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Site Characteristics and Plant Invasion: Light Limitation of Invasive Establishment and Impacts of *Elaeagnus Umbellata* on Soil Nitrogen Availability and Co-occurring Species

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SITE CHARACTERISTICS AND PLANT INVASION: LIGHT LIMITATION OF
INVASIVE ESTABLISHMENT AND IMPACTS OF *ELAEAGNUS UMBELLATA* ON
SOIL NITROGEN AVAILABILITY AND CO-OCCURRING SPECIES

A Thesis Presented

By

ERIN LYNN MOSTOLLER

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University of Massachusetts Amherst in partial fulfillment
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Plant Biology

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DEDICATION

To my brother, Eric Mostoller, for all of your support, encouragement and love.
Thank you for showing me that you can overcome any challenge that life throws your
way.

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CHAPTER 1

OVERVIEW

Invasive species have become an increasing threat to many habitats worldwide. While only a fraction of introduced species actually become successful invaders (Williamson and Fitter 1996), these species can cause severe economic and ecological consequences where they become established. It has been estimated that nonnative species cause over \$100 billion in damages each year in the United States (Pimentel et al. 2000). Ecological damage caused by invasive species includes reductions in native biodiversity (Wilcove et al. 1998), alterations of fire regimes (D'Antonio and Vitousek 1992), and disruptions of nutrient (Vitousek and Walker 1989) and hydrologic cycles (Wood et al. 2006).

In order to successfully become invasive, an introduced species must undergo several transitions. Species must be able to survive through the initial transport and introduction phases, then be able to establish and form self-sustaining populations leading to further spread (Kolar and Lodge 2001). Establishment of invasive plants is largely controlled by the ability of a species to germinate and survive under the environmental conditions at the site of introduction. Therefore, spread can be facilitated if the species can germinate and survive under a range of environmental conditions such as varying light or nutrient levels. My research addressed the questions of whether several invasive woody plants can germinate, survive and grow in light levels typical of an undisturbed forest understory, and also whether alteration of the nitrogen cycle by one invader is likely to increase the rate of invasion by others.

The ability to germinate and survive under many light levels can facilitate invasion into different types of habitat. Species that are able to establish in both low and high light habitats can take advantage of gaps in the forest understory in addition to surviving when the gaps close. These species will be able to invade open areas such as early-successional habitats as well.

In order to address these issues, I measured germination rates and early survival of common invasive woody shrubs under sun and shaded conditions in the greenhouse. Species selected for the study included *Elaeagnus umbellata*, *Rosa multiflora*, *Celastrus orbiculatus*, *Berberis thunbergii*, and *Rhamnus cathartica*. These species were selected because they were widespread throughout the study site and represented both shade tolerant and intolerant species. I found that all species had high germination and survival rates in both the sun and shade. The results of this experiment show that invasive species' intolerance to shade does not explain the lack of current invasion in the forest understory.

Once established, some invasive plant species have the ability to alter nutrient cycles, most commonly the nitrogen cycle. These invaders can form symbioses with soil microbiota and fix atmospheric nitrogen thereby increasing available soil nitrogen (Vitousek and Walker 1989, Yelenik et al. 2004, Hughes and Denslow 2005). When this occurs in areas with infertile soils, plant species that are not adapted to fertile soils will be at a disadvantage. Also, because many invasive plants have the ability to respond to additional nitrogen input, invasion by an N-fixing species could possibly facilitate further invasion (Ostertag and Verville 2002, Brooks 2003). The facilitation of invasives by

nitrogen fixing invaders has been observed in a variety of habitat types ranging from coastal prairies (Maron and Connors 1996) to volcanic sites (Vitousek and Walker 1989).

The second part of my research focuses on the ability of an invasive woody shrub, *Elaeagnus umbellata*, to increase soil nitrogen availability in an abandoned agricultural field. *Elaeagnus umbellata* has already successfully established and spread throughout New England. Other studies have shown that *E. umbellata* can increase soil nitrogen (Paschke et al. 1989, Baer et al. 2006). If it increases soil N availability in the New England habitat, it might promote growth of other invasives which could have significant management implications.

In a field study, I examined the possibility that the nitrogen-fixing *Elaeagnus umbellata* can facilitate the growth of additional invasive plants. I compared various soil and plant measurements in plots dominated by *E. umbellata* to those of an invasive non-nitrogen fixing shrub, *Lonicera morrowi*, and a native reference species, *Solidago rugosa*. There was a trend toward higher soil nitrogen availability in *E. umbellata* dominated plots as well as higher foliar nitrogen, chlorophyll content and growth in other plants. These results suggest that *E. umbellata* has the potential to alter soil properties and facilitate invasion of other species.

CHAPTER 2

EFFECTS OF LIGHT ON GERMINATION AND ESTABLISHMENT OF INVASIVE WOODY SPECIES

2.1 Introduction

Plant invasions can have serious impacts on native biodiversity and ecosystem processes. The presence of invasive woody species has resulted in a decline in native plant density and diversity including advanced regeneration of native tree species (Woods 1993, Wyckoff and Webb 1996, Hutchinson and Vankat 1997). Plant invasions also alter nutrient cycling processes (Vitousek and Walker 1989), which may facilitate future invasions.

In order to be a successful invader, an introduced species must be able to establish self-sustaining populations and subsequently spread. However, the ultimate success of establishment following dispersal is determined by the characteristics of the invasive plant species and the environment. Many site factors affect susceptibility to invasion, such as species richness (Elton 1958, Lonsdale 1999), nutrient availability (Huenneke et al. 1990, Stohlgren et al. 1999, Cassidy et al. 2004), light availability (Hutchinson and Vankat 1997), overstory species composition (Harrington and Ewel 1997), ability of seeds and seedlings to penetrate the forest litter layer (Ellsworth et al. 2004b) and type, frequency, or intensity of disturbance (Hobbs and Huenneke 1992).

Disturbance may facilitate invasion by increasing availability of light, nutrients, and safe sites for germination. A number of woody invasive species have become established in disturbed early successional habitats, including *Elaeagnus umbellata* (Munger 2003), *Rosa multiflora* (Munger 2002), *Acacia nilotica* (Brown and Carter 1998), and *Cytisus scoparius* (Bellingham 1998). However, although early successional

habitats and forest gaps are more suitable for germination and growth of a number of invasive plants, many can also survive in the understory. For example, while growth of *Celastrus orbiculatus* was greater under high light availability, this species was able to survive at 2% full sun (Ellsworth et al. 2004a) and to persist in forest understory habitats (Greenberg et al. 2001). Even *Elaeagnus umbellata*, a species considered shade intolerant, was able to survive and grow when planted in the understory (Sanford et al. 2003), suggesting that the lack of current invasion of *E. umbellata* in the understory cannot be explained by intolerance of seedlings to shade. Although rapid growth confers a competitive advantage in open sites, the ability to survive in low light allows species to persist in understory habitats. Thus, the ability of an invasive species to establish under both high and low light levels can contribute substantially to its success. Therefore, one objective of this study was to assess the effects of varying light levels on the germination and early survival of common invasive woody species of the Northeastern United States. I hypothesized that (i) species commonly established in early successional habitats but not found in understory habitats (shade-intolerant species) will have lower rates of germination and survival in shade than in sun, and (ii) that species capable of invading both open and understory habitats (shade-tolerant species) will have similar germination and survival rates in sun and shade.

Light is the major limiting resource in the understory, so species that can increase the amount of leaf area displayed, achieve greater light interception and increase photosynthesis (Santiago et al. 2000). When an increase in leaf area is a direct result of an increase in allocation to leaf biomass, there are high respiratory costs. However, species that increase leaf area ratio (LAR) in the shade by decreasing leaf mass per area

(LMA), not by increasing leaf biomass ratio (LBR), are able to maximize light interception without incurring the respiratory costs coupled with greater leaf biomass (Pattison et al. 1998). Therefore, another objective of this study was to determine if species capable of invading both open and understory habitats have greater morphological plasticity at the leaf level. I hypothesized that species with high seedling survival in both sun and shade will exhibit greater morphological plasticity in leaf mass per area (LMA) resulting in the ability to increase leaf area ratio (LAR) in the shade to increase light interception without the need for greater investment in leaf biomass.

