals, while its vining nature strangles young trees (Czarapata 2005).

Exotic species impacts are not equal in their severity. Some are particularly dangerous invaders because they have the ability to alter their invaded territory (Mack et al. 2000).

Plants in this category include: excessive utilizers of natural resources, providers of limiting resources, fire promoters and suppressors, soil (sediment, sand) stabilizers, erosion promoters, soil carbon modifiers and salt accumulators and redistributors (Mooney 2005; Richburg et al. 2002). Species with these features and additional functions such as nitrogen fixation are of immediate concern (Vitousek and Walker

1989) and due to their ability to alter habitat structure they can also influence the evolutionary trends of associated organisms (Mooney and Cleland 2001).

The Autumn olive (*Elaeagnus umbellata* Thunb.) is a soil stabilizer, a provider of a limited resource with the potential to alter habitat structure and therefore can be described as a dangerous invader. It is a multiple stemmed, deciduous shrub, native to East Asia. The shrub was imported to the United States in the early 1830s and since then has been widely planted to provide food and shelter for wildlife, stabilize and enrich soils in erosion prone areas such as mine reclamations and as protective hedges along roadways. Autumn olive grows up to 4.6 meters in height. The oval, simple, alternate leaves have entire margins, with the lower epidermis characterized by silvery coloration mixed with brown scales. Stems have thorns, often covered with coppery scales (Voss 1985). Plants produce up to 40 kilograms of bright red fruit, which is dispersed by birds (Ormont 1985). Autumn olive is highly invasive and has established itself in eastern North America, where it is abundant in most of the Midwest and found also in Wyoming, Washington and Oregon. It is listed as a noxious weed, prohibited and banned in West Virginia, New Hampshire, Massachusetts and Connecticut, respectively (USDA 2011). It is an established weed in Michigan, especially in parts of Lapeer County (Voss 1985) and has the potential of becoming highly problematic in the central and eastern United States (USDA-NRCS 2011).

In addition to the effects of invasive species on forests, excess nitrogen may be altering natural forest ecosystems. Concern over long-term, surplus nitrogen deposition to

forest soils has prompted multiple studies. Data suggest that nitrogen excess has negative consequences on forests (Vitousek et al. 1997b; Aber et al. 2003). Effects include decreased frost hardiness (Friedland et al. 1984), increased water stress, chlorosis of leaves (Van Dijk and Roelofs 1988), soil nutrient imbalances and deterioration and demise of conifers (Schultze 1989). In intact, mid-successional forests, decomposition of organic matter contributes to nitrogen deposition. Recycling is the major source of incoming nitrogen as opposed to atmospheric and biological fixation inputs (Vitousek 1982). However, since the 1960s, global anthropogenic nitrogen fixation has risen dramatically, from ~30 Tg N/year to ~150 Tg N/year (1Tg=10¹² g). Agricultural fertilizers contribute more than 80 Tg N/year, internal combustion engines 25 Tg N/year, and nitrogen fixing plants ~30 Tg N/year (Vitousek et al. 1997b). Additional nitrogen is released upon mechanical disturbance of soils, such as clear cutting, burning of vegetation and wetland drainage (Vitousek and Melillo 1979; Tilman and Lehman 2001). These additions to total global nitrogen have resulted in nitrogen saturation (Aber et al. 1989) and increased C: N ratios in terrestrial systems (Sprent 1987; Townsend et al. 1996). Because nitrogen is a limiting resource for many plants, increases in soil nitrogen result in increases in tree growth (Gessel 1960). Furthermore, any alteration in the nutrient assimilation process can stress plants (Hale and Orcutt 1987).

Nitrogen inputs to forest soils can also be attributed to nitrogen fixing plants, such as autumn olive. The shrub is colonized by *Frankia*, a gram positive, filamentous

Actinomycete. Hyphae penetrate the cells of the root epidermis and infect the intercellular spaces of the root cortex (Pawlowski and Bergman 2007). Infected cells, now occupied by the Actinomycete (=bacteroids, containing high concentrations of nitrogenase) become distorted and eventually form nodules. The relationship between autumn olives and *Frankia* is mutualistic because the plant provides dicarboxylates and the Actinomycete export the useable forms of ammonia and nitrates, which benefits the plant. However, *Frankia* is not confined to the nodules and can travel through the soil (Postgate 1978).

As an invasive, nitrogen-fixing shrub, autumn olive has been the subject of several studies. Researchers sampled soils from autumn olive plantings and discovered that they contained significantly higher amounts of amino-sugar nitrogen concentrations (Wang et al. 2005). Excess nitrogen deposited into soils by autumn olive can then leach into wetlands (Church et al. 2004). In another study, an analysis of soil water samples revealed that N mineralization and nitrification rates were higher beneath autumn olives (Goldstein 2007). A comparison of grassland to adjacent autumn olive plots showed that nitrogen mineralization potential was higher below the autumn olives (Baer et al. 2006). Black walnuts interplanted with autumn olives in southern Illinois exhibited dramatic increases in their growth (Funk et al. 1979).

In light of these findings, this study aims to examine the effect of surplus nitrogen deposited by *Frankia* on mature white oak trees (*Quercus alba* L.). White oak is a major constituent of several forest types including the oak-hickory forest of the Lapeer State

Game Area (LSGA), where this study was conducted (Appendix A). Much research has been conducted regarding the effects of nitrogen on plant growth. Less is known about the influence of excess nitrogen in natural ecosystems and at start date, no published data has been found describing the effect of autumn olives on mature white oak trees in Michigan. The research hypothesis states that autumn olive (*Elaeagnus umbellata* Thunb.) will increase the nitrogen content in soil and result in increased growth of mature oak trees. Because it has been suggested that invasive species affect forest regeneration (Stinson et al. 2006), this study also secondarily examined the effect of autumn olive on tree seedling and sapling abundance and diversity. The exploration of other forest components in relation to autumn olive may prove useful in understanding autumn olive effects on forests.

Materials and Methods

Research was conducted in May, 2010 through February, 2011 in the Lapeer State Game Area (LSGA) in Lapeer County, Michigan, latitude 43.17556, longitude -83.35472 (Figure 1). Study sites were chosen in Arcadia Township at T.8 N, R.11 E in sections 18 and 7. Multiple measures of luminosity were calculated to aid in plot selection (mean luminosity range = 7395 lum/m² to 8762 lum/m²). Three plots were then chosen showing increasing gradation of autumn olive concentration as described below. Each plot measures 60 meters by 15 meters, these dimensions determined by geographical boundaries. Autumn olives were counted in each plot. Shrubs measuring 0.5 meters or less and/or exhibiting a single stem were considered juveniles (Ormont 1985). Shrubs taller than one meter were considered adults and plants two meters and taller were noted. Autumn olives were further identified as single stemmed or multiple stemmed. Thirty autumn olives in Plot A and Plot B were randomly cut at three centimeters above the soil line and growth rings counted to determine age. Shrub stem diameter was measured and approximate height and number of stems noted. Autumn olive leaves were analyzed for nitrogen content (Kjeldahl nitrogen). The number of autumn olives within three meters of each oak was recorded. Only mature white oaks (*Quercus alba* L.), those with diameter at breast height greater than nine centimeters and taller than four meters were considered for this study. The oaks were identified and numbered with metal tags (Appendix B).

