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LIMITING IMPACTS OF INVASIVE GLOSSY BUCKTHORN IN SOUTHEASTERN NEW HAMPSHIRE WOODLANDS: STUDIES OF INTENSIVE CONTROL AND FOREST DYNAMICS

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LIMITING IMPACTS OF INVASIVE GLOSSY BUCKTHORN IN SOUTHEASTERN NEW HAMPSHIRE WOODLANDS: STUDIES OF INTENSIVE CONTROL AND FOREST DYNAMICS

BY

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THESIS

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This thesis has been examined and approved in partial fulfillment of the requirements for the degree of Master of Science in Natural Resources: Forestry by:

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Original approval signatures are on file with the University of New Hampshire Graduate School.

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ABSTRACT

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by

Nicholas B. Lanzer

University of New Hampshire, December, 2016

Invasive glossy buckthorn (*Frangula alnus* P. Mill) threatens forest communities in southeastern New Hampshire both ecologically and economically by outcompeting native regeneration and hampering forest management. Seventy-five white pine (*Pinus strobus* L.) seedlings surrounded mainly by buckthorn were identified at the MacDonald Lot property in Durham, NH. In spring 2015, fifty of these pines were encouraged to emerge from and overtop surrounding buckthorn by cutting all neighboring plants within 1 m; targeted herbicide was applied to cut stumps at 25 of these. Pine response was assessed after one growing season. Released pines showed increased diameter growth, foliar biomass, and stem non-structural carbohydrate content. No growth differences between pines treated with herbicide and those not treated were observed; however buckthorn did recover more strongly in untreated plots.

Buckthorn's response to forest succession is not known, nor is the status of the regional invasion. To determine a) if the invasion is continuing to invade new stands, and b) what successional factors predict buckthorn presence and abundance in forests, I resampled 20 of 22 sites in an old-field chronosequence in Durham, NH initially sampled 17 years prior. Site characteristics such as age since abandonment, overall shade tolerance, and degree of occupation by various vegetation were analyzed. Site age and shade tolerance were the strongest predictors of buckthorn presence and abundance. In these unmanaged old-field sites, the buckthorn invasion seems to have stabilized with no net gain in stands invaded.

CHAPTER I: Sapling white pine (*Pinus strobus* L.) exhibits growth response following removal of glossy buckthorn (*Frangula alnus* P. Mill) and associated vegetation

Introduction

Non-native invasive woody plants, increasing in both overall abundance and in number of species within the northeastern United States, present a challenge to forest management (Webster et al. 2006) not explicitly addressed by traditional silvicultural methods. Invasive species, or those "which establish a new range in which they proliferate, spread and persist to the detriment of the environment," (Mack et al. 2000) influence both the ecology of forests (Collier et al. 2002, Charles and Dukes 2007, Burnham and Lee 2010, Koning and Singleton 2013) and economic potential of forestry (Pimentel et al. 2000, Holmes et al. 2009) by altering tree growth, forest structure and community composition. Many invasive species were intentionally introduced to the U.S. as landscaping plants [e.g. burning bush (*Euonymus alatus*) (Brand et al. 2012)], for erosion control [e.g. kudzu (*Pueraria montana*) (Ma 2008)], or to benefit wildlife [e.g. autumn olive (*Elaeagnus umbellata*) (Moore et al. 2013)], while many others have been unintentionally introduced as a byproduct of global trade (Westphal et al. 2008, Hulme 2009). In New England, an estimated 30% of all plants are non-native (Ricketts et al. 1999), a testament perhaps to both the scale or rate of invasion and the resulting loss of native species.

The potential impacts of invasion are numerous. Invasive plants may establish in high densities, reducing growing space available to native species (Fagan and Peart 2004), and may indeed displace native forest vegetation via aboveground (Gioria and Osborne 2014) and/or belowground competition (Bais et al. 2003, Stinson et al. 2006). Displacement of native vegetation (and wildlife species reliant on that flora) by one or multiple invasive species may upset an entire ecosystem, as in the case of kudzu (Forseth and Innis 2004), and may compromise the services provided by that ecosystem (Charles and Dukes 2007) while simultaneously disrupting forest management and planning. Hydrologic cycling (Levine et al. 2003), fire regimes (Mack et al. 2000), carbon sequestration (Peltzer et al. 2010), and nutrient cycling (Ehrenfeld et al. 2001, Evans et al. 2001, Heneghan et al. 2006) in various ecosystems can be affected by the introduction of a novel species, with potentially costly results.

The set of hurdles to forest management posed by these exotic species is perhaps one of the least studied aspects of invasive ecology. Traits that make certain species successful invaders can effectively impede management in many scenarios. Invasive species often form dense seed banks, allowing rapid establishment following disturbance, or dense monocultures, excluding native or desired flora (Lonsdale 1999, Webster et al. 2006). Free from the suppressive effect of co-evolved predators and pathogens (Mitchell and Power 2003), invasives may grow quickly and spread prolifically through enhanced seed production and sprouting ability. These traits and others can jeopardize the commercial viability of management operations in heavily invaded areas (Holmes et al. 2009). Without at least some level of control, invasive species can become established permanently, potentially reverting forest to non-forest conditions (e.g. Collier et al. 2002), and large ecological and pecuniary impacts can result. The economic toll of invasive species control is well documented, at least at the large scale (Holmes et al. 2009). In the U.S., invasive plants alone are responsible for at least $34 billion annually in losses, damages and control costs (Pimentel et al. 2005).

Control of invasives is costly (Pimentel et al. 2005, Olson 2006). Once a non-native species has graduated from “introduced” to “invasive,” the prospects of eradicating it are usually small (Mack et al. 2000). Long-term monitoring of populations and ceaseless vigilance following control efforts are required to ensure an invasion has been successfully rectified. Eradication is often impossible, and efforts to completely eradicate some species can negatively affect native species (Kettenring and Adams 2011) or backfire (Zipkin et al. 2009). Perhaps more feasible in some systems is “maintenance control” (Mack et al. 2000), in which one or several invasive species, through some degree of management intensity, is kept at a non-threatening level of abundance.

The increasing importance of considering invasive species' impacts when planning for forestry activities is evident in the northeastern U.S., where now-commonplace invaders such as Japanese and European barberry (*Berberis thunbergii* and *B. vulgaris*), Norway maple (*Acer platanoides*), Asian (or Oriental) bittersweet (*Celastrus orbiculatus*), glossy buckthorn (*Frangula alnus*), common buckthorn (*Rhamnus cathartica*), Japanese knotweed (*Fallopia japonica*), autumn olive and others complicate forest management and silvicultural decisions (Silander and Klepeis 1999, Webb et al. 2000, Greenberg et al. 2001, Fagan and Peart 2004, Webster et al. 2006, Knight et al. 2007, Aguilera et al. 2010, Moore et al. 2013). Traditional goals of forestry (timber, water quality, wildlife, and recreation) are made difficult with the introduction of additional non-native plants.

One such invader is glossy buckthorn (hereafter simply "buckthorn"), a non-native shrub originating in Europe now common in much of the eastern U.S. and southeastern Canada (Figure 1.1). Buckthorn arrived by at latest 1898 in London, Ontario (Catling and Porebski 1994) and by at latest the 1940s in seacoast New Hampshire (Lee and Thompson 2012). Buckthorn is particularly effective at invading eastern white pine (*Pinus strobus*) forests and poses a challenge to the management of pine. In the northeastern U.S., buckthorn has been shown to associate with white pine (Fagan and Peart 2004) on all soil types, but especially where pine grows on clay and loam soils with thin organic layers and low herbaceous cover (Kozikowski 2016). Specific reasons for this association are unconfirmed but may include the preferential combination of light, moisture, dispersal agents, and lack of inhibitive hardwood leaf litter typical of white pine forests. Buckthorn exhibits many traits common to successful invaders which make it a threat to white pine-occupied forest, including high seed productivity, formation of a seed bank viable for upwards of three years (Godwin 1943), lack of native predators, and the ability to form near-monocultures (Reinartz 1997) from seed and basal sprouting. Particularly relevant to white pine is buckthorn's moderate shade tolerance (Frappier et al. 2003) which allows colonization beneath a closed pine canopy. Glossy buckthorn deploys leaves early in spring (Godwin 1943), while a close relative, common buckthorn, retains leaves longer in autumn than most native plants (Harrington et al. 1989). Glossy buckthorn seems similar to common buckthorn in this regard (author: personal observation) and creates shadier under-plant conditions than most natives. These characteristics make glossy buckthorn a challenge to native regeneration (Frappier et al. 2004).

Buckthorn's most immediate impact on forestry is via competition with desired vegetation. With its rapid growth (Webster et al. 2006) and early leaf-out (Godwin 1943), and an apparent lack of co-evolved specialist predators in North America, buckthorn can establish dense thickets which prohibit the development of native seedlings (Fagan and Peart 2004). By suppressing the establishment of a new stand of trees, a buckthorn invasion can inhibit forestland from producing trees. Another invasive which invades forests, Amur honeysuckle *(Lonicera maackii*), has been shown to diminish forest plant species richness and force a return to shrub condition (Collier et al. 2002), and even suppress the growth of overstory trees (Hartman and McCarthy 2007); it is not unlikely that, under the right conditions, buckthorn could do the same.

Invasion of buckthorn following colonization can be swift, especially if scattered stems already exist on a site or if a seed source is present nearby. Buckthorn will sprout vigorously from broken stems (Godwin 1943), and canopy disturbances increase light and warmth to the seed bank, encouraging germination (Burnham and Lee 2010). In the northeast U.S., seed banks are created near extant buckthorn populations when buckthorn's copious drupes are ingested by American robins, cedar waxwings, rose-breasted grosbeaks and other birds (Catling and Porebski 1994) and the seeds subsequently dispersed. Those seeds, viable for at least three years, accumulate in soil and germinate readily when conditions are favorable, for instance following a disturbance such as a mid-forest blowdown or a forestry operation. Those forestry activities common to pine management, such as clear-cutting or group selection, facilitate invasion and increased abundance of buckthorn relative to unmanaged pine forest (Burnham and Lee 2010, Lee and Thompson 2012), unintentionally promoting the creation of the same buckthorn thickets and nearby seed banks which challenge future forest stand development.

In the northeastern U.S. and southeastern Canada, eastern white pine (*Pinus strobus*) plays an important ecological and economic role. Timber production is high compared to other native species; white pine forms stands with high volume per unit area, and especially old trees, now rare in pine's native range (Figure 1.1), may reach well over 60 meters in height if unencumbered (Peattie 1948, 2013). Pine stands offer tremendous vertical diversity, valuable shelter for roosting birds and deer, nutritious seeds for birds and rodents, and snags for raccoons, wood ducks, woodpeckers and other animals to occupy (Wendel and Smith 1990). Deer, squirrels, porcupine, beaver, snowshoe hares and New England cottontails will eat the bark and foliage of young white pine.

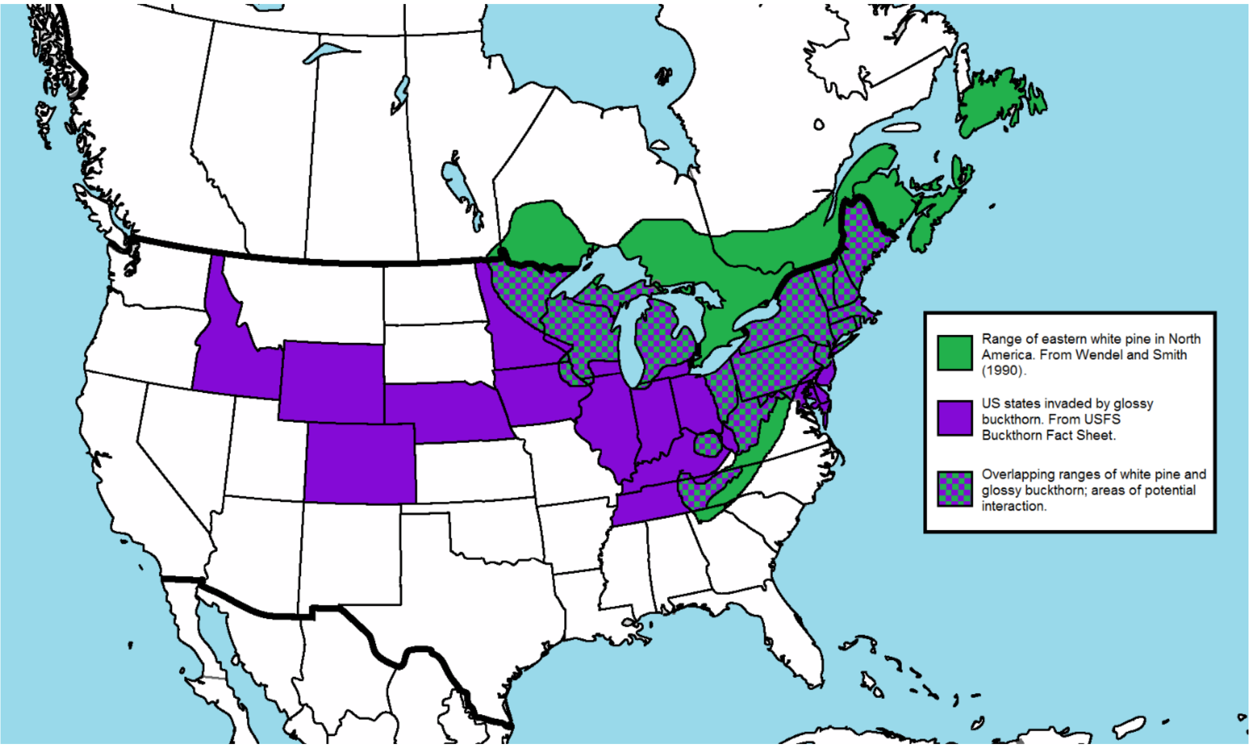


Figure 1.1. *Range of white pine in North America (from Wendel and Smith 1990), US states invaded by glossy buckthorn (from USFS Buckthorn Fact Sheet), and areas of overlap in the US. Buckthorn is also widespread in areas of Quebec and southern Ontario (Catling and Porebski 1994).*

Under appropriate conditions, white pine is able to create dense thickets of regeneration owing to mature trees' often prodigious seed production. Viable seeds, dispersed by wind, birds and squirrels, may exceed 4.4 million per hectare (Graber 1970). White pine seedlings grow slowly relative to seedlings of associated trees (Wendel and Smith 1990), but increase growth rate in the sapling phase. Pine's ability to withstand intermediate shade allows seedlings to establish beneath a mature canopy where gaps are present, but pines will of course colonize old fields (a classic New England occurrence), though susceptibility to damage and disfigurement from white pine weevil (*Pissodes strobi*) limits these trees' commercial utility (USFS 1995).

White pine's role in forestry is unparalleled in the northeastern U.S. In New Hampshire. Pine accounts for more timber volume than any other species (USFS 1997), and the wide range of uses of its lumber, from furniture to structural timbers to box making to pulp and biomass

(Howard 1985), illustrates the importance of white pine to forest managers. The historical use of large pines for ship masts is well known (Peattie 1948, Howard 1985), and the vast quantities of usable specimens in New England was a main driver of colonial settlement. At the time of this writing, stumpage price of pine sawlogs (payable to the landowner) ranges from $110-160 per thousand board feet (MBF) in southeastern New Hampshire (NHDRA 2016), exceeded in value only by oak, yellow birch and hard maple. When accounting for the densities commonly attained in pine stands, the financial incentive for landowners to manage for white pine becomes clear.

Many silvicultural regimes are appropriate for managing white pine (Wendel and Smith 1990). Shelterwood, seed-tree, patch and group cutting and under some conditions thinning have been used successfully to produce high-quality stands of white pine. However, logging activities in white pine stands increases susceptibility to invasion by non-native species, particularly glossy buckthorn (Frappier et al. 2003, Fagan and Peart 2004, Lee and Thompson 2012).

Though few peer-reviewed studies of invasive species control actually include an estimate of control costs (Kettenring and Adams 2011), it is assumed that buckthorn is highly expensive to eradicate due to plant characteristics, the difficulties in controlling seed dispersal, and the persistent effort required (Pergams and Norton 2006). Buckthorn can be controlled via chemical methods (e.g. herbicides such as glyphosate or triclopyr), mechanical means (e.g. pulling or cutting), or by targeted burning, and a combination of two or more methods is commonly employed [Reinartz 1997, Pergams and Norton 2006, Lee et al. 2016 (unpublished)]. Buckthorn foliage is somewhat fire-resistant (USFS Fact Sheet 2005). Timing of any buckthorn control treatment is an important consideration due to its ability to re-sprout (Reinartz 1997, Zuidema 2014) and repeat treatments within the same growing season are often required. Multiple cuttings or flame treatments implemented within the same growing season have been shown to be successful [Lee et al. 2016 (unpublished), Zuidema 2014], though non-target vegetation is easily damaged without extreme care. To conduct a campaign to eradicate buckthorn from a pine forest, or following a harvest operation when both buckthorn and pine co-establish, would likely be prohibitively challenging and expensive [Lee et al. 2016 (unpublished)] if preserving any pine regeneration was a stated goal. It follows, then, that some level of control which promotes pine regeneration while minimizing time and cost expended to treat buckthorn may be ideal, at least for forest management purposes.