2.2 Methods

2.2.1 Study species

The following species were selected for the study: *Elaeagnus umbellata* (autumn olive), *Rosa multiflora* (multiflora rose), *Celastrus orbiculatus* (Oriental bittersweet), *Berberis thunbergii* (Japanese barberry), and *Rhamnus cathartica* (common buckthorn). All species are woody invasives that are bird dispersed but differ in their distribution. *E. umbellata* and *R. multiflora* are widely established in early successional habitats but are generally absent from understory habitats. *B. thunbergii*, *C. orbiculatus* and *R. cathartica* are established in both early successional and understory habitats. Many of these invasives have negative impacts on native plant species. *E. umbellata*, originally planted for wildlife value, is threatening native plant communities in Ontario and the U.S. (Catling et al. 1997). Records of the distribution of *Celastrus* species in the New York metropolitan flora have gone from about 90% of the native American bittersweet (*Celastrus scandens*) in 1960 to 94% of the invasive *C. orbiculatus* in 1990-1999

(Steward et al. 2003). *Celastrus orbiculatus* can overtop native species in gaps and along roadsides and is considered a pest by land managers (Dreyer et al. 1987, McNab and Meeker 1987). *R. cathartica* has been shown to double soil nitrogen as well as increase soil carbon by 80% in the Midwest (Heneghan et al. 2006).

2.2.2 Experimental design and measurements

Fruits of the five study species were collected in October 2005 at the Poland Brook Wildlife Management Area, Conway, MA. In order to collect seed, pulp was removed from the fruits by hand, and seeds were floated in water. Seeds floating to the top were discarded. Seeds were cold stratified at 4°C for 90 days. In January 2006 seeds were sown in potting soil in the greenhouse in a randomized block design with five species in two treatments (sun and shade) in four replicate blocks. The sun treatment was ambient light in the greenhouse (60% incident). Pots in the shade treatment were placed in shade houses with a 5% incident light level. Ten seeds of each individual species were sown in 4" x 4" pots with four replicate pots per species per treatment for a total of 400 seeds. Pots were checked daily for germinants and watered as needed. Each new germinant was marked and the day of germination recorded. Plants were left in the pots until harvested.

In June 2006 survival and height of all plants were recorded. Aboveground biomass of all plants was then harvested, and leaves and stems were separated, oven dried at 70° C and weighed. Leaf area was calculated using a computer scanner and Adobe Photoshop. LMA (leaf mass per unit leaf area), LBR (leaf biomass ratio, leaf biomass per unit total plant biomass) and LAR (leaf area ratio, leaf area per unit total plant biomass) were calculated using biomass and leaf area data. Percent survival was

calculated for each pot, and height, biomass and allocation data were collected. Analyses of variance (SPSS version 11) were conducted to test for any significant differences between the light treatments within a species. The model used the following terms (and degrees of freedom): species (4), block (3), light (1), species X light (4), light X block (3), species X block (12), species X block X light (12).

2.3 Results

2.3.1 Germination and Survival

All five species germinated successfully in both sun and shade treatments. In the shade, germination ranged from 50% for *Elaeagnus umbellata* to 80% for *Celastrus orbiculatus*. Germination in the sun ranged from 67.5% for *Rosa multiflora* to 87.5% for *Celastrus orbiculatus*. *C. orbiculatus* had the highest percent germination in both light treatments (Figures 2.1a-e). Germination began between days 5 and 13 in the shade and days 5 and 16 in the sun. Under both light conditions, *Berberis thunbergii* was the first to germinate while *Rhamnus cathartica* was the last (Figures 2.1a-e).

Each of the five species also demonstrated high seedling survivorship. For seedlings in the sun, *C. orbiculatus* had the lowest survival at 64%, and both *R. cathartica* and *R. multiflora* had 100% survival of seedlings that germinated (Table 2.1). In the shade, survival ranged from 73% for *R. multiflora* to 97% for *R. cathartica* (Table 2.1). *C. orbiculatus* was the only species showing a significant difference in mean seedling survival between light treatments, while survival of *B. thunbergii*, *E. umbellata*, *R. cathartica* and *R. multiflora* seedlings did not differ between sun and shade (Table 2.1).

2.3.2 Height and Biomass Allocation

R. cathartica had the shortest plants in both the sun and shade, while *R. multiflora* had the tallest plants in the sun and shade, (Table 2.1). *B. thunbergii* and *C. orbiculatus* were the only species to show a significant height difference having taller plants in the shade compared to the sun, although they differed in the magnitude of the difference. *B. thunbergii* was approximately 35% taller in the shade, while height of *C. orbiculatus* in the shade was two times the height it reached in the sun treatment (Table 2.1). However, while not significant, *E. umbellata*, *R. cathartica*, and *R. multiflora* showed a similar trend with taller plants in the shade. Despite greater height in the shade, all five species had significantly greater above ground biomass in the sun compared to the shade. None of the species showed a significant difference in leaf area between light treatments.

All five species had significantly greater LAR in the shade relative to the sun (Table 2.2). However, the greater LAR observed in the shade was not a result of significantly greater investment in leaf biomass. *C. orbiculatus*, *E. umbellata*, and *R. cathartica* showed significantly greater LBR in the sun compared to the shade, while the other two species showed the same trend but the differences were not significant (Table 2.2). The five species had significantly greater LMA in the sun relative to the shade by at least two-fold (Table 2.2). The ability of these species to increase LAR in the shade without a concurrent increase in LBR while maintaining a lower LMA in the shade suggests that the increase in LAR in the shade is a result of leaf level morphological plasticity.

2.4 Discussion

This study has demonstrated that a light level resembling that of a small gap, 15% full sun, (Denslow et al. 1998) does not limit germination or early seedling survival in five common woody invasive plants of the Northeast. All five species were able to decrease their LMA and increase their LAR. Three of the species significantly decreased LBR without decreasing survival. These species display ample morphological plasticity in order to compensate for a low light level in the short term.

One of my objectives was to assess if the absence of certain invasive species in low light environments is a result of low germination success and low seedling survival in the shade. Although the experiment was relatively short term, the focus was on first season survival, and under low light conditions, short term survival was high. In addition the seedlings had a growing season (germination to senescence) of 8 months, which is longer than the first year growing season under natural field conditions in southern New England. This experiment did not address overwinter seedling mortality, but Sanford et al. (2003) observed high winter survival of *E. umbellata* in open (88%) and understory (79%) plots in a field experiment.

All species exhibited high germination success and high survival under both sun and shaded conditions in this study. Absence of certain invasive species in low light habitats can be a result of a number of constraints. First there could be a lack of propagules dispersed to the site. Alternatively dispersal could occur but conditions are not favorable for successful germination and seedling establishment. For instance the inability of seeds to penetrate the forest litter layer could decrease germination rates and establishment. Ellsworth et al. (2004b) showed that seedling emergence of one of the

species studied here, *Celastrus orbiculatus*, was not prevented by a fragmented litter layer. The seedlings also had high emergence rates under intact litter layers (Ellsworth et al. 2004b). Finally, seedlings may become easily established but experience high early mortality. Future research on limits of invasion for these species could involve exploring factors such as seed dispersal, forest litter layer, and seed and seedling predation.

Another objective was to assess whether species invading open and understory habitats display greater morphological plasticity at the leaf level. My results suggest that shade tolerant species (*B. thunbergii*, *C. orbiculatus*, and *R. cathartica*) were all able to decrease LMA and increase LAR without increasing LBR. These results are consistent with the work of Ellsworth et al. (2004a) who also showed a decrease in LMA and an increase in LAR in the shade for *C. orbiculatus* seedlings, which could ultimately increase its invisibility in understory habitats. Shade intolerant species (*E. umbellata* and *R. multiflora*) also decreased LMA and increased LAR in the shade. *E. umbellata* was shown to behave in a similar manner when planted in the forest understory. Sanford et al. (2003) found a mean LMA of 29.3 g/m² while seedlings from my greenhouse experiment showed a mean LMA of 21.7 g/m². Sanford et al. (2003) and my LMA results for *E. umbellata* under high light conditions were similar as well (56.7 g/m² and 52.5 g/m²). Although Sanford et al. (2003) found a decrease in LBR and LAR in their seedlings, the seedlings were older with more woody stems. The similar LMA results demonstrate that while my seedlings were smaller and not grown under field conditions, the plasticity at the leaf level observed was not artificially induced under greenhouse conditions. These results suggest that species typically not found in the understory are still capable of adjusting to the low light levels by altering leaf morphological characteristics.

