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Relating soil fertility and plant competition to *Rhamnus cathartica* L. (common buckthorn)

invasion success

By

Julia Lynn York

A thesis submitted to the Department of Environmental Science and Biology of the State
University of New York College at Brockport in partial fulfillment of the requirements for the
degree of Master of Science

07-18-2016

Relating soil fertility and plant competition to *Rhamnus cathartica* L. (common buckthorn)
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Abstract

Rhamnus cathartica (common buckthorn) is a shrub or small tree that is invasive in the northern and central United States and southern and eastern Canada. Buckthorn invades a wide variety of habitat types, including open areas and forests. Impacts of buckthorn invasion include the loss of native species, alterations to soil nutrient cycling and decay rates, and increases in non-native earthworm abundances. Although it is shade-tolerant, buckthorn grows rapidly in high light. However, the effects of competition on buckthorn growth are more pronounced in high light environments. Therefore, buckthorn may be particularly adapted to succeed in habitats with intermediate light regimes, which provide ample light for growth and decreased competition. Habitats with low soil fertility may also be especially vulnerable to buckthorn invasion due to buckthorn's ability to increase soil nitrogen while limiting the growth of herbaceous competitors. An observational and experimental study was performed to determine how habitat, competition, and soil nutrient status affect buckthorn success. I hypothesized that seedlings would have greater success in 1) shrubland habitats than meadow or forest edge habitats and 2) plots with decreased soil fertility than plots with increased or unaltered soil fertility. For the observational study, I measured vegetation and soil characteristics and leaf litter decomposition rates in one meadow, shrubland, and forest edge habitat at six sites in western New York. Meadows were different from shrub and forest habitats in vegetation, but not soil characteristics. Meadows had more herbaceous vegetation and fewer seedlings and saplings than the shrub and forest habitats. There were no differences in herbaceous vegetation cover, woody vegetation abundances and diameters, or in soil characteristics

between the shrub and forest habitats. Buckthorn leaf litter decayed faster than a native species mix. For the experiment, I measured the effect of habitat, competition, and soil nutrients on the growth and photosynthetic rates of transplanted buckthorn seedlings at the six sites. Although photosynthetic rates and light levels were greater in the meadows than the shrub and forest habitats, buckthorn seedlings displayed increased height loss in the meadows that was likely due to seedling herbivory and desiccation. While herbivory and desiccation likely exerted the strongest effects on seedling growth in the meadows, light availability exerted the strongest effects in the shrub and forest habitats. In contrast with my hypotheses, competition had no effect on seedling growth, and soil fertility affected only a small subset of seedlings. As meadow habitats were less susceptible to invasion than shrub and forest habitats, management efforts should prioritize shrublands and forests for buckthorn removal. As the competition and soil nutrient treatments had no effect on buckthorn growth in the shrubs and forests, management practices based on manipulating soil fertility or planting native competitors to inhibit buckthorn are not indicated. Instead, buckthorn monitoring and removal practices in forest and shrub habitats should focus on areas with increased light availability, which may create an invasion window for buckthorn.

Introduction

Rhamnus cathartica L.

Rhamnus cathartica L. (common buckthorn) is a deciduous shrub or small tree that is invasive throughout the northern and central United States and southern and eastern Canada (Kurylo *et al.* 2007). Native to Eurasia and northern Africa (Godwin 1943), buckthorn was introduced to North America in the late 1700s (Kurylo and Endress 2012) and became common in New England by the early 1800s, where it was used ornamentally and as a shelterbelt tree (Archibold *et al.* 1997). It is dioecious, reproducing sexually through bird-dispersed fruits (Godwin 1943). As a habitat generalist, buckthorn invades a variety of habitat types, including wetlands and uplands, open areas, and forest interiors (Kurylo *et al.* 2007). Buckthorn exhibits rapid growth (Harrington *et al.* 1989b, Grubb *et al.* 1996, Stewart and Graves 2004), high fecundity (Archibold *et al.* 1997), shade tolerance (Grubb *et al.* 1996), and production of secondary metabolites (Izhaki 2002, Seltzner and Eddy 2003). Buckthorn has been observed to produce leaves earlier and senesce later than co-occurring native species within its invasive range (Harrington *et al.* 1989a, Archibold *et al.* 1997).

Buckthorn invasion affects habitats on the community and ecosystem levels. On the community level, buckthorn invasion has been shown to decrease germination rates, survival, growth, and reproduction of native herbaceous species (Klionsky *et al.* 2011) and decrease the establishment of native canopy trees (Mascaro and Schnitzer 2011). On the ecosystem level, buckthorn invasion has been found to increase soil nitrogen, carbon, pH, and moisture levels, while decreasing soil carbon: nitrogen ratios (Heneghan *et al.* 2006). Unlike other members of the Rhamnaceae family that form associations with nitrogen-fixing *Frankia* species (Benson and Silvester 1993), buckthorn alters soil properties through its

nitrogen-rich leaf litter, which decays more rapidly than native litter (Heneghan *et al.* 2002). The alterations to nutrient cycling and decomposition caused by buckthorn have been associated with significant decreases in soil microarthropod abundances (Heneghan *et al.* 2009) and changes in substrate-use patterns of soil microbes (Heneghan *et al.* 2004). Buckthorn's ecosystem-altering effects can lead to further community-level effects by shifting the distributions of common mammalian species (Vernon *et al.* 2014).

Buckthorn invasion can also facilitate exotic earthworm invasion success, which produces further alterations in soil processes and structure (Heneghan *et al.* 2007, Madritch and Lindroth 2009, Klionsky *et al.* 2011). Heneghan *et al.* (2007) characterized the interaction between buckthorn and exotic earthworms as a modest invasional meltdown [a positive interaction between two or more non-native species in which the interacting species facilitate one another's invasion success synergistically (Simberloff and Von Holle 1999)] with a potential for legacy effects due to soil alterations and invasions by additional exotic species. Another study found that exotic earthworms were associated with increased abundance and biomass of buckthorn seedlings, providing further evidence of the interactive nature of buckthorn and earthworm invasion (Roth *et al.* 2015).

Buckthorn often forms dense monocultures in the habitats it invades (Boudreau and Willson 1992, Archibold *et al.* 1997), which may increase the severity of community and ecosystem effects. Shifts in ecosystem and soil processes may lead to changes in plant community structure and functioning (Heneghan *et al.* 2009). While no studies have directly measured the effects of buckthorn-induced soil alterations on plant communities, other studies of invasive plants have shown that alterations to soil nutrient levels and cycling can reshape plant communities by decreasing the abundances of or excluding native species

that are not adapted to the novel soil nutrient conditions produced by invaders (Vitousek *et al.* 1987, Chapin *et al.* 2000, Ehrenfeld *et al.* 2001, Allison and Vitousek 2004).

Interactions among competition, light availability, and invasion success

Buckthorn's invasion success may be due in large part to its physiological and life-history traits. Buckthorn is unique in that it is both shade-tolerant (Grubb *et al.* 1996, Archibold *et al.* 1997, Knight 2006) and highly responsive to increased light availability (Harrington *et al.* 1989a, Grubb *et al.* 1996). This ability to take advantage of fluctuating light levels may increase buckthorn's success in forest canopy gaps (Knight *et al.* 2007) and other habitats with periodic light fluctuations. Studies measuring buckthorn performance in a range of light levels found that buckthorn seedling survival (Gourley 1985), biomass (Grubb *et al.* 1996, Knight 2006), percent cover (Scriver 2005), and height (Willert 2000, Scriver 2005) were greater in intermediate to high light levels. On an absolute scale of light availability, buckthorn's preference might best be described as intermediate (i.e., halfway between full sunlight and darkness); however, an intermediate absolute light availability is likely to be described as relatively high light availability within forest understories due to the shady conditions within forests.

Light availability is often linked to growth rates via photosynthetic capacity. A comparison of the photosynthetic rates of buckthorn shrubs growing in a forest understory and an open hedgerow habitat found that hedgerow shrubs had greater photosynthetic rates and daily carbon accumulation rates than understory shrubs, which were limited by light availability; also, buckthorn's photosynthetic rates were roughly twice those of the co-occurring native shrub, *Cornus racemosa* (Harrington *et al.* 1989a). Buckthorn's phenology

also influenced its total annual carbon gain, with photosynthesis occurring prior to leaf emergence and extending after the senescence of native species (Harrington *et al.* 1989a).

While buckthorn is sensitive to both aboveground and belowground competition, the effects of competition are dependent on light availability. Herbaceous species decreased the growth of buckthorn seedlings in hardwood forest canopy gaps by decreasing light and soil NO₃; despite the negative effects of herbaceous competitors, buckthorn growth and survival were greater in canopy gaps than in closed canopy understory (Knight 2006). Similarly, two studies investigating the re-invasion of buckthorn in oak savannas following restoration found that tree canopy thinning increased buckthorn height (Willert 2000, Scriver 2005). Planting with native grasses and forbs initially decreased buckthorn growth (Willert 2000), but this effect did not persist over time; a follow-up study found that planting native grasses and forbs had no effect on buckthorn cover, stem density, or height (Scriver 2005), demonstrating that canopy-level light availability was more important over time for buckthorn performance than competition. Also, increased canopy cover in late-successional fields in an abandoned agricultural field chronosequence was associated with a reduction in buckthorn percent cover (Copenheaver 2008). Thus, while herbaceous competitors can decrease buckthorn's success, the negative effects of this competition can be negated by increased light availability.

Effects of soil fertility on invasion success

Multiple studies have shown that the competitive effects of neighboring vegetation vary with soil fertility (Grime 1974, Huston 1979, Gaucherand *et al.* 2006). For example, low soil fertility can decrease the competitive effects of herbaceous species on neighboring

individuals because low fertility environments are likely to exhibit lower plant abundances than high fertility environments, which decreases the likelihood of competitive interactions. A competition experiment in abandoned agricultural fields in Canada found that while the removal of native competitors significantly increased invasive cover in fertile sites, invasive cover in less fertile sites was not affected by neighbor removal (Reader and Best 1989). Similarly, a study measuring the effects of neighboring vegetation on three tree species found that inhibition of seedling growth was most pronounced in favorable sites, where seedling growth was greatest with competitors removed (Berkowitz *et al.* 1995). Inhibition was much weaker in unfavorable sites, and in some unfavorable sites, neighboring vegetation facilitated seedling growth (Berkowitz *et al.* 1995).

Buckthorn's positive effects on soil nitrogen availability may enhance its ability to invade low fertility environments while maintaining a competitive advantage. A study measuring the competitive effects of buckthorn on understory forbs found that increases in soil fertility associated with buckthorn invasion did not lead to greater success for native species (Klionsky *et al.* 2011). Forbs growing in invaded plots exhibited decreased survival, growth, and reproduction despite increased soil fertility; the authors posited that buckthorn decreased the performance of native forbs by decreasing light availability and through allelopathy (Klionsky *et al.* 2011). Thus, the drivers of buckthorn invasion success may vary with resource availability. In fertile habitats, competition from herbaceous species may decrease invasion success. In less fertile habitats, buckthorn invasion success may increase due to decreased competition and buckthorn's capacity to increase soil nitrogen availability while maintaining a competitive advantage over native herbaceous species.

Buckthorn's phenology and physiology may make it particularly adapted to invade low-fertility environments. Some of buckthorn's life history traits, such as its long leaf lifespan and production of secondary metabolites, are associated with increased resource-use efficiency (Chapin 1980, Coley *et al.* 1985). Invasive plants can sometimes exhibit greater efficiency than native plant species that are adapted to low-fertility environments. A study comparing the performance of invasive species with native Hawaiian species in low-resource environments found that invasives had greater carbon assimilation rates in light-, nutrient-, and water-limited environments and greater light-use efficiency, instantaneous nitrogen-use efficiency, and instantaneous energy-use efficiency in light- and nutrient-limited environments (Funk and Vitousek 2007). The longer leaf lifespans of the native species, however, led to similar total nutrient uptake levels for natives and invasives over time (Funk and Vitousek 2007). Buckthorn, however, retains its leaves longer than common competing native species within its invasive range (Harrington *et al.* 1989a, Archibold *et al.* 1997). Buckthorn's adaptations to low-fertility environments may be especially important in areas of the northeastern United States that were exposed to intensive agricultural practices followed by abandonment after soils were depleted. Agricultural activities generally decrease soil carbon and nitrogen levels (McLauchlan 2006). Communities formed on abandoned agricultural fields may be more susceptible to invasion because the native species therein are not adapted to low-fertility environments; the disturbance to soil properties from agricultural activities creates a window for invaders with greater resource-use efficiencies than native competitors.

Objective

Buckthorn is a common invasive plant in many parts of North America that can invade a variety of habitats. While the effects of buckthorn invasion are becoming increasingly well-documented, there have been few experimental manipulations performed using buckthorn. The effects of light availability, competition, and soil fertility must be separated to understand the mechanisms underlying buckthorn's success. Meadows, shrublands, and forests are three common habitat types within the northeastern United States that are invaded by buckthorn. As light availability varies among these habitats, habitat type can be used to provide a light availability gradient. The objective of this study was to determine how habitat, competition, and soil fertility interact to influence buckthorn growth and photosynthesis.