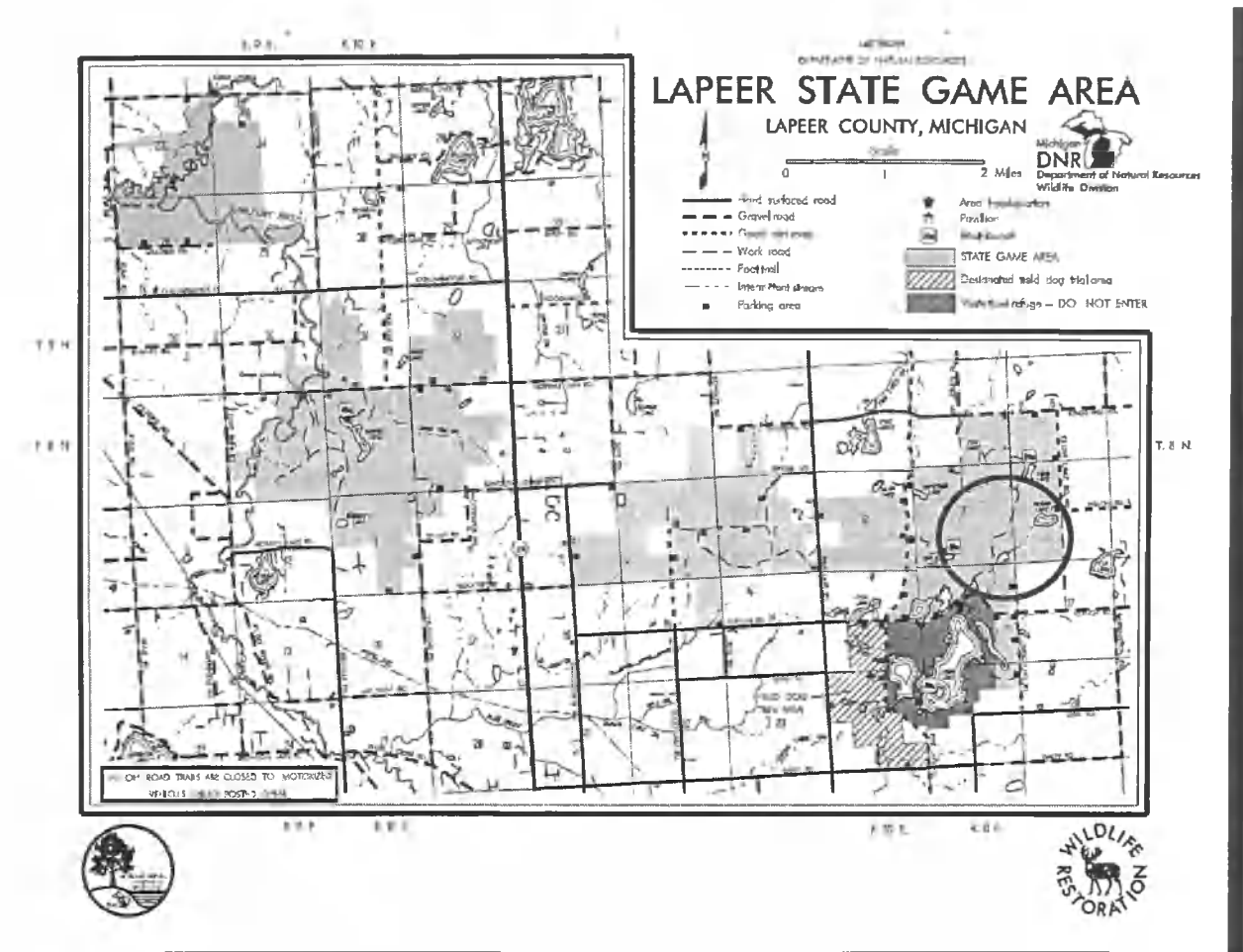


Figure 1. Red outline indicates location of experimental plots A and B, control Plot C (Used with permission from the Lapeer State Game Area, Department of Natural Resources 2011).

The following white oak properties were measured in each plot: tree height, tree stem diameter, growth of tree. White oak leaves were analyzed for nitrogen content (total Kjeldahl nitrogen). Overall appearance of the oaks was observed.

Tree growth was assessed by extracting cores from 15 mature white oaks with a minimum of 50 annual rings. Cores were extracted from oaks growing within three meters of autumn olives at a height of 48 centimeters from the base. Cores were

allowed to dry at room temperature, were affixed into grooved trays and sanded to expose the annual rings. Growth rings were observed with a dissecting microscope at 6X magnification. Annual radial growth was measured (mm) and recorded. The Pearson correlation coefficient was calculated to determine the strength of the relationship between annual radial growth and number of autumn olive. Data was analyzed by One-Way ANOVA.

We collected 637 sun leaves from the crown of 15 mature white oaks in Plots A, B and C between mid -July and mid –August, 2010. Canopy leaves were chosen in order to diminish the possibility of variation due to light competition. Leaves were severed from the ends of canopy or epicormic branches at no less than 30 meters above ground. After removing petioles, leaves were pressed in conventional leaf presses and then dried at 32° C in an electric convection oven. Dry leaves were digitally scanned and leaf area was calculated (cm²) using the APS Assess 2.0 Image Analysis Software. Leaf tissue from 380 leaves was sent to the Michigan State University Soil and Plant Nutrient Laboratory where tissue was analyzed for total Kjeldahl nitrogen. The Pearson correlation coefficient was calculated for leaf area and number of autumn olive; leaf nitrogen and number of autumn olive. Data was analyzed by One-Way ANOVA.

Soil samples were collected from all plots. One half liter of soil was removed from random areas within three meters circumference of oak trees and other site locations. Digging depth was restricted to approximately five centimeters of the A horizon because tree surface roots are found here (Rogers 2010). Twenty three soil samples were

collected, eight from Plot A, eight from Plot B and 7 from Plot C. Samples were sent to the Michigan State University Soil and Plant Nutrient Laboratory where they were analyzed for sand, silt and clay composition (%). Soil phosphorus (P), potassium (K), calcium (Ca), manganese (Mg) content and levels of nitrate (NO₃), ammonium (NH₄), and pH were also measured (ppm). Comprehensive soil tests were completed to ensure that soil changes could be attributed to autumn olive influence and to verify similarity in soil profiles, ensuring that plot differences were due to changes in the nitrogen levels. Soil chemistry data was analyzed by One-Way ANOVA.

Oak and other tree juveniles (seedlings and saplings) were randomly sampled per plot. The seedlings and saplings will be considered as a group, referred to as juveniles. Five 25 m² subplots were randomly chosen in each plot and each juvenile species was identified and counted per subplot. A paired samples *t* –Test was calculated to compare the mean frequencies of tree juveniles to plot. The Simpson Diversity Index (*D*) was computed and a Dominance-Diversity Curve plotted to quantify plot diversity.

A basic contingency table was constructed to determine plot dependence for single-stemmed and multiple-stemmed autumn olives.

RESULTS

Plot A, the most heavily infested plot, contains 163 autumn olives, 20 single stemmed and 107 multiple stemmed with 36 of the latter being equal to or greater than two meters tall (Table 1).

Table 1. Autumn olive characteristics compared by plot.

PLOT AUTUMN OLIVE CHARACTERISTICS					
PLOT	Mean age (years)	Single stemmed	Multiple stemmed	≥ 2m	Total
A	7.57	20	107	36	163
B	10.55	30	36	14	80
C	n/a	0	0	0	0

Shrub cover is extensive and nearly continuous within six meters north of the trail and three meters south of the trail (Figure 2). Autumn olive mean age is 7.57 years and the mean stem diameter is 2.37 centimeters. The shrubs cluster closely along the trail and are also numerous distributed throughout the plot. A particularly dense growth of autumn olives occupies a 42m² area just north of the trail. Twelve mature white oaks were identified and tagged. Soils consist of 72.9% sand, 16.0% silt and 11.1% clay and are classified as sandy loam.



Figure 2. Plot A.

Plot B is located just west of Plot A. Autumn olive density is slightly less than one half that of Plot A with 80 total individuals, 30 single stemmed and 36 multiple stemmed. Fourteen autumn olives are \geq two meters tall. Autumn olive mean age is 10.55 years and the mean stem diameter is 2.46 centimeters. Shrub concentration is mainly within four meters of the trail and some smaller plants are found throughout. Thirteen mature white oaks were identified. Soils consist of 74.9% sand, 15.0% silt, 10.1% clay and are classified as sandy loam.

Plot C, with no autumn olives was designated as the control. It is located west of Plots A and B. Twelve white oaks were counted. Soils consist of 83.4% sand, 6.5% silt, 10.1% clay and are classified as loamy sand.

Statistical analysis confirms plot choice. A Pearson correlation coefficient was computed for the relationship between number of autumn olives and plot. A strong positive correlation ($r(32) = 0.951, p < 0.001$) was found, representing a significant linear relationship between number of autumn olives and plot.

The mean soil nitrate (NO₃) content for total collected samples in Plot A was 0.71 ± 1.31 parts per million (ppm), in Plot B was 0.49 ± 0.93 ppm and in Plot C was 0.17 ± 0.07 ppm (Figure 3, Table 2, Appendix C1).

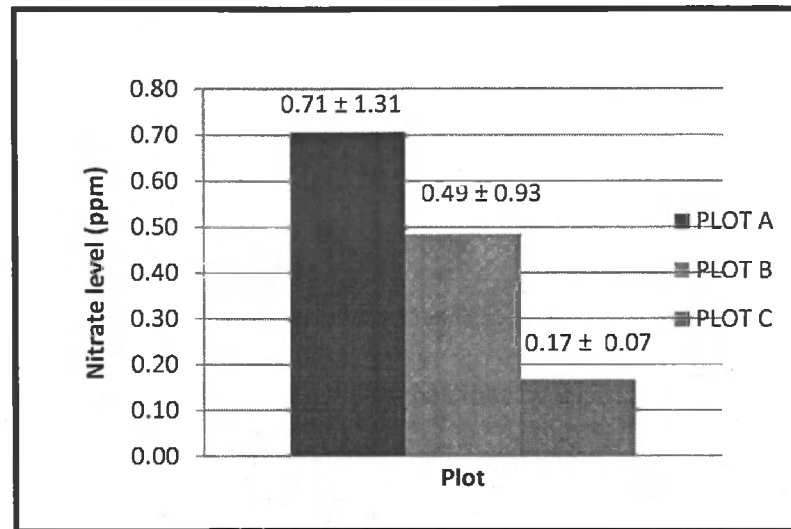


Figure 3. Comparison of soil nitrate concentrations across plots. Concentrations differ between plots, however the differences are not significant.

Table 2. Comparisons of mean and standard deviation between plots for leaf area, leaf nitrogen, stem diameter, trunk height and annual ring diameter. *Leaf areas in Plot A and B were significantly larger than Plot C ($p < 0.001$, $p < 0.002$ respectively) **Annual radial growth in Plot A and B was significantly greater than Plot C ($p < 0.001$, $p < 0.001$ respectively).