In conclusion, the results of this experiment suggest that absence of certain species from the forest understory may not be due to the intolerance of the species to shade. The species studied here have the ability to germinate and establish in a low light environment similar to that of a small forest gap, which could be a great concern for land managers. Forest fragmentation, which increases gap and edge habitats (Saunders et al. 1991), is on the rise in New England. Increases in the availability of these habitat types could lead to a greater chance that invasive bird-dispersed species, such as those studied here, will be dispersed into the forest understory. Further invasion could have a dramatic effect on the future structure and composition of New England's forests.

Figures 2.1a-e: Percent germination of five invasive plant species (+/- SE). All pots were monitored daily for approximately six months. The end of each line represents the last day a new germinant was observed. Lines with solid circles represent 5% full sun.

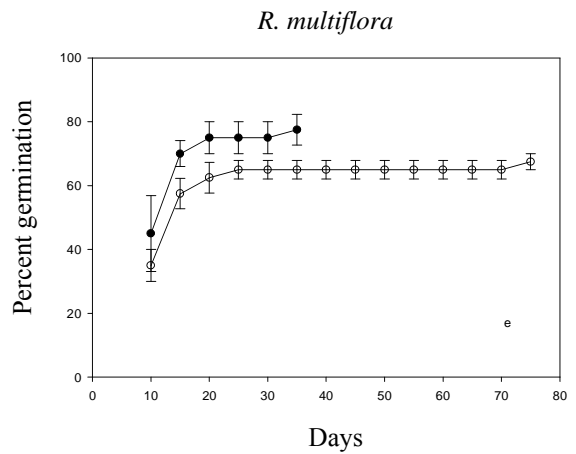
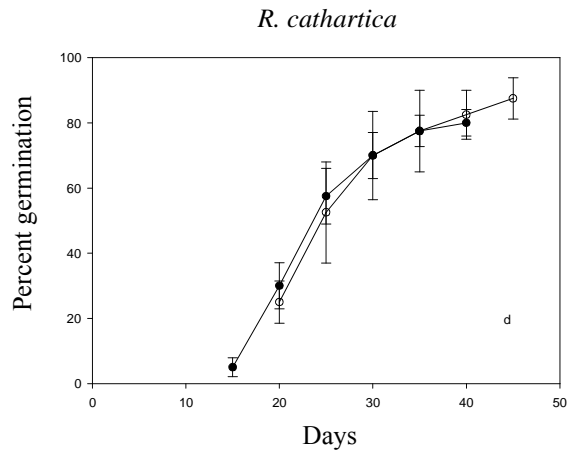
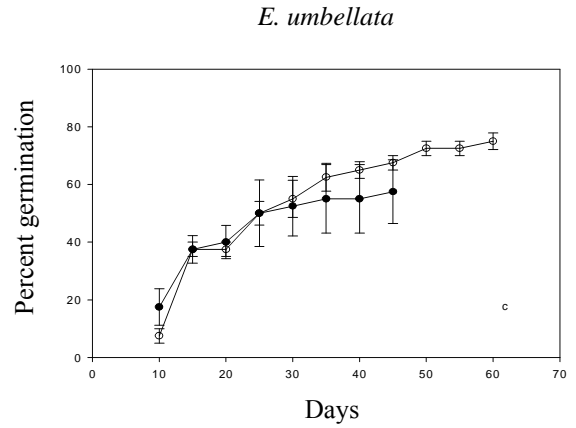
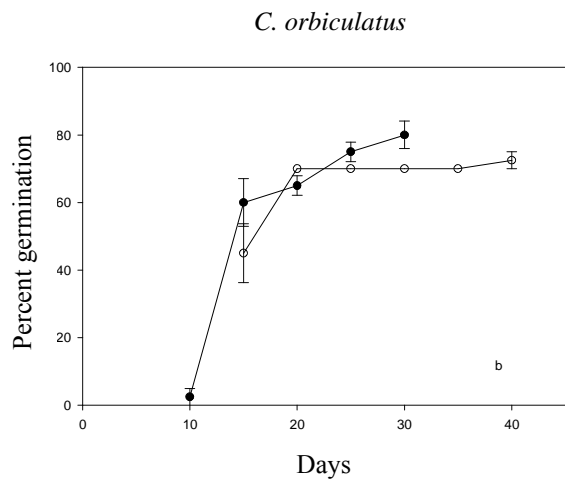
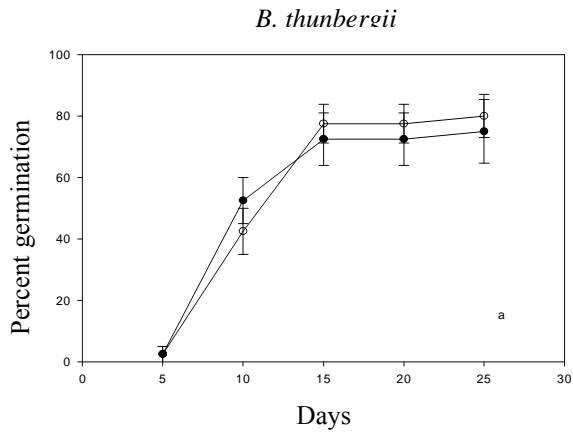


Table 2.1: Comparison of plant height (cm), biomass (g), leaf area (cm²) and percent survival of five invasive species under differing light conditions (60% full sun, shade (5% full sun)). Values are the means (se) of the four replicates. Values in bold indicate significant differences between light treatments within a species (P=0.05).

Species	Light	Height (cm)	Biomass (g)	Leaf area (cm ²)	Survival (%)
<i>B. thunbergii</i>	Sun	3.5 (0.4)	0.10 (0.001)	9.4 (0.14)	87.5 (8.0)
	Shade	4.8 (0.7)	0.03 (0.004)	7.7 (0.96)	84.7 (6.1)
<i>C. orbiculatus</i>	Sun	4.7 (0.3)	0.26 (0.048)	7.1 (2.32)	63.8 (5.1)
	Shade	10.5 (1.3)	0.11 (0.018)	10.1 (2.80)	82.3 (7.3)
<i>E. umbellata</i>	Sun	7.4 (0.7)	0.13 (0.024)	11.2 (5.51)	96.9 (3.2)
	Shade	8.4 (0.7)	0.02 (0.002)	4.8 (0.83)	85.2 (5.4)
<i>R. cathartica</i>	Sun	3.3 (0.2)	0.10 (0.016)	5.4 (1.92)	100.0 (0.0)
	Shade	4.0 (0.4)	0.02 (0.002)	4.7 (0.79)	97.2 (2.8)
<i>R. multiflora</i>	Sun	11.2 (0.7)	0.40 (0.015)	5.9 (1.54)	100.0 (0.0)
	Shade	14.8 (1.5)	0.07 (0.017)	11.0 (4.10)	72.8 (17.2)

Table 2.2: Comparison of mean LMA (leaf mass per unit leaf area), LBR (leaf biomass ratio, leaf biomass per unit total plant biomass) and LAR (leaf area ratio, leaf area per unit total plant biomass) of five invasive species under differing light conditions (60% full sun, shade (5% full sun)). Values are the means of the four replicates. Standard errors are in parentheses. Values in bold indicate significant differences between light treatments within a species (P=0.05).