Driving my research is this very question: is it possible to successfully manage for timber in the presence of an invasive species through some level of control which stops short of eradication?

To address this question I have developed and implemented a simple silvicultural procedure combining elements of crop tree release with localized invasive species control—in effect, timber stand improvement (TSI) in miniature—in which pine saplings are liberated from direct competition with buckthorn and associated vegetation either by A: cutting adjacent vegetation, or B: cutting adjacent vegetation and applying herbicide to cut stumps, both within a small pre-determined radius of the pine sapling. Pines released in this manner should, in theory, then gain an advantage over neighboring vegetation by utilizing increased growing space (light, soil moisture, physical space, etc.). Ultimately, the method, designed to be implemented quickly and at low cost, must give pines the “boost” needed to emerge from (and stay atop) a surrounding buckthorn thicket in order to be worthwhile. The novelty of such an approach lies in the single, localized treatment of invasive species as opposed to stand-wide eradication [e.g. Zuidema (2014) and Lee et al. (2016, unpublished)], the young age at which “crop trees” (saplings) are released, the targeted use of herbicide to suppress buckthorn recovery, and the acceptance of a persistent invasive population, without attempting eradication, provided aims of forestry are achievable.

Success will be assessed by evaluating three pine physiological responses: foliar biomass, foliar nitrogen concentration, and stem non-structural carbohydrates. **Foliar biomass:** Trees with access to higher resource levels (e.g., physical space, soil moisture, but especially light) should accrue leaf biomass more rapidly than trees with more limited access (Niinemets 1997). Foliar biomass should serve as a reliable indicator of a tree's net photosynthetic capability, such that a pine sapling with greater leaf biomass than a neighboring sapling should produce and store more carbohydrates (Reich et al. 1999). **Foliar nitrogen:** Trees not limited by light availability should assimilate more nitrogen (Chapin et al. 1987) and produce more of the nitrogen-rich molecule rubisco (Mooney et al. 1978, Field 1983), an enzyme involved in carbon fixation, than trees which are light-limited. Also, trees with fewer competitors for soil nutrients should assimilate more nutrients from the relatively larger pool of available resources (Craine and Dybzinski 2013), for instance to create chlorophyll or rubisco from nitrogen, allowing accelerated growth. **Stem non-structural carbohydrates:** Trees not limited by light should produce more non-structural carbohydrates (NSC; starch and sugars) through photosynthesis than conspecifics which are light-limited (Kozlowski et al. 1991), which will be allocated to leaf, branch, stem (xylem and bark) and root tissues (Dietze et al. 2014, Richardson et al. 2015). My experiment examined NSC content of stem tissues (xylem and bark) only. The term "bark" is used here to include all tissues outside of the vascular cambium: secondary phloem, cortex, phelloderm, phellogen (cork cambium), and periderm.

Hypotheses

H1: During the growing season following a localized, spring cut or cut and herbicide treatment, treated (released) pine saplings will respond to the increased availability of resources by accruing additional leaf biomass when compared to unreleased control specimens, indicating enhanced photosynthetic (and therefore growth) capacity.

H2: Leaf nitrogen concentration will be greater in treated (released) pine saplings versus controls.

H3: Stem non-structural carbohydrates will be found in xylem and bark tissues in greater concentrations in treated (released) pine saplings versus controls.

A probable consequence of release is that treated trees will emerge from the buckthorn thicket more quickly than untreated trees (if these emerge at all) due to the enhanced growth spurred by increased photosynthetic activity following release. However, the limited amount of time available to conduct this study (one growing season) precludes some measurements which would allow more concrete conclusions to be drawn; the growth variables indicated in the hypotheses instead serve as proxies for more definitive growth observations (e.g., radial and height growth). Future measurement of study trees is intended, and measurement of these should provide the ultimate judgment of the success of the experiment.

Methods

Site

Research was conducted at MacDonald Lot in Durham, New Hampshire, a forested 31.9-hectare property (Figure 1.2) owned and managed by the University of New Hampshire. Soils beneath study plots are in the Scantic silt loam and Hollis-Charlton fine sandy loam series. Forest cover is white pine, pine-oak (red, black and white; *Quercus rubra*, *Q. velutina*, and *Q. alba*, respectively), and mixed hardwoods, which include white ash (*Fraxinus americana*), shagbark hickory (*Carya ovata*), black birch (*Betula lenta*) and red maple (*Acer rubrum*). Much of the understory, especially under white pine, has been colonized and is now dominated by glossy buckthorn.

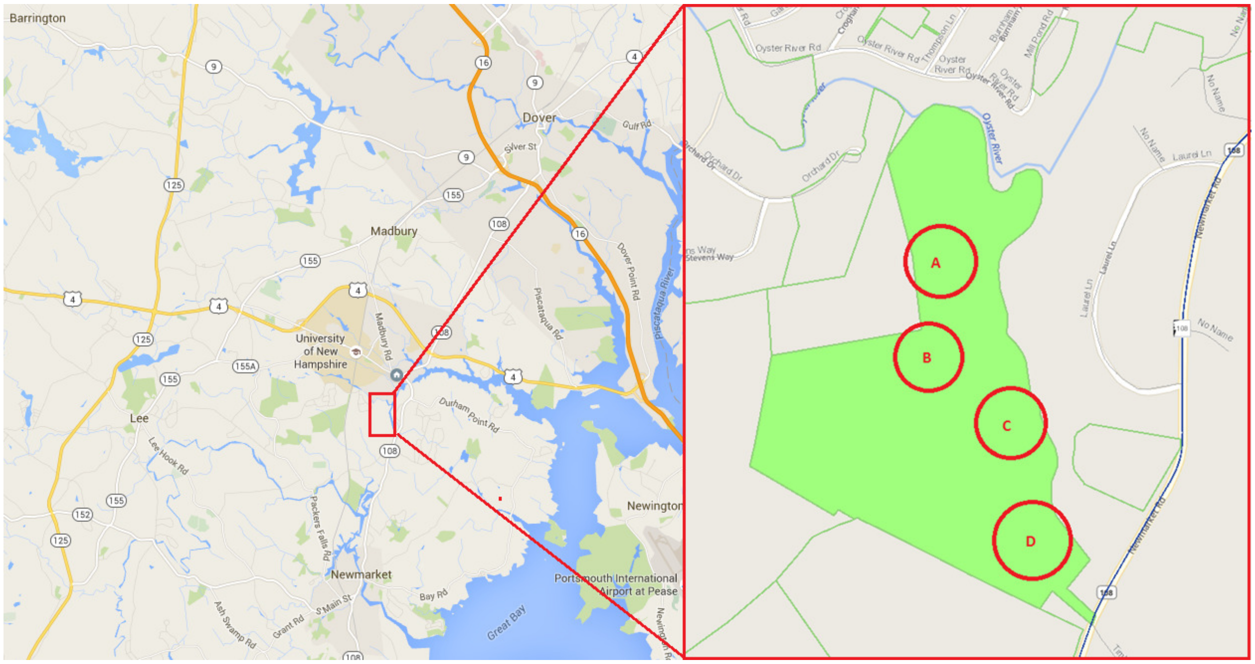


Figure 1.2. *Map of MacDonald Lot, Durham, NH. General locations of study units (A, B, C and D) are outlined.*

Several treatments designed to suppress glossy buckthorn and promote white pine regeneration have been conducted at MacDonald Lot and predate the present study [Lee et al. 2016 (unpublished), Zuidema 2014]. The UNH Office of Woodlands and Natural Areas logged portions of mature white pine forest during the winter of 2009-2010, creating four clear-cut units (A, B, C and D in Figure 1.2) of 0.4 ha each [Lee et al. 2016 (unpublished)]. Areas within units A, B and C that did not overlap with plots utilized by Zuidema (2014) were considered eligible for the purposes of the present experiment, and 28 of the 75 pine saplings studied are located within these. A fourth 2 ha unit (D, Figure 1.2) was clear-cut the same winter; it is here that the remaining 47 study saplings are located. Because 2009 was a productive white pine seed year, pine established successfully following all cutting operations, alongside which buckthorn also established in dense thickets both from seed as well as through sprouting from stems crushed during harvesting. Buckthorn density observed at some study pines exceeded 30 stems m^{-2}

(300,000 stems ha^{-1}) prior to treatment. In addition to buckthorn, many other invasive species were observed within study plots (Table 1.1) though not in comparable densities.

***Table 1.1**. Invasive species observed within study plots at MacDonald Lot, Durham, NH.*

Common name	Scientific name
barberry	*Berberis spp.*
burning bush	*Euonymous alatus*
common buckthorn	*Rhamnus cathartica*
honeysuckle	*Lonicera spp.*
multiflora rose	*Rosa multiflora*
Oriental bittersweet	*Celastrus orbiculatus*
common privet	*Ligustrum vulgare*

For this study, research plots were located in these four harvested units of MacDonald Lot (Figure 1.2), set in areas of regenerating pine and buckthorn and with minimal extraneous species present.

Study Design

Tree selection

On May 18th, 2015, 75 pine saplings for study were identified, each meeting the following selection criteria: 1) was at least 2 m from an opening or cut edge; 2) was surrounded by at least 10 buckthorn stems of any diameter (within a 1 m radius of pine sapling); 3) had foliage at least as full its nearest neighbors; 4) was at least as tall as its nearest neighbors; 5) was at least 3 m from next closest study pine; 6) was at least 5 m from forest edge; 7) was five years old or younger (based on number of branch whorls); 8) its shape was not negatively influenced by surrounding vegetation; and 9) exhibited growth form and vigor likely to result in a mature tree with economic value. (If sapling was stunted, broken or chlorotic, it was excluded.)

These criteria were designed to ensure some testable level of competition between buckthorn and pine, and to mimic the decisions made by a forest technician who, equipped with a brush saw or chainsaw, would make quick on-the-ground judgments as to which saplings warranted release.

Saplings from all four study units (A, B, C and D) were randomly assigned to one of the treatments based on 1) initial sapling height and 2) equal representation of treatments within each unit and within the experiment as a whole. Once identified, all study saplings in a given unit were sorted by height; the tallest three were each randomly assigned to one of the three treatments, the next tallest three likewise, and so on until each treatment contained 25 saplings.

Treatments

Cut treatments, implemented on May 28th, 2015, coincided with first flush of new buckthorn growth including full expansion of first leaves, helping ensure that root stores were maximally exhausted (Canham et al. 1994), sprout response would be minimized, and herbicide application would be least challenged by sap flow.

Cut only ("cut"): all buckthorn and other vegetation within a 1 meter radius of the study pine stem were removed, cutting as close to ground level as was operationally feasible, (Reinartz 2002) using a brush saw (Stihl Incorporated, Virginia Beach, VA USA). Those plants originating outside the 1 m clearance area but which intruded in some way were trimmed back to the plot circumference.

Cut and herbicide ("cut + herb"): a 1 m radius circle was cut (as above), and immediately thereafter an herbicide mix of 50% water and 50% Rodeo® (Dow Agrosciences, Indianapolis, IN USA), was applied directly to cut stems (Reinartz 1997). Rodeo® is 53.75% glyphosate; concentration of applied mixture was ~26.9% glyphosate after dilution.

No treatment ("control"): no vegetation was removed or treated with herbicides.

Response variables

Pine growth

Pre-treatment and post-growing season metrics were collected on all study pines to examine a growth response to treatment. Initial measurements were taken from May 20-22, 2015, before treatment implementation, and final measurements were taken from August 21-26, 2015 near the end of the growing season. Variables measured (and used in statistical analysis) were stem diameter at ground level (in cm to nearest mm with calipers) and height from ground level to tip of leader (in cm to nearest mm with meter stick).

Light (PAR)

A Sunfleck® ceptometer (Decagon Devices, Pullman, WA USA) was used to measure photosynthetic photon flux density (PPFD, in µmoles of photons m^{-2} sec^{-1}) at a randomly-selected subset of 10 pines per treatment. Each study sapling was visited on three nearly cloudless occasions during midsummer: once at ~09:00, once at ~12:00 and once at ~15:00. Two readings were taken with the ceptometer, one read while pointed north and the other while pointed south, while simultaneously a reading was obtained using a LI-180 quantum sensor (LI-COR Inc., Lincoln, NE USA) in full sun at a nearby reference station. Both devices were calibrated before field readings were taken. The mean percent of maximum PPFD was calculated for each sapling for each occasion.

Pine foliar and leader biomass

Ten randomly-selected study saplings from each treatment were harvested on August 28th to analyze both pine foliar and leader biomass and non-structural carbohydrate concentration (below). The needles and leader from the 2015 growing season were removed from the tree, separated, air dried and weighed.

Pine foliar nitrogen concentration

Two previous-year (2014) fascicles were haphazardly picked from the top whorl of each study sapling on May 22nd, before treatments were implemented, and again (this time from the 2015 whorl) in mid-August near the end of the growing season. Fascicles were air dried and analyzed using a CHN 2400 Series II Elemental Analyzer (PerkinElmer, Waltham, MA USA) at the UNH Water Quality Analysis Laboratory (181 James Hall, 56 College Rd, Durham, NH 03824). Procedures described by Bremner (1996) were followed and percent nitrogen of each fascicle was reported.

Pine non-structural carbohydrate (NSC) concentration

The 30 pines harvested for the foliar and leader biomass examination (above), plus an additional two pines from the “control” treatment and one pine from the “cut only” treatment (accidentally destroyed), were analyzed for non-structural carbohydrate (starch and sugar) concentration. A 10 cm segment from the base of each sapling’s stem was removed. Bark tissue was manually removed and xylem (stem wood) was divided into quarters for drying. After a one-minute microwave pre-treatment to minimize NSC losses from drying [*sensu* Pelletier (2010)], bark and xylem tissues were air dried. NSC concentrations were analyzed following Chow and Landhäusser (2004) and was conducted by the Huggett Lab at Bates College (44 Campus Ave, Lewiston, ME 04240).

Vegetation removed

Before treatment implementation, a careful inventory of vegetation surrounding each study sapling (all buckthorn stems and their sizes, all pine stems and their sizes, and stems of other species) was conducted in order to estimate total stems removed in the “cut only” and “cut and herbicide” treatments. This inventory was intended for the purpose of detecting a difference in how pine saplings responded to the removal of buckthorn versus the removal of pine and other vegetation.

Buckthorn response

To assess the response of buckthorn to the two treatments (“cut only” and “cut and herbicide”), the number of living buckthorn stems within each treated pine’s clearance circle was tallied in September 2015. Number of stump sprouts versus number of stems originating from seed was distinguished for 12 of the pines in the “cut only” treatment and 11 in the “cut and herbicide” treatment, chosen in the field after realizing the value of such a distinction and after roughly half of all trees had already been visited.

Statistical analyses

The statistics program JMP Pro 12 (SAS, Cary, NC USA) was used to perform all statistical analyses. One-way analysis of variance (ANOVA) was used to verify that treatment groups did not differ in height characteristics *a priori* and to examine how percentage of maximum PPFD differed between treatments. A two-way ANOVA was used to examine NSC differences (in xylem and bark tissues) between treatments. Analysis of covariance (ANCOVA) with initial diameter as covariate was used to test for differences between treatments in pine radial and height growth and foliar and leader biomass; ANCOVA with pre-treatment foliar nitrogen as covariate was used to analyze post-treatment foliar nitrogen concentration. Response variables were transformed as appropriate to meet the assumptions of these tests.

The vegetation removed from the 1 m radius circle surrounding pines in the “cut” and “cut and herbicide” treatments varied in species composition and in density. To assess the influence of the various components, stepwise regression was used. Specifically, I examined how pine diameter responded relative to the number of buckthorn stems, pine stems, or stems of miscellaneous species removed. A post-hoc Student’s *t*-test was used to examine the response of buckthorn following treatment. Regression inputs included number of buckthorn stems less than 1 cm in basal diameter, buckthorn > 1 cm, pine < 1 cm, pine > 1 cm, number of stems of miscellaneous species, treatment type, and initial basal diameter.

Results

Pine growth

Study saplings were analyzed to ensure treatment groups did not differ in mean height or diameter *a priori*. Neither initial height (one-way parametric ANOVA, d.f. = 2, F = 0.167, p = 0.847) nor initial diameter (one-way parametric ANOVA, d.f. = 2, F = 0.422, p = 0.658) varied significantly between treatments.

The final basal diameter of pine saplings did vary significantly across treatments after controlling for initial diameter (one-way parametric ANCOVA on log-transformed data, $F_{3,72}$ = 363.502, $p < 0.001$); treated pines exhibited on average 12.4% greater diameter than controls (Table 1.2, Figure 1.3). A Tukey-Kramer “Honestly Significant Difference” (HSD) post-hoc test revealed that the “cut only” and “cut and herbicide” treatments each varied significantly when compared with the control group ($p < 0.001$, $p = 0.005$, respectively) but did not vary when compared with each other ($p = 0.361$). No difference in final height was observed between treatments. Three saplings from the “cut and herbicide” treatment, that died following treatment implementation, were not included in analysis. The terminal leaders of three additional “cut and herbicide” specimens and one from the “cut only” treatment, which *were* included in this analysis, died over the course of the growing season; the trees themselves remained alive. No trees in the “control” group died.