I hypothesized that buckthorn would have greater success in shrub habitats than meadows or forests because shrublands provide the most advantageous light availability regime for buckthorn. The tall shrubs that characterize shrublands offer buckthorn seedlings protection from desiccation and limit competition from herbaceous competitors by decreasing the average light availability. As buckthorn is shade tolerant (Grubb *et al.* 1996) and has a longer leaf lifespan than co-occurring native woody species (Harrington *et al.* 1989a, Archibold *et al.* 1997), the light limitation that decreases the competitive effects of herbaceous species is expected to have minimal effects on buckthorn's success. I also predicted that soil fertility and competition would have a positive interaction such that as soil fertility decreased, the effects of competition on buckthorn success would also decrease. Buckthorn's long leaf lifespan, defensive chemicals, and responsiveness to light availability may confer a competitive advantage in low-fertility environments, whereas

native plants in the northeastern United States may be less adapted to low-fertility environments, making them less effective competitors in such environments.

To test my hypotheses, I conducted an experimental manipulation using transplanted buckthorn seedlings exposed to habitat, competition, and soil fertility treatments. I also performed an observational study within each of the study sites to compare the vegetation, soil, and litter decomposition characteristics among habitats in order to determine which parameters were most important for buckthorn success.

Methods

Study sites

Both the observational and experimental studies were conducted in one meadow, shrubland, and forest edge habitat in each of six sites in western New York: Hunters Creek County Park, Erie County; Iroquois National Wildlife Refuge, Orleans County; Isaac Gordon Nature Park, Monroe County; Knox Farm State Park, Erie County; Montezuma National Wildlife Refuge, Seneca County; and Northern Montezuma Wildlife Management Area (NMWMA), Cayuga County (Figure 1). Mean annual precipitation values for the region range from 75 mm to 100 mm, and mean temperatures range from -6°C to -4°C in January and 20°C to 22°C in July based on 1981-2010 climate normals (Northeast Regional Climate Center 2016). Common tree species included *R. cathartica*, *Fraxinus pennsylvanica* (green ash), *Populus deltoides* (eastern cottonwood), and *Ostrya virginiana* (American hophornbeam). Common shrub species included *R. cathartica*, *Cornus racemosa* (gray dogwood), and *Lonicera tatarica* (Tartarian honeysuckle). Herbaceous vegetation was not identified to species; however, the meadow sites contained mixtures of grasses and forbs

interspersed with the occasional shrub or tree. Each site had pre-existing buckthorn populations.

Observational study - vegetation and soil measurements

During September and October 2013, I randomly established three 5 m² plots with two nested 1 m² subplots within each habitat. I measured the diameter at breast height (DBH) of all woody species greater than 1.4 m tall in the 5 m² plots. Individuals with a DBH ranging from 2.5 to 12.7 cm were characterized as sapling species, and individuals with a DBH greater than 12.7 were characterized as tree canopy species. I measured seedling abundance, herbaceous vegetation percent cover, soil moisture, and soil organic matter content within the 1 m² subplots. I measured seedling abundance by counting the number of woody individuals less than 1.4 m tall. Whereas trees and saplings were all identified to species, due to the difficulty of identifying seedling species and the large numbers of seedlings present, I identified buckthorn seedlings to species and counted all other seedlings as "Other." Seedling abundances were averaged by species (buckthorn and other) for each habitat/site combination. The percent cover (0 – 100%) of herbaceous vegetation was visually estimated. Soil characteristics were determined by collecting one 2-cm-diameter, 15-cm-depth soil core from the center of one 1-m² subplot per 5-m² plot. The three cores per habitat were pooled into one sample and sieved (2 mm). I measured soil moisture by oven drying known volume samples at 105°C for 48 hours. The dried samples were then combusted at approximately 360°C for two hours to calculate the loss on ignition (LOI) to determine soil organic matter content.

Observational study – litter decay rates by habitat and litter type

Leaf litter decay rates were measured by determining the change in mass of a known amount of litter placed in mesh litterbags. All leaf litter was collected from Iroquois National Wildlife Refuge during October and November 2012 using a shade-cloth placed on the soil surface to capture litterfall. The collected litter was dried at room temperature and separated into buckthorn litter and native leaf litter. The predominant native species were green ash, *F. americana* (white ash), *Crataegus monogyna* (hawthorn), eastern cottonwood, and *Acer saccharinum* (silver maple). One gram of dry litter was sealed into 10-cm²-mesh litterbags. Twelve buckthorn litterbags and 12 native litterbags were staked onto the soil surface in each habitat at each site in April 2013. Four replicates of each litter type were collected at each of three harvests occurring in July/August 2013, October 2013, and November/December 2013. After retrieval, the litterbags were air-dried at room temperature and then oven-dried at 60°C for 48 hours. Mass loss during transport and drying was accounted for using 10 calibration bags for each litter type. A correction factor for each litter type was calculated by dividing the oven-dried mass of the litter by the air-dried mass of the litter. I calculated decomposition rates using a single exponential decay model, $\frac{X_t}{X_0} = e^{-kt}$ where $\frac{X_t}{X_0}$ is the fraction of original mass remaining at time t in years and k is the annual decay constant (Olson 1963). I used a linear model to determine the annual decomposition rate (k), which is equal to the slope of the line produced by regressing the natural logarithm of the mean proportion of mass remaining over time in years. The four replicates at each time-point were averaged to calculate the mean proportion of mass remaining.

Observational study – statistical analyses

One-way ANOVAs were used to analyze the effect of habitat on seedling abundance, sapling abundance, sapling DBH, tree abundance, tree DBH, herbaceous vegetation percent cover, soil moisture, and LOI. Data were averaged across each plot and subplot to calculate the mean value for each site. The six sites were used as replicates.

The abundance of buckthorn was analyzed using a two-way ANOVA with habitat type and size class (seedling, sapling, and tree) as the main effects. The abundances of buckthorn within each size class were averaged across the three plots and two subplots at each site. Site was used as the level of replication. Leaf litter decomposition rates were analyzed using a two-way ANOVA, with habitat and litter type as the main effects. The six sites were used as replicates.

The datasets met most of the assumptions of the ANOVAs. The dependent variables were continuous, the observations were independent, and the dependent variables approximated normality in each cell of the design as determined using normal Q-Q plots. Five of the datasets were transformed to remove outliers. The seedling, sapling, and tree abundance datasets and the total buckthorn abundance dataset were all logarithm transformed. The litter decay rate dataset was transformed by multiplying each value by negative one and taking the square root of the product. This transformation was chosen using trial and error. The seedling abundance dataset contained one outlier after transformation. This dataset was analyzed twice—once with the outlier included and once with the outlier removed. The statistical trends were the same with and without the outlier; results are reported for the dataset containing the outlier. For clarity, untransformed mean values are reported in the text and figures for all transformed datasets.

Levene's Test of Equality of error variances was used to assess homogeneity. The seedling abundance, sapling abundance, sapling DBH, tree DBH, soil moisture, LOI, and buckthorn abundance datasets met the assumption of homogeneity of the variance. The ratio of the largest within-group variance to the smallest within-group variance (F_{\max}) was calculated for the datasets with heterogeneous variances. F_{\max} was greater than three for all of these datasets, indicating that the heterogeneity of the variances was likely to cause alpha inflation (Keppel 1991). As such, the level of significance was reduced from $\alpha = 0.05$ to $\alpha = 0.025$ for the tree abundance, herbaceous vegetation percent cover, and litter decay rate datasets.

Significant results were further analyzed using Tukey *post hoc* tests for multiple comparisons. All statistical analyses were performed using IBM SPSS Statistics (version 22).

Experimental study – buckthorn relative growth rates and biomass

Between July and October 2012, 54 transplant plots (0.33 m x 0.33 m, 6 replicates per habitat per site, $n = 108$) were established within each of the three habitat types (meadow, shrubland, and forest edge) at the six study sites. One buckthorn seedling was transplanted into the center of each plot. The seedlings were all harvested from a forested area within the Montezuma National Wildlife Refuge up to one week prior to planting. The initial seedling height and diameter at the root collar (mean \pm SD: 23.4 \pm 11.3 cm and 0.96 cm \pm 0.46 cm, respectively) were measured after transplanting. Two treatments, soil nutrient level and plant competition, were applied to the experimental plots in a factorial design. The plant competition treatment was applied when the plots were established (July-October 2012) and consisted of three levels: aboveground competition (AG), belowground

competition (BG), and no competition (NC). The AG plots were situated so that herbaceous and/or woody subcanopy plant competitors covered at least 75% of the plot. In habitats lacking a sufficient abundance of interspecific competitors, other buckthorn individuals were used as plot competitors. In the BG plots, aboveground biomass from herbaceous and woody subcanopy competitors was tied back using rope and cable ties to minimize competition for sunlight. In the NC plots, all existing vegetation (excluding canopy trees) was cut at ground level and cleared from the plot. The competition treatments were maintained throughout the experiment.

The soil nutrient treatment consisted of a single application of three levels: decreased (FS), increased (FN), and ambient (FO) soil nitrogen. To decrease soil nitrogen, sawdust (44.0 g per plot) was spread on the soil surface in May 2013. Plant fertilizer (0.80 g NH_4NO_3 per plot) was applied to the surface of plots in July 2013. Soil nitrogen levels were not altered in the ambient treatment.

I measured buckthorn seedling height and diameter three times for each seedling. Height measurements were taken using a meter stick, and diameter measurements were taken using calipers. The initial measurements were performed in July 2013. This measurement was taken after the competition treatments and the sawdust treatment were applied and before the fertilizer treatment was applied. I assumed that the competition and sawdust treatments would take longer to produce a measurable effect due to the length of time needed for plant growth in response to altered competition and the length of time required for the sawdust to decrease soil nitrogen levels. Although the seedlings were measured directly following transplanting, which occurred from July to October 2012, these measurements were not included in the analysis because many seedlings died and were

replaced from October 2012 to July 2013. Thus, all the seedlings were re-measured in July 2013 to standardize the length of time between subsequent measurements.

The first measurement following the application of all treatments was taken in September 2013. The final measurement was taken in November and December 2013. Seedlings that died or were browsed were not replaced following the initial July 2013 measurement. Thus, for any seedling, the initial height or diameter measurements could be greater than the subsequent measurements due to height or diameter loss from breakage, herbivory, or desiccation.

At the conclusion of the experiment, the aboveground and belowground biomass of the buckthorn seedlings was measured. The seedlings were harvested from the experimental plots by digging, washed to remove soil from the roots, and oven-dried at 60°C for 24 hours. The aboveground and belowground portions of the dried seedlings were separated and massed. Then, the ratio of aboveground to belowground biomass was calculated by dividing the aboveground mass by the belowground mass.

Experimental study – buckthorn photosynthetic rate and PAR

Net photosynthetic rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) was measured for a sub-sample of buckthorn seedlings using a LiCor 6400 portable CO₂ analyzer with a leaf chamber at constant CO₂ and ambient light. External photosynthetically active radiation (PAR, $\mu\text{mol m}^{-2} \text{ s}^{-1}$) was also measured at that time using a light sensor mounted to the leaf chamber. The instrument was calibrated to maintain relative humidity within a favorable range. Photosynthesis and PAR were each measured two times during the experiment. The initial photosynthesis and PAR measurements were taken in July and August 2013 when the

nitrogen fertilizer was applied to plots. The second photosynthesis and PAR measurements were taken in September 2013. The photosynthesis and PAR measurements were organized into four datasets: initial photosynthetic rate (PS Pre), initial PAR (PAR Pre), final photosynthetic rate (PS Post), and final PAR (PAR Post). One seedling was selected for measurement from each treatment-level combination for each site and habitat (n = 9 per habitat, 27 per site) based on the presence and number of leaves. Leaves that were large enough to fill the leaf chamber and appeared healthy were preferentially selected for measurement. Many of the seedlings' leaves were smaller than the leaf chamber. Other seedlings had no leaves or loosely attached leaves, particularly during the second measurement. Many of the treatments only had one or two seedlings with suitable leaves for measurement. If possible, the same seedling was measured on both dates; however, in some cases, another seedling had to be substituted due to a lack of leaves for sampling.

Experimental study – statistical analyses

The effects of habitat, competition, and soil nutrient levels on buckthorn seedling growth rates were analyzed using three-way ANOVAs. First, I calculated the relative growth rate (RGR) of each seedling for both height and diameter by subtracting the initial measurement from the final measurement and dividing by the number of days between measurements.

$$RGR_{height} = \frac{(H_f - H_i)}{T_{days}}$$

$$RGR_{diameter} = \frac{(D_f - D_i)}{T_{days}}$$

A number of seedlings had negative RGR values, presumably due to a combination of desiccation and herbivory. To differentiate between the effects of the treatments on height/diameter accumulation and height/diameter loss, analyses were performed for positive height and diameter RGR values, and then further analyses were performed for both positive and negative height and diameter RGR values. I analyzed the height and diameter RGRs separately. The six sites were considered the level of replication, so the six pseudo-replicates within each site were averaged, and these averages were used for the analyses. The buckthorn biomass ratio, photosynthesis, and PAR measurements were analyzed similarly, with the six sites used as replicates.

Three-way factorial ANOVAs were used to measure the effects of habitat, competition, and soil nutrient levels on the nine dependent variables (positive HRGR, positive DRGR, all values HRGR, all values DRGR, buckthorn biomass ratio, PS Pre, PS Post, PAR Pre, and PAR Post). The datasets met most of the assumptions of the three-way ANOVAs. The dependent variables were continuous, the observations were independent, and the dependent variables approximated normality in each cell of the design as determined using normal Q-Q plots. All of the datasets contained outliers. Three datasets were transformed to remove the outliers (positive HRGR—square root transformation, PAR Pre and PAR Post—logarithm transformation). For clarity, untransformed values are reported in the text and figures. For the remaining datasets, no transformations were found that removed the outliers. These datasets were analyzed twice—once with the outliers included and once with the outliers removed. The statistical trends were the same with and without the outliers for all of the untransformed datasets. Results are reported for the datasets containing outliers.