Species	Light	LAR (cm ² /g)	LBR (g/g)	LMA (g/m ²)
<i>B. thunbergii</i>	Sun	98.9 (1.8)	0.60 (0.02)	60.4 (0.9)
	Shade	223.3 (7.2)	0.54 (0.02)	24.4 (0.6)
<i>C. orbiculatus</i>	Sun	98.5 (4.4)	0.74 (0.01)	75.4 (4.0)
	Shade	344.7 (28.1)	0.65 (0.01)	19.4 (1.9)
<i>E. umbellata</i>	Sun	130.7 (8.0)	0.68 (0.01)	52.5 (2.8)
	Shade	260.2 (19.3)	0.56 (0.03)	21.7 (0.7)
<i>R. cathartica</i>	Sun	126.0 (6.7)	0.73 (0.01)	57.9 (2.6)
	Shade	244.4 (14.9)	0.58 (0.01)	23.8 (1.3)
<i>R. multiflora</i>	Sun	94.3 (3.3)	0.58 (0.01)	61.0 (1.7)
	Shade	441.9 (29.6)	0.62 (0.01)	14.1 (0.7)

CHAPTER 3

THE EFFECT OF *ELAEAGNUS UMBELLATA* ON SOIL NITROGEN AVAILABILITY AND NATIVE AND INVASIVE PLANTS.

3.1 Introduction

Invasive plant species have had a negative impact on native plant biodiversity in a number of habitats (Woods 1993, Wyckoff and Webb 1996, Wilcove et al. 1998). Some species are also able to alter ecosystem level processes, and these impacts are difficult to reverse even after eradication of the invasive species (Zavaleta et al. 2001). In particular, some very successful invasive plant species establish nitrogen-fixing associations that not only increase invasiveness but also increase soil nitrogen availability. Because many invasive plants have the ability to respond to additional nitrogen input, invasion by a nitrogen-fixing species could possibly facilitate further invasion (Vitousek and Walker 1989, Maron and Connors 1996, Von Holle et al. 2006). The objective of this study is to determine whether the nitrogen-fixing *Elaeagnus umbellata* increases soil N resulting in increased N availability to other plants.

Several types of habitats have been invaded by nitrogen-fixing invasive species. *Acacia saligna* has successfully invaded the fynbos of South Africa and significantly increased total soil nitrogen availability (Yelenik et al. 2004). In Hawaiian wet lowland forests, nitrogen availability increased up to 121 times and phosphorous availability was up to 24 times higher depending on the age of the site in stands invaded by the invasive tree *Falcataria moluccana* (Hughes and Denslow 2005). Nitrogen fixers have also invaded habitats and increased soil nitrogen availability in coastal prairies of California (Maron and Connors 1996), upland coastal systems of the Cape Cod National Seashore (Von Holle et al. 2006) and young volcanic sites in Hawaii (Vitousek and Walker 1989).

By increasing N availability nitrogen-fixing invasive species may facilitate invasion of other nonnative species into plant communities across differing habitat types. For example, in the Mohave Desert, adding nitrogen in the form of ammonium nitrate or NPK fertilizer increased biomass of nonnative plants while decreasing biomass of natives (Brooks 2003). In montane forests of Hawaii, N-limited plots fertilized with nitrogen and phosphorous resulted in an increased density of nonnative ginger along with a decrease in abundance of natives in response to both nitrogen addition and NP addition (Ostertag and Verville 2002). These studies suggest that if nitrogen fixers invade habitats, there is great potential for additional invasions or increased dominance of nonnative species.

Autumn olive (*Elaeagnus umbellata* Thunb.) is an actinorhizal, nitrogen-fixing, invasive woody shrub that has successfully established and spread throughout New England. It was introduced to the U.S. from its native range in China, Korea and Japan around 1830 (Rehder 1940). Autumn olive was commonly planted for wildlife value, and its fleshy fruits are readily consumed and dispersed by birds (Edgin and Ebinger 2001). Autumn olive can facilitate the growth of native species. For example, it has been planted as a nurse crop with black walnut (*Juglans nigra*) to enhance productivity and has also been shown to increase white ash (*Fraxinus americana*) growth in Central Hardwood forest ecosystems (Ponder 1988). The effects in these ecosystems are likely a result of increased nitrogen availability near *Elaeagnus* (Paschke 1989, Wang et al. 2005).

If *E. umbellata* can facilitate the growth of native species, it is likely that it can facilitate invasive species as well. The invasive plants Japanese barberry (*Berberis thunbergii*) (Cassidy et al. 2004, Harrington et al. 2004) and glossy buckthorn (*Frangula*

alnus) (Knapp 2006) have been shown to respond positively to nitrogen additions and are common in the New England landscape. If invasive species have a greater N response than native species in *E. umbellata* invaded habitats, native species could be at a competitive disadvantage. Therefore my overall objective was to assess the impacts that *E. umbellata* has on an invaded area including (i) soil nitrogen availability, (ii) foliar nitrogen and chlorophyll content of naturally co-occurring native *Solidago rugosa* and (iii) growth rates of planted seedlings of a co-occurring invasive species, *Celastrus orbiculatus*.

I hypothesized that *E. umbellata* increases soil nitrogen availability relative to open areas and areas under a non-N-fixing invasive shrub, *Lonicera morrowi*. Therefore, I predicted that soil percent N is higher near *E. umbellata* relative to open areas and areas under a non-N-fixing invasive shrub, *L. morrowi*. I also hypothesized that the increase in soil percent N is not related to the presence of other shrubs or high soil moisture content and that nitrogen mineralization and nitrification are higher near *E. umbellata* relative to open areas and areas near *L. morrowi*. Since soils naturally contain more ^{15}N than air and nitrogen-fixing species that can obtain N from the isotopically lighter air, I predicted if nitrogen is derived from fixation, then ^{15}N will be lower in soil near *E. umbellata*.

Furthermore, I hypothesized that the additional N input from *E. umbellata* is available to other co-occurring plants and could conceivably facilitate growth of other invasive plants. I tested this hypothesis in two ways: first, I tested the prediction that the native *Solidago rugosa* would have higher foliar N and chlorophyll content when grown under *E. umbellata* than when grown under *L. morrowi*; second, *Celastrus orbiculatus* seedlings will have higher chlorophyll content, growth and survival under *E. umbellata*

than under *L. morrowi*. In addition, I examined whether there is a shading or general shrub effect that could possibly affect *C. orbiculatus* seedling growth or survival by comparing foliar ^{13}C values of the reference *Solidago rugosa* found in the three treatment areas. If there is a shading effect that could reduce water stress, I predicted that the foliar ^{13}C values of *S. rugosa* found under *E. umbellata* and *L. morrowi* shrubs will be more negative than those of *S. rugosa* in open areas. ^{13}C values can be used as an indicator of water stress in plants due to Rubisco's strong discrimination against ^{13}C when plants are not water stressed.

3.2 Methods

3.2.1 Site selection and experimental design

All field work was conducted at the Poland Brook Wildlife Management Area in Conway, MA. In order to randomly select points invaded by *E. umbellata*, I plotted points on a grid system every 10 m in the field in a north-south, east-west direction for a total of 149 points and noted if *E. umbellata* was present within a 1 m radius around the point. A random subsample of 10 points containing *E. umbellata* with nearby *Lonicera morrowi* and open areas inhabited primarily by *S. rugosa* was selected allowing for a blocked design with 10 replicates of three species. The three species allow for comparisons between an invasive nitrogen fixing shrub (*E. umbellata*), an invasive non-nitrogen fixing shrub (*L. morrowi*) and open areas dominated by *S. rugosa*.

3.2.2 Soil measurements

In July a pair of soil cores was taken from the top 10 cm of soil at all 30 points for a total of 60 soil cores. The soil cores were placed in polyethylene bags and taken to the

lab. One soil core from each pair was analyzed for initial nitrate and ammonium concentration using KCl extractions the day after collection. Soil cores were sieved to remove rocks and homogenize soils. A subsample of 10 g was taken from each soil core and placed in 100 mL of 1N KCl solution. This mixture was shaken vigorously then left to settle. An additional 10 g subsample was used for calculating soil moisture content. Soils were dried at 70° C. The remaining soil cores were incubated in the lab at room temperature and a constant moisture level for 30 days then processed. After processing, initial and final KCL extracts were sent to the University of Georgia Stable Isotope Lab, Athens, GA for analysis of ammonium and nitrate. Total N mineralization was calculated from the difference between initial and final ammonium plus nitrate concentrations. Nitrification was calculated from the difference between initial and final nitrate concentrations. In addition, subsamples of the soil were sent to the University of Georgia Stable Isotope Lab, Athens, GA for soil N, ¹⁵N, C and ¹³C analyses.