Variable	PLOT A		PLOT B		PLOT C	
	N	mean ± sd	N	mean ± sd	N	mean ± sd
Leaf area (cm ²) *	163	19.35 ± 7.46	166	18.76 ± 7.53	168	15.97 ± 7.43
Leaf nitrogen (%)	163	2.085 ± 0.263	166	2.021 ± 0.189	168	2.171 ± 0.168
Stem diameter (cm)	16	39.43 ± 13.37	19	44.51 ± 11.23	13	39.64 ± 14.13
Trunk height (m)	12	19.54 ± 5.32	14	18.50 ± 4.75	12	19.15 ± 5.10
Annual radial growth (mm)**	50	44 ± 10	50	36 ± 7	50	26 ± 11

No significant difference was found between high autumn olive density Plot A and control Plot C, nor between intermediate Plot B and the control ($F(2, 24) = 10.42, p > 0.05$). The mean soil ammonium (NH_4) content for samples in Plot A was 4.77 ± 3.60 ppm, in Plot B 5.12 ± 2.04 ppm and in Plot C 4.79 ± 1.25 ppm ; ($F(2, 20) = 0.047, p > 0.05$) (Figure 4).

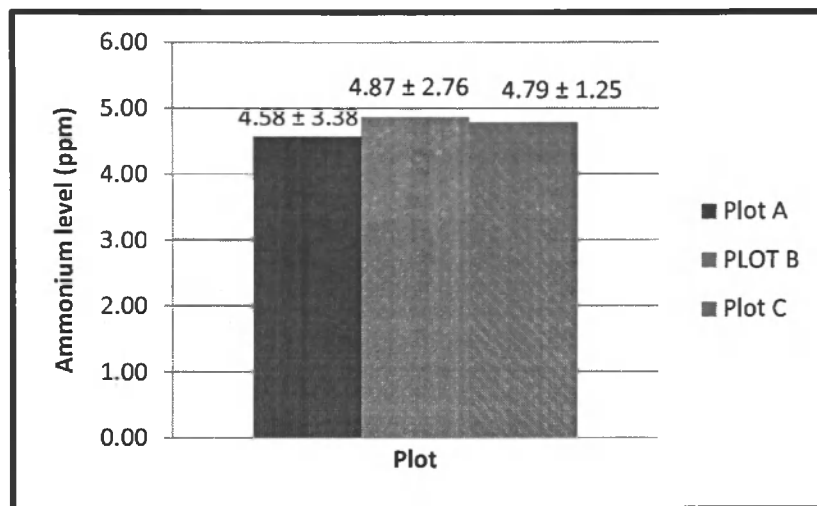


Figure 4. Comparison of mean and standard deviation of soil ammonium concentrations in Plots A, B and C.

Soil nitrate and ammonium concentrations vary significantly ($t(22) = -7.16, p < 0.001$) (Figure 5). Much higher soil ammonium concentrations were found across all plots compared to soil nitrate concentrations. Phosphorus sample mean for Plot A was 12.0 ± 7 ppm, Plot B 20 ± 13 ppm and for Plot C 20 ± 7 ppm ; ($F(2, 15) = 3.12, p > 0.05$). Mean soil calcium content for Plot A was 287 ± 231 ppm, for Plot B 362 ± 118 ppm and for Plot C 157 ± 41 ppm ; ($F(2, 14) = 56.87, p > 0.05$). Mean magnesium content for Plot A was 51 ± 41 ppm, for Plot B 71 ± 19 ppm and for Plot C 40 ± 11 ppm ; ($F(2, 15) = 26.50, p > 0.05$). Significant differences were found between and within plots ($F(2, 15) = 19.20, p <$

0.05) for soil potassium content; means per plot were 45 ± 6 ppm for Plot A, 51 ± 12 ppm for Plot B and 37 ± 12 ppm for Plot C. The mean pH soil levels for Plot A were 4.8 ± 0.7 , for Plot B 4.8 ± 0.2 and for Plot C 4.3 ± 0.2 ; ($F(2, 45) = 7.65, p < 0.01$). Single soil samples analyzed for iron showed 189.9 ppm in Plot A, 150.3 ppm in Plot B and 217.0 in Plot C.

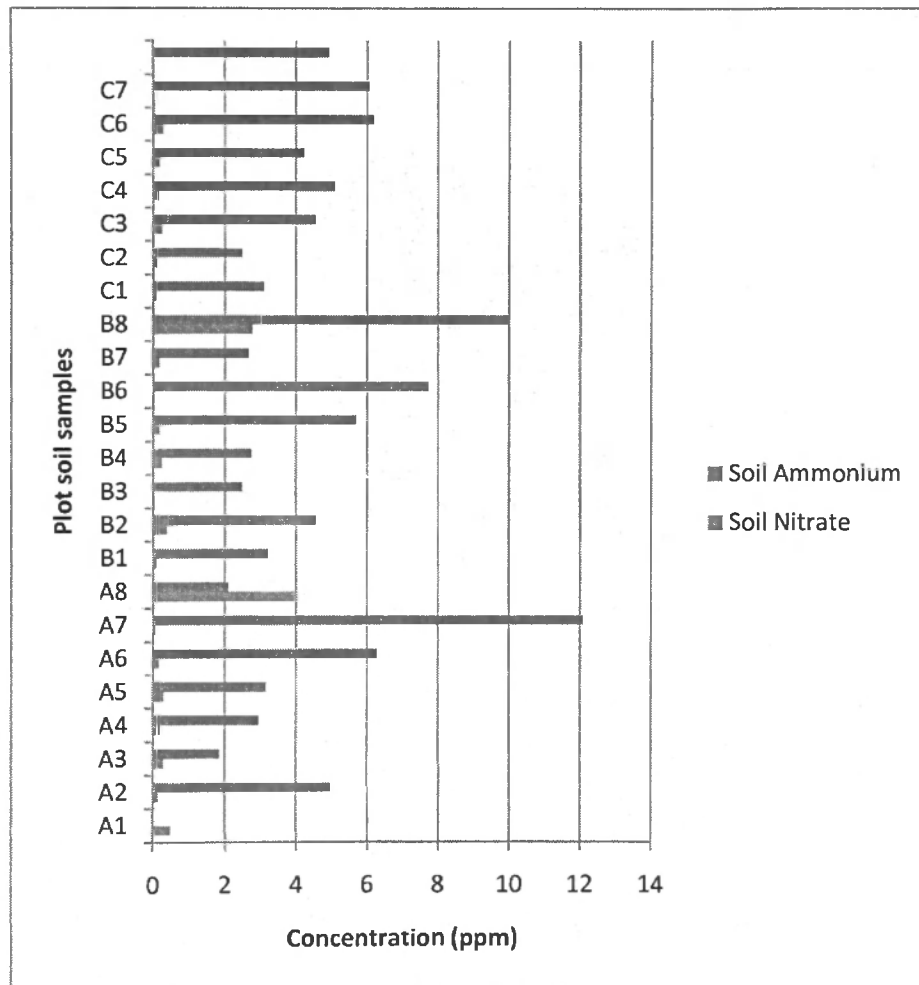


Figure 5. Comparison of soil ammonium to soil nitrate concentrations across plots. Variation in mean values is significantly different.

Mean leaf area for trees in Plot A was $19.35 \pm 7.46 \text{ cm}^2$, in Plot B $18.76 \pm 7.32 \text{ cm}^2$ and $15.97 \pm 7.44 \text{ cm}^2$ in Plot C (Figure 6). A significant difference was found between plots ($F(2, 632) = 7.45, p < 0.05$). Leaves of trees in plot A are larger than leaves in Plot B, which are larger than those in Plot C, however there is no significant difference between leaf areas in Plot A and Plot B ($p = 0.879$). A significant positive linear relationship exists between leaf area and numbers of autumn olives ($r(633) = 0.084, p < 0.07$). Leaf area is positively correlated with leaf nitrogen ($r(633) = 0.083, p < 0.001$).

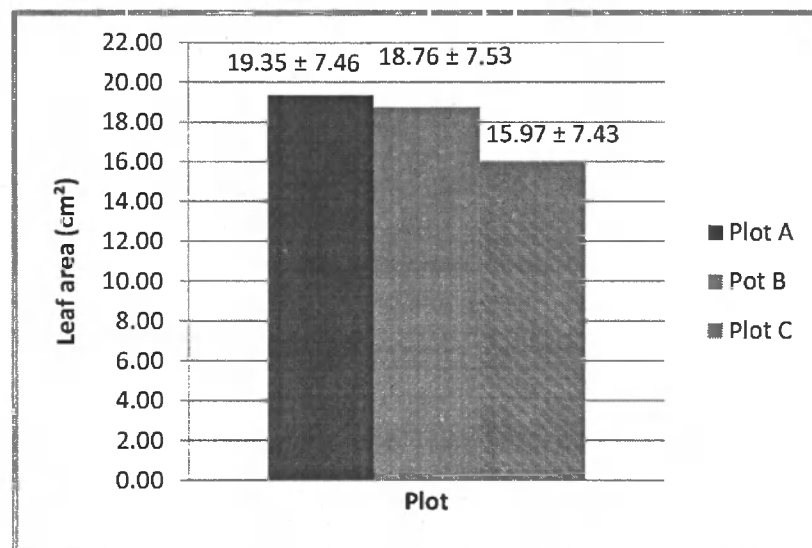


Figure 6. Comparison of mean and standard deviation of leaf area across plots. Differences in the mean values are significant.