Levene's Test of Equality of error variances was used to assess homogeneity. Only the positive DRGR dataset met the assumption of homogeneity of the variance. F_{\max} was greater than three for the datasets with heterogeneous variances, so the level of significance was reduced from $\alpha = 0.05$ to $\alpha = 0.025$ (Keppel 1991) for all datasets except the positive DRGR dataset. Significant results were further analyzed using Tukey *post hoc* tests for multiple comparisons.

Results

Observational study – vegetation and soil measurements

Habitat had no significant effect on soil moisture, LOI, sapling DBH, tree abundance, or tree DBH (Tables 1 and 2). Although the difference was non-significant, mean tree abundances were lowest in the meadows and greatest in the forest habitats (Table 2). Habitat had a significant effect on seedling abundance ($F_{2,13} = 11.540$, $p = 0.001$) and sapling abundance ($F_{2,11} = 8.574$, $p = 0.006$). Seedling abundances were significantly lower in the meadow habitats (mean \pm standard error, $13,056 \pm 5,716$ seedlings/ha) than the shrub ($273,056 \pm 118,601$ seedlings/ha) and forest ($320,833 \pm 153,869$ seedlings/ha) habitats (Figure 2). Shrub and forest seedling abundances were not significantly different. Sapling abundance was significantly lower in the meadow habitats (178 ± 153 saplings/ha) than the shrub ($4,200 \pm 1,120$ saplings/ha) and forest ($2,978 \pm 672$ saplings/ha) habitats (Figure 3). The shrub and forest sapling abundance values were not significantly different.

Habitat had a significant effect on herbaceous vegetation percent cover ($F_{2,15} = 14.216$, $p < 0.001$). Herbaceous vegetation percent cover was significantly greater in the meadow habitats ($98.47 \pm 1.02\%$) than the shrub ($56.89 \pm 13.62\%$) or forest ($31.51 \pm 7.40\%$)

(Figure 4). Herbaceous percent cover in the forest and shrub habitats was not statistically different.

Observational study – buckthorn abundance by habitat and size class

Size class ($F_{2,19} = 34.664$, $p < 0.001$), but not habitat, had a statistically significant effect on buckthorn abundance. *Post hoc* analyses revealed that the abundance of buckthorn seedlings ($112,500 \pm 55,244$ individuals/ha) was significantly greater than the abundance of buckthorn saplings (733 ± 297 individuals/ha) and buckthorn trees (207 ± 78 individuals/ha) (Figure 5).

Observational study – litter decay rates by habitat and litter type

Litter type had a statistically significant effect on decomposition rates ($F_{1,30} = 46.215$, $p < 0.001$). Habitat and the interaction term were both non-significant. Buckthorn litter ($k = -6.04 \pm 0.82$) had faster decomposition rates than the leaf litter of native species ($k = -1.44 \pm 0.16$) (Figure 6).

Experimental study – buckthorn relative growth rates

None of the treatments had a statistically significant effect on buckthorn seedling height RGR within the positive-values-only HRGR dataset (Table 3). For the positive values DRGR dataset, there was a significant interaction between the habitat and soil nutrient treatments ($F_{2,102} = 7.40$, $p = 0.001$, Figure 7). Seedlings in the meadows (0.0017 ± 0.0003 cm/day) had greater diameter RGRs when nitrogen was added to plots than seedlings in the shrub (0.0008 ± 0.0002 cm/day) or forest habitats (0.0009 ± 0.0001 cm/day). There was no difference between the diameter RGRs of the shrub and forest seedlings.

For the HRGR dataset including both positive and negative values, buckthorn seedling height RGR varied significantly among habitats ($F_{2,135} = 11.857$, $p > 0.001$). Height RGR was less negative in the shrub (-0.0058 ± 0.0019 cm/day) and forest habitats (-0.0057 ± 0.0019 cm/day) than the meadow habitats (-0.0214 ± 0.0038 cm/day) (Figure 8). For the DRGR dataset including both positive and negative values, the treatments had no significant effects on diameter RGR (Table 4).

Experimental study – buckthorn biomass

Habitat ($F_{2,127} = 4.749$, $p = 0.010$), competition ($F_{2,127} = 5.917$, $p = 0.003$), and soil nutrient levels ($F_{2,127} = 5.483$, $p = 0.005$) all had statistically significant effects on buckthorn seedling AG:BG biomass ratios, although none of the interactions were significant (Table 5). *Post hoc* multiple comparisons showed that the AG:BG biomass ratio was lower in the meadow habitat (0.8973 ± 0.0369) than the shrub (1.0388 ± 0.0450) and forest (1.0316 ± 0.0326) habitats (Figure 9). The NC treatment (0.9052 ± 0.0373) had a lower biomass ratio than the AG (1.0824 ± 0.0397) treatment (Figure 10). The BG treatment (0.9801 ± 0.0377) was not statistically different from the NC or AG treatments. The FN soil nutrients treatment (1.0881 ± 0.0488) had a significantly greater biomass ratio than the FS (0.9386 ± 0.0325) and F0 (0.9410 ± 0.0313) treatments (Figure 11).

Experimental study – buckthorn photosynthetic rate and PAR

For the PS Pre dataset, habitat had a statistically significant effect on buckthorn seedling photosynthesis ($F_{2,134} = 12.336$, $p < 0.001$, Table 6). Net photosynthetic rates were greater in the meadow habitats (3.6 ± 0.4 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) than the shrub (1.3 ± 0.3 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) or forest (0.5 ± 0.6 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) habitats (Figure 12). Habitat also had a

significant effect on photosynthesis in the PS Post dataset ($F_{2,135} = 15.067$, $p < 0.001$, Table 6). Net photosynthetic rates were greater in the meadow habitats ($3.8 \pm 0.4 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) than the shrub ($1.7 \pm 0.4 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) or forest ($1.2 \pm 0.2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) habitats (Figure 12).

For the PAR Pre dataset, PAR levels varied significantly among habitat ($F_{2,134} = 89.811$, $p < 0.001$) and soil nutrient ($F_{2,134} = 5.773$, $p = 0.004$) treatments (Table 7). PAR was greater in the meadow ($713 \pm 81 \mu\text{mol m}^{-2} \text{ s}^{-1}$) habitats than the shrub ($115 \pm 36 \mu\text{mol m}^{-2} \text{ s}^{-1}$) or forest ($93 \pm 31 \mu\text{mol m}^{-2} \text{ s}^{-1}$) habitats (Figure 13). The sawdust-added soil nutrients treatment ($395 \pm 71 \mu\text{mol m}^{-2} \text{ s}^{-1}$) had greater PAR than the nitrogen-added ($277 \pm 66 \mu\text{mol m}^{-2} \text{ s}^{-1}$) or ambient ($252 \pm 63 \mu\text{mol m}^{-2} \text{ s}^{-1}$) treatments (Figure 14). For the PAR Post dataset, PAR was significantly different among habitats ($F_{2,135} = 45.612$, $p < 0.001$, Table 7). The meadow habitat ($875 \pm 90 \mu\text{mol m}^{-2} \text{ s}^{-1}$) had greater PAR than the shrub ($242 \pm 56 \mu\text{mol m}^{-2} \text{ s}^{-1}$) or forest ($110 \pm 32 \mu\text{mol m}^{-2} \text{ s}^{-1}$) habitats (Figure 13). PAR levels were also greater in the shrub habitats than the forest habitats.

Across both measurement dates, PAR levels statistically significantly predicted photosynthetic rates ($F_{1,49} = 71.634$, $p < 0.001$), accounting for 59.4% of the variation in photosynthesis.

Discussion

Observational study – vegetation and soil measurements

The three habitat types showed no difference in many of the measured vegetation and soil parameters. Although abundances of all species of trees were lowest in the meadow habitats and greatest in the forest habitats (Table 2), these differences were not

significant. This finding is at least partially due to the use of forest edges, rather than forest interiors, which limited the amount of woody vegetation. Also, while the habitats were rigidly delineated for the purpose of the study, ecological boundaries are less strictly defined. The habitats tended to be situated near or directly adjacent to one another, often forming a matrix of meadow, shrub, and forest patches. Also, study sites were chosen based on the presence of pre-existing buckthorn populations. As buckthorn tends to displace native species through competitive and possibly allelopathic effects (Klionsky *et al.* 2011), the habitats were likely already degraded. In addition to buckthorn, other invasive species were present. These species included *Elaeagnus umbellata* (autumn olive), *L. periclymenum* (European honeysuckle), Tartarian honeysuckle, and *Rosa multiflora* (multiflora rose). Thus, the lack of a significant difference in tree abundances among the habitats may also have been due to pre-existing effects of buckthorn invasion, which can lead to a shift from large trees to smaller trees in forest habitats and a shift from herbaceous species to woody species in meadow habitats (Mascaro and Schnitzer 2011).

The main differences among the habitats were in sapling and seedling abundances and herbaceous vegetation percent cover. The results were as expected; the meadows contained fewer saplings and seedlings and more herbaceous vegetation than the forests and shrub habitats.

Observational study - buckthorn abundance by habitat and size class

The finding that buckthorn seedlings were more abundant than buckthorn saplings and trees was expected, as many seedlings do not survive to reach maturity. The large difference between the abundance of seedlings and saplings/trees (Figure 5) suggests that

buckthorn seedling mortality is relatively high in these habitats. Thus, buckthorn invasion may be most limited during colonization. As buckthorn seeds are bird-dispersed (Godwin 1943), the abundances and feeding preferences of avian populations and the availability of perch sites are likely to play an important role in determining buckthorn recruitment rates.

The lack of a difference in buckthorn abundance among habitats is likely due to selection bias. Sites were chosen based on the presence of buckthorn populations, with preference given to areas within sites with greater buckthorn abundances.

Observational study - litter decay rates by habitat and litter type

Buckthorn leaf litter had faster decay rates than a native leaf litter mix within all habitat types. These results are similar to other decomposition studies, which also found that buckthorn litter had greater decomposition rates than native species litter, presumably due to the greater nitrogen content found in buckthorn litter (Heneghan *et al.* 2002, Heneghan *et al.* 2007). Buckthorn invasion is associated with increased soil nitrogen, carbon, moisture, and pH and decreased soil carbon: nitrogen ratios (Heneghan *et al.* 2006). Based on these results, the sites in this study and similar buckthorn-invaded habitats are likely to have different soil characteristics than non-invaded areas. The soil parameters measured in this study, soil moisture and soil organic matter, did not differ among the habitats. This finding may be the result of buckthorn invasion. However, the soil measurements were only taken once during the growing season, so it is possible that differences among the habitats occur at other time points. Further research is needed, particularly comparisons of the soil characteristics of invaded and non-invaded areas.

Experimental study - buckthorn relative growth rates

By separating the positive values from the total dataset, the effects of the experimental treatments on buckthorn seedling height and diameter accumulation were distinguished from the effects on height and diameter loss. As this experiment took place in the field with many uncontrolled factors, using a dual approach allowed a greater understanding of the different stressors acting on the seedlings. While buckthorn seedling height loss was greatest in the meadow habitats, seedlings had greater diameter growth in this habitat when nitrogen was added to plots. These results indicate that habitat had the greatest effect on buckthorn seedling success of the experimental treatments, with the meadow habitats exerting different effects than the shrub and forest habitats.

The increase in diameter RGRs in the nitrogen-addition treatment of the meadow habitats suggests that seedling growth was limited by nitrogen availability in the meadows. Although nitrogen addition led to increased diameter growth rates for seedlings in the meadow habitats, this boon did not lead to increased height growth rates. It appears that other factors prevented these seedlings from increasing in height. The pattern of height loss sheds light on this finding. Seedlings in all competition and soil nutrient treatments in the meadow habitats had greater height loss than seedlings in the shrubs and forests. In an experiment using seedlings transplanted into shade frames within its native range, buckthorn produced the greatest dry mass and shoot height in nutrient-rich soils with high light availability; however, herbivores were excluded, and water was not limited (Grubb *et al.* 1996). In the present study, buckthorn's ability to thrive in nutrient-rich environments with high light appeared to be limited or negated by herbivory and/or desiccation. As the meadows had greater light levels than the shrubs and forests (Figure 13), desiccation may

have prevented height accumulation in the meadows. While herbivory was not measured, many seedlings showed evidence of herbivory, such as being clipped at the base of the stem. The clipping of seedlings at or near ground level is characteristic of herbivory by meadow voles (*Microtus pennsylvanicus*) (Ostfeld *et al.* 1997). Meadow vole herbivory is more prevalent in old field habitats than forest edges, particularly in old fields dominated by herbaceous rather than woody vegetation (Ostfeld *et al.* 1997), as was the case for the meadow habitats in this study. Also, herbivory by small mammals was the primary cause of mortality for buckthorn seedlings transplanted into old fields in central New York (Gill and Marks 1991). Thus, it is likely that desiccation and herbivory prevented seedlings in the meadows from gaining a height advantage and, in fact, led to a greater decrease in height than seedlings in the other habitats.