3.2.3 Plant measurements

3.2.3.1 Foliar Chemistry

To test whether *E. umbellata* had higher foliar N concentration and chlorophyll content than the non-fixing shrub, *L. morrowi*, or the native *S. rugosa*, foliage was collected from the three species at all ten points in August 2006. The samples were dried and ground to a fine powder using a Wiley mill and sent to the University of Georgia Stable Isotope Lab, Athens, GA for foliar N, ¹⁵N, C and ¹³C analyses.

Because *S. rugosa* was so widespread and common at the site, I used this species to test whether native plant species respond to increased soil N availability in the proximity of *E. umbellata*. I randomly selected one healthy *S. rugosa* individual from

each of the 30 plots. Each *S. rugosa* selected was located within 1 m of the selected treatment shrub in plots in the *E. umbellata* and *L. morrowi* treatments. Leaves from the selected plants were removed then taken to the lab for processing. The leaves were ground to a fine powder using a Wiley mill then sent to the University of Georgia Stable Isotope Lab, Athens, GA for foliar N, ^{15}N , C and ^{13}C analyses. Prior to removing leaves from the plants, chlorophyll content was recorded using a CCM-200 chlorophyll meter (Opti-Sciences). Chlorophyll content was measured as an additional index of foliar N content since the two should be positively correlated.

3.2.3.2 *Celastrus orbiculatus* seedling transplants and measurements

Celastrus orbiculatus seedlings were collected from the Mill River Recreation Area, North Amherst, MA in July 2006. The seedlings were then transplanted into the field at Poland Brook Wildlife Management Area, Conway, MA in four of the ten original plots. In addition to the previous three treatments, a competitive removal treatment was added where all standing vegetation was removed from a 0.5m x 1m plot. Eighteen *C. orbiculatus* seedlings were transplanted in 0.5m x 1m plots in all four treatments within each block for a total of 288 seedlings. Immediately after planting, seedlings were watered and heights were measured. Seedlings were replaced if they died within the first few days. Final heights of the seedlings were measured in September. Chlorophyll content of all healthy seedlings with leaves large enough for measurement was also recorded in September using a CCM-200 chlorophyll meter (Opti-Sciences).

3.2.3.3 Statistical Analyses

SPSS (version 11) was used for all statistical analyses. Analyses of variance were performed to test for significant species effects and interactions of species and soil

moisture content on soil nitrogen variables. Species and block were entered as fixed factors and moisture as a covariate. If the interaction was not significant, it was dropped from the model, and the ANOVA was run again. If the moisture covariate did not significantly affect the dependent variable, it was removed from the model, and the ANOVA was run again. When species significantly affected the dependent variable, LSD post-hoc comparisons were done to determine which species were different from one another. The basic model used the following terms (and degrees of freedom): species (2), block (9), species X block (18). Soils under *E. umbellata* have n=9 due to a missing sample. Analyses were performed in the same manner for the foliar variables but without using soil moisture as a covariate in the model. Percent survival data were arcsine square root transformed and net N-mineralization, nitrification, and seedling growth data were log transformed.

3.3 Results

3.3.1 Soil measurements

There was a tendency for higher nitrogen in areas near *E. umbellata* (Table 3.1). However, total soil nitrogen below *E. umbellata* did not differ from that under *Lonicera morrowi* or in open areas. Soil ¹⁵N did not differ significantly between treatments but tended to be lower in *E. umbellata* dominated plots, which is expected with N-fixing species (Table 3.1). Soil C:N also did not differ among treatments.

Net N-mineralization was not significantly different among the three treatments, but again there was a trend of increased mineralization rates under *Elaeagnus* (P=0.11) which covaried with soil moisture (Figure 3.1). There was a higher rate of net N-

nitrification near *E. umbellata* ($P=0.02$) which also covaried with soil moisture (Figure 3.2). The proportion of N mineralized from the total soil N was almost twice as high under *E. umbellata* as under *Solidago rugosa* but was not significant (Table 3.2).

3.3.2 Plant measurements

3.3.2.1 Foliar Chemistry

Elaeagnus umbellata had greater foliar N than both *Lonicera morrowi* and *Solidago rugosa* ($P<0.001$) (Table 3.3). In addition, *E. umbellata* foliar C:N was lower than *L. morrowi* and *S. rugosa* ($P<0.001$) (Table 3.3).

Foliar N of *S. rugosa* was significantly greater in areas near *E. umbellata* than in the open areas ($P=0.008$) (Table 3.4). Foliar N of *S. rugosa* growing near *L. morrowi* was intermediate and did not differ significantly from the other two treatments (Table 3.4). *S. rugosa* foliar C:N decreased under *E. umbellata* ($P=0.002$) compared to under *L. morrowi* by 11% and in open areas by 19%. While chlorophyll contents of *S. rugosa* next to *L. morrowi* and open areas were similar, chlorophyll content was significantly higher near *E. umbellata* by at least 21% ($P=0.001$). *S. rugosa* found near *E. umbellata* had more negative foliar ^{13}C values than that found in the other treatment plots ($P=0.008$) (Table 3.4). This result suggests that there was more water stress under *L. morrowi* shrubs and open areas dominated by *S. rugosa*.

3.3.2.2 *Celastrus orbiculatus* seedling transplants and measurements

Celastrus orbiculatus seedlings grew less in areas dominated by *Solidago rugosa* than under either shrub or in cleared areas (Table 3.5). This pattern could be due to competitive inhibition that could be partly explained by nitrogen, since chlorophyll

content was lower than under *E. umbellata* or where vegetation was removed. However, *C. orbiculatus* seedlings had lower chlorophyll content under *L. morrowi* suggesting that other factors are important. Seedlings planted under *E. umbellata*, *L. morrowi* and *S. rugosa* had high survival rates ranging from 89-96%. *Celastrus orbiculatus* seedlings planted in areas with the standing vegetation removed had significantly lower survival, approximately 60%. There were many wilting and brown seedlings in the vegetation removal plots so this observation could be a result of increased water stress for seedlings in these areas.

3.4 Discussion

The current study demonstrated that *Elaeagnus umbellata* has the potential to alter soil properties and also to facilitate the growth of other invasive plant species as well as co-occurring natives. Increased soil nitrogen availability in plots associated with *E. umbellata* compared to *L. morrowi* and *S. rugosa* was observed although the difference was not significant. Net nitrification was significantly higher under *E. umbellata* and increased as soil moisture increased. In addition, net N-mineralization and the proportion of nitrogen mineralized per unit of soil nitrogen were higher under *E. umbellata* but were not significant. While Baer et al. (2006) also found a non-significant trend toward total extractable soil N being higher under *E. umbellata*, net N-mineralization and nitrification were significantly higher. However, the investigators were comparing *E. umbellata* to rates in C₃ grasses while we compared *E. umbellata* to an invasive non-nitrogen fixing shrub and a forb. This approach was used in order to try to explain whether our results could be attributed to a general shrub effect or that of a nitrogen fixer. Higher soil N,

lower soil ^{15}N , higher net N-mineralization and nitrification coupled with significantly higher foliar N and lower foliar C:N suggest higher N availability in the *E. umbellata* samples than in the *L. morrowi* samples indicating that the results seen are not simply due to a shrub effect.

The impacts of a species on soil properties can be related to foliar properties of the individual species. For example, foliar N of *E. umbellata* was significantly higher than both *L. morrowi* and *S. rugosa* and higher nitrogen availability was observed under *E. umbellata*. In addition foliar C:N was significantly lower for *E. umbellata*. While this variable was not measured in our study, it is general knowledge that higher foliar nitrogen and lower foliar C:N result in higher decomposition rates (Melillo et al. 1982, Constantinides and Fownes 1994). Higher foliar N and lower foliar C:N suggest that *E. umbellata* foliage has a higher litter decomposition rate.