The mean oak leaf total Kjeldahl nitrogen for Plot A was $2.085 \pm 0.263\%$, for Plot B $2.021 \pm 0.189\%$ and for oak leaves in Plot C was $2.171 \pm 0.168\%$. No significant difference was found between plots ($F(2, 16) = 0.660, p > 0.05$). Autumn olive leaves from Plot A contained 3.908% nitrogen and from Plot B 4.019% . Leaf nitrogen content is significantly related to numbers of autumn olive ($r(17) = 0.176, p < 0.01$).

The mean stem diameter in Plot A was 39.43 ± 13.37 cm, in Plot B 44.51 ± 11.23 cm and in Plot C was 39.64 ± 14.13 cm. Stem diameters did not vary significantly between plots ($F(2, 57) = 0.792, p > 0.05$). The mean tree height for Plot A was 19.14 ± 5.32 meters, for Plot B 18.50 ± 4.75 m and for Plot C, 19.15 ± 5.10 m. Tree height does not vary significantly by plot ($F(2, 57) = 1.80, p > 0.05$).

The mean annual radial growth for trees in Plot A was 44 ± 10 mm, in Plot B 36 ± 7 mm and in Plot C 26 ± 11 mm (Figure 7). A moderately strong positive correlation was found ($r(748) = 0.390, p < 0.01$) between annual radial growth and plot. A significant difference in annual radial growth was found between the plots ($F(2, 747) = 67.78, p < 0.05$), as well as among the plots ($F(2, 12) = 6.69, p < 0.05$) when examining annual radial growth in the context of autumn olive density.

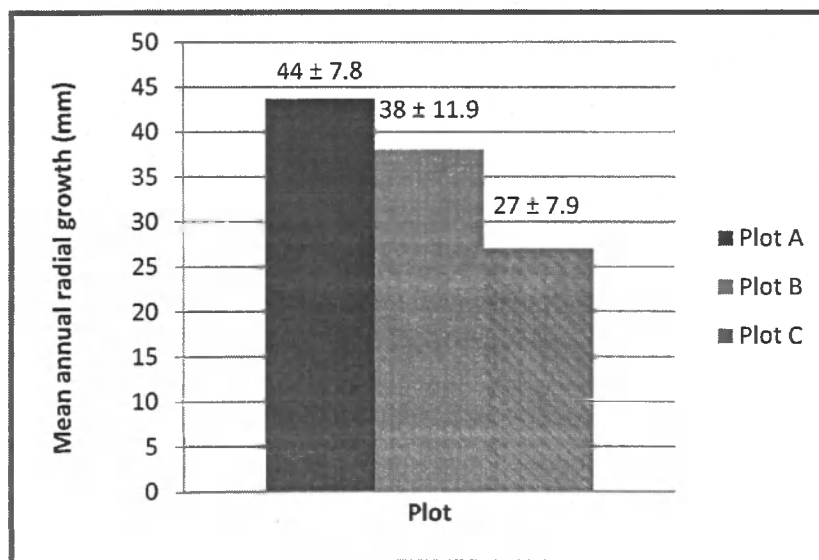


Figure 7. Comparison of mean and standard deviation of annual radial growth across plots.

Plot A contains 165 juveniles, 171 grow in Plot B and 447 in Plot C (Table 3).

Table 3. Juvenile mean frequencies across plots. Values were obtained by sampling five 25m² sub-plots.

Species	Plot A	Plot B	Plot C
<i>Acer saccharum</i>	23	12	249
<i>Amelanchier arborea</i>	0	0	27
<i>Carpinus caroliniana</i>	0	0	0
<i>Carya ovata</i>	2	6	2
<i>Cornus florida</i>	17	3	14
<i>Crataegus spp.</i>	3	12	7
<i>Fagus grandifolia</i>	1	0	1
<i>Fraxinus americana</i>	3	18	18
<i>Hammamelis virginiana</i>	13	40	43
<i>Ostrya virginiana</i>	7	11	8
<i>Prunus serotina</i>	26	52	8
<i>Quercus alba</i>	38	6	9
<i>Quercus rubra</i>	17	11	18
<i>Sassafras albidum</i>	15	0	43
Total	165	171	447

The mean occurrence of juveniles in Plot A is 13.75 ± 11.38 individuals, in Plot B 17.10 ± 16.04 and in Plot C 34.38 ± 65.93 . Plot C contains significantly more juvenile tree species than Plot A and Plot B ($t(69) = -1.73, p < 0.05$), ($t(69) = -1.67, p < 0.05$). No difference was found between the means of Plot A and Plot D ($t(69) = 0.20, p > 0.05$). A dominance-diversity curve showed that the majority of the samples represent common species and the remaining groups are less common, indicating that there is some “dominance” of a particular species in the plots (Figure 8). Dominance was expressed by sugar maple (*Acer saccharum*), black cherry (*Prunus serotina*), witch hazel (*Hammamelis virginiana*) sassafras (*Sassafras albidum*) and American ash (*Fraxinus americanus*). Computed Simpson Diversity Index (*D*) for Plot A = 38.54, for Plot B = 57.58 and Plot C = 47.35.

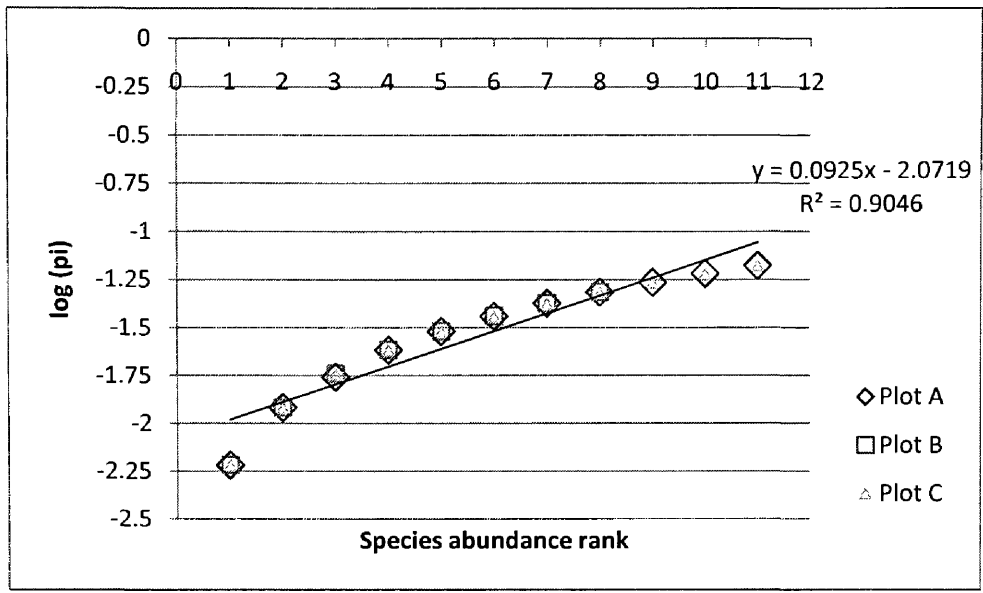


Figure 8. The dominance- diversity curve plots the number of species (represented by pi, a proportion of the total number) as a function of that species abundance rank. The slope indicates dominance.

DISCUSSION

The objective of this study was to explore the effects of autumn olive on mature white oak trees in a secondary growth forest in the Lapeer State Game Area (LSGA). Water acquisition being similar, nitrogen availability should be the most important limiting factor for forest trees. An increase in nutrients may cause initial growth spurts, but prolonged chronic nitrogen addition leads to nitrogen saturation, resulting in stress and forest decline (Aber et al. 2003). Because autumn olive fixes nitrogen via a mutualistic relationship with *Frankia*, research focused on the effects of supplemental nitrogen deposition to forest soils and resultant effects on tree height, stem width, annual tree growth, leaf nitrogen content and leaf area. In addition, autumn olive effects on tree juveniles were observed.

Higher concentrations in autumn olive infested plots due to *Frankia* activity were expected, but only slight differences exist between plots. Plots A, B and C show similar ammonium levels and are not significantly different. Ammonium concentration in all plots is much higher than the expected average (averages provided by Michigan State University Soil and Plant Nutrient Laboratory) (Appendix C2). The reason for this is unclear. Soil samples collected in the spring would have higher ammonium content than those collected later, due to greater bacterial activity (Jon Dahl, Michigan State University, East Lansing, MI, personal communication). These soil samples were collected in mid to late summer when perhaps greater accumulation of organic debris

may also support greater bacterial populations. Mean nitrate levels were highest in Plot A, followed by Plot B and Plot C.