Experimental study - buckthorn biomass

The differences in buckthorn biomass ratios were concordant with the trends in seedling relative growth rates. The lower biomass ratios in the meadow habitats were likely due to a combination of decreased nutrient availability (Brouwer 1962, Bloom *et al.* 1985, Lambers and Poorter 1992, Olff 1992, Aerts and Chapin 1999) and water stress (Brouwer 1962, Bloom *et al.* 1985, Poorter and Nagel 2000). In the meadows, the average biomass ratio was less than one, indicating that seedlings had greater belowground biomass than aboveground biomass. Fast-growing species often respond to competition for belowground resources, particularly soil nitrogen, by increasing belowground biomass production (Brouwer 1962, Boot and den Dubbelden 1990, Lambers and Poorter 1992, Olff 1992, Aerts and Chapin 1999). As the addition of nitrogen led to greater stem-diameter

growth rates, it is reasonable to conclude that soil fertility limited seedling growth rates in the meadows to some extent. Also, the greater rate of seedling height loss in the meadows probably contributed to the lower biomass ratios, as both herbivory and desiccation can cause large decreases in aboveground biomass. Buckthorn seedling AG:BG biomass ratios were greater in the nitrogen-addition treatment across all habitats, indicating that aboveground biomass production was stimulated when nitrogen was added to soils. Buckthorn biomass ratios were also greater in the aboveground competition treatment than the no-competition treatment in all habitats. Aboveground biomass production is a common response to the presence of aboveground competition for light (Bloom *et al.* 1985, Geber 1989, Olf 1992, Dudley and Schmitt 1996, Ballaré *et al.* 1997), so this finding is not unexpected. It is interesting, however, that the competition and soil nutrient treatments affected seedling biomass ratios but not seedling height and diameter RGRs, except for increased diameter growth rates in the meadows. These results suggest that any effects of the competition and soil nutrient treatments on seedling height and diameter were obscured or negated by stronger forces. As discussed above, herbivory and desiccation appear to be the limiting factors in the meadows. These factors were probably also at play in the shrubs and forests, although to a lesser extent. Light availability may have also been a limiting factor in the shrub and forest habitats.

Experimental study - buckthorn photosynthetic rate and PAR

The greater photosynthetic rates and PAR availability found in the meadows demonstrate the importance of light availability for buckthorn photosynthesis. PAR was approximately 1.5 times greater in the meadows on both measurement dates. The

photosynthetic rates in the meadows were more than two times greater than those in the shrub habitats and more than three times greater than the forests. Photosynthetic rates and PAR increased in all habitats later in the season. While the increase in PAR on the second measurement date was greatest in the shrub habitat, the increase in photosynthesis was greatest in the forest. Mean photosynthesis in the forests increased by $0.7 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, while mean PAR only increased by $17 \mu\text{mol m}^{-2} \text{ s}^{-1}$. Whereas in the shrubs, mean PAR increased by $127 \mu\text{mol m}^{-2} \text{ s}^{-1}$, and mean photosynthesis only increased by $0.4 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. A previous study found a positive correlation between buckthorn leaf nitrogen content and maximum photosynthetic rates in open hedgerow habitats, but not in forest habitats; in forests, photosynthetic rates were limited by light availability (Harrington *et al.* 1989). In the same overall study, buckthorn had a greater aboveground growth rate in the open habitat than in the forest habitat (Harrington *et al.* 1989), demonstrating the interaction between light availability, nitrogen availability, photosynthetic rates, and buckthorn growth rates. Seedlings in the meadow habitats in the present study, however, showed the opposite effect. The open habitat in the experiment of Harrington *et al.* (1989a) was a hedgerow composed primarily of buckthorn, *Lonicera X bella* (Bell's honeysuckle), gray dogwood, and *Prunus serotina* (black cherry). This habitat most closely resembles the shrub habitats in the present study. Based on the results of Harrington *et al.* (1989a), I would expect seedlings in the shrub habitats in the present study to have greater photosynthetic rates than those in the forest during the second measurement period due to the increased PAR availability at that time. The lack of an increase in photosynthesis is puzzling, especially as neither the soil nutrients nor competition treatments had a significant effect on photosynthetic rates. As the nitrogen-addition treatment in my study was applied in July, it

is possible that the effects of N-addition would not be apparent in September, which would explain why the soil nutrients treatment had no effect on photosynthesis in the shrublands on the second measurement date. However, the shrub seedlings' lack of response to increased light availability remains unexplained.

The preexisting buckthorn populations in the shrub and forest habitats may have altered soil nitrogen levels prior to the initiation of this study. As buckthorn invasion is associated with an increase in soil nitrogen (Heneghan *et al.* 2006, Klionsky *et al.* 2011), heavily invaded areas are likely to experience increases in nitrogen availability. Adding nitrogen to the shrub and forest plots would not have influenced buckthorn growth rates if those soils were already at the level of saturation.

PAR was greater in the sawdust-addition plots than the ambient and nitrogen-addition plots during the summer. The cause and implications of this result are unclear. The addition of sawdust to plots may have caused a decrease in the aboveground biomass of competitors due to decreased nitrogen availability (Brouwer 1962, Boot and den Dubbelden 1990, Lambers and Poorter 1992, Olf 1992, and Aerts and Chapin 1999), leading to an increase in PAR levels. However, if this were so, it seems likely that this effect would have been present in the fall as well. This finding may be the result of the chance positioning of the gas analyzer/PAR sensor. It is also possible that bias was introduced into the positioning of the experimental plots such that the sawdust-addition plots had greater light availability.

Synthesis of observational and experimental study results

Knight *et al.* (2007) suggested that buckthorn may have an advantage within canopy gaps of forests due to the combined effects of buckthorn's shade tolerance and

responsiveness to increased light availability. Using the same line of reasoning, I hypothesized that buckthorn seedlings would perform better in shrub habitats than meadows or forests because shrublands offer an intermediate light environment with more protection from desiccation than meadows and greater light availability than forests. While the shrub habitats in this study appeared to present an intermediate light environment, with similar PAR availability to the forests in the summer and greater PAR availability than the forests in the fall, buckthorn seedling growth rates were not greater in the shrub habitats. The shrub and forest habitats had similar effects on buckthorn seedling growth and photosynthetic rates. Additional light availability in the fall did not translate into an increase in height or diameter growth rates or even an increase in photosynthesis for seedlings in the shrub habitats. There was no difference in soil moisture levels or soil organic matter content between the shrub and forest habitats, so it is unlikely that photosynthetic rates were limited by these factors. Nor was there a difference in photosynthetic rates among the soil nitrogen treatments, suggesting that photosynthesis was not limited by nitrogen availability. It appears that the seedlings in the shrub habitats were unable to respond effectively to the increased light availability due to biological constraints, such as leaf-level photosynthetic capacity or leaf area index (LAI), rather than environmental conditions. Previous studies found that increased light availability was correlated with increased aboveground biomass production in buckthorn shrubs (Harrington *et al.* 1989b) and seedlings (Grubb *et al.* 1996). While the seedling biomass ratios measured in this study were altered by the competition treatments, greater light availability did not lead to a concrete increase in biomass. The seedlings in this experiment were transplanted, which may have limited the seedlings' ability to respond to increased light availability by

decreasing the overall health of the plants and limiting leaf production and/or leaf longevity. Buckthorn shrubs growing in Wisconsin retained their leaves until mid-November (Harrington *et al.* 1989a), but in the present study most seedlings had few leaves remaining by September, when the second photosynthesis measurement was taken.

Competition had no effect on buckthorn growth or photosynthesis in this experiment. A previous study measuring the effects of aboveground and belowground competition on the growth of transplanted seedlings in abandoned agricultural fields in central New York found that buckthorn biomass was greater in the absence of competition and greater in plots with only belowground competition than in plots with only aboveground competition (Gill and Marks 1991). The lack of an effect in my experiment may have been the result of the experimental conditions and/or study duration. Gill and Marks (1991) used a combination of physical partitions and herbicide application to achieve their competition treatments. Due to the scale of this experiment and land-use restrictions, the use of physical partitions and chemical application was not feasible. The manual methods employed in this study may not have been sufficient to separate competitive effects. Also, Gill and Marks (1991) performed their study over two growing seasons, whereas my study took place over a single growing season. Competition may have become more important to seedling performance if my study had been extended, especially if the negative effects of transplanting decreased seedling growth and survival.

Another confounding factor in the competition treatment was the difference in plot competitors among the habitats. Seedlings in the meadow habitats were more likely to be competing with grasses and herbaceous species, whereas seedlings in the shrub and forest habitats were competing with a mixture of herbaceous and woody species that was often

dominated by buckthorn. Thus, intraspecific competition was more frequent in the shrub and forest habitats, and interspecific competition was more frequent in the meadow habitats. Some researchers have suggested that buckthorn shrubs may facilitate the growth of buckthorn seedlings (Kollmann and Grubb 1999, Knight 2006), however there is evidence that inhibition may also occur (Gourley 1985). The conflation of intraspecific and interspecific competition and herbaceous and woody competitors may have decreased the probability of detecting the effects of competition on buckthorn seedling growth, particularly if conspecific facilitation was occurring.

While light availability differed among habitats, the competition treatments had no significant effect on PAR levels. As the competition treatments were applied to separate the effects of competition for light from competition for belowground resources, this result indicates that the competition treatments did not alter light availability as intended. Therefore, any differences among competitive effects were not detectable. The large difference in light availability among the habitats may have obscured differences in light availability among the competition treatments. However, these findings indicate that caution should be used when interpreting the experimental results. The apparent lack of an effect of competition on buckthorn seedling growth may be the result of the experimental conditions rather than environmental or physiological effects. As PAR was measured in only a subset of the plots on two measurement dates, the lack of a difference among the competition treatments in PAR values is not necessarily proof that the treatments were not effective. The biomass ratios of the seedlings did show a response to the competition treatments, with greater belowground biomass production when competitors were removed from plots and greater aboveground growth in plots with aboveground

competitors. These results represent typical growth responses to the absence and presence of competitors, lending support to the conclusion that the competition treatments were at least somewhat effective. The relatively short duration of the experiment may have limited the effects of the competition treatments on buckthorn growth rates. A single growing season may not have been adequate to produce detectable differences in growth rates.

I hypothesized that buckthorn would gain a competitive advantage in low fertility habitats due to the decreased competitive effects of neighboring plants associated with low fertility environments. The results of the soil nutrients treatment in this experiment did not support my hypothesis. In fact, for seedlings with positive growth rates, soil nutrient levels interacted with habitat such that seedlings in the meadow habitats had greater diameter growth rates when nitrogen fertilizer was added to soils, while competition had no effect on growth rates. This result suggests that soil fertility is more important than competition for buckthorn diameter growth but only within high light environments. A study measuring the effects of light and nutrient availability on the growth of 10 woody species found that most of the species, including buckthorn, only responded to increased nutrient availability in at least moderately high light environments (Grubb *et al.* 1996). Meadow habitats, therefore, may be more susceptible to buckthorn establishment than shrub or forest habitats in the presence of increased soil nitrogen due to the greater light availability in meadows.

Buckthorn management

Based on the results of this study, different buckthorn management strategies may be necessary for meadows than shrub or forest habitats. In environments with both high light availability and high soil nitrogen levels, such as heavily invaded or anthropogenically

altered meadows, management strategies that focus on decreasing soil fertility may decrease buckthorn's success by limiting its competitive advantage. Previous studies have shown that native grasses and/or forbs can outcompete or limit the growth of buckthorn in both early-successional old fields and forested habitats (Gill and Marks 1991, Willert 2000, Knight 2006). Management efforts with a focus on returning the soil nitrogen content to historical levels may give native species sufficient advantage to outcompete buckthorn seedlings during establishment, thereby limiting the need for costly and labor-intensive buckthorn removal activities.

Despite the greater light availability, buckthorn seedlings were less successful in the meadow habitats than the shrub or forest habitats. Herbivory and desiccation appeared to limit the seedlings' growth. Thus, invaded meadows are potentially less likely to support large buckthorn populations and may be less of a priority for management than shrub or forest habitats. However, buckthorn can still establish and attain maturity in meadows. While single or small numbers of individuals are unlikely to exert ecosystem-level effects, these individuals can act as seed sources for surrounding areas that are more vulnerable to buckthorn invasion.

For all habitat types, the removal of well-established individuals could limit the establishment of buckthorn seedlings and perhaps prevent buckthorn dominance. Also, as buckthorn is dioecious (Godwin 1943), the strategic removal of fruiting trees could be used in conjunction with other methods to reduce buckthorn reproduction and establishment (Archibold *et al.* 1997).

Differences in buckthorn distribution patterns among habitats may also affect management strategies. A study of the distribution of buckthorn in old fields, maple-beech

forests, and conifer plantations found that buckthorn seedling populations in old fields tended to be concentrated near mature buckthorn trees, whereas in the maple-beech forests, buckthorn was limited to canopy gaps and trail edges (McCay *et al.* 2009). Buckthorn seedling density increased with light availability in the two forest habitats (McCay *et al.* 2009). Another study also found that buckthorn cover in forested habitats increased with light availability (Knight and Reich 2005). Thus, for shrub and forest habitats, it may be more fruitful to focus management efforts on disturbed areas, such as canopy gaps and trails, and areas with greater light availability, such as forest edges, because these locations are more likely to be invaded. In meadow habitats, targeting mature buckthorn trees for removal may be a more effective strategy.