Table 1.2. *Magnitude of release of pine saplings relative to untreated controls. "Cut" = cut only, "Cut + herb" = cut and herbicide. For “Diameter” and “Foliar/leader biomass,” figures are based on adjusted means with effects of initial stem diameter removed with ANCOVA.*

Response	Cut	Cut + herb	Average Release
Diameter	+14.6%	+10.1%	+12.4%
Foliar/leader biomass	+77.2%	+73.7%	+75.4%
Bark starch	+119%	+160%	+140%

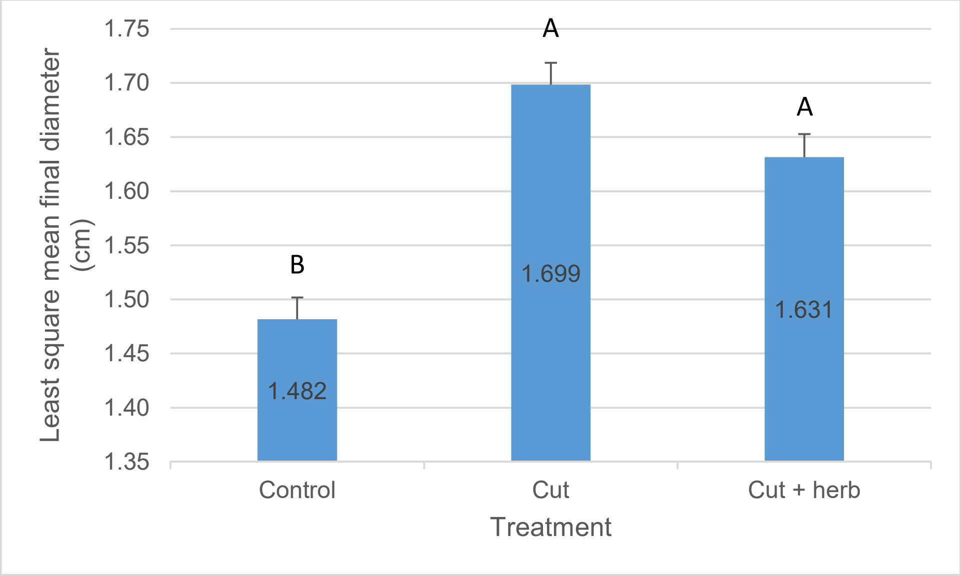


Figure 1.3. *Diameter (cm) of pine saplings at MacDonald Lot, UNH, Durham NH following treatment and seasonal growth. Final diameter varied significantly between treated saplings ("Cut" and "Cut + herb" treatments) and controls. Figure includes group mean, standard error, and connecting letter designation from Tukey-Kramer HSD post-hoc test. Treatments not connected by the same letter are significantly different (p < 0.05).* $n_{control}$ *and* n_{cut}*=25;* $n_{cut+erb}$*=22.*

Light (PAR)

Photosynthetically-active radiation (PAR, reported as the mean percent of maximum PPFD of three measurements per replicate), measured five weeks after treatments were implemented, varied significantly between control and treatments (one-way parametric ANOVA with arcsine-square root transformed data, d.f. = 2, F = 13.086, p < 0.001); treated trees received more solar radiation than controls (Figure 1.4). A Tukey-Kramer HSD post-hoc test revealed that the "cut only" and the "cut and herbicide" treatments each had significantly greater – nearly double – PPFD than the control group (p < 0.001, p = 0.003, respectively) but did not vary when compared with each other (p = 0.388).

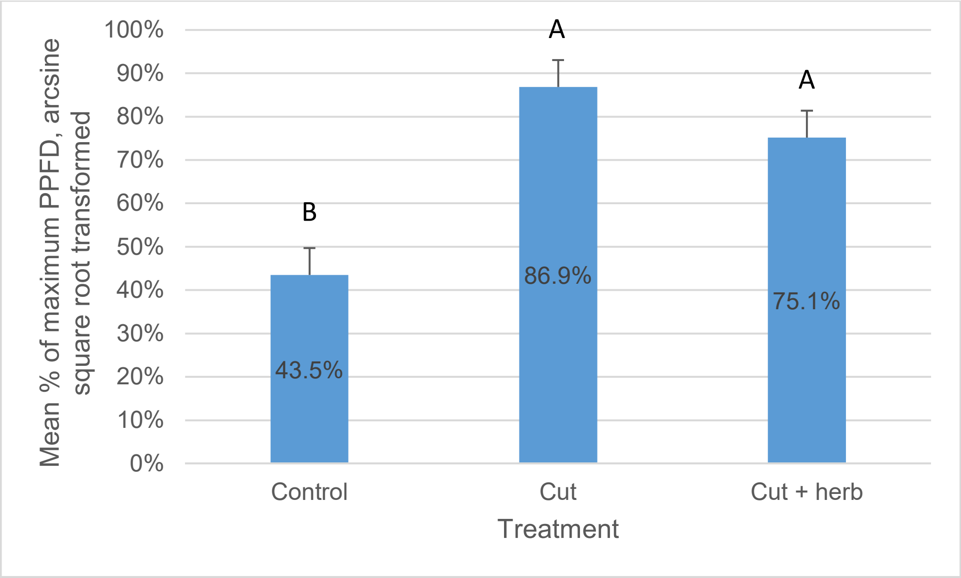


Figure 1.4. *Arcsine square root transformed percentages of maximum PPFD observed at subset of pine saplings at MacDonald Lot, UNH, Durham NH, presented as mean of three observations. Percent of maximum PPFD varied significantly between treated saplings ("Cut" and "Cut + herb" treatments) and controls. Figure includes group mean, standard error, and connecting letter designation from Tukey-Kramer HSD post-hoc test. Treatments not connected by the same letter are significantly different ($p < 0.05$). n=10 for all treatments.*

Pine foliar and leader biomass

Measured at the end of the growing season, current year dry biomass of the pine sapling leader, both stem and foliage, varied significantly between treatments after controlling for initial diameter (one-way parametric ANCOVA with log-transformed data, $F_{3,29} = 35.813$, $p < 0.001$) (Figure 1.5). A Tukey-Kramer HSD post-hoc test revealed that the "cut only" and the "cut and herbicide" treatments each had mean values more than 73% higher than the control group ($p = 0.011$, $p = 0.014$, respectively; Table 1.2) but did not vary when compared with each other ($p = 0.993$).

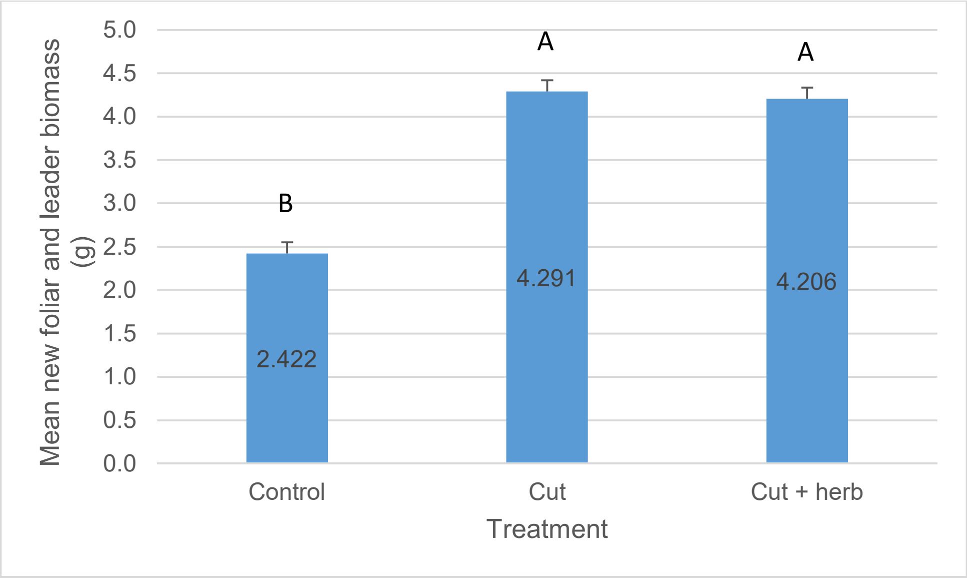


Figure 1.5. *Current year dry biomass (g) of pine sapling leader, including foliage, of subset of saplings at MacDonald Lot, UNH, Durham NH following treatment and seasonal growth. Biomass varied significantly between treated saplings ("Cut" and "Cut + herb" treatments) and controls. Figure includes group mean, standard error, and connecting letter designation from Tukey-Kramer HSD post-hoc test. Treatments not connected by the same letter are significantly different ($p < 0.05$). n=10 for all treatments.*

Pine foliar nitrogen concentration

Needles collected from each study sapling pre-treatment, as well as needles collected following treatment and seasonal growth, were analyzed for percent nitrogen content. Average late-season nitrogen content did not differ significantly across treatments after controlling for pre-treatment nitrogen content (control: 1.80% N; "cut": 1.91%; "cut + herb": 1.86%. Standard errors < 0.001 for all groups. One-way parametric ANCOVA with arcsine-square root transformed data, $F_{3,66} = 1.974$, $p = 0.127$). Treatment sample sizes varied slightly because some fascicles could not be satisfactorily analyzed: $n_{control}=23$; $n_{cut}=25$; $n_{cut+herb}=19$.

Pine non-structural carbohydrate (NSC) concentration

Non-structural carbohydrate content (starch and sugar) from bark and xylem tissues was analyzed. Starch content in phloem varied significantly among treatments (two-way parametric ANOVA of log-transformed data, $F_{3,63} = 119.883$, $p < 0.001$) (Figure 1.6). A Tukey-Kramer HSD post-hoc test revealed that the “cut only” and “cut and herbicide” treatments together exhibited on average 140% greater bark starch values than the control group ($p < 0.001$ for both treatments; Table 1.2) but did not vary when compared with each other ($p = 0.861$). No significant difference in xylem starch content or in bark or xylem sugar content was observed between treatments.

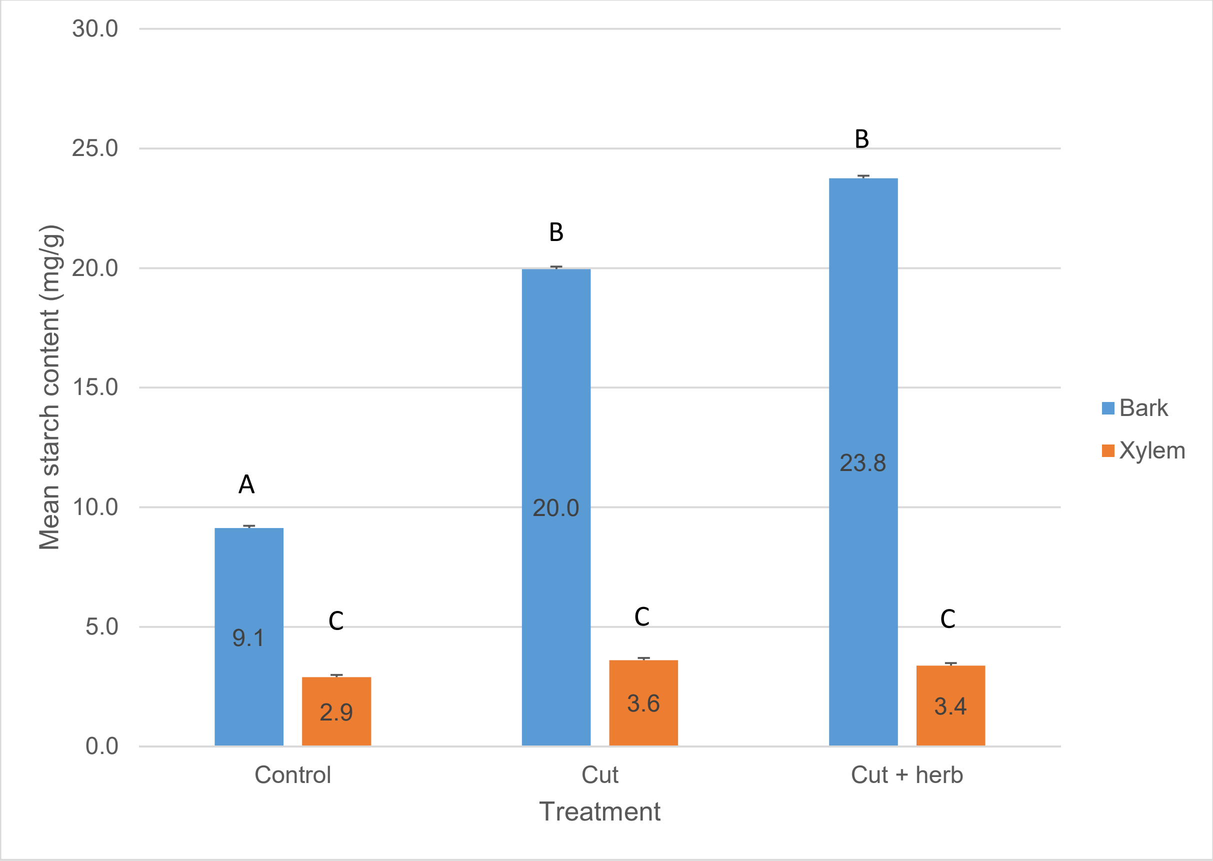


Figure 1.6. *Starch content (mg/g) of subset of pine saplings at MacDonald Lot, UNH, Durham NH following treatment and seasonal growth. Bark starch varied significantly between treated saplings (“Cut” and “Cut + herb” treatments) and controls while xylem starch did not. Figure includes group mean, standard error, and connecting letter designation from Tukey-Kramer HSD post-hoc test. Treatments not connected by the same letter are significantly different ($p < 0.05$). $n_{control}=23$, $n_{cut}=21$, $n_{cut+herb}=20$.*

Vegetation removed

Treatment groups did not differ in the amount or composition of vegetation surrounding each study pine (and in the case of the “cut” and “cut and herbicide” treatments, vegetation removed; Table 1.3). On average, regardless of treatment, buckthorn comprised ~66% of stems within 1 m of the study pine, though this number ranged from 19% to 97% across all plots. Pine averaged 23% of stems and ranged from 0% to 61%. Miscellaneous species averaged 14% and ranged from 0% to 63%.

Variation in the densities of buckthorn, pine, and other species removed did not seem to affect pine growth. Specifically, based on minimum AICc, the final diameter of treated study saplings was not significantly related to any model inputs (number of buckthorn stems less than 1 cm in diameter, buckthorn > 1 cm, pine < 1 cm, pine > 1 cm, number of stems of miscellaneous species, treatment type, and initial diameter) except initial diameter.

Table 1.3*. Average numbers of buckthorn (FA), white pine (PS) and other species occupying (Control) or removed (Cut, Cut + herb) from study pines (per 3.14 m^2) by treatment type.*

Treatment	FA <1	FA >1	FA total	PS <1	PS >1	PS total	Other spp. total	All stems
Control	71.13	47.88	119	29.53	6.53	36.07	26.64	181.71
Cut	70.75	47.88	118.63	35.81	6.28	42.1	16.59	177.31
Cut + herb	80.68	38.33	119	38.7	5.78	44.48	21.99	185.48

Buckthorn response

At the end of the growing season, in the “cut only” treatment, an average of 142.2 stems per plot were tallied (80.5% of these from sprouts), whereas in the “cut and herbicide” treatment, an average of 66.1 stems per plot were tallied (56.0% from sprouts; Figure 1.7). With sprouts included, buckthorn recovery was significantly higher in the “cut only” treatment (Student’s *t* adjusted for pre-treatment buckthorn density as covariate, d.f. = 46, *t* = -4.313, p < 0.0001) than the “cut and herbicide” treatment. With sprouts excluded, the number of buckthorn stems present was nearly identical in both treatments (27.7 stems in “cut only” vs. 29.1 stems in “cut and herbicide”).