Since density of autumn olive is greatest in Plot A and intermediate in Plot B compared to control Plot C, nitrate levels were expected to be highest in Plot A and lowest in Plot C. Nitrate levels in Plot A are higher than average, those in Plot B attain nearly average levels, while Plot C nitrate concentration is well below average. These differences however are not significant. The lack of significant soil nitrate differentials can be attributed to microbial assimilation (Davison et al. 1992).

Previous studies completed in southern Michigan demonstrated autumn olive ability to lower soil pH (Spiguel 1990). Lower than average pH levels facilitate the rapid absorption of NO_3 , while the acidic conditions depress NH_4 absorption resulting in higher soil levels (Foth 1984). Nitrate is also easily leached from the sandy soil possibly explaining the pronounced difference between NO_3 and NH_4 amounts within plots ($t(22) = -7.16, p < 0.01$).

Production of ammonium by *Frankia* associated with autumn olive and the shrub's high nitrogen leaf litter is expected to raise soil nitrogen levels. Soil saturation of NH_4 and therefore a decrease in its absorption may increase other cation levels. Plots A and B show above average levels of potassium (K), calcium (Ca) and Magnesium (Mg). Plot C shows lower than average cation concentrations, suggesting increased NH_4 absorption. Correlation with autumn olive abundance is difficult to ascertain, since no significant difference was found in ammonium levels between plots. Significant differences exist

between pH levels across plots; however, Plot C exhibits highest acidity without the presence of autumn olive and therefore does not provide an explanation for differences in ion exchange.

Study site soils contain very high amounts of iron (Fe) compared to the average.

Although not examined statistically, the presence of high iron content may be associated with the low pH levels, because iron solubility increases with increasing acidity (Jon Dahl, Michigan State University, East Lansing, MI, personal communication).

Any interference with nutrient availability or ion exchange can result in stress. The white oaks may be susceptible to iron toxicity.

It is well known that plant growth increases with added fertilizers. Several studies examine tree height correlations with nitrogen supplementation (Mitchell and Chandler 1939; Lea et al. 1979). Another study demonstrated that tree seedlings sprayed with nitrogen compounds grew 20% taller over a two year period compared to the control (Gessel 1960). The trees in Plot A, which also show more variability are on average tallest, followed by those in Plot C and then Plot B, although these differences are not significant. The forest plot trees receive similar amounts of light and moisture and are close in age (mean = 92.4 years) and therefore their vertical growth should be fairly uniform. Average stem diameters in Plot A and Plot C were nearly the same. Trees in Plot B grew larger, but not significantly. Data analysis showed that as nitrate levels increase, stem diameter increases, suggesting that the white oaks may respond to

higher levels of nitrogen. Stem diameter also significantly increased with increased pH, suggesting that white oaks may prefer a more basic soil.

Research has shown that annual radial growth increases with nitrogen supplementation. In one study, red oak (*Quercus rubra* L.), chestnut oak (*Quercus montana* Willd.), red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), pignut hickory (*Carya glabra* Mill.) and other forest trees showed an increase in annual radial growth with fertilizer application, while white oak radial increments did not significantly increase (Mitchell and Chandler 1939). Later studies illustrate the variability in the response of forest trees to fertilization. For example, sugar maple (*Acer saccharum* L.), increases in growth, whereas American beech (*Fagus grandifolia* L.) does not (Lea et al. 1979). In the Lapeer forest, the autumn olives are expected to supplement the soil with additional nitrogen. Soil samples collected beneath autumn olives in Plots A and B reveal high amounts of nitrate (mean = 3.36 ppm) compared to Plot A overall mean 0.43 ppm and Plot B overall mean 0.22 ppm. Since white oak fibrous root systems can extend as far as 30 meters from the base (Thomas 2000), it is likely that the roots have access to these nitrogen pools. Annual radial growth varied significantly between plots. Trees in Plot A grew more on average than trees in Plots B and C, because their mean annual ring width is significantly greater compared to Plot C. These results are expected because Plot A contains significantly more autumn olive than Plots B and C and Plot B contains significantly more autumn olive than Plot C. As the number of autumn olive increases, radial incremental growth also increases. The chronic release of nitrogen compounds into experimental plot soils possibly contributes to white oak annual growth.

Because tree foliage analysis may provide clues to soil fertility, leaf area and leaf nitrogen were examined. In addition to absorbing and metabolizing atmospheric nitrogen-NH₃ (Hutchinson et al. 1972), the oak leaves were expected to contain higher amounts of nitrogen due to autumn olive presence.

Higher leaf nitrogen concentration may have resulted in larger leaves even though differences were not significant. When analyzed in the context of autumn olive density, leaf nitrogen concentration increases significantly with increasing autumn olive density ($p < 0.01$). Soil nitrogen levels were highest in Plot A and therefore vegetative growth was expected to be greatest in that plot. Oak leaves growing in the presence of many autumn olives were larger compared to control Plot C. The numbers of multiple stemmed autumn olive in particular, have a positive correlation with leaf area. The data suggest that the 163 autumn olives in Plot A, by contributing additional amounts of nitrogen to the soil, allow the trees to absorb and utilize this nutrient towards tissue manufacture.

Although the investigation of juvenile tree species abundance and diversity was not the focus of the hypothesis, an examination of other forest components in relation to autumn olive may prove useful in understanding autumn olive effects on forests. More than double seedlings and saplings grow in Plot C than in Plots A and B, primarily due to the high abundance of sugar maple, witch hazel and sassafras. Adult forms of the latter two species were numerous along the path and in open areas. One of the more important sub-canopy juveniles, the serviceberry (*Amelanchier arborea*) grows

abundantly in Plot C and is absent from the other plots. Herbaceous groundcover was more diverse and abundant in Plot C, which is characterized by a more open canopy due to missing autumn olives. Smaller white oak crown leaves may also contribute to increased solar radiation to the forest floor. Although species occurrence may be dictated by habitat characteristics, the absence of autumn olive in Plot C seems to encourage greater variety and larger herbaceous plant populations, sub-canopy and understory juvenile and red oak juvenile populations.

Plots A and B have significantly less juveniles. This is expected because dense autumn olive clumps crowd and shade out young trees and other herbaceous seedlings, especially spring ephemerals. Where a clear-cut exists in Plot A, twenty white oak juveniles grow in association with Bracken fern (*Pteridium aquilinum*) and Pennsylvania sedge (*Carex pensylvanica*). Despite higher abundance of juveniles in Plot C, results of a Simpson Diversity computation show Plot B as most diverse, followed by Plot C and Plot A. The lack of evenness in the abundance distribution of species in Plot C (skewed by high numbers of sugar maple) influences diversity values. Because this community is dominated by several species it is considered to be less diverse compared to plot B, but not plot A. Higher abundance and higher diversity in plots C and B may be indicators of forest health in those plots. Further studies are needed to link autumn olive density to juvenile tree species abundance and diversity.

The importance of light availability cannot be overestimated in terms of forest regeneration. White oak is classified as an intermediate in shade tolerance and can

persist in the understory for many years, given at least 35% of full sunlight (Rogers 2010). Growth however can only occur with release from shade. Northern red oak is also intermediate, but cannot survive in low light conditions. Sassafras juveniles must receive nearly full light in order to mature. Sugar maple and particularly black cherry regenerate under heavy shade. Many more black cherry juveniles were counted in Plots A and B. With the exception of the clear-cut, conditions for light demanding juveniles may not be optimal in Plots A and B. By shading out competitors, autumn olive may cause a decrease in juvenile tree abundance. Autumn olive has also been implicated as an inhibitory agent to native tree seedlings (Orr et al. 2005). It is possible then, that juvenile growth may be influenced by allelopathic effects of autumn olive.

CONCLUSION

Excess nitrogen deposition from industrial and agricultural sources has intensified since the 1940's (Aber et al. 2003). In addition to human health concerns (Kirby 2007), surplus nitrogen disturbs natural ecosystems by affecting soil processes (Aber et al. 1995) and potentially altering plant composition. These effects may be particularly distressing to forests (Schulze 1989). This investigation intended to examine autumn olive nitrogen contributions and their effect on mature forest white oak trees.

No significant differences were found in nitrogen concentrations between plots.

Perhaps lack of significance is due to the small sample size rather than an incorrect hypothesis. Experimental design was also limited to plot choice as opposed to transect design due to topographical restraints and the tendency of autumn olive to grow along the trail. Future studies should explore alternative sampling methods with increased sample size.

White oak leaf area differed significantly between plots. Leaf size was greatest in the autumn olive dense plot, less in the intermediate plot and least in the control plot.

Annual radial growth differed significantly between plots. Trees growing in the presence of many autumn olives showed higher annual increases than those with less or no autumn olives. Significantly more juvenile tree species and higher diversity were found in the control and Plot B compared to the heavily infested plot A. The data suggest that chronic autumn olive nitrogen deposition may be increasing white oak vegetative growth and inhibiting juvenile tree growth.

An increase in vegetative growth of desirable plants may seem beneficial from the human perspective. Although surplus nitrogen initially increases biomass, chronic excess deposition may ultimately result in decreased growth and diminished species richness (Vitousek 1994). Increases in fertilization also decrease the production and setting of fruit. Disruption of reproductive potential may occur and in conjunction with soil process alterations, forest integrity may decline.