As competition and soil nutrient treatments had no effect on buckthorn growth rates in the shrub and forest habitats, management strategies based on restoring historical soil fertility levels or planting native competitors to reduce buckthorn dominance are not indicated. As other studies have found a positive relationship between buckthorn abundance and light availability in forested habitats (Knight and Reich 2005, McCay *et al.* 2009), management promoting mid- and late-successional canopy forest species, particularly evergreen species, may limit buckthorn establishment and growth. However, buckthorn's shade-tolerance and responsiveness to light (Harrington *et al.* 1989b, Grubb *et al.* 1996) limit the effectiveness of this strategy. Additionally, in heavily invaded forests, buckthorn can alter stand characteristics, potentially halting succession (Mascaro and Schnitzer 2007, 2011). Buckthorn-dominated forests are likely to require highly intensive management over a number of years, underscoring the importance of monitoring and decisive action in areas with low-to-moderate buckthorn populations.

Conclusions

Buckthorn is a frequent invader within the northern and central United States and southern and eastern Canada that can cause both community (Klionsky *et al.* 2011, Mascaro and Schnitzer 2011) and ecosystem effects (Heneghan *et al.* 2006, Heneghan *et al.* 2007, Madritch and Lindroth 2009). This project included an observational study of vegetation and soil characteristics in buckthorn-invaded habitats and an experimental study using a factorial design to separate the effects of habitat, competition, and soil nutrient availability on buckthorn seedling growth rates, biomass allocation, and photosynthetic rates. In the observational study, buckthorn abundances did not differ by habitat type. In the experimental study, however, habitat type exerted the strongest effects on buckthorn seedling height and diameter relative growth rates and biomass ratios, with greater height loss and greater allocation to belowground biomass in the meadows. This effect may be due to seedling herbivory by meadow voles and desiccation. On average, seedlings displayed negative growth rates in all habitats. When only seedlings with positive growth rate values were analyzed, the addition of nitrogen fertilizer resulted in increased diameter growth rates in the meadow habitats. This result suggests that the meadow habitats were N-limited, but the effects of nitrogen limitation were overshadowed by herbivory and desiccation. Based on these findings, buckthorn management efforts should focus on shrub and forest habitats. Management practices relying solely on the planting of native competitors or alteration of soil nutrient levels are unlikely to lead to significant reductions in buckthorn seedling growth. Light availability may be more important to buckthorn success in shrub and forest habitats, which had significantly lower photosynthetic rates and PAR levels than the meadows. As such, buckthorn control efforts should focus on areas

within shrub and forest habitats with greater light availability, such as canopy gaps, trails, and other disturbed areas, for monitoring and removal activities.

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Figures

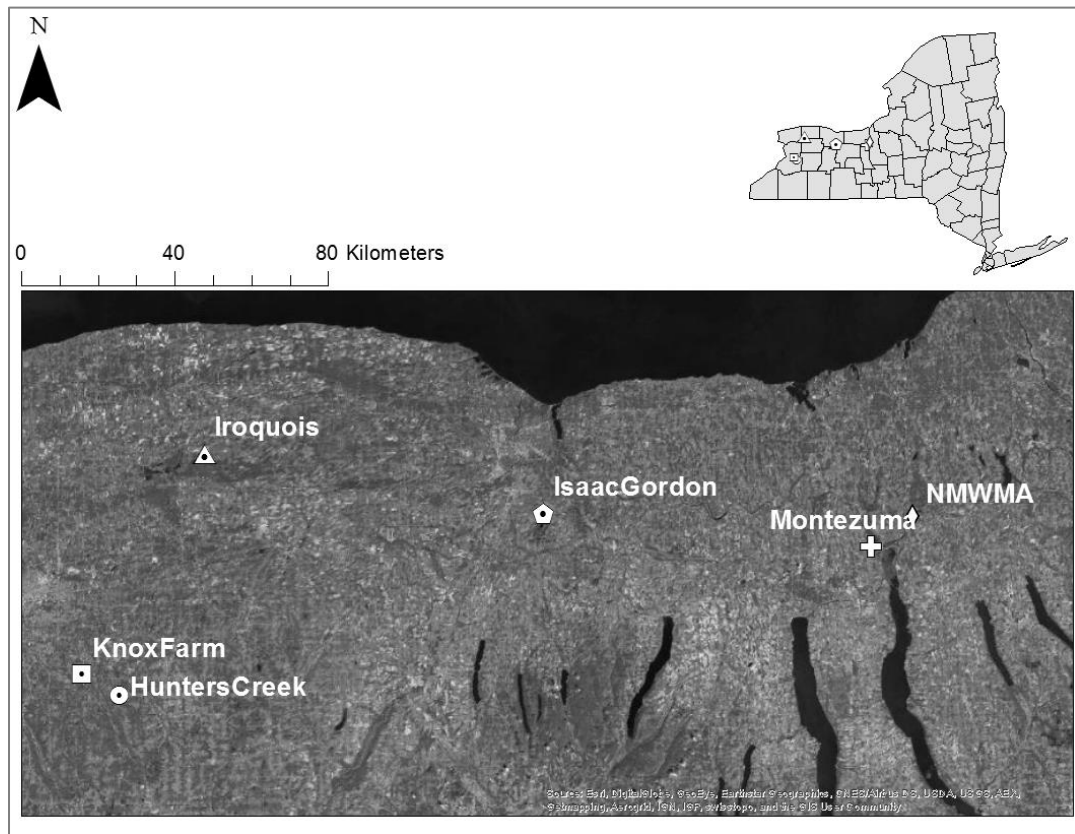


Figure 1. Map of six sites in New York used in a study measuring the effects of competition, soil fertility, and habitat on invasive *Rhamnus cathartica* growth and photosynthesis. The sites were Hunters Creek County Park, Erie County (HuntersCreek); Iroquois National Wildlife Refuge, Orleans County (Iroquois); Isaac Gordon Nature Park, Monroe County (IsaacGordon); Knox Farm State Park, Erie County (KnoxFarm); Montezuma National Wildlife Refuge, Seneca County (Montezuma); and Northern Montezuma Wildlife Management Area, Cayuga County (NMWMA).

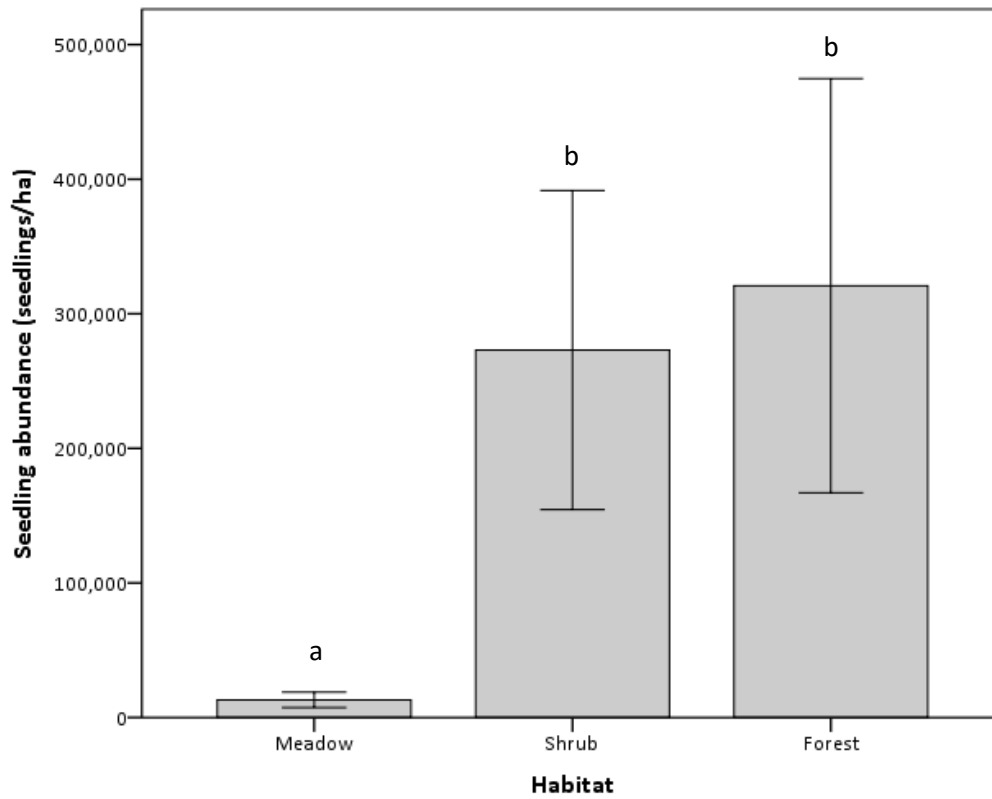


Figure 2. Seedling abundance (mean \pm SE) in three habitats measured in an observational study at six sites in western New York between September and October 2013. A one-way ANOVA ($F_{2,13} = 11.540$, $p = 0.001$) was performed on the log-transformed data. The untransformed data are shown above. Letters indicate significant differences.

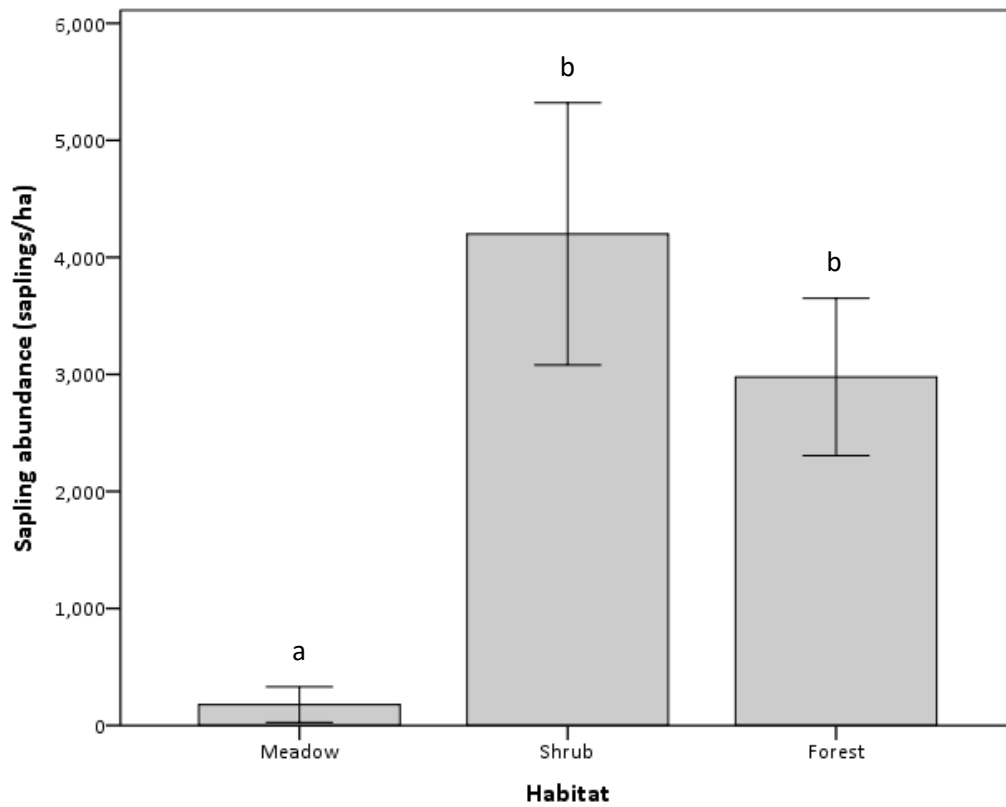


Figure 3. Sapling abundance (mean \pm SE) in three habitats measured in an observational study at six sites in western New York between September and October 2013. A one-way ANOVA ($F_{2,11} = 8.574$, $p = 0.006$) was performed on the log-transformed data to measure the effect of habitat on sapling abundance. The untransformed data are shown above. Letters indicate significant differences.

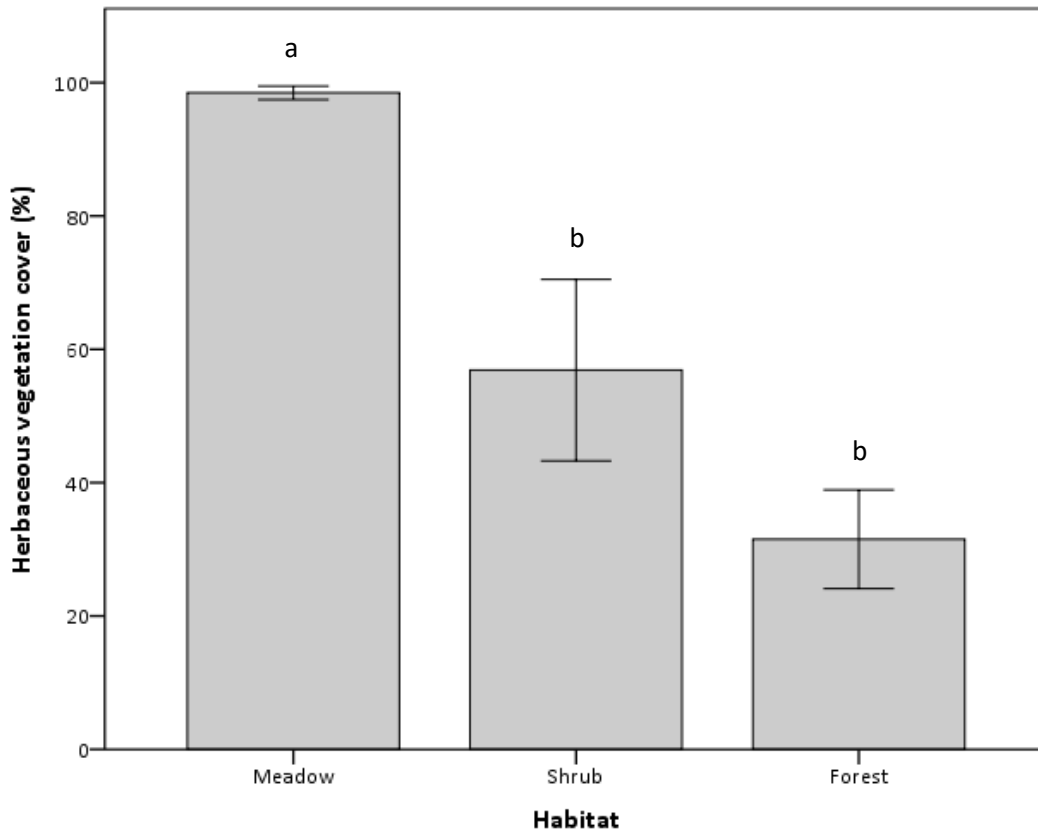


Figure 4. Herbaceous vegetation percent cover (mean \pm SE) in three habitats analyzed using a one-way ANOVA ($F_{2,15} = 14.216$, $p < 0.001$, $\alpha = 0.025$). Herbaceous vegetation was measured during an observational study at six sites in western New York in September and October 2013. Letters indicate significant differences.