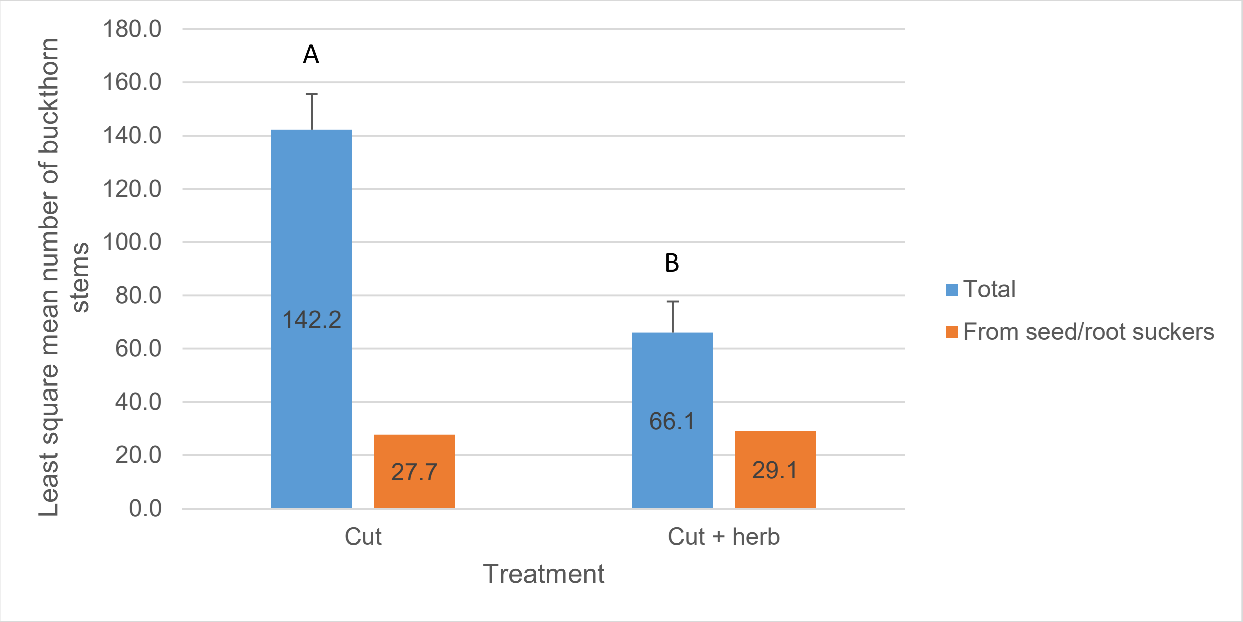


***Figure 1.7**. Number of tallied buckthorn stems within treatment radii at MacDonald Lot, UNH, Durham NH following treatment and seasonal growth. Total number of buckthorn stems varied significantly between treatment groups ($p < 0.0001$) whereas those not originating from sprouts did not. Connecting letter designation from Student's* t *post-hoc test. Standard error is included with each "Total" column.*

Discussion

As hypothesized, pine saplings responded to release from competition with increased foliar biomass, increased starch content of bark tissues, and increased foliar nitrogen (as a function of increased biomass), though nitrogen concentration did not vary. Additionally, basal diameter growth of released pines was greater than control specimens, but height growth was not. Release effects were not measurably enhanced by the use of herbicide in addition to cutting; all measured variables were similar between "cut only" and "cut and herbicide" treatments.

Foliar and leader biomass

The increase in foliar mass observed in released trees (those from the "cut only" and "cut and herbicide" treatments) suggests that the released pines are utilizing some enhanced resource (increased light, water, and/or nutrients) unavailable to the control group to grow more needles, longer needles, or both. It is evident that this increase in needle mass translates into increased whole-plant net photosynthesis, driving greater rates of basal diameter growth and starch production of treated pines. Pacala et al. (1994) describe that white pine radial growth is rapid under high light and slow in low light conditions; this can plausibly be linked to the associated increase in photosynthetic capacity from additional foliar biomass in high light scenarios. Height growth (shoot elongation) is related more to the previous growing season's root stores (Dickson 1989) so any differences between treatments should be observable following the 2016 growing season.

Foliar nitrogen and xylem/bark NSC content

As hypothesized, foliar nitrogen of released trees increased as a function of mass when compared to controls. The late-season N percent, however, did not increase and was stable across all treatments, controls included. Yet, because all pines had, on average, the same amount of foliage to start with and as treated pines *did* accrue additional foliar mass, which would have required additional rubisco, there was likely an undetected spike in foliar nitrogen concentrations a short time after treatment, followed by the observed increase in foliar mass (and an associated bulk gain in foliar nitrogen) and then a decrease in N concentration. Seasonal fluctuation of foliar N has been observed in white pine in Ontario (Munson et al. 1995) and Ohio (Scherzer et al. 1998) and is likely to have occurred here, though the two points in time at which fascicles were sampled for our nitrogen analysis appear to have captured moments in which concentrations did not vary significantly relative to pre-treatment levels.

Another component of the nitrogen equation is uptake and assimilation. In many temperate forests, inorganic nitrogen is a major limiting factor to tree growth and is quickly taken up by plants (Dickson 1989). By removing immediately neighboring competitors from pine saplings' root zones, released pines should display a greater rate of nitrogen uptake than controls, owing to a probable short-term increase in available labile nitrogen and to increased need by those pines. This may indeed be the case within our study system, in that released saplings quickly assimilated enough additional nitrogen to accrue added foliar biomass, but perhaps the fact that control saplings did not differ from treated trees in late-season nitrogen concentration could be due to some other factor, for instance an “artificially” inflated pool of labile nitrogen available to all study pines. Stokdyk and Herrman (2014) found that glossy buckthorn litter modified forest soil characteristics by increasing extractable nitrogen via enhanced microbial nitrogen mineralization. It is plausible that increased availability of nitrogen in soils occupied by glossy buckthorn lessens the competition for it, and is also feasible that pines from outside of our experimental system, e.g. those not surrounded by glossy buckthorn, may have had lower foliar nitrogen concentrations, though this was not tested.

In released pines, non-structural carbohydrates (NSC, starch and sugars) increased only in bark tissues, and then in starch only. Neither bark sugar nor xylem starch or sugar increased significantly compared to controls. In some pines (e.g. *Pinus sylvestris* and *P. cembra*), xylem tissues store low amounts of NSC relative to bark/phloem tissues (Hoch et al. 2003, Gruber et al. 2013). Little data on NSC storage of white pine are available, yet my analysis is consistent with how NSC is allocated in these other pine species.

The increased levels of starch in bark tissues of released pines is likely attributable to lower physiological stress and higher overall photosynthate production (from increased needle biomass). Because some pines (e.g. *P. sylvestris*) respond to drought stress by reallocating free NSC to the roots (Gruber et al. 2012), leaving less within phloem tissues to nourish the cambium and spur diameter growth, it is possible that the general physiological stress experienced by control specimens in this study (e.g. through lowered light levels and competition from buckthorn and other neighboring vegetation for soil moisture and nutrients) explains the lower bark starch concentrations observed in controls. The low sugar content of both xylem and bark tissues, which did not differ across treatments, could be explained by an undetected seasonal fluctuation (e.g. Terziev 1997, who demonstrated that sugar concentrations within sapwood of *P. sylvestris* vary depending on time of year, with lowest concentrations in spring and summer). Perhaps an amplified (and statistically significant) signal would have been apparent if sampling had been conducted in autumn or winter. An alternative explanation is that sugars, more mobile and readily used compounds than starches, which are generally for long-term use, were at the time of sampling still being generated and utilized quickly, preventing buildup within the sampled tissues. Regardless of the mechanism, the increased production and storage of starch in bark tissues is evidence that treated pines were more photosynthetically active than controls, and these stored reserves bode well for next year's growth.

Release from competing vegetation

While it is clear that competitors affect the success of white pine seedlings, it is difficult to know how much of the pine release is due to the removal of any one component (buckthorn, other white pine, miscellaneous species). The variation (or lack thereof) in the composition of each study pine's "circle of competition" may explain the underwhelming results of this particular analysis. It is possible that differing influences of each competitive component may have been detected had there been greater variation in the "circles" of released trees. Of course, a certain amount of variation was intentionally designed out of the study: to be selected for inclusion, a pine sapling was required to be surrounded by at least 10 buckthorn stems. Without experimentally designing competitive mixtures that emphasize (or exclude) one component, the role of each competitor in the magnitude of the pine growth response is difficult to determine; the model results were therefore inconclusive. It can be stated that, in the mixtures encountered, buckthorn does not seem to be playing a disproportionate role in suppressing pine relative to other competitors, or conversely the removal of buckthorn does not better explain the resulting growth increase than removing any other species or combination of species. More likely, it is simply the concerted effects of many competitive neighbors that suppress pine growth, though the enhanced resource use efficiency of buckthorn (and other invasives present) could play an outsized (if undetected) role. Rather than attribute the treated pines' growth response to the removal of a specific competitor, it is likely the combination of increased sunlight, soil moisture and soil nutrients achieved through release which explain that response, suggesting that similar results could be achieved in many invaded systems and with many target tree species, though specific traits of some invasive species (e.g. allelopathy) may complicate realized effects.

The observed results are analogous to those attained through silvicultural weeding or cleaning (Nyland 2007), two timber stand improvement techniques commonly utilized in seedling or sapling stands of pine or other species to help achieve a desired species matrix or encourage desirable form or spacing. In essence, the utilized release method could be considered a combination crop tree release and cleaning operation on a constricted scale, and less an invasive control operation, though the method results in some level of invasive species suppression, especially if canopy cover (of released trees) is allowed to converge and shade out some of the remaining invasive component [*sensu* Cunard and Lee (2009)]. Clearly the removal of vegetation is promoting a growth response in those released trees, with the implication that the method used is perhaps a practical silvicultural option in the face of an invasion.

Treatment differences

No significant difference was observed between pines in the "cut only" and the "cut and herbicide" treatments, at least not following the first growing season post-treatment when this study was conducted. Buckthorn response did vary, however. Buckthorn sprouted much more vigorously from cut stumps in the "cut only" treatment than the "cut and herbicide" treatment, illustrating the effectiveness of glyphosate in subduing sprouting when applied to cut stumps;

however, the herbicide showed no effect on number of buckthorn stems emerging from the soil (whether by seed or via root suckering). Glyphosate, purported to have low volatility in soil due to microbial degradation (Franz et al. 1997), had no obvious effect on the seed bank or emergent seedlings, possibly due in part to limited soil exposure through judicious application; buckthorn seedlings emerging from soil were very similar across “cut” and “cut and herbicide” treatments.

Answering the question of economic viability of herbicide application, versus simply cutting, will require further analysis. Should pines grow sufficiently after a cutting treatment to overtop buckthorn sprouts, perhaps herbicide is unneeded; however, some buckthorn sprouts observed in September 2015 had already grown higher than the study pine. Though no growth differences were noted between study pines in the “cut only” and “cut and herbicide” treatments, the quick recovery of buckthorn in some plots suggests that herbicide may be required, at least in some cases. However, following treatment, a greater number of pines perished in the “cut and herbicide” treatment (six) than in the “cut only” treatment (one), a difference likely attributable to the herbicide itself. This leads to the question: does the more effective suppression of buckthorn sprouting when herbicide is used offset the increased risk of pine mortality incurred through its use? Radosevich et al. (1980) describe how certain pines and other coniferous tree species are susceptible to harmful effects from glyphosate during the spring and summer; it is likely that some pine seedlings were exposed to overspray, contributing at least in part to mortality. The timing of treatment was designed to affect buckthorn when root stores would be maximally exhausted, following leaf-out, but Reinartz (1997, 2002) reports higher effectiveness of glyphosate application on buckthorn in late fall or winter. Perhaps the optimal timing for the “cut only” treatment would differ from the “cut and herbicide” for these reasons but for practical purposes the treatments were implemented simultaneously.

Unanswered questions and future research

This study does not examine how species other than white pine or forest conditions different than those studied will respond to the method used, nor does the author presume to imply success in other systems. (Indeed, application of the method used here outside of the buckthorn/pine system is likely limited to those scenarios in which the target tree species is commercially valuable and is not preferred by deer or other local grazers; release may simply improve access and target trees may suffer increased predation.) In the white pine/buckthorn system, it cannot yet be determined which release treatment – cut only or cut and herbicide – fares better long term. Some future monitoring is required to determine if pines emerge from the buckthorn thicket following a simple cutting treatment, if an herbicide is also required, or if an even more intensive treatment than a single 1 m radius cut is necessary. The economics of the treatment determined to be most effective will require analysis; such treatment will need to make financial sense relative to silvicultural alternatives in order to be useful or widely applicable.

Conclusion

It is clear that the “cut only” and “cut and herbicide” treatments elicited a growth response from released pines. Pine basal diameter, foliar biomass and starch content of bark tissues all increased following the post-treatment growing season. The fate of pine within this system when treated in such a manner is promising; it is evident that growth has accelerated following release, and some measure of buckthorn suppression was achieved, though follow-up measurements will allow more concrete inference. Should those measurements strengthen my findings, the localized control tested will offer a viable (perhaps preferable) alternative to traditional invasive eradication techniques and should allow forestry operations to continue profitably in invaded systems. These initial findings imply that a forest heavily colonized by one or more troublesome woody invaders can still be managed for timber, and quality regeneration attained, provided some constrained measure of control is implemented. The most cost effective solution to managing an invaded forest may require holistic treatment at many management stages, but it bodes well that the control method studied here, implemented during the sapling stage, promises not only localized suppression of buckthorn but a robust response from treated pines.

CHAPTER II: Site age and composition predict presence and abundance of invasive glossy buckthorn (*Frangula alnus* P. Mill) in a post-agricultural forest stand chronosequence

Introduction

Invasive plant species, or those that colonize and succeed in novel environments, may alter forest health and dynamics (Mack et al. 2000, Webster et al. 2006). Invasive species can displace or suppress native species (Stinson et al. 2006, Gioria and Osborne 2014), alter ecosystem processes (Charles and Dukes 2007), and modify forest structure (Collier et al. 2002). These effects in turn modify succession, the process traditionally described as the subsequent (and predictable) replacement of communities, and more generously expressed as the “changes observed in an ecological community following a perturbation” (Connell and Slatyer 1977). Conversely, invasive species populations and behavior may be modified by forest succession. Forests in varying stages of succession should be variably susceptible to invasion. Clearly an understanding of forest dynamics is critical for ecologists and managers; so too is understanding how invasive species respond to and impact succession.

Though the specifics and mechanics of succession are hotly debated and, as such, many different models of succession exist (Connell and Slatyer 1977, Shugart and West 1980), common to nearly all models is that competition between component species (native or exotic) drives at least in part the changes in community composition over time (Tilman 1988). When physical space is made available following a disturbance, initially high resource levels result in low competition among the (potentially many) pioneers that colonize that space, but competition intensifies as individual plants and populations grow and resources decline; the poorer competitors are thus displaced (Tilman 1988). The decline with successional time of resources such as light (Howard and Lee 2003), and soil nutrient levels (Bormann et al. 1974) is well-documented. Community composition shifts as competing plants gain “transient dominance” of a site (Tilman 1988) until resource fluctuations favor different species. No one species is competitive at all resource levels due to physiological trade-offs between growth rate, seed production and requirement of resources (in forests, this resource is generally light). Species are differentiated by these trade-offs; in general, plants with a high resource requirement ("r*") grow and breed quickly while those tolerant of low resource levels grow slowly (Tilman 1985). Thus the most obvious shifts within forest communities is the trend, with time, toward trees and shrubs which tolerate deep shade (Martin et al. 2009); those requiring high light are excluded earlier than more efficient competitors which can withstand deeper shade. That most successful invasive species thrive in early successional stages and under associated high light conditions (Crawley 1987, Rejmanek 1989, Meiners et al. 2002, Martin et al. 2009) points to the difficulty of managing certain species or controlling invasions following anthropogenic disturbance (such as logging) (Lee and Thompson 2012) but hints at a possible management strategy for invasives with relatively high r* for light (Cunard and Lee 2009). Highly shade-tolerant invasive species are less numerous and less well-studied (Webb et al. 2000, Martin and Marks 2006).

Researchers keen to understand various mechanisms of forest dynamics are challenged by the time required to observe succession in action; in most systems, the time required for an abandoned field to proceed to climax forest is so long as to be impractical. As Tilman (1988) drolly notes, plants frequently live longer than scientists. Short-term studies of forest dynamics, while valuable in shedding light on transient dynamics, fail by default to provide conclusive long-term takeaways. A common workaround to this conundrum is to substitute space for time (Pickett 1989) by identifying forest patches in various stages of succession. This method, or "chronosequence" approach, relies on the critical assumption that sites vary in age only. Vast areas of agricultural land in the United States have been abandoned at various times (for example during wartime), creating many opportunities for chronosequence-style studies; old-field sites have thus been popular choices for successional experiments [e.g. Inouye (1987), Meiners (2002)]. But because of the difficulty in ensuring sites are similar in physiographic characteristics, land use history, propagule presence, and other variables, the chronosequence approach has been derided by some (Johnson and Miyanishi 2008). However, it remains the most practical tool from which to draw inference about forest succession because of the time scale at which forest succession unfolds.

Not all communities are created equal in terms of susceptibility to invasion (“invasibility”) (Crawley 1987, Rejmanek 1989) and of course the characteristics of the invading species themselves play a role (Rejmanek and Richardson 1996). Important factors influencing a forest’s invasibility include the availability of propagules from exotic species present in the landscape, the level of plant cover, and frequency of disturbance. Mesic sites are more prone to invasion than xeric or hydric sites (Rejmanek 1989). Forests in later stages of succession are generally less susceptible; probability of successful germination of seeds, native or exotic, is extremely low in these more mature communities (Rejmanek 1989). Resistance to invasion is generally seen to increase with forest age, with some exceptions, but how an invasion early on following abandonment might influence succession is not well known (Martin and Marks 2006, Martin et al. 2009).