Works Cited

- Aber JD, Nadelhoffer J, Steudler P, Melillo JP. 1989. Nitrogen Saturation in Northern Forest Ecosystems. *Bioscience* 39(6): 378-86.
- Aber JD, Magill A, McNulty SG, Boone RD, Naderhoffer KJ, Downs M, Hallett R. 1995. Forest biogeochemistry and primary production altered by nitrogen saturation. *Water, Air and Soil Pollution* 85: 1665-1670.
- Aber JD, Goodale CL, Ollinger SV, Smith LM, Magill AH, Martin ME, Hallett RA, Stoddard JL. 2003. Is nitrogen deposition altering the nitrogen status of northeastern forests? *Bioscience* 53(4): 375-388.
- Baer SG, Church JM, Willard KWJ, Groninger JW. 2006. Changes in Intrasystem N Cycling from Nitrogen Fixing Shrub Encroachment in Grassland: Multiple Positive Feedbacks. *Agriculture, Ecosystems and Environment* 115: 174-82.
- Brenner, FJ. 1979. Soil and plant characteristics as determining factors in site selection for surface coal mine reclamation. *Environmental Geochemistry and Health* (1):1 39-44.
- Chornesky EA, Bartuska AM, Aplet GH, Britton KO, Cummings-Carlson J, Davis FW, Eskow J, Gordon DR, Gorrschalk KW, Haack RA, Hansen AJ, Mack RN, Rahel FJ, Shannon MA, Wainger LA, Wigley TB. 2005. Science priorities for reducing the threat of invasive species to sustainable forestry 55(4):335-348.

- Church JM, Williard KWJ, Baer SG, and Zaczek JJ. 2004. Nitrogen Leaching below Riparian Autumn Olive Stands in the Dormant Season. Proceedings of the 14th Central Hardwoods Forest Conference: 211-16.
- Cipollini D, Gruner B. 2007. Cyanide in the chemical arsenal of garlic mustard (*Alliaria petiolata*). *Journal of Chemical Ecology* 33: 85-94.
- Czarapata EJ. 2005. Invasive plants of the Upper Midwest. Madison, Wisconsin: University of Wisconsin. 215 p.
- Davison EA, Hart SC, Firestone MK. 1992. Internal cycling of nitrate soils of a mature coniferous forest. *Ecology* 73: 1146-1158.
- Foth HD. 1984. Fundamentals of soil science. 7th ed. New York: John Wiley and Sons. 435 p.
- Friedland AJ, Gregory RA, Karenlampi L, Johnson AH. 1984. Winter damage as a factor in red spruce decline. *Canadian Journal of Forestry* 14: 963-965.
- Funk DT, Schlesinger RC, Ponder Jr F. 1979. Autumn olive as a nurse plant for black walnut. *Botanical Gazette* 140: S110-114.
- Gessel SP. 1960. Progress and problems in mineral nutrition of forest trees. In: Kozłowski T, editor. *Tree growth*. New York: The Ronald Press Company. p 231.

- Goldstein CL. 2007. Nitrogen dynamics associated with autumn olive stands at field and watershed scales. [thesis]. Carbondale IL: Southern Illinois University-Carbondale. 109 p. Available from University of Michigan, Ann Arbor MI.
- Graney DL. 1977. Site index predictions for red oaks and white oak in the Boston Mountains of Arkansas. New Orleans, LA: Southern Forest Experiment Station, Forest Service, U. S. Dept. of Agriculture. Research Paper SO-139.
- Hale MG, Orcutt DM. 1987. Physiology of plants under stress. New York: John Wiley and Sons. 206 p.
- Hutchinson GL, Millington RJ, Peters DB. 1972. Atmospheric ammonia: absorption by plant leaves. *Science* 175: 771-772.
- Kirby EA. 2007. Plant growth in relation to nitrogen supply. In: Clark FE, Rosswall T, editors. *Terrestrial nitrogen cycles*. Stockholm: Swedish natural science council. p 249-50.
- Lea R, Tierson WC, Leaf AL. 1979. Growth response of northern hardwoods to fertilization. *Forest Science* 25(4): 597-604.
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological Applications* 10(3): 689-710.

- Mitchell HL, Chandler Jr RF. 1939. The nitrogen nutrition and growth of certain deciduous trees of Northeastern United States. *The Black Rock Bulletin* 11: 1-102.
- Mooney HA, Cleland EE. 2001. The evolutionary impact of invasive species. *PNAS* 98(10): 5446-451.
- Mooney HA. 2005. Invasive alien species: the nature of the problem. In: Mooney HA, Mack RN, McNeely JA, Neville LE, Schei PJ, Waage JK, editors. *Invasive alien species, a new synthesis*. Washington DC: Island Press. p 2-10.
- Mortensen CE. 2002. Invasive plants of the southern tier. USDA Forest Service. 43 p.
- National Climatic Data Center. [cited 2011 Feb 16]. MDA Michigan weather service. (no author). Available at <http://www.ncdc.noaa.gov>
- Nuzzo V. 1999. Invasion pattern of the herb garlic mustard (*Alliaria petiolata*) in high quality forests. *Biological Invasions* 1: 169-179.
- Ormont WE. 1985. Evaluation of the soil conservation service's plant materials program, with special emphasis on autumn olive, *Elaeagnus umbellata* [thesis]. Madison, WI: University of Wisconsin-Madison. 198 p. Available from University of Michigan, Ann Arbor, MI.
- Orr SP, Rudgers JA, Clay K. 2005. Invasive plants can inhibit native tree seedlings: testing potential allelopathic mechanisms. *Plant Ecology* 181:153-65.

Pawlowski K, Bergman B. 2007. Plant symbioses with frankia and cyanobacteria. In:

Bothe H, Ferguson SJ, Newton WE, editors. Biology of the nitrogen cycle.

Amsterdam: Elsevier. p 166.

Pimentel D, Lach L, Zuniga R, Morrison D. 2000. Environmental and economic costs of nonindigenous species in the United States. *Bioscience* 50 (1): 53-65.

Postgate J. 1978. Nitrogen fixation. London: Edward Arnold Limited. 68 p.

Richburg JA, Dibble AC, Patterson WA. 2002. Woody invasive species and their role in altering fire regimes of the Northeast and Mid-Atlantic states. In: Galley KEM and Wilson TP, editors. Proceedings of the invasive species workshop: the role of fire in the control and spread of invasive species. Miscellaneous publication no.11, Tall Timbers Research Station, Tallahassee, FL.

Rogers R. (no date) [Cited 2010 April 24]. Silvics manual, volume 2 [internet]. Available from <http://www.na.fs.fed.us/spfo/pubs/silvicsmanual/volume2/quercus/alba>.

Schulze ED. 1989. Air pollution and forest decline in a spruce (*Picea abies*) forest.

Science 244: 776-83.

Spiguel M. 1990. Nitrogen cycling and nitrogen availability in three oak ecosystems in southeastern Michigan [dissertation]. Ann Arbor MI: University of Michigan Ann Arbor. 112 p. Available from: University of Michigan Ann Arbor.

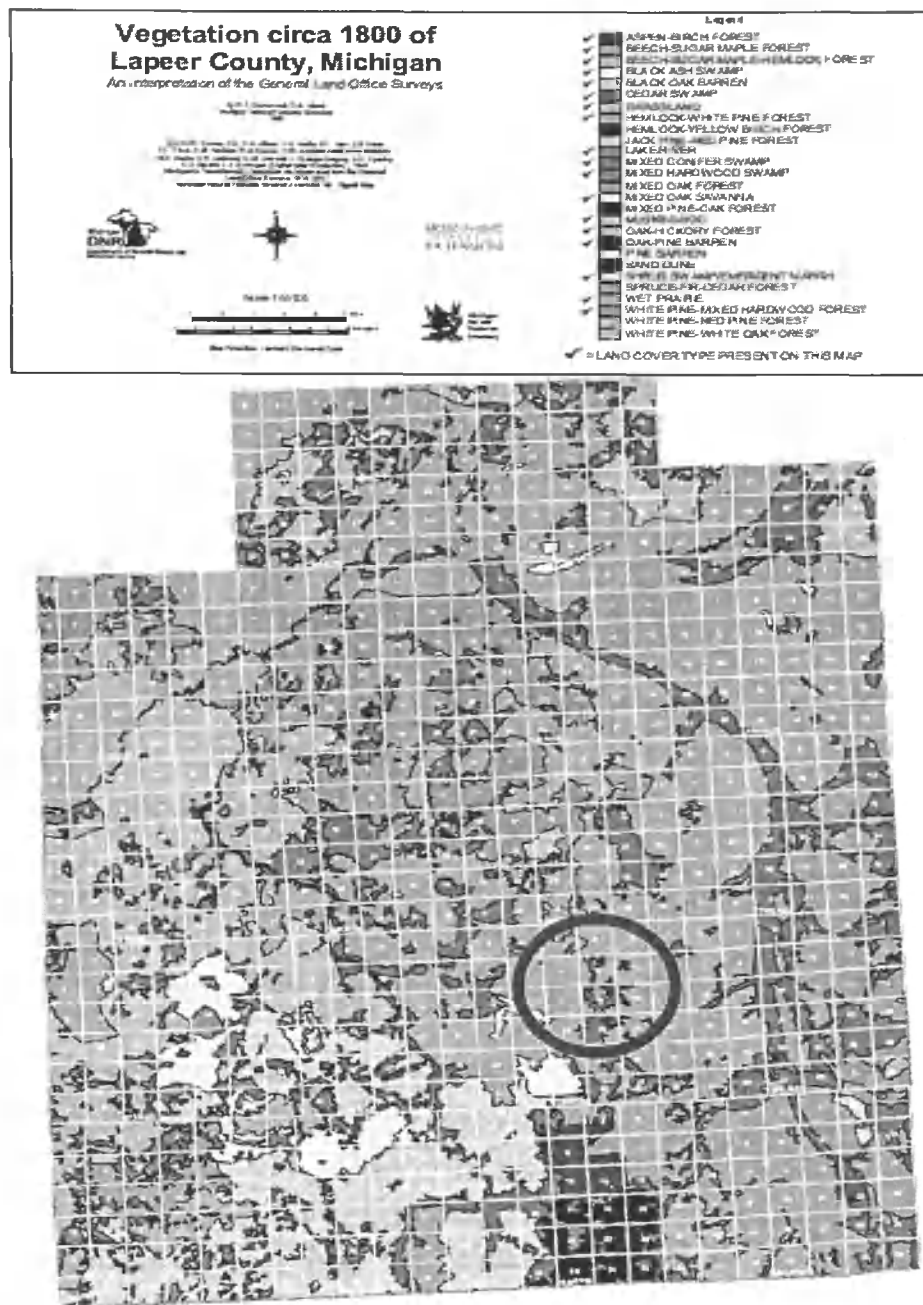
Sprent, JI. 1987. The ecology of the nitrogen cycle. Cambridge: Cambridge University Press. 151 p.