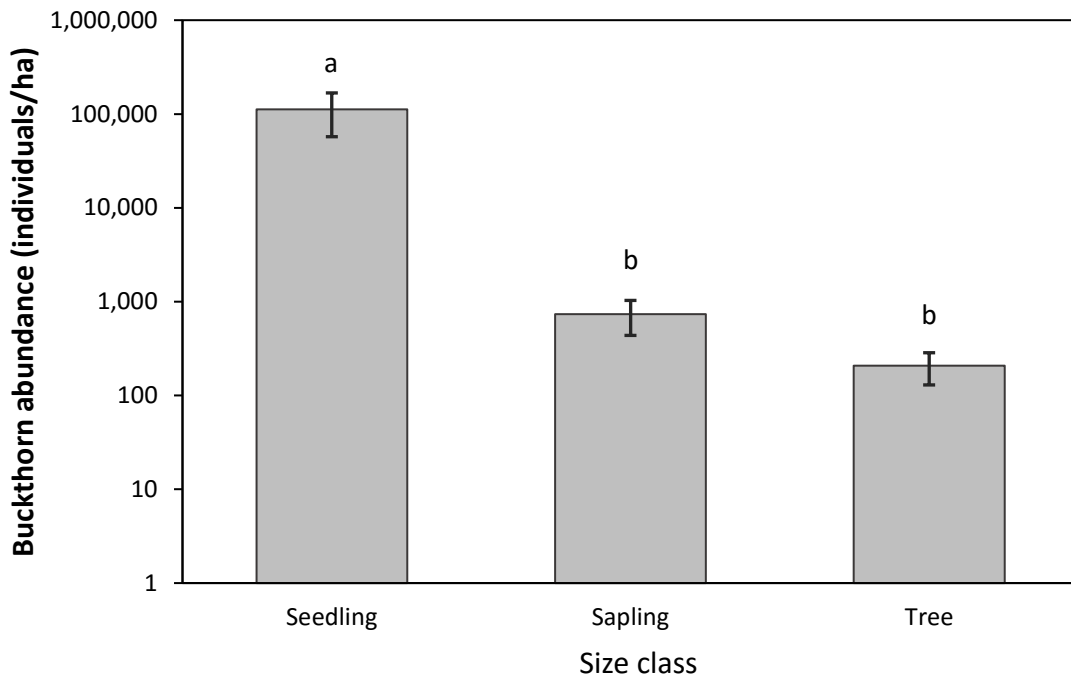


Figure 5. Buckthorn abundance (mean \pm SE) by size class measured during an observational study at six sites in western New York in September and October 2013. A two-way ANOVA ($F_{2,19} = 34.664$, $p < 0.001$) comparing the effects of habitat and size class on buckthorn abundance was performed using log-transformed data. The untransformed data are shown above. Letters indicate significant differences. Note the logarithmic scale of the y-axis.

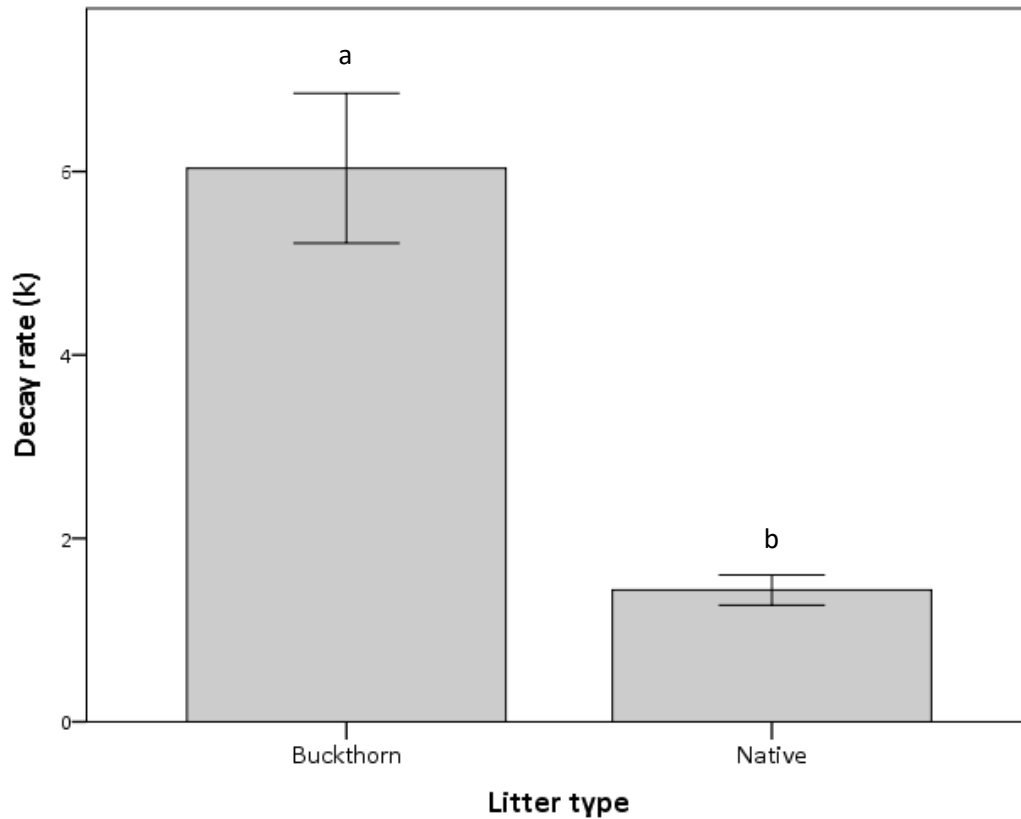


Figure 6. Effect of leaf litter type on decay rate (mean \pm SE) measured during an observational study using mesh litterbags deployed in six sites in western New York from April to December 2013. A two-way ANOVA ($F_{1,30} = 46.215$, $p < 0.001$) comparing the effects of habitat and litter type on decay rates was performed using transformed data (square root of decay rate multiplied by negative one). The untransformed data are shown above. Letters indicate significant differences.

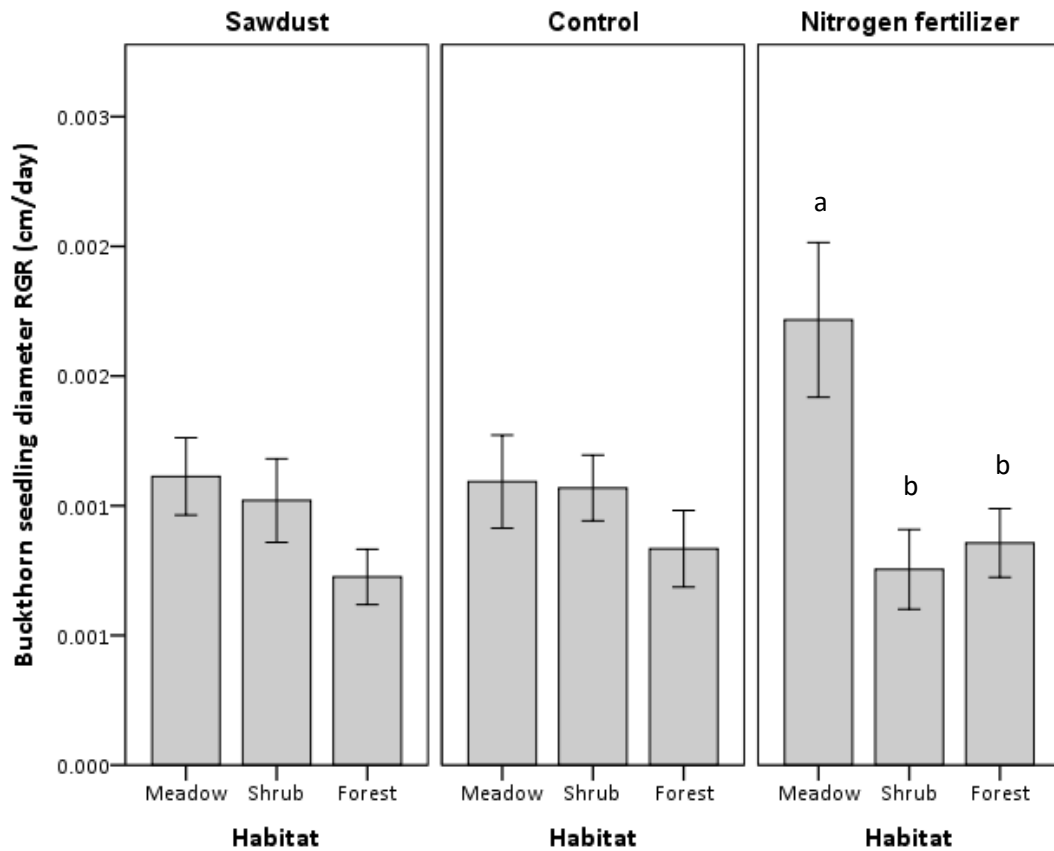


Figure 7. Buckthorn seedling diameter relative growth rates (RGR) (mean \pm SE) of the habitat and soil nutrient interaction term for seedlings exhibiting positive growth (negative values excluded). A three-way ANOVA ($\alpha = 0.05$) was used to compare the effects of habitat, competition, and soil nutrient levels on diameter RGRs of buckthorn seedlings in an experimental study in six sites in western New York. Habitat had a significant effect on diameter RGR within the nitrogen fertilizer level of the soil nutrients treatment ($F_{2,102} = 7.40$, $p = 0.001$). Letters indicate significant differences.

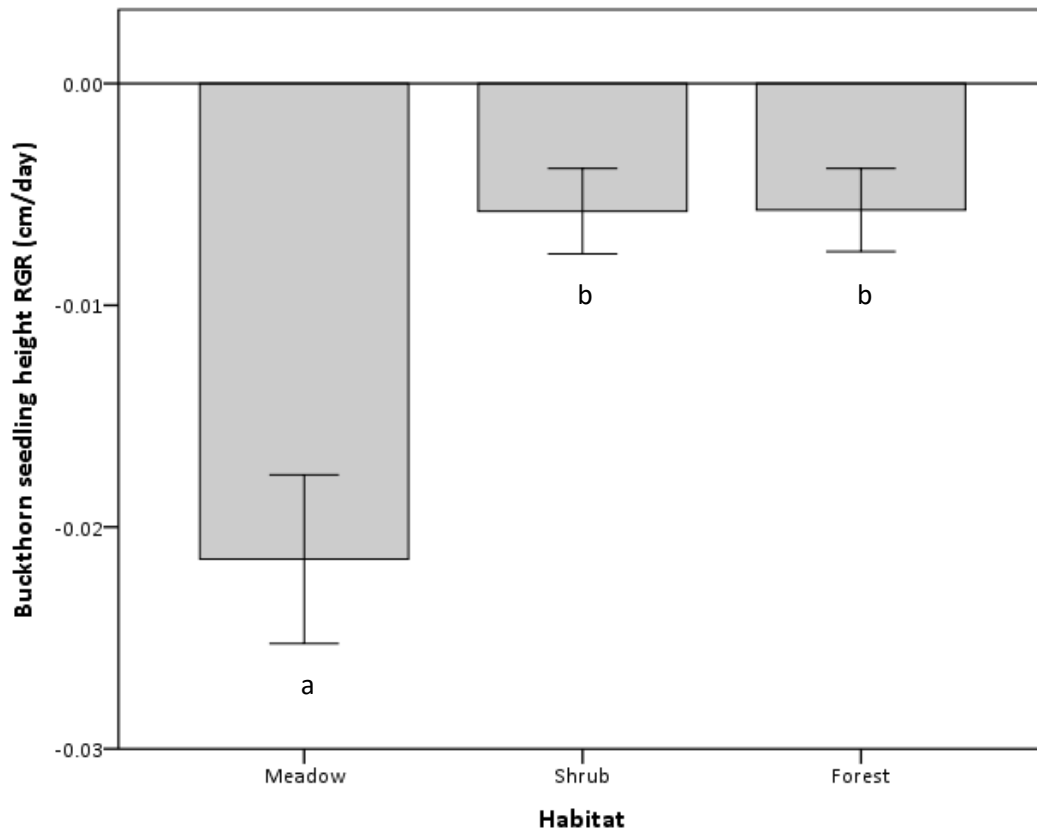


Figure 8. Buckthorn seedling height relative growth rates (RGR) (mean \pm SE) measured in three habitats during an experimental study in six sites in western New York from July to December 2013. A three-way ANOVA ($F_{2,135} = 11.857$, $p > 0.001$, $\alpha = 0.025$) was used to compare the effects of habitat, competition, and soil nutrient levels on height RGRs of transplanted buckthorn seedlings. Letters indicate significant differences.