In the northeastern US and southeastern Canada, glossy buckthorn (*Frangula alnus*) has, in a relatively short period, invaded a variety of forest community types since its introduction to the region in the late 1800s (Catling and Porebski 1994). In New England, early and mid-successional forests of old-field eastern white pine (*Pinus strobus*) are frequently colonized (Frappier et al. 2003, Fagan and Peart 2004, Lee and Thompson 2012, Kozikowski 2016). Buckthorn produces copious seed, which survives for three or more years in the seed bank, and sprouts vigorously when damaged (Godwin 1943). These traits allow buckthorn to respond quickly following disturbance, but may hint at a trade-off in which buckthorn’s competitive ability may decrease over successional time, as at least one study shows an increase in buckthorn mortality as shade tolerant trees become abundant and light diminishes (Cunard and Lee 2009).

Presumably, there is some relationship between buckthorn's abundance in a forest and that forest's successional stage; abundance, as limited by competitive ability, should vary with different resource levels. Yet, an examination of buckthorn's response across many successional stages has not been conducted, nor has a study of which variables predict buckthorn presence or abundance in old-field sites been published (to the author's knowledge).

As forests in buckthorn's invaded range occupy a variety of successional stages, buckthorn poses a very real problem to landowners and managers; understanding whether the invasion is growing or declining, and how it relates to forest type, is the first step in prescribing control solutions. More effective management of land invaded by buckthorn requires that these effects and relationships be made apparent. Control strategies could conceivably be informed by a better understanding of buckthorn's successional dynamics and the invasibility characteristics of forests.

Howard (1999, see Howard and Lee 2002, 2003) explored how successional factors structured plant communities in southern New Hampshire in a 22 site old-field chronosequence sampled in 1998. Howard recorded abundance data for all vascular plant species present at these sites, including glossy buckthorn. Although these data could have been used to answer questions about buckthorn presence and abundance at these sites over successional time (research question 2, below), resampling these sites in 2015 allowed further assessment of the invasion status by comparing the same sites at two different points in time.

Research questions and hypotheses

1. Did buckthorn presence and abundance differ in 1998 and 2015 in Howard's chronosequence sites? Buckthorn might not have yet fully invaded by 1998, in which case buckthorn presence and abundance may have increased by 2015. If, however, competition from the local woody flora increased as sites aged, and if buckthorn declines

with competition as the literature suggests, one might expect a decrease in buckthorn in older sites. Assuming that its peak “transient dominance” had not yet been reached in younger sites, an increase may be expected in some stands due to continued recruitment.

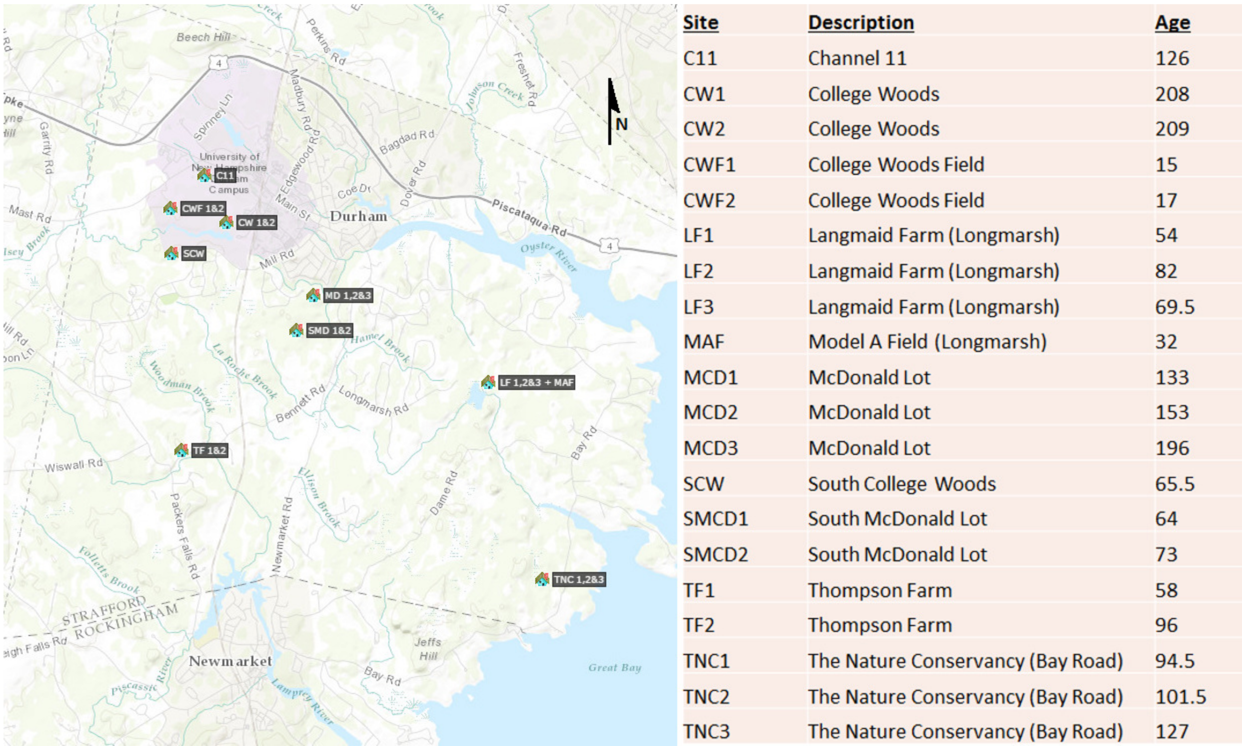
2. What, if any, succession-related factors predict the (a) presence and (b) abundance of buckthorn at these sites? I hypothesized that buckthorn presence and abundance would decline with site age (years since agricultural abandonment) or degree of shade tolerance of the vegetation, or both, as the literature suggests that buckthorn can be competitively displaced as resource levels drop.

Methods

Site selection

Howard [1999, 2002 (with TD Lee), 2003 (with TD Lee)] identified 22 sites in Durham, NH along an old-field abandonment chronosequence, keeping constant factors such as land use history, soil type, and bedrock. All sites chosen, each at least 100 m from any other, exhibited “clear agricultural history, as indicated by the presence of stone walls” (Howard 1999) and no site was logged following abandonment. Sites ranged from 14 to 209 years since agricultural abandonment, and a continuum of forest stages, from recently abandoned fields to climax forest, was represented. Vegetation at these sites ranged accordingly from highly shade intolerant (e.g. gray birch, *Betula populifolia*) to mid-tolerant (e.g. red oak, *Quercus rubra*) to very tolerant species (e.g. eastern hemlock, *Tsuga canadensis*) In 1998, each site was sampled with four subplots (details on size follow) each located a random distance along one of the four cardinal compass directions from plot center, and each with its corner nearest the center marked with rebar (Figure 2.2a).

Of the original 22 sites, 20 were resampled in the summer of 2015 and these ranged in age from 31-226 years (Figure 2.1). A private landowner would not grant permission to resample two sites, and one subplot at site TF1 (Figure 2.1) could not be resampled due to an incursion from a neighboring landowner which compromised subplot vegetation.



Site	Description	Age
C11	Channel 11	126
CW1	College Woods	208
CW2	College Woods	209
CWF1	College Woods Field	15
CWF2	College Woods Field	17
LF1	Langmaid Farm (Longmarsh)	54
LF2	Langmaid Farm (Longmarsh)	82
LF3	Langmaid Farm (Longmarsh)	69.5
MAF	Model A Field (Longmarsh)	32
MCD1	McDonald Lot	133
MCD2	McDonald Lot	153
MCD3	McDonald Lot	196
SCW	South College Woods	65.5
SMCD1	South McDonald Lot	64
SMCD2	South McDonald Lot	73
TF1	Thompson Farm	58
TF2	Thompson Farm	96
TNC1	The Nature Conservancy (Bay Road)	94.5
TNC2	The Nature Conservancy (Bay Road)	101.5
TNC3	The Nature Conservancy (Bay Road)	127

Figure 2.1. *Map of Durham, NH with 20 sample sites identified.*

Data collection, organization, and pre-analysis

In the summer of 2015, I collected data at 20 of Howard's (1999) original 22 sites. Sampling methodology was identical in 1998 and 2015 and was conducted at three scales: **tree**, **shrub**, and **herb** (Figure 2.2). Only the tree and shrub strata were used for this study after it was determined that the herb stratum did not influence results. In each plot, the **tree stratum,** comprising all woody stems > 1.3 cm in diameter at breast height (DBH, 1.3 m from the ground), was sampled in four 10 x 10 m quadrats (100 m^2 in each subplot; total 400 m^2 per site) (Howard 1999). All trees were identified to species and measured with a metric diameter tape. Basal area at 1.3 m for each tree was calculated and then summed by species. The **shrub stratum** included all woody or semi-woody specimens > 40 cm tall but too small to fit into the trees category, and was sampled with three 4 x 4 m (16 m^2) quadrats (total 48 m^2 per subplot and 192 m^2 per site) nested within the tree stratum. Number of stems per species was recorded in each quadrat. Both true shrubs and tree saplings were included (Howard 1999). Shrub counts were later expanded to the same scale as the tree stratum (by dividing tallies by 0.48). It was assumed, *sensu* Howard (1999), that each shrub counted had a DBH of 0.5 cm; basal areas were calculated accordingly and then summed by species.

Howard (1999) used tree ring counts to estimate the age of each site in two ways. First, the largest tree at each site was cored and its age determined by counting its annual rings; it was assumed that the largest tree was the oldest specimen present, and that the age of this tree would reflect the time elapsed since site abandonment. An admitted limitation of this assumption is the possible presence of pasture trees prior to abandonment, resulting in an inflated site age. The second method addressed this shortcoming by coring several older trees of similar size and identifying a period of accelerated growth, assuming that this signaled abandonment; the age of the plot was thus calculated. Howard preferred this second method, which he termed “abandonment index,” and for the purposes of this study this figure was used as the best estimate of site age except when unavailable. [At three older sites (C11, CW1 and MCD3), no release signal was detected in tree ring analysis, so for these sites the oldest tree was used as the best estimate of site age.] See Howard (1999) for additional detail on aging methodology.

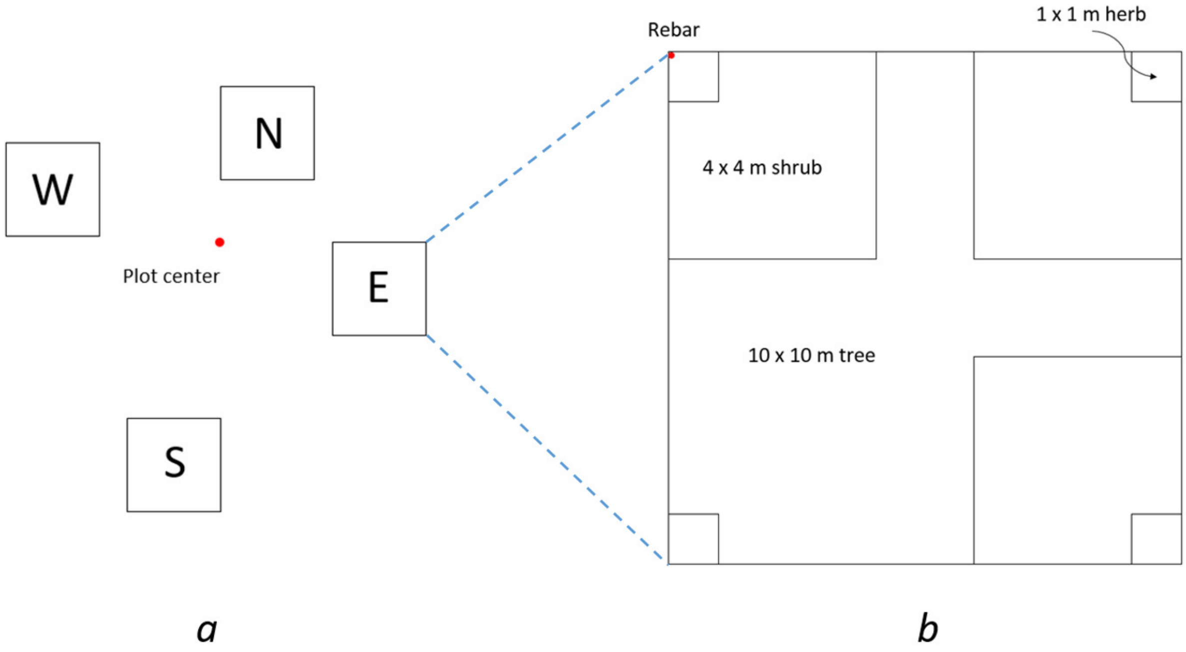


Figure 2.2. *a) Stylistic diagram of plot layout with N, S, E and W subplots; b) detail of one subplot with each stratum [tree, shrub, herb (not used here)] indicated.*

As one of my goals was to relate buckthorn abundance to abundance of shade tolerant and intolerant trees at each site, some index of shade tolerance was required. For this study, tolerance values from Niinemets and Valladares (2006), ranging from 0 (highly intolerant) to 5 (highly tolerant), were used for most species. For species not included in this index (31 of the 79 woody species in this study), "climax adaptation number" (CAN) values from Howard (1979) were converted to the 5-point scale (Appendix A) for compatibility with the Niinemets and Valladares values. Based on these tolerance values, I assigned each species to one of three tolerance classes: intolerant (0-1.66), mid-tolerant (1.67 to 3.33) and tolerant (3.34 to 5) for use in some analyses.

Additionally, I used tolerance values (0-5) to compute a tolerance index for each site. Each species' basal area at the site was multiplied by its tolerance value and these products summed and divided by the total basal area at the site Tolerance index is therefore the average tolerance of species present weighted by their basal areas. Shade tolerance of the woody vegetation at a site increases with the site's tolerance index.

Statistical analysis

Analyses were designed to address three objectives: 1) to determine if and how the local buckthorn population changed between 1998 and 2015, 2) to determine which of the measured site age and shade tolerance variables best predicted buckthorn presence at a site, and 3) to determine which of the measured site age and shade tolerance variables best predicted buckthorn abundance at a site. An information theoretic approach was used for objectives 2 and 3 (Burnham and Anderson 2002). All data analyses were performed in JMP Pro 12 (SAS, Cary, NC USA).

Change in Buckthorn Abundance from 1998 to 2015

At sites which changed in buckthorn abundance between 1998 and 2015, I calculated the difference in buckthorn stem density, which I then log-transformed (ln of absolute value; in case of decrease, negative re-applied after calculation). Using linear regression, I then determined whether these increases or decreases were attributable to either site age, initial (1998) buckthorn density, or tolerance index. Welch's *t*-tests were used to understand how the *increase* group and *decrease* group differed.

Buckthorn Presence

The variables predicting presence of buckthorn at each site in 1998, and again in 2015, were tested using nominal logistic regression. Buckthorn presence was regressed against a suite of parameters (Table 2.1) singly and in combination.

Buckthorn Abundance

All sites: Buckthorn abundance (stem counts) was log-transformed (ln+1) to meet the assumption of normality and regressed against a suite of parameters (Table 2.1) singly and in combination using multiple linear regression (see below). Note: basal area data used in models was scaled to cm^2 400 m^{-2}, thus parameter estimates and standard errors apply at this scale only.

Sites with less than 10 m^2 of hemlock BA per hectare: To minimize the effects of zero-inflation during multiple linear regression, I excluded many sites with no buckthorn present. Since age was the most consistent predictor of buckthorn presence as revealed through nominal logistic regression (see Results), I considered simply excluding older sites. However, one very old site (MCD3) did indeed have buckthorn, and I did not want to leave this out of analysis due to the already-low number of sites with buckthorn present. Another variable revealed through nominal logistic regression to predict buckthorn presence was hemlock basal area. No sites with greater than 3.5 m^2 ha^{-1} of hemlock also contained buckthorn; sites with extremely high hemlock basal area (10 m^2 ha^{-1}; six sites) were then excluded. The same suite of multiple linear regression analyses performed on all sites was again performed on the subset of sites without high hemlock influence (1998: n = 16; 2015: n = 15).