Since we were unable to separate the effects of soil N on foliar characteristics from intrinsic differences in species, we measured foliar traits in a single species, *Solidago rugosa*, found in the three treatment areas. These results were consistent with those of the three individual species. *Solidago rugosa* found near *E. umbellata* had higher foliar N, lower C:N, and higher chlorophyll content than when found near *L. morrowi* or in *S. rugosa* dominated areas. More negative foliar ^{13}C was observed in *S. rugosa* found near *E. umbellata*. This suggests an interaction with water availability such that either *E. umbellata* colonizes wetter microsites or that the shade from *E. umbellata* reduces water stress in *S. rugosa* growing under the shrub. I found, however, that there was no significant difference in soil moisture among the three treatments (Table 3.1).

Transplanted *Celastrus orbiculatus* seedlings also demonstrated that the slightly

higher nitrogen available under *E. umbellata* was associated with higher seedling chlorophyll content when compared to *L. morrowi* and *S. rugosa*. Chlorophyll content was somewhat higher where vegetation was removed, but it is possible that vegetation removal allowed for a larger pool of soil N available for seedlings leading to potential increases in chlorophyll content. Seedling growth was also highest under *E. umbellata*. After post-hoc comparisons, seedlings growing under *L. morrowi* shrubs and in areas with the standing vegetation removed had similar growth rates while seedlings growing in areas with standing *S. rugosa* had very low growth, which could be attributed to intense shading within the *S. rugosa* plots. Percent survival was very high in *E. umbellata*, *L. morrowi*, and *S. rugosa* plots. The very low growth coupled with high survival of *C. orbiculatus* seedlings in areas dominated by *Solidago* is consistent with the “sit and wait” strategy of *C. orbiculatus* described by Greenberg et al. (2001).

Numerous studies have shown that nitrogen fixing invasive plants have had detrimental impacts on ecosystems worldwide. The presence of *Acacia saligna* more than doubled soil total N compared to fynbos vegetation in South Africa (Yelenik et al. 2004). In addition, Von Holle et al. (2006) observed almost double total soil nitrogen in *Robinia pseudoacacia* stands than in paired native stands in Cape Cod, MA. The increase in soil N availability often translates into increased growth of co-occurring invasive or weedy species.

High survival under *E. umbellata* is consistent with the results from Orr et al. (2005) who showed that Eastern cottonwood (*Populus deltoides*) seedlings that were treated with either extract from fresh or minced *E. umbellata* leaves had about 80% survival compared to about 50% survival of seedlings treated with only sterile water.

However, the high survivorship of *C. orbiculatus* under all vegetation could be a characteristic of the species. Ellsworth et al. (2004a) observed 43% survivorship of *C. orbiculatus* in full sun and 70% in 28% sun. I also saw similar results with *C. orbiculatus* seedlings grown in the greenhouse with 64% survival in 60% sun and 82% in the shade (5% sun) (Chapter 2, Table 2.1). Areas with standing vegetation removed had significantly lower survival, possibly due to high light conditions and increased heat stress.

The results of this study support the idea that the invasive nitrogen fixing shrub, *Elaeagnus umbellata*, has a higher foliar N content and increased soil nitrogen availability when compared to a non N-fixing invasive shrub, *Lonicera morrowi*, and the forb, *Solidago rugosa*. These properties can lead to increased foliar N, chlorophyll, and growth of both native and invasive co-occurring plant species. The aforementioned properties could have serious management implications for the control of invasive species that inhabit areas where *E. umbellata* invades. Impacts of this facilitation, however, will be a function of the relative performance of the individual species. In addition, the ability of *E. umbellata* to increase soil N availability can have long lasting effects on soil chemistry. Even after the species is removed, the additional nitrogen will remain in the soil causing a legacy effect that can hinder restoration efforts. In order to avoid a potential legacy effect, early eradication of *E. umbellata* and invasive nitrogen-fixing species is of great importance.

Table 3.1: Mean values for soil nitrogen composition under native and invasive plants. Standard deviations are in parentheses.

SPECIES	Soil %N	Soil ¹⁵ N	Soil C:N	Moisture
<i>E. umbellata</i>	0.53 (0.14)	4.83 (0.81)	12.47 (3.26)	0.50 (0.12)
<i>L. morrowi</i>	0.50 (0.10)	5.35 (0.79)	11.70 (6.40)	0.46 (0.09)
<i>S. rugosa</i>	0.44 (0.13)	5.10 (0.89)	15.96 (6.52)	0.53 (0.05)

Figure 3.1: Relationship between moisture and net nitrogen mineralization for two invasive species (*Elaeagnus umbellata* and *Lonicera morrowi*) and the native *Solidago rugosa*.

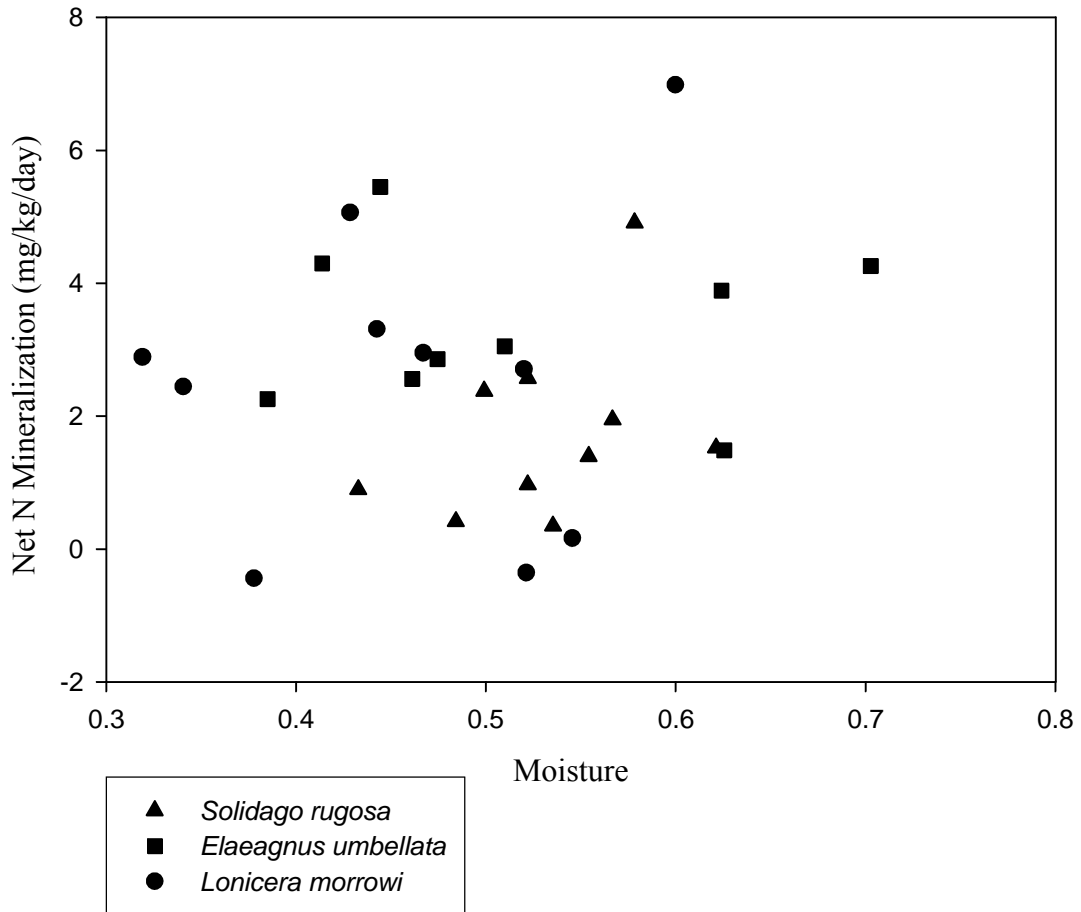


Figure 3.2: Relationship between moisture and net nitrification for two invasive species (*Elaeagnus umbellata* and *Lonicera morrowi*) and the native *Solidago rugosa*.