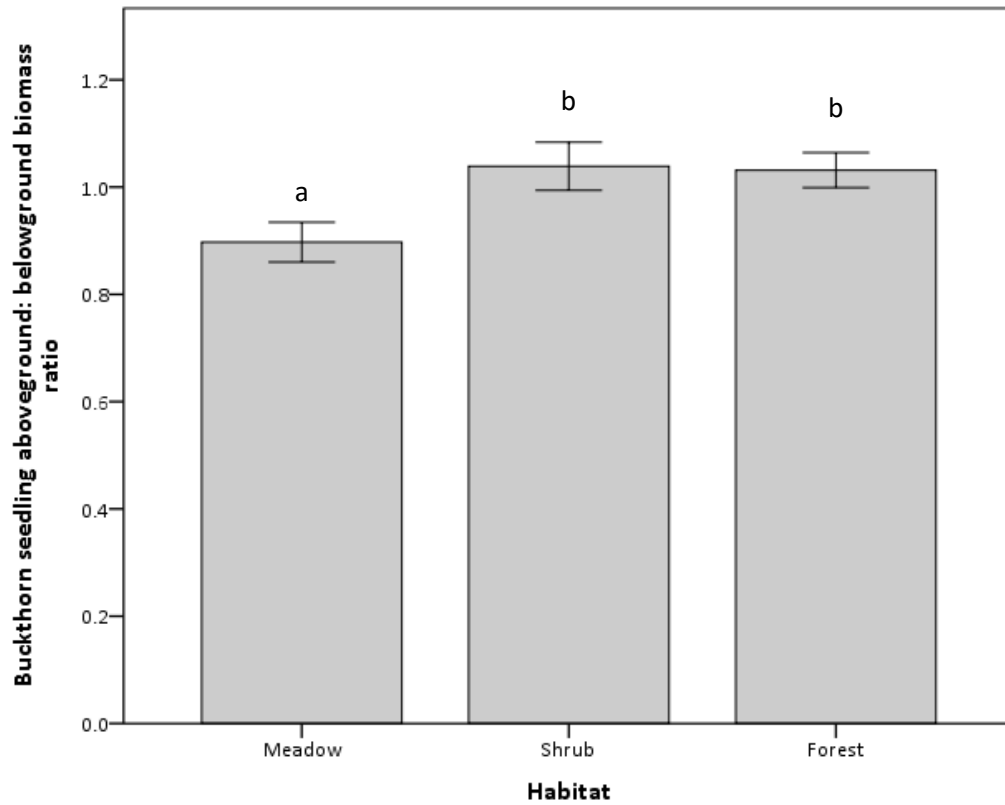


Figure 9. Main effects of the habitat treatment in a three-way ANOVA ($F_{2,127} = 4.749$, $p = 0.010$) comparing the aboveground: belowground biomass ratios (mean \pm SE) of buckthorn seedlings exposed to habitat, competition, and soil nutrient treatments during an experimental study at six sites in western New York from July to December 2013. Letters indicate significant differences ($\alpha = 0.025$).

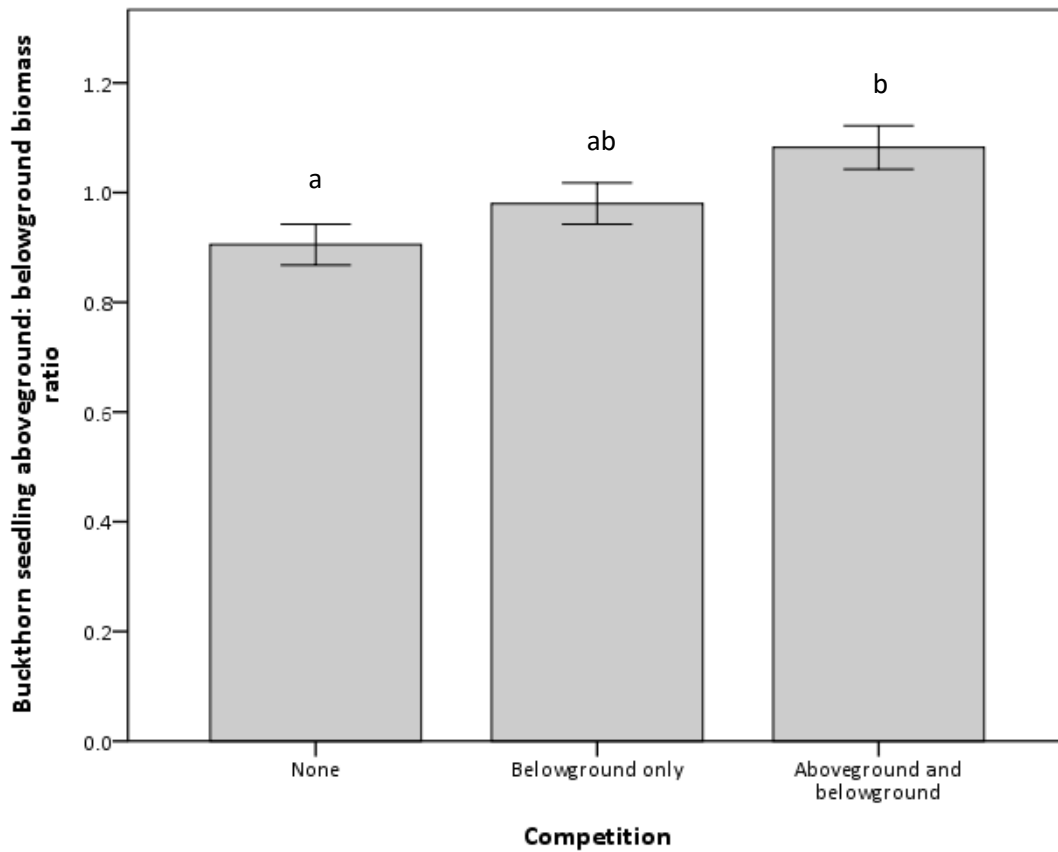


Figure 10. Main effects of the competition treatment in a three-way ANOVA ($F_{2,127} = 5.917$, $p = 0.003$) comparing the aboveground: belowground biomass ratios (mean \pm SE) of buckthorn seedlings exposed to habitat, competition, and soil nutrient treatments during an experimental study at six sites in western New York from July to December 2013. Letters indicate significant differences ($\alpha = 0.025$).

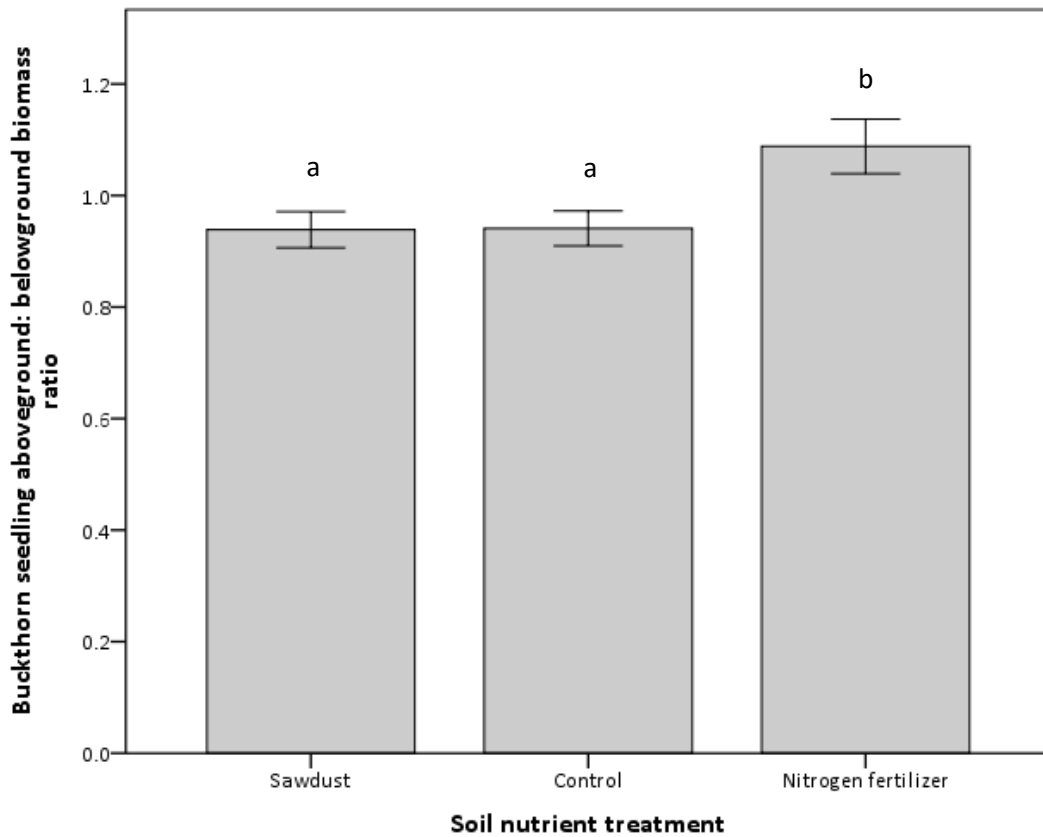


Figure 11. Main effects of the soil nutrient treatment in a three-way ANOVA ($F_{2,127} = 5.483$, $p = 0.005$) comparing the aboveground: belowground biomass ratios (mean \pm SE) of buckthorn seedlings exposed to habitat, competition, and soil nutrient treatments during an experimental study at six sites in western New York from July to December 2013. Letters indicate significant differences ($\alpha = 0.025$).

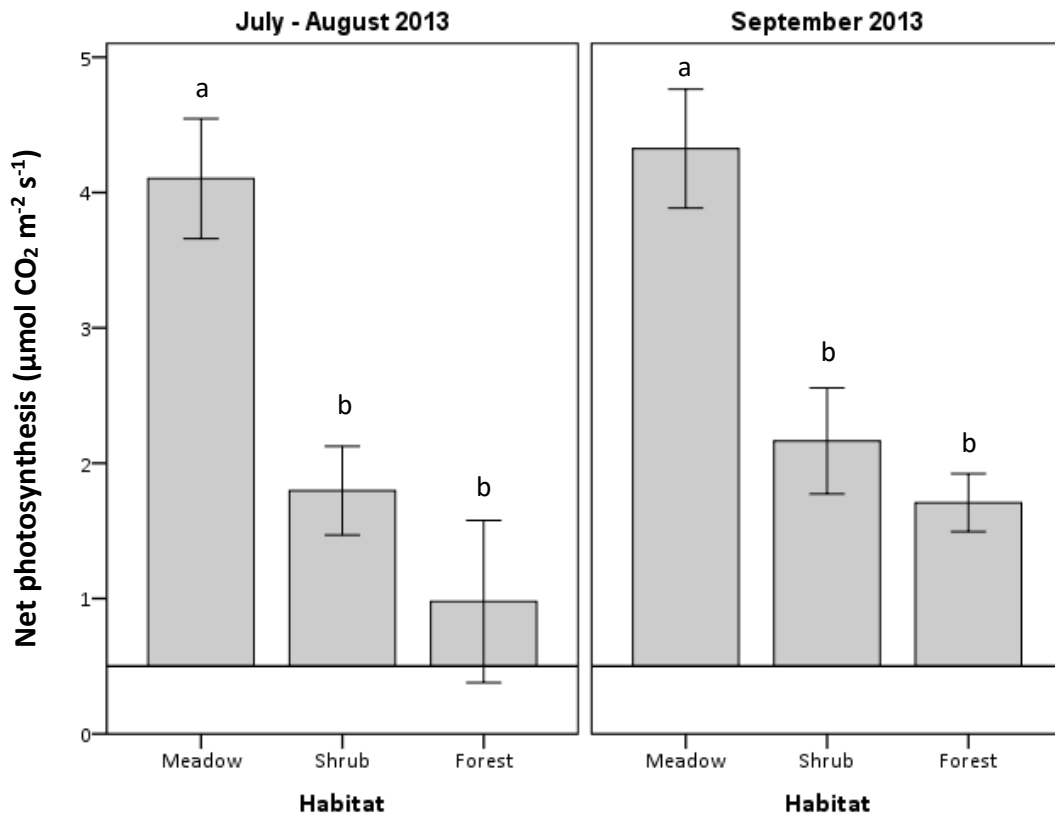


Figure 12. Net photosynthetic rate (mean \pm SE) of buckthorn seedlings by habitat and measurement date. Transplanted buckthorn seedling photosynthesis was measured using a leaf chamber attached to a portable CO₂ analyzer during an experimental study at six sites in western New York. The two measurement periods were analyzed separately using two three-way ANOVAs (July – August 2013: $F_{2,134} = 12.336$, $p < 0.001$, $\alpha = 0.025$; September 2013: $F_{2,135} = 15.067$, $p < 0.001$, $\alpha = 0.025$). Significant differences are indicated by letters.