- Stinson KA, Stuart AC, Powell JR, Wolfe BE, Callaway RM, Thelen GC, Hallett SG, Prati D, Klironomos JN. 2006. Invasive plant suppresses the growth of native tree seedlings by disrupting belowground mutualisms. *PLoS Biology* 4(5): 727-731.
- Thomas P. 2000. *Trees: their natural history*. New York: Cambridge University Press. 286 p.
- Tilman D, Lehman C. 2001. Human-caused environmental change: impacts on plant diversity and evolution. *PNAS* 98(10): 433-440.
- Tisdale SL, Werner LN, Beaton JD. 1985. *Soil fertility and fertilizers*. 4th ed. New York: Macmillan Publishing Company. 754 p.
- Townsend AR, Braswell BH, Holland EA, Penner JE. 1996. Spatial and temporal patterns in terrestrial carbon storage due to deposition of fossil fuel nitrogen. *Ecological Applications* 6(3): 806-14.
- United States Department of Agriculture. [2001 May 18, cited 2011 Feb 16]. Invasive exotic species of management concern. USDA Forest Service, Southern Region (no author). Available from <http://www.usda.fs.gov>
- United States Department of Agriculture, Natural Resources Conservation Service [cited 2011 Feb 16]. Invasive and noxious weeds. (no author). Available from <http://www.plants.usda.gov>
- United States Geological Survey [cited 2011 Feb 16]. USGS Barnes Lake Quad. (no author). Available from <http://www.topozone.com>

- Van Dijk HFG, Roelofs JGM. 1988. Effects of excessive ammonium deposition on the nutritional status and condition of pine needles. *Physiology of Plants* 73: 494-501.
- Vitousek PM, Melillo JM. 1979. Nitrate losses from disturbed forests: patterns and mechanisms. *Forest Science* 25 (4): 605-619.
- Vitousek PM. 1982. Nutrient cycling and nutrient use efficiency. *American Naturalist* 119: 553-572.
- Vitousek PM, Walker LR. 1989. Biological invasion by *Myrica faya* in Hawai'i. Plant demography, nitrogen fixation, ecosystem effects. *Ecological Monographs* 59: 247-265.
- Vitousek PM. 1994. Beyond global warming: ecology and global change. *Ecology* 75(7): 1861-1876.
- Vitousek P, D'Antonio CM, Loope LL, Rejmanek M, Westbrooks R. 1997a. Introduced species: a significant component of human-caused global change. *New Zealand Journal of Ecology* 2(1): 1-16.
- Vitousek P, Aber JD, Howarth RW, Likens GE, Matson PA, Schindler DW, Schlesinger DH, Tilman D. 1997b. Human alteration of the global nitrogen cycle: sources and consequences. *Ecological Applications* 7(3): 737-50.
- Voss EG. 1985. Michigan Flora Part II. Bloomfield MI: Cranbrook Institute of Science. 724 p.

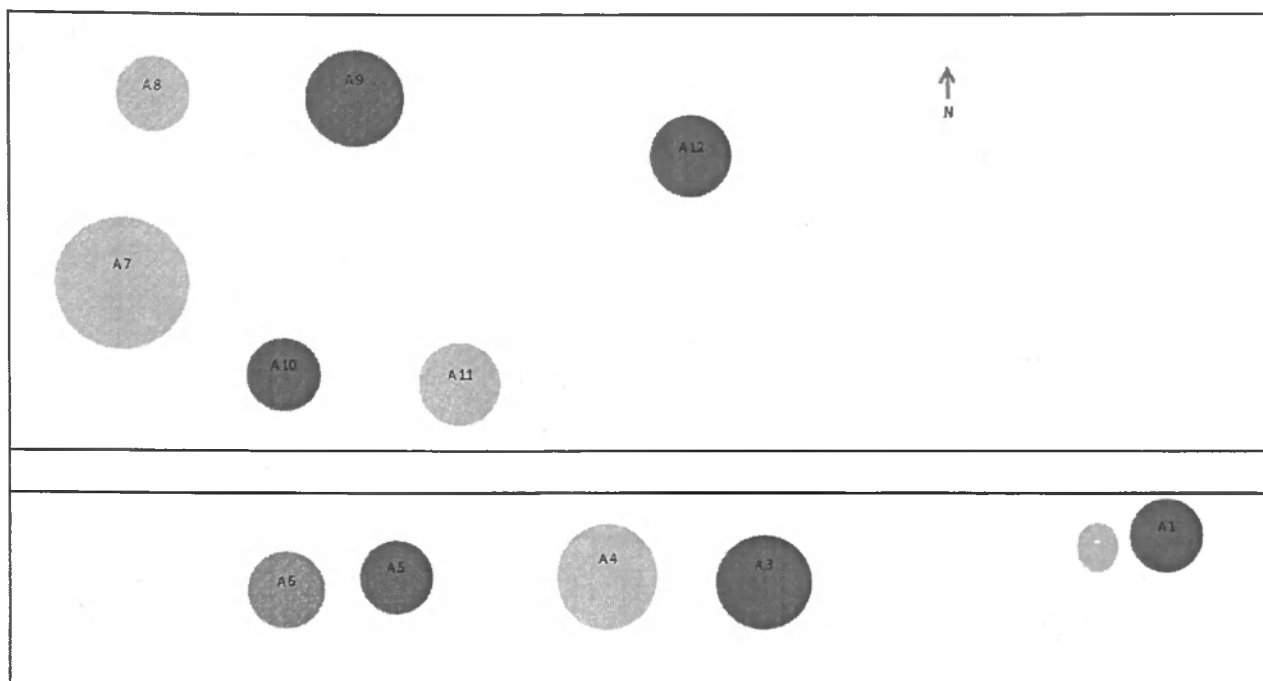
Wang J, Kahn SA, Dawson JO. 2005. Nitrogen fixing trees influence concentrations of ammonium and amino sugar-nitrogen in soils. AFTA 2005 Conference Proceedings: 1-17.

Appendix A



Map illustrates pre-settlement ecosystem types of Lapeer County, Michigan (Used with permission from Michigan Natural Features Inventory 2011). Lapeer State Game Area (circled in red) was originally characterized by oak-hickory forest and conifer swamp. Today's forest is deciduous, dry mesic, dominated by white oak in the uplands and red oak in the lower habitats. Geology is characterized by end moraines of coarse textured till with glacial outwash sand and gravel and postglacial alluvium. Elevation at center is 246 meters (USGS 2011). Average annual precipitation is approximately 80.3 centimeters. Average annual temperature is 8.5°C (NCDC 2011).