***Table 2.1.** All model parameters used in nominal logistic regression and multiple linear regression analyses. Each parameter was tested singly, and combinations were tested by grouping one or more "a" parameters with* either *"b" or "c" parameters; in all models with more than one parameter, site age was included. All model iterations tested are listed in Appendix B.*

Model parameter	Description
site age^a	Years elapsed following agricultural abandonment, based on "abandonment index" or if unavailable, age of oldest tree on site
intolerant BA^b	Combined basal area of all species in the "intolerant" group [those ranging from 0-1.66 on Niinemets/Valladares (2006) tolerance scale or if unavailable, CAN value from Howard (1979)] in cm^2 400 m^{-2}
mid-tolerant BA^b	Combined basal area of all species in the "mid-tolerant" group [those ranging from 1.67-3.33 on Niinemets/Valladares (2006) tolerance scale or if unavailable, CAN value from Howard (1979)] in cm^2 400 m^{-2}
tolerant BA^b	Combined basal area of all species in the "tolerant" group [those ranging from 3.34-5 on Niinemets/Valladares (2006) tolerance scale or if unavailable, CAN value from Howard (1979)] in cm^2 400 m^{-2}
hemlock BA^c	Amount of hemlock basal area in cm^2 400 m^{-2}
white pine BA^c	Amount of white pine basal area in cm^2 400 m^{-2}
red oak BA^c	Amount of red oak basal area in cm^2 400 m^{-2}
*site age * x*$^{a,b \text{ or } c}$	Interaction between site age and another model parameter ("*x*")

total BA^a	Total basal area (all species) in cm^2 400 m^{-2}
tolerance index^a	Value of tolerance index calculation from 0-5

Important particulars of analyses

Candidate models for regression analyses of buckthorn presence and abundance were designed to minimize the ratio of predictor variables to number of observations, though in some cases up to seven parameters were included in a model. [Burnham and Anderson (2002) leave the selection of parameters to be included in models up to the researcher; I chose variables or combinations of variables that, given the small size of my data sets (n_{1998} = 22, n_{2015} = 20), represented clear tests of my hypotheses without overly confounding results.] In addition to site age, parameters included in models were related to the abundance of a species or group of species; I've classed these as *holistic* ("total BA" and "tolerance index"), *grouped* ("intolerant BA," "mid-tolerant BA," and "tolerant BA") or *species-specific* ("white pine BA," "red oak BA," and "hemlock BA". These represent the three most abundant species across the entire data set). Except when testing the effects of a particular parameter in isolation, candidate models with more than one parameter included site age and one or more variables from the holistic, grouped, or species-specific classes. Grouped and species-specific parameters (Table 2.1; superscript "b" and "c," respectively) were never tested together to avoid redundancy.

Generalized linear regression, a zero-inflated modeling approach often appropriate for ecological data because of its ability to model within Poisson or negative binomial distributions instead of the normal distribution, was not used for the "buckthorn abundance" analysis since all Studentized residuals of top-performing multiple linear regression models conformed to the normal distribution (Shapiro-Wilk goodness-of-fit test on normal distribution: for all models $p > 0.05$, where small p-values reject hypothesis that data is from the normal distribution). In the "buckthorn presence" and "buckthorn abundance" analyses, the corrected Akaike Information

Criterion (AICc) was used to evaluate model performance. All candidate models considered have Δ AICc values ≤ 2 from the “best” model. Burnham and Anderson (2002) recommend retaining models within 2 to 4 points of the lowest AICc value; here the lower threshold of 2 points was chosen to restrict the large number of competing models returned. Multicollinearity of included parameters was assessed by examining variance inflation factors (VIFs) within the model results; VIFs ≥ 2.5, though very rare, indicated multicollinearity between parameters higher than what is generally considered dismissible, and model results rejected.

Results

Change in Buckthorn Abundance from 1998 to 2015

Buckthorn presence varied little between 1998 and 2015. Buckthorn was present in 11 of 22 sites in 1998, nine of 20 sites in 2015, and absent from 11 sites in both years. (The two sites sampled in 1998 but inaccessible in 2015, LMF1 and LMF2, had buckthorn present. It is probable that they still did in 2015.) One site not invaded in 1998 had gained buckthorn by 2015, and one site with buckthorn present in 1998 was free of buckthorn in 2015. In five sites, buckthorn abundance decreased from 1998 to 2015 (average decrease = -63.2 stems 400 m^{-2}, $\sigma = 85.3$), while in four sites buckthorn abundance increased over the same period (average increase = 201.5 stems 400 m^{-2}, $\sigma = 225.4$; Welch’s *t*-tests, Table 2.2). (One site with buckthorn present in both years stayed the same.)

Linear regression revealed that neither *site age* ($p = 0.995$, adj. $r^2 = -0.143$), *initial (1998) buckthorn density* ($p = 0.273$, adj. $r^2 = 0.049$), nor *tolerance index* ($p = 0.302$, adj. $r^2 = 0.029$) were significant predictors of the magnitude or direction of the log-transformed difference in buckthorn abundance at a given site.

Buckthorn presence/absence

Logistic regression was used to determine which factors best predict buckthorn presence in sites sampled in 1998. Seven highly-competitive (Δ AICc ≤ 2) models were retained (Table 2.3) in this analysis. *Site age* was included in all seven models, and was consistently negatively related to buckthorn presence (Table 2.3). The most competitive model (model 1, Δ AICc = 0) included *site age* and *hemlock basal area (BA)*, which was also negatively related to buckthorn presence. The most parsimonious model (3b) included *site age* only. The only variable in any candidate model that was positively related to buckthorn presence was *intolerant species' BA* (model 7). Because of the strong relationship between *tolerance index* and *hemlock BA* (r^2_{adj} = 0.64, Figure 2.3), models 1 and 3a were highly similar and can be considered functionally equivalent.

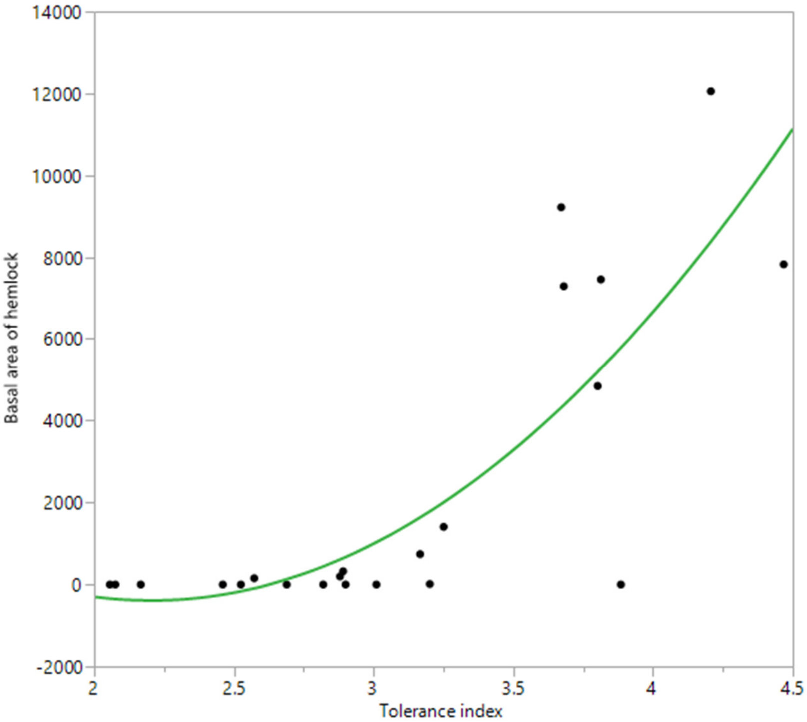


Figure 2.3. *Hemlock basal area by tolerance index at 22 sites in Durham, NH in 1998. Adjusted r^2 = 0.64.*

In the logistic regression run on 2015 presence/absence data, three models (Δ AICc ≤ 2, Table 2.4) were retained. The two most competitive models (models 1a and 1b, in which AICc scores were the same) included *site age*, *hemlock BA* and *red oak BA*. Model 1a (Δ AICc = 0) also included *white pine BA*, which had a positive effect on buckthorn presence, as an additional regressor, while 1b (Δ AICc = 0) included the *interaction between site age and red oak BA* which also had a positive effect. However, both models the models perfectly predicted the response, resulting in unstable parameter estimates, so inference may be limited. More preferred is model 3 (Δ AICc = 0.65) which yielded stable estimates and is more parsimonious. Model 3 included *site age* (which had a negative effect on buckthorn), *hemlock BA* (negative effect) and *red oak BA* (positive effect).

Buckthorn abundance

Buckthorn abundance varied greatly among sites in both 1998 and 2015. In 1998, in the 11 sites where buckthorn was present, buckthorn stem density ranged from 52 to over 20,000 stems per hectare. Similarly, in 2015, density ranged from 52 to nearly 15,000 stems per hectare in the nine sites which included buckthorn.

Multiple linear regression analysis designed to explain buckthorn abundance at the 22 sites sampled in 1998 retained 11 models (Δ AICc ≤ 2, Table 2.5); all of these included *site age*, which was negatively related to buckthorn abundance in all cases. The most competitive model (model 1, Δ AICc = 0, r^2_{adj} = 0.49) included *site age* and *tolerance index* which, like age, had a negative effect on buckthorn abundance. The next most competitive model (model 2; Δ AICc = 0.10, r^2_{adj} = 0.54) included *site age*, *tolerant species' BA*, and the *interaction between age and tolerant BA*. In model 2, *tolerant BA* and the *interaction between site age and tolerant BA* were also negatively related to buckthorn abundance but parameter estimates were very slight (-0.0002 and > -0.0001, respectively). Again, the most parsimonious model (model 7) included

Table 2.2. *Results of two-sample Welch's t-tests (assuming unequal variances) comparing sites in Durham, NH which increased in buckthorn abundance (n=4) or decreased (n=5) between 1998 and 2015.*

Test variable	$\mu_{increase}$	$\mu_{decrease}$	t Ratio	DF	p>|t|	p>t	p<t
Mean site age	93.50	67.60	0.5986	3.403	0.587	0.294	0.707
Mean 1998 buckthorn density (ln+1)	2.58	3.92	-0.9005	5.617	0.405	0.798	0.202
Mean tolerance index	2.74	2.97	-1.0015	5.560	0.358	0.821	0.179

Table 2.3. *Results of nominal logistic regression on presence/absence of glossy buckthorn at 22 sites in Durham, New Hampshire sampled in 1998. ΔAICc = corrected Akaike Information Criterion differences. Bold p-values indicate significance at α = 0.05. Positive or negative (+ / -) signs on parameter estimates indicate parameter's direction of influence on buckthorn presence. Asterisk (*) indicates an interaction; dagger (†) indicates unstable parameter estimates as modeled.*

Model parameters	Rank	AICc	Δ AICc	Parameter estimate	Standard error	Log likelihood	Akaike weight	Evidence ratio
site age hemlock basal area	1	15.21	0	-0.0748 -0.0007	0.047 0.002	1	0.21	2.36
site age† intolerant spp. basal area† site age * intolerant spp. basal area†	2	15.69	0.48	-159.3245 -3.5466 -0.2720	557,734.800 12,423.195 952.301	0.79	0.16	1.86
site age tolerance index	3	15.72	0.51	-0.0822 -2.8280	0.044 2.074	0.77	0.16	1.83
site age	4	15.72	0.51	-0.0940	0.049	0.77	0.16	1.83
site age tolerant spp. basal area	5	16.31	1.10	-0.0723 -0.0003	0.044 >0.001	0.58	0.12	1.36
site age total basal area	6	16.60	1.39	-0.0785 -0.0003	0.054 >0.001	0.50	0.10	1.18
site age intolerant spp. basal area	7	16.93	1.72	-0.0935 +0.0013	0.051 0.001	0.42	0.09	1

Table 2.4. *Results of nominal logistic regression on presence/absence of glossy buckthorn at 20 sites in Durham, New Hampshire sampled in 2015. ΔAICc = corrected Akaike Information Criterion differences. Positive or negative (+ / -) signs on parameter estimates indicate parameter’s direction of influence on buckthorn presence. Asterisk (*) indicates an interaction; dagger (†) indicates unstable parameter estimates as modeled.*

Model parameters	Rank	AICc	Δ AICc	Parameter estimate	Standard error	Log likelihood	Akaike weight	Evidence ratio
site age†	1 (tie)	14.29	0	-2.5092	3345.573	1	0.37	1.38
white pine basal area†				+0.0105	15.212			
hemlock basal area†				+0.0864	113.699			
red oak basal area†				-0.1000	135.708			
site age†	1 (tie)	14.29	0	-18.5292	97,257.023	1	0.37	1.38
hemlock basal area†				-0.6281	3,286.0191			
red oak basal area†				+0.5290	2,771.188			
site age * red oak basal area†				+0.0006	3.804			
site age	3	14.94	0.65	-0.6035	1.004	0.72	0.27	1
hemlock basal area				-0.0232	0.036			
red oak basal area				+0.0193	0.031			

site age only. In all 11 models, the only variables positively related to buckthorn abundance were *intolerant BA* and some interaction terms.

In the regression analysis of 2015 abundance data, four models were retained (Δ AICc ≤ 2, Table 2.6), all of which—as with 1998 data—included *site age*. The relationship between *site age* and buckthorn abundance was negative in all models. The most competitive model (model 1, AICc = 0, $r^2_{adj} = 0.67$), also the most parsimonious, included *tolerance index* (which had a negative relationship with buckthorn abundance) and the *interaction between site age and tolerance index* (which had a very slight positive relationship). The next most competitive model (model 2, AICc = 0.04, $r^2_{adj} = 0.72$) included *intolerant BA* (positive effect), *tolerant BA* (negative effect), and the *interaction between site age and tolerant BA* which, as in model 2 in 1998 (Table 2.5), exerted a (very slight) negative effect on buckthorn abundance. Multicollinearity was high in model 3 (VIFs of age = 3.11, intolerant BA = 7.67, site age * intolerant BA = 5.23) so the model was disregarded.

Buckthorn abundance at sites with < 10 m^2 ha^{-1} of hemlock BA

In 1998, buckthorn was present at 11 of 16 sites with less than $10m^2$ of hemlock BA per hectare. These sites range in age from 14 to 196 years following abandonment. In 2015, nine of 14 sites below this hemlock limit contained buckthorn, ranging from 31 to 213 years since abandonment.

In the analysis of the 1998 data, three multiple linear regression models (Δ AICc ≤ 2, Table 2.7) were retained which best explained buckthorn abundance at these sites. Three parameters (*site age, intolerant BA*, and *tolerance index*) were included in these, with *site age* alone (model 1, $r^2_{adj} = 0.40$; Figure 2.4) having the lowest AICc value (Δ AICc = 0). The next most competitive model (model 2, Δ AICc = 0.05, $r^2_{adj} = 0.48$) included *intolerant BA* with *site age*, while the third most competitive model (model 3, Δ AICc = 1.82, $r^2_{adj} = 0.42$) included *site* *age* and *tolerance index*. In all three candidate models, *site age* was negatively related to buckthorn abundance. In model 2, *intolerant BA* was positively related to buckthorn abundance. In model 3, *tolerance index* had a negative relationship.

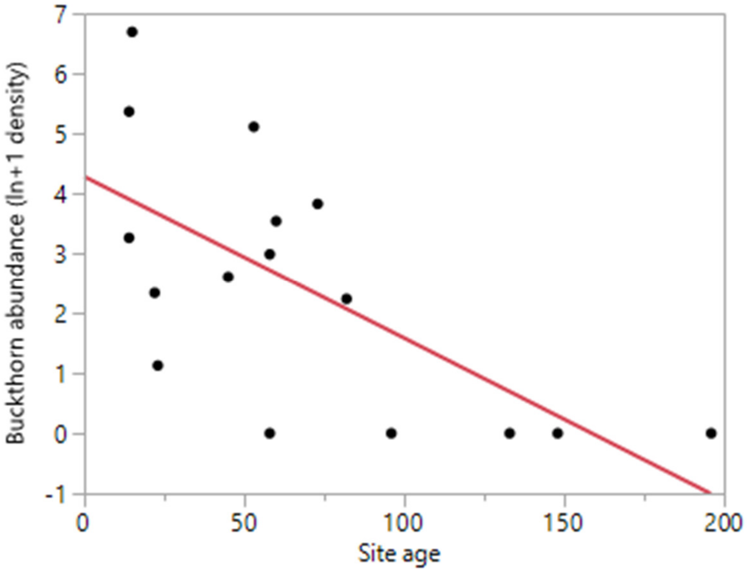


Figure 2.4. *Buckthorn abundance by site age at 16 sites with less than 10 m^2 ha^{-1} of hemlock basal area in Durham, NH in 1998. Adjusted r^2 = 0.40.*

For 2015 data, only two models resulted in Δ AICc values less than 2 (Table 2.8), each with only one parameter. Model 1 (Δ AICc = 0, r^2_{adj} = 0.59; Figure 2.5) included *intolerant BA*, while model 2 (Δ AICc = 0.97, r^2_{adj} = 0.56) included *tolerance index*. As with 1998 data, as *intolerant BA* increased, buckthorn density also increased (model 1). As *tolerance index* increased, buckthorn abundance decreased (model 2).