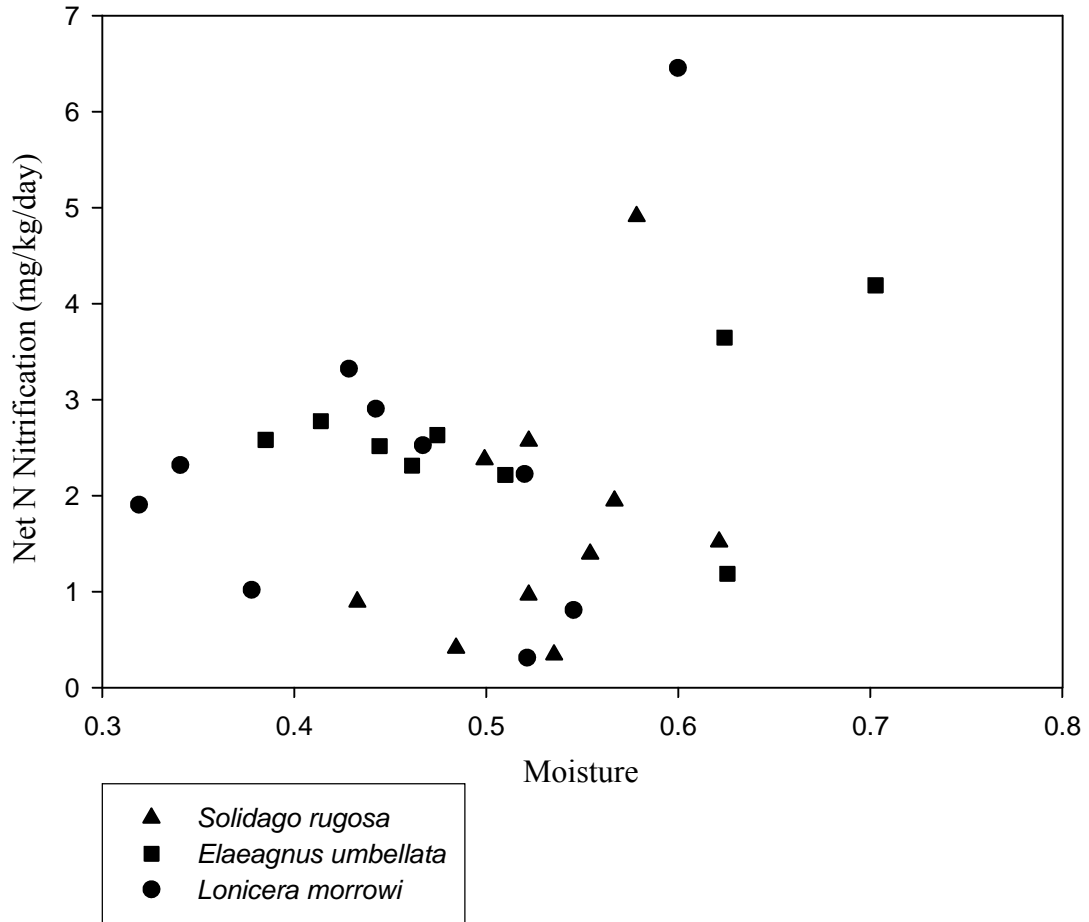


Table 3.2: Nitrogen availability under native and invasive plants. Standard deviations are in parentheses.

SPECIES	Net N mineralization (mg/kg/day)	Net N nitrification (mg/kg/day)	NMin/Soil N (mgN/kg soil)
<i>E. umbellata</i>	3.34 (1.23)	2.67 (0.85)	0.023 (0.009)
<i>L. morrowi</i>	2.57 (2.36)	2.38 (1.72)	0.017 (0.016)
<i>S. rugosa</i>	2.18 (1.53)	1.73 (1.35)	0.013 (0.010)

Table 3.3: Mean foliar nitrogen and foliar C:N of invasive and native plants. Standard deviations are in parentheses. Species with the same letter do not differ in their mean values for a given characteristic (P=0.05).

Species	Foliar %N	Foliar C:N
<i>E. umbellata</i>	3.81 (0.30) ^a	13.01 (1.05) ^a
<i>L. morrowi</i>	2.12 (0.20) ^b	22.88 (2.04) ^b
<i>S. rugosa</i>	2.22 (0.46) ^b	20.95 (2.59) ^c

Table 3.4: Mean values for *S. rugosa* foliar characteristics found near invasive shrubs and in open areas. Standard deviations are in parentheses. Species with the same letter do not differ in their mean values for a given characteristic (P=0.05).

Treatment	Foliar %N	Foliar C:N	Chlorophyll	¹³ C
<i>E. umbellata</i>	2.74 (0.41) ^a	16.98 (2.60) ^a	17.28 (3.27) ^a	-32.01 (1.53) ^a
<i>L. morrowi</i>	2.45 (0.21) ^{ab}	19.09 (1.50) ^b	13.60 (2.44) ^b	-30.99 (0.87) ^b
<i>S. rugosa</i>	2.22 (0.46) ^b	20.95 (2.59) ^c	12.29 (1.66) ^b	-30.38 (0.65) ^b

Table 3.5: Mean chlorophyll, growth and percent survival of *C. orbiculatus* seedlings planted near invasive shrubs, native *S. rugosa* or in areas where vegetation was removed. Growth was calculated by subtracting the initial height from the final height of the seedlings. Standard deviations are in parentheses. Species with the same letter do not differ in their mean values for a given characteristic (P=0.05).

Species	Chlorophyll	Growth (cm)	% Survival
<i>E. umbellata</i>	10.97 (2.22) ^a	2.99 (0.92) ^a	89 (20) ^a
<i>L. morrowi.</i>	7.18 (1.14) ^b	2.12 (0.99) ^a	92 (10) ^a
<i>S. rugosa</i>	8.20 (1.04) ^b	0.33 (0.52) ^b	96 (8) ^a
Cut vegetation	11.59 (2.04) ^a	1.78 (2.51) ^a	58 (27) ^b

BIBLIOGRAPHY

- Baer, S.G., C.H. Church, K.W.J. Williard, and J.W. Groninger. 2006. Changes in intrasystem N cycling from N-2-fixing shrub encroachment in grassland: multiple positive feedbacks. *Agriculture Ecosystems and Environment* **115**:174-182.
- Bellingham, P. J. 1998. Shrub succession and invasibility in a New Zealand montane grassland. *Australian Journal of Ecology* **23**:562-573.
- Brooks, M. L. 2003. Effects of increased soil nitrogen on the dominance of alien annual plants in the Mojave Desert. *Journal of Applied Ecology* **40**:344-353.
- Brown, J. R., and J. Carter. 1998. Spatial and temporal patterns of exotic shrub invasion in an Australian tropical grassland. *Landscape Ecology* **13**:93-102.
- Cassidy, T. M., J. H. Fownes, and R. A. Harrington. 2004. Nitrogen limits an invasive perennial shrub in forest understory. *Biological Invasions* **6**:113-121.
- Catling, P. M., M. J. Oldham, D. A. Sutherland, V. R. Brownell, and B. M. H. Larson. 1997. The recent spread of autumn-olive, *Elaeagnus umbellata*, into southern Ontario and its current status. *Canadian Field-Naturalist* **111**:376-380.
- Constantinides, M. and J. H. Fownes. 1994. Nitrogen mineralization from leaves and litter of tropical plants: Relationship to nitrogen, lignin and soluble polyphenol concentrations. *Soil Biology and Biochemistry* **26**:49-55.
- D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle and global change. *Annual Review of Ecology and Systematics* **23**:63-87.
- Denslow, J. S., A. M. Ellison, and R. E. Sanford. 1998. Treefall gap size effects on above- and below-ground processes in a tropical wet forest. *Journal of Ecology* **86**: 597-609.
- Dreyer, G. D., L. M. Baird, and C. Fickler. 1987. *Celastrus-Scandens* and *Celastrus-Orbiculatus* - Comparisons of Reproductive Potential between a Native and an Introduced Woody Vine. *Bulletin of the Torrey Botanical Club* **114**:260-264.
- Edgin, B., and J. E. Ebinger. 2001. Control of autumn olive (*Elaeagnus umbellata* Thunb.) at Beall Woods Nature Preserve, Illinois, USA. *Natural Areas Journal* **21**:386-388.
- Ellsworth, J. W., R. A. Harrington, and J. H. Fownes. 2004a. Survival, growth and gas exchange of *Celastrus orbiculatus* seedlings in sun and shade. *American Midland Naturalist* **151**:233-240.