Appendix B



Numbers of autumn olive

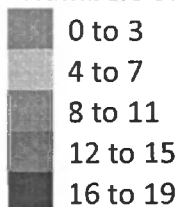
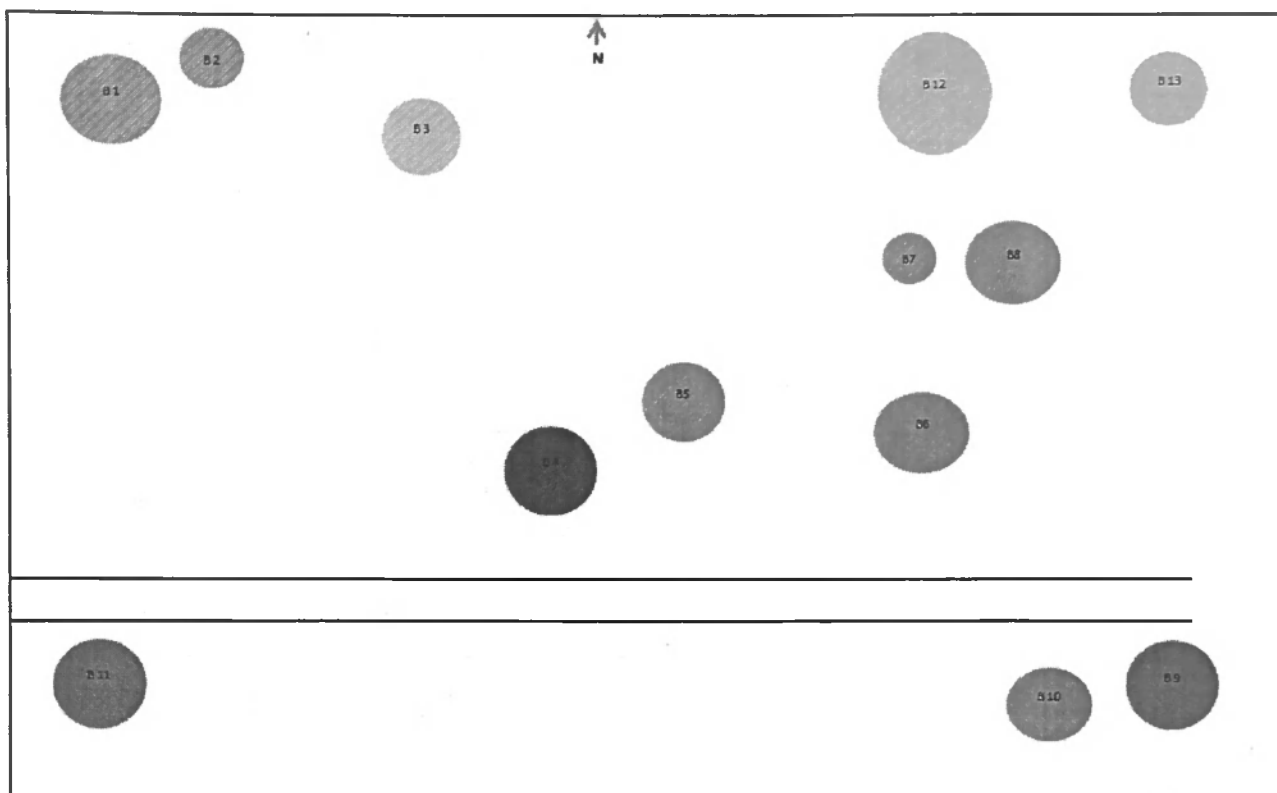


Diagram illustrates relative white oak positions and diameter ($N = 12$) in Plot A in relation to the trail (black outlines). Four to seven autumn olives grow within 3 meters of 42% of the white oaks, 12-15 autumn olives grow within 3 meters of 50% of the oaks and only one tree is associated with 0-3 autumn olives. All the oaks grow with juvenile and large autumn olives ($>2m$) within the 3 meters circumference, with the exception of Tree A11, which is surrounded by shrubs that are 1 meter and less in height.



Numbers of autumn olive

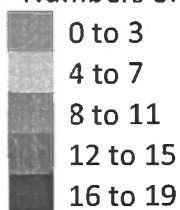


Diagram illustrates relative white oak positions and diameter ($N = 13$) in relation to the trail in Plot B. One oak (B4) is associated with 23 autumn olives, 2 oaks or 15% grow near 12-15 autumn olives, 23% grow with 8-11 and 4-7 shrubs, and 31% grow with 3 or less autumn olives in a 3 meter radius around the trunk. Trees surrounded by 7 or less autumn olives grow farthest from the trail.

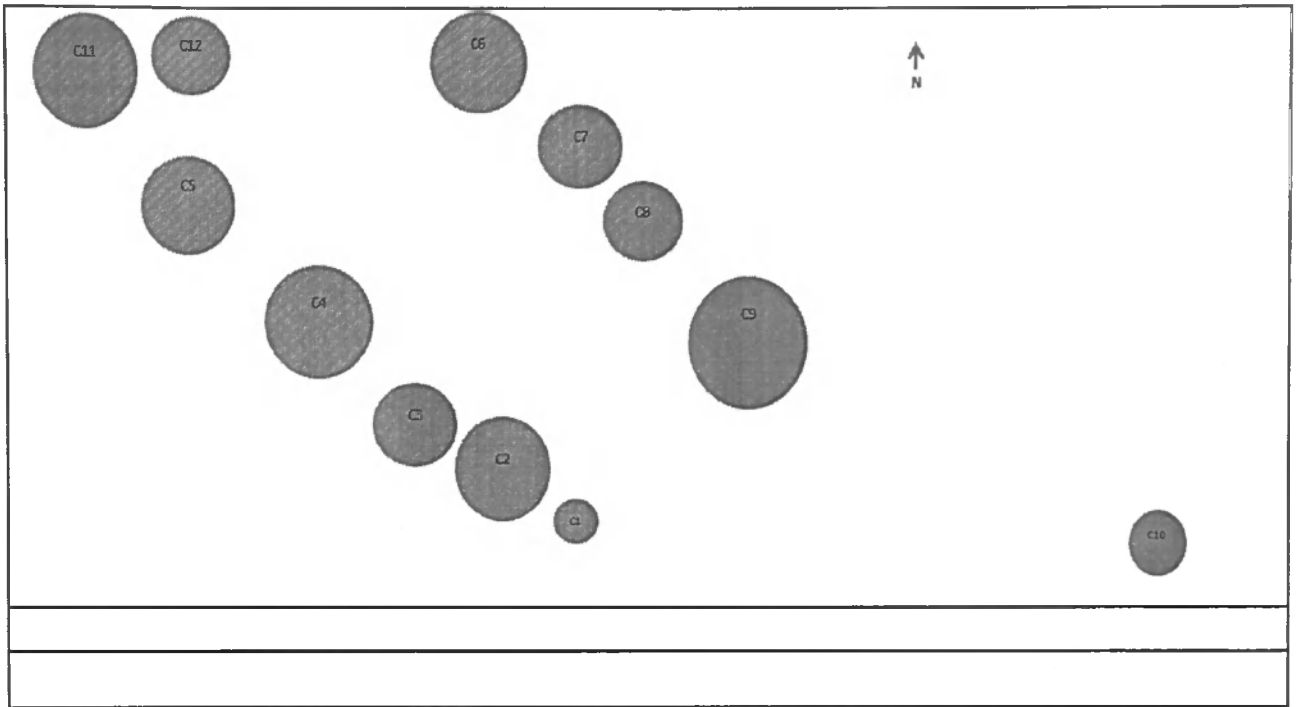


Diagram illustrates relative white oak positions and diameter (N = 12) in Plot C in relation to the trail. No autumn olive grows here.

Appendix C

	NO₃	NH₄	P	K	Ca	Mg	Fe	pH
PLOT A								
Sample 1	0.48	4.99	8	49	269	34		4.8
Sample 2	0.14	1.85	8	50	613	112		5.7
Sample 3	0.29	2.95						
Sample 4	0.24	3.15					189.8	
Sample 5	0.30	6.29	9	41	78	21		4.1
Sample 6	0.16	12.10	25					
Sample 7	0.10	2.09	12	38	188	35		4.5
Sample 8	3.94	3.20						
Mean ± sd	0.71 ± 1.31	4.58 ± 3.38	12 ± 7	45 ± 6	287 ± 231	51 ± 41		4.8 ± .7
PLOT B								
Sample 1	0.11	4.56						
Sample 2	0.39	2.48	10	38	516	98	150.3	4.8
Sample 3	0.01	2.75						
Sample 4	0.24	5.70	14	67	316	64		
Sample 5	0.17	7.74	38	46	237	53		4.7
Sample 6	0.01	2.66						
Sample 7	0.18	9.96						
Sample 8	2.77	3.10						
Mean ± sd	0.49 ± 0.93	4.87 ± 2.76	21 ± 15	50 ± 15	356 ± 144	72 ± 23		4.8 ± .1
PLOT C								
Sample 1	0.08	2.48	17	39	211	56		4.4
Sample 2	0.11	4.56						
Sample 3	0.24	5.1	20	28	145	41		4.2
Sample 4	0.16	4.22	10	30	130	34	217.0	4.0
Sample 5	0.17	6.19						
Sample 6	0.28	6.06	27	31	112	27		4.5
Sample 7	0.13	4.93	26	58	187	43		
Mean ± sd	0.17 ± 0.07	4.79 ± 1.25	20 ± 7	37 ± 12	157 ± 41	40 ± 11		4.3 ± .2

Table C1. Soil chemistry values for Plots A, B and C. Concentrations are measured in parts per million.

Soil component	ppm
Nitrate	< 0.5
Ammonium	< 0.5
Phosphorus	19
Potassium	24
Calcium	243
Magnesium	32
Iron	<50

Table C2. Average soil component values for dry-mesic forest in Michigan. Data retrieved by MSU soil analysis lab.