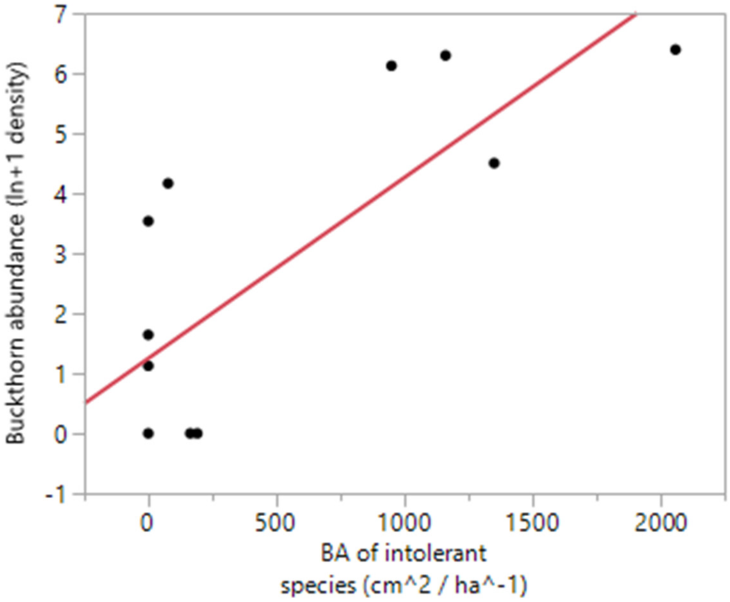


Figure 2.5. *Buckthorn abundance by BA of intolerant species at 14 sites with less than 10 m^2 ha^{-1} of hemlock basal area in Durham, NH in 2015. Adjusted r^2 = 0.59.*

Table 2.5. *Results of multiple linear regression on log-transformed (ln+1) abundance of glossy buckthorn density at 22 sites in Durham, New Hampshire sampled in 1998. ΔAICc = corrected Akaike Information Criterion differences. Positive or negative (+ / -) signs on parameter estimates indicate parameter's direction of influence on buckthorn abundance. Asterisk (*) indicates an interaction.*

Model parameters	Rank	AICc	Δ AICc	Adj. r^2	Parameter estimate	Standard error	Log likelihood	Akaike weight	Evidence ratio
site age tolerance index	1	87.92	0	0.49	-0.0152 -1.2101	0.007 0.596	1	0.14	2.13
site age tolerant spp. basal area site age * tolerant spp. basal area	2	88.02	0.10	0.54	-0.0182 -0.0002 >-0.0001	0.006 <0.001 <0.001	0.95	0.13	2.02
site age intolerant spp. basal area site age * intolerant spp. basal area	3	88.22	0.30	0.53	-0.0269 +0.0004 >-0.0001	0.008 0.001 <0.001	0.86	0.12	1.83
site age intolerant spp. basal area tolerant spp. basal area site age * tolerant spp. basal area	4	88.71	0.79	0.58	-0.0144 +0.0007 -0.0002 <+0.0001	0.006 <0.001 <0.001 <0.001	0.67	0.09	1.43
site age intolerant spp. basal area	5	88.75	0.83	0.47	-0.0178 +0.0009	0.006 0.001	0.66	0.09	1.40
site age tolerance index site age * tolerance index	6	88.76	0.84	0.52	-0.0182 -1.0826 +0.0109	0.007 0.584 0.007	0.66	0.09	1.40
site age	7	89.22	1.30	0.41	-0.0231	0.006	0.52	0.07	1.11
site age tolerant spp. basal area	8	89.30	1.38	0.46	-0.0173 -0.0002	0.007 <0.001	0.50	0.07	1.07
site age hemlock basal area site age * hemlock basal area	9	89.35	1.43	0.51	-0.0204 -0.0002 <+0.0001	0.006 <0.001 <0.001	0.49	0.07	1.04
site age intolerant spp. basal area tolerant spp. basal area	10	89.37	1.45	0.51	-0.0130 +0.0009 -0.0001	0.007 0.001 <0.001	0.48	0.07	1.03
site age hemlock basal area	11	89.43	1.51	0.46	-0.0187 -0.0002	0.006 <0.001	0.47	0.06	1

Table 2.6. *Results of multiple linear regression on log-transformed (ln+1) abundance of glossy buckthorn density at 20 sites in Durham, New Hampshire sampled in 2015. ΔAICc = corrected Akaike Information Criterion differences. Positive or negative (+ / -) signs on parameter estimates indicate parameter's direction of influence on buckthorn abundance. Asterisk (*) indicates an interaction.*

Model parameters	Rank	AICc	Δ AICc	Adj. r^2	Parameter estimate	Standard error	Log likelihood	Akaike weight	Evidence ratio
site age	1	79.81	0	0.67	-0.0158	0.007	1	0.35	2.59
tolerance index					-2.3123	0.746			
site age * tolerance index					+0.0270	0.008			
site age	2	79.85	0.04	0.72	-0.0109	0.007	0.98	0.34	2.53
intolerant spp. basal area					+0.0017	0.001			
tolerant spp. basal area					-0.0002	<0.001			
site age * tolerant spp. basal area					<+0.0001	<0.001			
site age	3	81.14	1.33	0.65	-0.0265	0.010	0.51	0.18	1.33
intolerant spp. basal area					-0.0005	0.002			
site age * intolerant spp. basal area					>-0.0001	<0.001			
site age	4	81.71	1.90	0.69	-0.0191	0.010	0.39	0.13	1
intolerant spp. basal area					-0.0002	0.002			
site age * intolerant spp. basal area					>-0.0001	<0.001			
tolerant spp. basal area					-0.0001	0.000			

Table 2.7. *Results of multiple linear regression on log-transformed (ln+1) abundance of glossy buckthorn density at 16 sites with less than 10 m^2 ha^{-1} of hemlock BA in Durham, New Hampshire sampled in 1998. ΔAICc = corrected Akaike Information Criterion differences. Positive or negative (+ / -) signs on parameter estimates indicate parameter's direction of influence on buckthorn abundance.*

Model parameters	Rank	AICc	Δ AICc	Adj. r^2	Parameter estimate	Standard error	Log likelihood	Akaike weight	Evidence ratio
site age	1	67.67	0	0.40	-0.0270	0.008	1	0.42	0.40
site age intolerant spp. basal area	2	67.72	0.05	0.48	-0.0206 +0.0010	0.008 <0.001	0.98	0.41	0.41
site age tolerance index	3	69.49	1.82	0.42	-0.0229 -1.1831	0.009 0.948	0.40	0.17	1

Table 2.8. *Results of multiple linear regression on log-transformed (ln+1) abundance of glossy buckthorn density at 14 sites with less than 10 m^2 ha^{-1} of hemlock BA in Durham, New Hampshire sampled in 2015. ΔAICc = corrected Akaike Information Criterion differences. Positive or negative (+ / -) signs on parameter estimates indicate parameter's direction of influence on buckthorn abundance.*

Model parameters	Rank	AICc	Δ AICc	Adj. r^2	Parameter estimate	Standard error	Log likelihood	Akaike weight	Evidence ratio
intolerant spp. basal area	1	59.73	0	0.59	+0.0030	<0.001	1	0.62	0.62
tolerance index	2	60.70	0.97	0.56	-6.8172	1.618	0.62	0.38	1

Discussion

Invasion status

Contrary to my hypotheses, older sites did not predictably or consistently lose more buckthorn than did younger sites, nor did young sites gain more buckthorn than older sites. The change in buckthorn abundance at each site from 1998 to 2015 was minimal, and the fact that that change—positive or negative—was unrelated to site age, initial buckthorn density, or tolerance index, suggests a) these changes were random, and b) the invasion of these sites has stabilized at the landscape level. This is not sufficient evidence to state that the buckthorn invasion in the Durham area or seacoast NH region at large is unchanging. Rather, this study suggests that in unmanaged old-field forests in the region, perhaps an equilibrium has been reached, or at least that buckthorn levels are changing more slowly than would be detectible over a period of 17 years. But because many more forests in the region are either managed, increasingly fragmented or converted from forest to another land use (conditions that favor buckthorn recruitment), an intensification of the buckthorn invasion at the landscape scale is plausible.

The ability of buckthorn to persist in a community is not known for our sites. Once occupied, how long buckthorn is likely or able to persist—that is, how long its transient dominance lasts relative to successional time—has not been studied. Persistence may depend on site conditions at the time of colonization or how much buckthorn establishes (e.g. if many stems establish, persistence may be more likely than if only a few do). Studies have demonstrated that buckthorn can persist, at least for a time, beneath a white pine canopy (Lee and Thompson 2012) but is unlikely to survive beneath shade tolerant trees (Cunard and Lee 2009). A better understanding of how buckthorn persists within communities, and what effect initial population density has, is needed to predict how forest composition will be affected over longer time scales; answering whether the invasion has yet peaked requires this information.

Presence of buckthorn

The strongest and most consistent predictor of buckthorn presence at the 22 sampled sites in both years was the amount of time elapsed following agricultural abandonment (site age), consistent with my hypotheses. Though most candidate models also included at least one other parameter, site age alone offers a compelling ecological story and is compatible with succession literature. Put simply, older sites tended to resist buckthorn while younger sites were less likely to do so.

Site age and degree of occupation are related, so it seems logical that as total basal area increases (that is, as the site becomes more fully occupied by trees and resources thus more fully exploited), the likelihood of buckthorn being present declines. Young (newly abandoned) sites are easily colonized by buckthorn due to nearly unlimited light, space, and soil nutrients and the low competition for those resources. As sites age, they become less invasible (Crawley 1987, Rejmanek 1989) likely because older stands have more biomass and roots, fewer soil nutrients, and less light at the forest floor. Regardless of species composition, it seems that older sites, which should be structured by competition and where resources are therefore constrained, should pose more of a hurdle to invasion than younger ones; this is strongly supported by my data.

Certain shade-tolerance characteristic(s) of the site vegetation were related to buckthorn presence. For example, as basal area of hemlock increased, buckthorn was less likely to be found at that site, consistent with Cunard and Lee (2009). Tolerant tree species like hemlock cast darker shade than do intolerant species (Pacala et al. 1996), resulting in decreased light levels at the forest floor in which buckthorn cannot establish. The most competitive logistic models included amount of hemlock basal area, tolerance index, and tolerant BA, all of which were associated with buckthorn absence; BA of intolerant species and of red oak (a mid-tolerant tree, appearing in 2015 models only) were associated with buckthorn presence. These model results were consistent with my hypotheses. (Age and tolerance are related; old sites tend toward more shade tolerant vegetation than young sites, where intolerant trees are favored.) Whether the tendency toward more tolerant vegetation with age (and therefore less light at the forest floor) is an important component of age's effect on buckthorn presence is difficult to extract from my analyses; it is probable that age alone is the strongest determinant.

Buckthorn lifespan itself may partly be responsible for its absence from old sites, and the processes of succession may exclude it after an initial cohort dies off. If buckthorn established early on following farm abandonment, as is likely, then pioneer individuals may have persisted until they reached old age and died. [Godwin (1943) notes specimens of 32 years old; Lee (personal communication) has collected specimens 40 or more years old.] At least a partial canopy of intolerant trees would be expected at this point, and release of mid-tolerant and tolerant tree and shrub saplings following the deterioration of the buckthorn cohort (plus new buckthorn stems) would occur. At this stage, depending on canopy closure and ambient light levels, germination of buckthorn seeds (and survival of seedlings) becomes less likely, except a) beneath certain canopy species [e.g. pine: Lee and Thompson (2012)] or b) following stochastic disturbance events (e.g. gap formation) which free up resources. Any recruitment at this point should cease if tolerant vegetation can establish. Thus, though site age itself has no inherent effect on buckthorn, the ecological and chronological characteristics associated with abandoned field sites which undergo succession do indeed affect buckthorn presence/absence or abundance.

Ascribing predictive power to site age comes with an asterisk. Because buckthorn did not invade the Durham, NH area until probably the 1920s [1940s at latest (Lee and Thompson 2012)], the older sites sampled here were not invaded during their early successional beginnings. It is therefore hard to say with conviction that the relationships detected between site age and buckthorn presence are anything more than historical artifact, and point toward the often-criticized limitations of substituting space for time (Johnson and Miyanishi 2008). In fact, several sites existed buckthorn-free for more than a century before the wider invasion. Further, in the 1998 data no sites abandoned earlier than 1916 had any buckthorn (n=8), while in the 2015 data only one site abandoned earlier than 1925 had any buckthorn while nine of these did not. Whether old sites actually *repel* buckthorn due to the high amount of tolerant vegetation or full resource exploitation (or some other reason), or whether the lack of an initial buckthorn cohort precluded a continuous colonization lineage cannot be inferred from this study. As propagule pressure from a regionally blooming buckthorn population intensified, these sites were perhaps already in a state prohibitive to invasion, or were at least geographically separate enough from concentrated seed sources to thwart colonization. Though the limitations of our methodology have been made obvious, it is merely academic to propose that a proper experiment would more satisfactorily address these questions.

Buckthorn abundance

The same factors acting on whether buckthorn would be present or not in a given site were also consistent in predicting buckthorn abundance. In 1998, site age again was included in all models; it is clear that as the age of our studied sites increased, the less buckthorn was likely to be present. However, this again begs the question: are old sites resilient to invasion *or* were the conditions in which the site aged different enough from those in sites colonized by buckthorn to explain this phenomenon?

It is plausible that the relationship between high site age and low buckthorn abundance falls apart once the dominant forest trees begin to experience mortality associated with old age. When old hemlocks, for instance, start experiencing canopy damage, or when large white pines blow over, gaps are created in which buckthorn could invade. Extremely old sites in the “old growth” stage (Oliver and Larson 1996) may indeed harbor more buckthorn than somewhat younger sites. As might defy a typical successional pattern, should more long-lived trees such as hemlock fail to establish and occupy the canopy, providing that there was a seed source nearby buckthorn could feasibly colonize forests of different canopy compositions at different times, eroding the relationship between site age and buckthorn abundance. (The tolerance index value for a site whose canopy is deteriorating is not likely to change drastically since it is based on the basal area contributions of its components; a flush of new mid-tolerant stems in a gap will likely occupy less area than, say, one older tolerant tree. Smaller trees and shrubs wield less influence upon the tolerance index.) Whether buckthorn that establish in these gaps are able to competitively displace other gap colonizers is not well-studied, but it seems unlikely unless the gaps are large enough to “reset” succession to a level which provides enough light and other resources to allow buckthorn to outpace its competitors. More likely are gap-sized inclusions of buckthorn which appear and disappear as conditions permit.

In both 1998 and 2015, variables related to tolerance were included in the most competitive models. As the overall tolerance of a site increased, buckthorn was less likely to be found in abundance. Again this is consistent with literature (Cunard and Lee 2009) and theory (Pacala et al. 1996). However, partially attributing the abundance (or simply presence) of buckthorn to a site’s shade tolerance characteristics is not without potential error for (at least) two reasons. First, shade tolerance is difficult to quantify precisely, and subscribing to a particular index of tolerance [e.g. Niinemets and Valladares (2006)] not only requires faith in its accuracy, but also places results and inference within the constraints of that index. Site age, by contrast, is explicit and subject to far less methodological ambiguity. Second, much of a site’s incident radiation (light) enters from beyond its borders. The conditions just beyond a site’s southern edge may drastically influence the amount of light reaching the site floor and therefore its composition. For instance, a large hemlock or two might cast deep shade upon a site, causing lower light levels (and conditions less favorable to germination) than might simply be explained by extant vegetation. Or, a site may be located on a hillside; a southerly aspect would allow higher levels of incident radiation and may increase the likelihood of buckthorn occupation regardless of what vegetation is directly overhead. Therefore, because a site's tolerance characteristics are shaped by both the index used and *ex situ* factors, tolerance as a proxy for understanding the light conditions at a site is imperfect. A better method would be to systematically evaluate PAR at each site with light measurement equipment to understand how incident light levels, rather than vegetative tolerance, might affect presence or abundance of buckthorn, but such an approach was logistically impractical under the scope of this study.

Buckthorn abundance at sites with low hemlock component

The factors influencing buckthorn abundance on sites with less than 10 m^2 of hemlock BA per hectare differed in 1998 and 2015. Site age again best predicted buckthorn abundance on 1998 data, but in 2015 the amount of BA of intolerant species and the tolerance index were the best predictors. I strongly suspect that site age no longer factored into the best 2015 models because two sites (LMF1 and LMF2), in early-successional stage in 1998 (22 and 14 years old, respectively) and colonized by buckthorn at that time, could not be resampled in 2015 due to site access issues. It is expected that buckthorn still occupies these sites. The inclusion of these two sites would have added considerably to analysis, and site age would presumably have again been an important predictor of abundance.

Without these sites, intolerant BA alone best predicted buckthorn abundance in 2015, supporting the positive relationship revealed in the presence/absence analysis. Here, the more intolerant BA a site contains, the more buckthorn it is also likely to contain, regardless of total basal area. Conceivably, a completely overstocked site composed of white birch (*Betula papyrifera*) or bigtooth aspen (*Populus grandidentata*) or other intolerant trees would exclude buckthorn—there is only so much space within which buckthorn could grow, after all—though none of our sites appears to have reached this limit so the relationship holds, at least statistically. It can be inferred that since buckthorn abundance rises with BA of intolerants, the converse should be true that buckthorn decreases with BA of tolerant species; this was of course found in other analyses, and is bolstered by the second most-competitive model for 2015 which shows that tolerance index alone predicts buckthorn (with a negative relationship). With hemlock absent, other shade-tolerant species such as sugar maple (*Acer saccharum*) or American beech (*Fagus grandifolia*) common to southeastern NH should, in high enough abundance, suppress or exclude buckthorn. It is worth entertaining scenarios in which hemlock is indeed absent from old stands, where it is currently a common component, since hemlock woolly adelgid and another non-native insect, elongate hemlock scale (*Fiorinia externa*) may cause severe mortality.