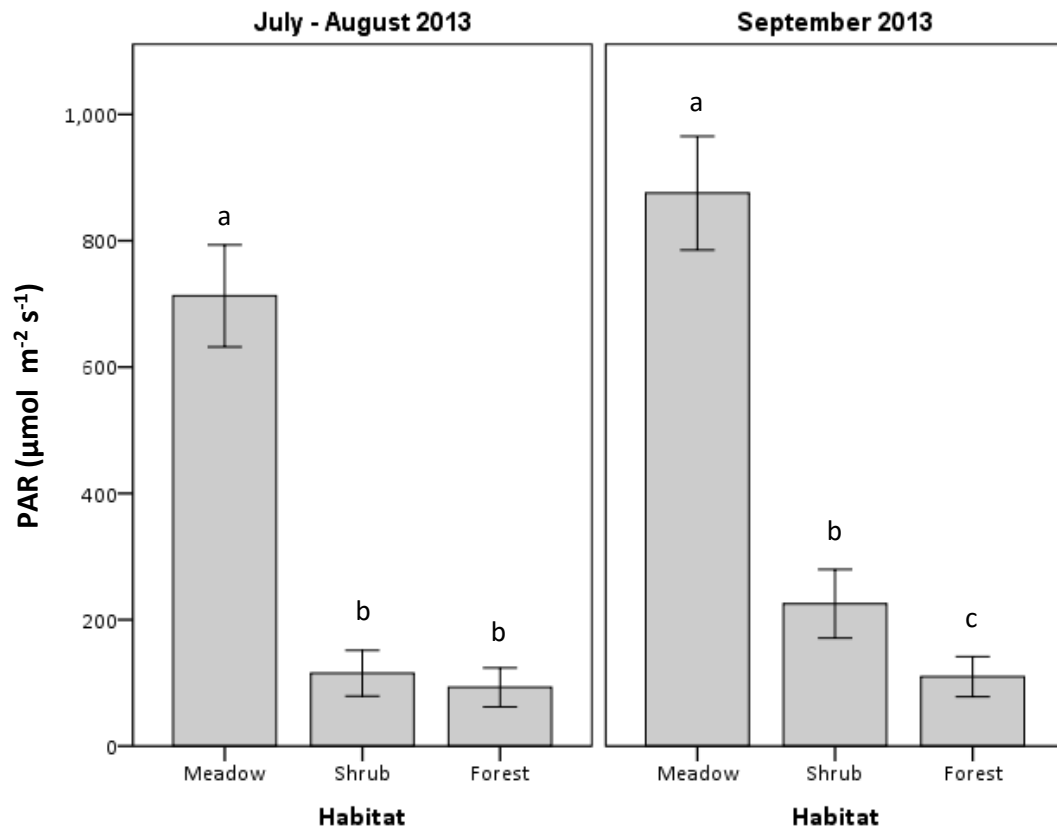


Figure 13. Photosynthetically active radiation (PAR) levels (mean \pm SE) in three habitats on two measurement dates. PAR was measured using a light sensor on the outside of a leaf chamber attached to a portable CO₂ analyzer during an experimental study at six sites in western New York. The two measurement periods were analyzed separately using two three-way ANOVAs (July – August 2013: $F_{2,134} = 89.811$, $p < 0.001$, $\alpha = 0.025$; September 2013: $F_{2,135} = 45.612$, $p < 0.001$, $\alpha = 0.025$). Both datasets were log-transformed for analysis; the untransformed data are shown above. Significant differences are indicated by letters.

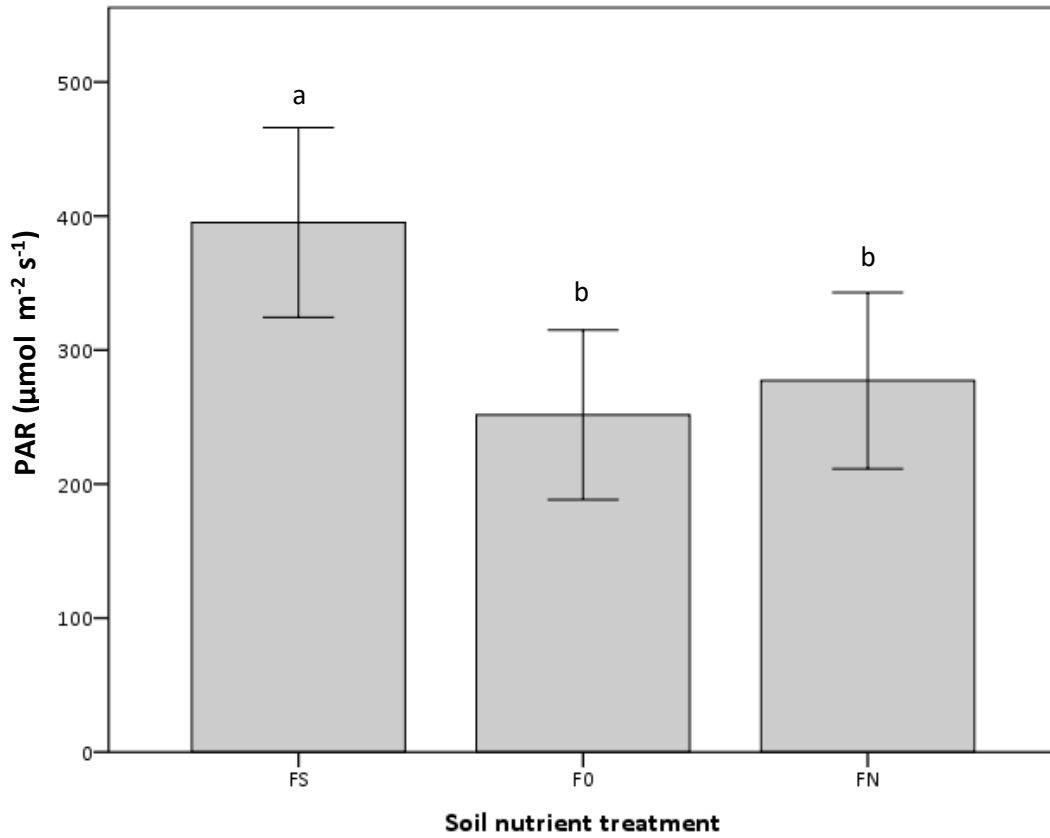


Figure 14. Photosynthetically active radiation (PAR) levels (mean \pm SE) measured in experimental plots exposed to three soil nutrient treatments (FS = sawdust, FO = control, FN = nitrogen fertilizer). PAR measurements were taken using a light sensor outside a leaf chamber attached to a portable CO₂ analyzer in July and August 2013 at six sites in western New York. Data were log-transformed and analyzed with a three-way ANOVA ($F_{2,134} = 5.773$, $p = 0.004$, $\alpha = 0.025$); the untransformed data are shown above. Significant differences are indicated by letters.

Tables

Table 1. Effect of habitat on soil moisture (%), loss on ignition (g/kg), sapling diameter at breast height (DBH) (cm), tree abundance (individuals/ha), and tree DBH (cm) as measured using one-way ANOVAs for each variable. Variables were measured in an observational study in six sites in western New York in September and August 2013.

Variable	One-way ANOVA results for habitat treatment			Transformation	Alpha
	df	F	P		
Soil moisture	2	0.068	0.934	None	0.05
LOI	2	0.314	0.735	None	0.05
Sapling DBH	2	0.763	0.489	None	0.05
Tree abundance	2	4.695	0.034	Logarithm	0.025
Tree DBH	2	1.039	0.386	None	0.05

Table 2. Mean (\pm SE) soil moisture, loss on ignition (LOI), sapling diameter at breast height (DBH), tree abundance, and tree DBH values in meadow, shrub, and forest edge habitats measured in an observational study in September and October 2013 at six sites in western New York. Habitat had no significant effect on any of these parameters.

Habitat	Soil moisture (%)	LOI (g/kg)	Sapling DBH (cm)	Tree abundance (#/ha)	Tree DBH (cm)
Meadow	31.30 \pm 3.89	71.83 \pm 12.01	6.12 \pm 1.68	67 \pm 30	21.50 \pm 4.75
Shrub	32.31 \pm 2.40	73.39 \pm 11.69	5.01 \pm 0.55	711 \pm 287	21.72 \pm 1.59
Forest	32.90 \pm 2.95	84.71 \pm 13.83	6.05 \pm 0.66	756 \pm 171	27.96 \pm 4.24

Table 3. Results of two three-way ANOVAs measuring effects of habitat, competition, and soil nutrients on buckthorn seedling height (HRGR) and diameter (DRGR) relative growth rates for seedlings displaying positive height and diameter growth values. Measurements were taken between July and December 2013 during an experimental study on buckthorn seedlings transplanted into six sites in western New York. (* $\alpha = 0.025$, † $\alpha = 0.05$)

Source	HRGR (Positive values)			DRGR (Positive Values)		
	df	F	P*	df	F	P†
Overall Model	24	0.714	0.806	26	1.29	0.188
Main effects						
Habitat (HBT)	2	1.609	0.214	2	7.19	0.001
Competition (COMP)	2	1.743	0.189	2	0.41	0.662
Soil Nutrients (SN)	2	0.743	0.482	2	0.77	0.465
Interactions						
HBT X COMP	4	0.192	0.941	4	0.36	0.835
HBT X SN	4	0.465	0.761	4	2.69	0.036
COMP X SN	4	0.796	0.535	4	0.87	0.484
HBT X COMP X SN	6	0.453	0.838	8	0.78	0.622

Table 4. Results of two three-way ANOVAs ($\alpha = 0.025$) measuring effects of habitat, competition, and soil nutrients on buckthorn seedling height (HRGR) and diameter (DRGR) relative growth rates for seedlings displaying both positive and negative height and diameter growth values. Measurements were taken between July and December 2013 during an experimental study on buckthorn seedlings transplanted into six sites in western New York. Both datasets were transformed prior to performing ANOVAs.

Source	df	HRGR (All values)		DRGR (All values)	
		F	P	F	P
Overall Model	26	2.083	0.004	0.308	1.000
Main effects					
Habitat (HBT)	2	11.857	< 0.001	0.260	0.772
Competition (COMP)	2	2.418	0.093	0.479	0.620
Soil Nutrients (SN)	2	0.600	0.550	0.579	0.562
Interactions					
HBT X COMP	4	1.678	0.159	0.425	0.790
HBT X SN	4	0.930	0.449	0.180	0.948
COMP X SN	4	1.325	0.264	0.053	0.995
HBT X COMP X SN	8	1.085	0.378	0.341	0.948

Table 5. Results of a three-way ANOVA ($\alpha = 0.025$) measuring the effects of habitat, competition, and soil nutrient levels on the ratio of aboveground to belowground biomass of buckthorn seedlings in an experimental study at six sites in western New York from July to December 2013.

AG:BG biomass			
Source	df	F	P
Overall Model	26	1.956	0.007
Main effects			
Habitat (HBT)	2	4.749	0.010
Competition (COMP)	2	5.917	0.003
Soil Nutrients (SN)	2	5.483	0.005
Interactions			
HBT X COMP	4	0.970	0.426
HBT X SN	4	1.494	0.208
COMP X SN	4	1.237	0.298
HBT X COMP X SN	8	0.470	0.875

Table 6. Results of two three-way ANOVAs ($\alpha = 0.025$) measuring effects of habitat, competition, and soil nutrient levels on net photosynthetic rates of buckthorn seedlings measured in July and August 2013 (PS Pre) and September 2013 (PS Post) before and after the addition of fertilizer to the plots. Seedlings were part of an experimental study in six sites in western New York.

Source	df	PS Pre		PS Post	
		F	P	F	P
Overall Model	26	2.144	0.003	2.012	0.005
Main effects					
Habitat (HBT)	2	12.336	< 0.001	15.067	< 0.001
Competition (COMP)	2	0.779	0.461	1.781	0.172
Soil Nutrients (SN)	2	0.262	0.771	2.719	0.070
Interactions					
HBT X COMP	4	1.742	0.144	0.402	0.807
HBT X SN	4	0.484	0.747	0.904	0.464
COMP X SN	4	1.476	0.213	0.797	0.529
HBT X COMP X SN	8	1.746	0.093	0.595	0.781

Table 7. Results of two three-way ANOVAs ($\alpha = 0.025$) comparing photosynthetically active radiation (PAR) levels outside a leaf chamber while measuring photosynthetic rates of buckthorn seedlings exposed to habitat, competition, and soil nutrient level treatments. PAR was measured in July and August 2013 (PAR Pre) and September 2013 (PAR Post) in an experimental study at six sites in western New York before and after the addition of fertilizer to the plots. Both datasets were log-transformed for analysis.

Source	df	PAR Pre		PAR Post	
		F	P	F	P
Overall Model	26	8.146	< 0.001	4.323	< 0.001
Main effects					
Habitat (HBT)	2	89.811	< 0.001	45.612	< 0.001
Competition (COMP)	2	1.917	0.151	1.382	0.255
Soil Nutrients (SN)	2	5.773	0.004	1.592	0.207
Interactions					
HBT X COMP	4	0.775	0.544	0.973	0.425
HBT X SN	4	0.391	0.815	0.184	0.946
COMP X SN	4	0.398	0.810	1.352	0.254
HBT X COMP X SN	8	1.351	0.224	0.648	0.736