- Ellsworth, J. W., R. A. Harrington, and J. H. Fownes. 2004b. Seedling emergence, growth, and allocation of Oriental Bittersweet (*Celastrus orbiculata*): effects of seed input, seed bank, and forest floor litter. *Forest Ecology and Management* **190**:255-264.
- Elton, C. S. 1958. *The Ecology of Invasions by Animals and Plants*. University of Chicago Press, Chicago.
- Greenberg, C. H., L. M. Smith, and D. J. Levey. 2001. Fruit fate, seed germination and growth of an invasive vine-an experimental test of 'sit and wait' strategy. *Biological Invasions* **3**:363-372.
- Harrington, R. A., and J. J. Ewel. 1997. Invasibility of tree plantations by native and non-indigenous plant species in Hawaii. *Forest Ecology and Management* **99**:153-162.
- Harrington, R. A., J. H. Fownes, and T. M. Cassidy. 2004. Japanese Barberry (*Berberis thunbergii*) in Forest Understory: Leaf and Whole Plant Responses to Nitrogen Availability. *American Midland Naturalist* **151**:206-216.
- Heneghan, L., F. Fatemi, L. Umek, K. Grady, K. Fagen, and M. Workman. 2006. The invasive shrub European buckthorn (*Rhamnus cathartica*, L.) alters soil properties in Midwestern US woodlands. *Applied Soil Ecology* **32**: 142-148.
- Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, Diversity, and Invasion - Implications for Conservations. *Conservation Biology* **6**:324-337.
- Huenneke, L. F., S. P. Hamburg, R. Koide, H. A. Mooney, and P. M. Vitousek. 1990. Effects of Soil Resources on Plant Invasion and Community Structure in Californian Serpentine Grassland. *Ecology* **71**:478-491.
- Hughes, R. F., and J. S. Denslow. 2005. Invasion by a N-2-fixing tree alters function and structure in wet lowland forests of Hawaii. *Ecological Applications* **15**:1615-1628.
- Hutchinson, T. F., and J. L. Vankat. 1997. Invasibility and effects of Amur honeysuckle in southwestern Ohio forests. *Conservation Biology* **11**:1117-1124.
- Knapp, L.B., 2006. Photosynthesis, growth, and survival of native and invasive woody species: trade-offs and plasticity across open and understory environments. Ph.D. dissertation, University of Massachusetts, Amherst. 194 pp.
- Kolar, C. S., and D. M. Lodge. 2001. Progress in invasion biology: predicting invaders. *Trends in Ecology & Evolution* **16**:199-204.

- Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* **80**:1522-1536.
- Maron, J. L., and P. G. Connors. 1996. A native nitrogen-fixing shrub facilitates weed invasion. *Oecologia* **105**:302-312.
- McNab, W., and M. Meeker. 1987. Oriental bittersweet: A growing threat to hardwood silviculture in the Appalachians. *Northern Journal of Applied Forestry* **4**:174-177.
- Melillo, J. M., J. D. Aber, and J. F. Muratore. 1982. Nitrogen and Lignin Control of Hardwood Leaf Litter Decomposition Dynamics. *Ecology* **63**:621-626.
- Munger, G. T. 2002. *Rosa multiflora*. In: Fire Effects Information System, [Online]. *in*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory.
- Munger, G. T. 2003. *Elaeagnus umbellata*. In: Fire Effects Information System. *in*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory.
- Orr, S. P., J. A. Rudgers, and K. Clay. 2005. Invasive plants can inhibit native tree seedlings: testing potential allelopathic mechanisms. *Plant Ecology* **181**:153-165.
- Ostertag, R., and J. H. Verville. 2002. Fertilization with nitrogen and phosphorus increases abundance of non-native species in Hawaiian montane forests. *Plant Ecology* **162**:77-90.
- Paschke, M. W., J. O. Dawson, and M. B. David. 1989. Soil nitrogen mineralization under black walnut interplanted with autumn-olive or black alder. *in* G. B. Rink, Carl A, editor. Proceedings, 7th central hardwood conference. Gen. Tech. Rep. NC-132. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station, Carbondale, IL.
- Pattison, R. R., G. Goldstein, and A. Ares. 1998. Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rainforest species. *Oecologia* **117**:449-459.
- Pimentel, D., L. Lach, R. Zuniga, and D. Morrison. 2000. Environmental and economic costs of nonindigenous species in the United States. *Bioscience* **50**:53-65.
- Ponder, F., Jr. 1988. Weed control and autumn-olive affect early growth and survival of black walnut in a hardwood clearcut. *New Forests* **2**:195-201.
- Rehder, A. 1940. Manual of cultivated trees and shrubs hardy in North America., 2nd edition. Macmillan, New York.

- Sanford, N. L., R. A. Harrington, and J. H. Fownes. 2003. Survival and growth of native and alien woody seedlings in open and understory environments. *Forest Ecology and Management* **183**:377-385.
- Santiago, L. S., T. S. Lau, P. J. Melcher, O. C. Steele, and G. Goldstein. 2000. Morphological and physiological responses of Hawaiian *Hibiscus tiliaceus* populations to light and salinity. *International Journal of Plant Sciences* **161**:99-106.
- Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological Consequences of Ecosystem Fragmentation - a Review. *Conservation Biology* **5**:18-32.
- Steward, A. M., S. E. Clemants, and G. Moore. 2003. The concurrent decline of the native *Celastrus scandens* and spread of the non-native *Celastrus orbiculatus* in the New York City metropolitan area. *Journal of the Torrey Botanical Society* **130**:143-146.
- Stohlgren, T. J., D. Binkley, G. W. Chong, M. A. Kalkhan, L. D. Schell, K. A. Bull, Y. Otsuki, G. Newman, M. Bashkin, and Y. Son. 1999. Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs* **69**:25-46.
- Vitousek, P. M., and L. R. Walker. 1989. Biological invasion by *Myrica faya* in Hawai'i: plant demography, nitrogen fixation, ecosystem effects. *Ecological Monographs* **59**:247-265.
- Von Holle, B., K. A. Joseph, E. F. Largay, and R. G. Lohnes. 2006. Facilitations between the introduced nitrogen-fixing tree, *Robinia pseudoacacia*, and nonnative plant species in the glacial outwash upland ecosystem of cape cod, MA. *Biodiversity and Conservation* **15**:2197-2215.
- Wang, J.S., S. A. Khan, and J. O. Dawson. 2005. Nitrogen fixing trees influence concentrations of ammonium and amino sugar-nitrogen in soils. Pages 1-17 in K. N. Brooks, and P.F. Ffolliott, editor. *Moving agroforestry into the mainstream. The 9th North American Agroforestry Conference Proceedings*. Dept. of Forest Resources, University of Minnesota, St. Paul, MN., St. Paul, Minnesota.
- Wilcove, D. S., D. E. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying Threats to Imperiled Species in the United States. *Bioscience* **48**:607-615.
- Williamson, M., and A. Fitter. 1996. The varying success of invaders. *Ecology* **77**:1661-1666.
- Wood, Y. A., T. Meixner, P. J. Shouse, and E. B. Allen. 2006. Altered ecohydrologic response drives native shrub loss under conditions of elevated nitrogen deposition. *Journal of Environmental Quality* **35**:76-92.

- Woods, K. D. 1993. Effects of Invasion by *Lonicera-Tatarica* L on Herbs and Tree Seedlings in 4 New-England Forests. *American Midland Naturalist* **130**:62-74.
- Wyckoff, P. H., and S. L. Webb. 1996. Understory influence of the invasive Norway maple (*Acer platanoides*). *Bulletin of the Torrey Botanical Club* **123**:197-205.
- Yelenik, S. G., W. D. Stock, and D. M. Richardson. 2004. Ecosystem level impacts of invasive *Acacia saligna* in the South African fynbos. *Restoration Ecology* **12**:44-51.
- Zavaleta, E. S., R. J. Hobbs, and H. A. Mooney. 2001. Viewing invasive species removal in a whole-ecosystem context. *Trends in Ecology and Evolution* **16**:454-459.