Implications and applications

It is clear that, of the variables assessed, site age and some indicator of composition related to shade tolerance both predict a site's likelihood of permitting or supporting a buckthorn population and to what degree. Evidence from this study suggests that buckthorn is transient in its dominance of a forest community in that its life history characteristics allow it to "temporarily competitively suppress other species," (Tilman 1988). Though buckthorn might appear to form monocultures in which no other species can establish, there is no scientific evidence that suggests that buckthorn lowers overall site richness. (This is not necessarily true of other diversity measures such as evenness.) Crawley (1987) highlights the lack of evidence that invasives competitively exclude any other species from a community, and in my data, no negative relationship between buckthorn abundance and site richness was detected. (In fact, the sites in which buckthorn abundance was greatest tended to have higher than average species richness, which is suggestive of the successional state in which buckthorn is most competitive.) It must be assumed, therefore, that by overwhelming and outnumbering native plants with intense propagule pressure and rapid growth, and by reducing the density of tree seedlings (Frappier et al. 2003, Fagan and Peart 2004), buckthorn is merely slowing the successional trajectory of our forest sites and not redirecting or derailing it entirely, and that with time it will be displaced by more efficient competitors, as was hypothesized by Cunard and Lee (2009). Site age, as an indication of a forest's degree of occupation and thus its competitive environment, should therefore predict the presence and or abundance of buckthorn. An estimate of a site's invasibility should clearly include site age. However, it may well serve a manager or landowner to redefine site age as "time elapsed since last significant disturbance," since any management activity or substantial natural perturbation should invite new species—possibly buckthorn—into that community.

The results of this study reinforce for buckthorn what has been shown with other species: that time is the enemy of poor competitors. Buckthorn, by no means a *poor* competitor, is of course poorer than some. A land manager would do well to identify and encourage (through appropriate silviculture) local species which could eventually competitively exclude buckthorn, if allowed to mature and spread. Of course, foresters with a keen economic sense may object that such a strategy is an opportunity cost and that battling an invasion through more traditional means is a more appropriate tactic if control costs can be recouped, conceivably through timber and regeneration now unencumbered by buckthorn. A rebuttal to that line of thought would emphasize the difficulty and high cost of controlling buckthorn (Lee et al. 2016, unpublished). The targeted, localized treatment of buckthorn around valuable tree specimens may be warranted (see Chapter 1 of this thesis) but more broad-scale control will likely result in economic losses no matter the resulting timber gains.

Johnson and Miyanishi's (2008) critique of the chronosequence approach should be remembered in trying to distill broadly-applicable lessons or strategies from this study. To illustrate, consider that an agricultural field abandoned today is unlikely to look in 215 years like the oldest sites studied (abandoned c. 1800) look today, for a variety of reasons. A relatively enormous increase in propagule pressure from buckthorn and other now-common invasive species, many of which were not present in 1800, would likely delay or otherwise influence succession. Farm practices today are quite different from those practiced two centuries ago, and as a result, fields abandoned today are likely very different in terms of soil and vegetation characteristics, potentially shaping the forest recovery. Certain native tree species common in 1800 (e.g. American elm and chestnut) are now functionally extinguished from local forests, and additional species are severely threatened. [Ash trees (namely white and black ash, *Fraxinus americana* and *F. nigra*), common in early and mid-succession on moist enriched soils, are currently under threat from an invasive insect, the emerald ash borer (*Agrilus planipennis*). Eastern hemlock, the most shade-tolerant species in the studied forests, is experiencing mortality from the hemlock woolly adelgid (*Adelges tsugae*). Maple species could see declines from Asian longhorned beetle (*Anoplophora glabripennis*).] Additionally, climate change may encourage some plant and insect species and discourage others, or potentially foster further invasions. Global commerce continues to introduce novel species which may alter communities further. The predictive nature of the models presented therefore extend only so far as the environment remains constant. Ultimately, forests at the landscape and regional scales are subject to complex and interactive dynamic forces which defy tidy generalizations.

So, how can findings from this study be applied in the woods? Forest managers confronted with a buckthorn invasion might use careful silviculture, such as weeding or cleaning treatments, to encourage competitive native species. Harvest operations in invaded stands could be delayed until a dense understory of mid-tolerant and tolerant vegetation has established, minimizing buckthorn response, provided care is exercised during felling and extraction not to damage the understory. Single-tree selection may be employed to minimize gap size (Burnham and Lee 2010) and favor more tolerant regeneration. Any of these recommendations paired with judicious herbicide use (Reinartz 1997) might increase the chances that buckthorn abundance could be reduced, if not eliminated. Of course, no individual recommendation should substitute a clear understanding of a particular forest system, its various components, and how and where it is oriented within the greater landscape.

Those disheartened by any specific invasion should take comfort in being reminded that, with time, forests tend to exclude those pernicious species which so brashly confront us following a disturbance, natural or anthropogenic. [An exception to this may be kudzu (*Pueraria montana*), which actually climbs atop and smothers other extant vegetation (Forseth and Innis 2004). Luckily most invaders in the northeastern US do not possess this trait.] Invasive species, including glossy buckthorn, are and will remain part of the landscape, though any given stand may well proceed over successional time to a stage in which they cannot compete, barring some stochastic disaster or infestation. The best management solution, depending on the species and forest conditions, may simply be to “hurry up and wait.”

Conclusion

In the studied 22-stand old-field chronosequence in southeastern New Hampshire, forest age is the best predictor of whether buckthorn will be present in a stand and in what abundance; older stands are less likely to be invaded, and if buckthorn is present it is likely to be at a lower abundance in an older stand than could be expected at a younger site. Additional factors such as high tolerance index or abundance of hemlock are also associated with buckthorn decline. In sites occupied by more intolerant vegetation (such as white pine), buckthorn may be able to persist. A caveat is that the regional buckthorn invasion began at earliest in the 1920s and that the oldest sites in the chronosequence grew for over 100 years before buckthorn could colonize.

At the landscape level, the glossy buckthorn invasion appears to be at an equilibrium, as inferred from two observations 17 years apart. However, because of the long timescale at which succession unfolds, this time span is likely insufficient to confirm or reject that the invasion is indeed stable. To conclusively answer this question will require future investigation.

Finally, insight into buckthorn’s response to and influence upon forest succession might allow forest managers to use silviculture to modify stand composition and discourage a buckthorn population. The intensity of management will vary with community composition and the severity of the invasion. In many systems, a passive approach may be logistically and financially preferable.

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APPENDIX A: Plant scientific names and tolerance values

Scientific names, common names and tolerance values [from Niinemets and Valladares (2006); values in italics are CAN values from Howard (1979) converted to 5-point scale] of all woody species included in Chapter II.

Scientific Name	Common Name(s)	Tolerance
Acer rubrum	red (soft, swamp) maple	3.44
Acer saccharum	sugar (hard) maple	4.76
Amelanchier arborea	downy serviceberry, shadbush	4.33
Amelanchier spp.	juneberry, serviceberry, etc.	*1.50*
Berberis thunbergii	Japanese barberry	*4.00*
Berberis vulgaris	European (common) barberry	*1.50*
Betula alleghaniensis	yellow birch	3.17
Betula lenta	black (sweet) birch	2.58
Betula papyrifera	paper (white) birch	1.54
Betula populifolia	gray birch	1.50
Carpinus caroliniana	blue beech, musclewood, eastern hornbeam	4.58
Carya glabra	pignut hickory	2.69
Carya ovata	shagbark hickory	3.40
Celastrus orbiculatus	Oriental bittersweet	*3.00*
Comptonia peregrina	sweetfern	*1.00*
Cornus alternifolia	alternate-leafed dogwood, pagoda dogwood	4.00
Cornus racemosa	gray (red-panicle) dogwood	4.00
Cornus sericea or *C. stolonifera*	red-osier dogwood	2.86
Corylus cornuta	beaked hazelnut	3.00
Crataegus spp.	hawthorn	*1.50*
Diervilla lonicera	bush honeysuckle	*2.50*
Elaeagnus angustifolia	Russian olive	1.35
Elaeagnus umbellata	autumn olive	*2.00*
Euonymous alatus	burning bush	4.33
Fagus grandifolia	American beech	4.75
Fraxinus americana	white ash	2.46
Hamamelis virginiana	witchhazel	3.00
Ilex verticillata	winterberry holly	3.00
Juniperus communis	common juniper	1.71
Juniperus virginiana	eastern redcedar	1.28
Ligustrum vulgare	common privet	2.29
Lonicera canadensis	American fly honeysuckle	*3.50*
Lonicera morrowii	Morrow's honeysuckle	*2.50*

Malus spp.	apple	*1.50*
Ostrya virginiana	hophornbeam, ironwood	4.58
Parthenocissus quinquefolia	Virginia creeper	*3.50*
Picea abies	Norway spruce	4.45
Pinus resinosa	red (Norway) pine	1.89
Pinus strobus	white pine	3.21
Populus balsamifera	balsam poplar	1.27
Populus grandidentata	bigtooth aspen	1.21
Populus tremuloides	quaking (trembling) aspen	1.21
Prunus pensylvanica	pin (fire) cherry	*1.00*
Prunus serotina	black cherry	2.46
Prunus virginiana	chokecherry	2.59
Quercus alba	white oak	2.85
Quercus rubra	red oak	2.75
Quercus velutina	black oak	2.72
Rhamnus cathartica	common buckthorn	1.93
Rhamnus frangula	glossy buckthorn (now *Frangula alnus*)	2.66
Rhus glabra	smooth sumac	1.78
Rhus typhina	staghorn sumac	1.56
Robinia pseudoacacia	black locust	1.72
Rosa multiflora	multiflora rose	*1.00*
Rubus allegheniensis	(common, Allegheny) blackberry	2.50
Rubus hispidus	bristly dewberry	*1.00*
Rubus idaeus	red raspberry	2.66
Rubus occidentalis	black raspberry	*1.00*
Rubus spp.	rubus	*1.00*
Spirea alba	meadowsweet	*1.00*
Spirea latifolia	broadleaf meadowsweet	*1.00*
Spirea tomentosa	steeplebush	*1.00*
Taxus canadensis	American yew	*5.00*
Tilia americana	basswood	3.98
Toxicodendron radicans	poison ivy	*2.00*
Tsuga canadensis	eastern hemlock	4.83
Ulmus americana	American elm	3.14
Vaccinium angustifolium	lowbush blueberry	*2.00*
Vaccinium corymbosum	highbush blueberry	2.00
Vaccinium pallidum	pale blueberry	*2.00*
Viburnum acerifolium	maple-leaved viburnum	*4.50*
Viburnum dentatum	arrowwood	4.00
Viburnum lentago	nannyberry	4.00
Viburnum trilobum	highbush cranberry	*3.00*

Vitis labrusca	fox grape	*1.00*
Vitis spp.	grape	*1.00*

APPENDIX B: All model iterations tested for nominal linear and multiple linear regression

Model parameter(s) included in iteration
hemlock BA
intolerant BA
mid-tolerant BA
red oak BA
site age
tolerance index
tolerant BA
total BA
white pine BA
site age, hemlock BA
site age, intolerant BA
site age, mid-tolerant BA
site age, red oak BA
site age, tolerance index
site age, tolerant BA
site age, total BA
site age, white pine BA
site age, hemlock BA, red oak BA
site age, hemlock BA, site age*hemlock BA
site age, intolerant BA, mid-tolerant BA
site age, intolerant BA, site age*intolerant BA
site age, intolerant BA, tolerant BA
site age, mid-tolerant BA, tolerant BA
site age, red oak BA, site age*red oak BA
site age, tolerance index, site age*tolerance index
site age, tolerant BA, site age*tolerant BA
site age, total BA, site age*total BA
site age, total BA, tolerance index
site age, white pine BA, hemlock BA
site age, white pine BA, red oak BA

site age, white pine BA, site age*white pine BA

site age, hemlock BA, red oak BA, site age*red oak BA

site age, hemlock BA, site age*hemlock BA, red oak BA

site age, intolerant BA, mid-tolerant BA, tolerant BA

site age, intolerant BA, site age*intolerant BA, mid-tolerant BA

site age, intolerant BA, site age*intolerant BA, tolerant BA

site age, intolerant BA, tolerant BA, site age*tolerant BA

site age, mid-tolerant BA, tolerant BA, site age*tolerant BA

site age, total BA, site age*total BA, tolerance index

site age, total BA, tolerance index, site age*tolerance index

site age, white pine BA, hemlock BA, red oak BA

site age, white pine BA, hemlock BA, site age*hemlock BA

site age, white pine BA, red oak BA, site age*red oak BA

site age, white pine BA, site age*white pine BA, hemlock BA

site age, white pine BA, site age*white pine BA, red oak BA

site age, hemlock BA, site age*hemlock BA, red oak BA, site age*red oak BA

site age, intolerant BA, mid-tolerant BA, tolerant BA, site age*tolerant BA

site age, intolerant BA, site age*intolerant BA, mid-tolerant BA, tolerant BA

site age, intolerant BA, site age*intolerant BA, tolerant BA, site age*tolerant BA

site age, total BA, site age*total BA, tolerance index, site age*tolerance index

site age, white pine BA, hemlock BA, red oak BA, site age*red oak BA

site age, white pine BA, hemlock BA, site age*hemlock BA, red oak BA

site age, white pine BA, site age*white pine BA, hemlock BA, red oak BA

site age, white pine BA, site age*white pine BA, hemlock BA, site age*hemlock BA

site age, white pine BA, site age*white pine BA, red oak BA, site age*red oak BA

site age, intolerant BA, site age*intolerant BA, mid-tolerant BA, tolerant BA, site age*tolerant BA

site age, white pine BA, hemlock BA, site age*hemlock BA, red oak BA, site age*red oak BA

site age, white pine BA, site age*white pine BA, hemlock BA, red oak BA, site age*red oak BA

site age, white pine BA, site age*white pine BA, hemlock BA, site age*hemlock BA, red oak BA

site age, white pine BA, site age*white pine BA, hemlock BA, site age*hemlock BA, red oak BA, site age*red oak BA

APPENDIX C: Results of multiple linear regression models with p-values included

Table 2.3. *Results of nominal logistic regression on presence/absence of glossy buckthorn at 22 sites in Durham, New Hampshire sampled in 1998. ΔAICc = corrected Akaike Information Criterion differences. Bold p-values indicate significance at α = 0.05. Positive or negative (+ / -) signs on parameter estimates indicate parameter's direction of influence on buckthorn presence. Asterisk (*) indicates an interaction; dagger (†) indicates unstable parameter estimates as modeled.*

Model parameters	Rank	AICc	Δ AICc	Effect likelihood ratio test p-value	Parameter estimate	Standard error	Log likelihood	Akaike weight	Evidence ratio
site age hemlock basal area	1	15.21	0	**0.008** 0.073	-0.0748 -0.0007	0.047 0.002	1	0.21	2.36
site age† intolerant spp. basal area† site age * intolerant spp. basal area†	2	15.69	0.48	**<0.001** 0.074 **0.039**	-159.3245 -3.5466 -0.2720	557,734.800 12,423.195 952.301	0.79	0.16	1.86
site age tolerance index	3a (tie)	15.72	0.51	**0.001** 0.101	-0.0822 -2.8280	0.044 2.074	0.77	0.16	1.83
site age	3b (tie)	15.72	0.51	**<0.001**	-0.0940	0.049	0.77	0.16	1.83
site age tolerant spp. basal area	5	16.31	1.10	0.100 0.147	-0.0723 -0.0003	0.044 >0.001	0.58	0.12	1.36
site age total basal area	6	16.60	1.39	**0.018** 0.178	-0.0785 -0.0003	0.054 >0.001	0.50	0.10	1.18
site age intolerant spp. basal area	7	16.93	1.72	**<0.001** 0.223	-0.0935 +0.0013	0.051 0.001	0.42	0.09	1

Table 2.4. *Results of nominal logistic regression on presence/absence of glossy buckthorn at 20 sites in Durham, New Hampshire sampled in 2015. ΔAICc = corrected Akaike Information Criterion differences. Bold p-values indicate significance at α = 0.05. Positive or negative (+ / -) signs on parameter estimates indicate parameter's direction of influence on buckthorn presence. Asterisk (*) indicates an interaction; dagger (†) indicates unstable parameter estimates as modeled.*

Model parameters	Rank	AICc	Δ AICc	Effect likelihood ratio test p-value	Parameter estimate	Standard error	Log likelihood	Akaike weight	Evidence ratio
site age†	1a (tie)	14.29	0	**0.001**	-2.5092	3345.573	1	0.37	1.38
white pine basal area†				**0.039**	+0.0105	15.212			
hemlock basal area†				**<0.001**	+0.0864	113.699			
red oak basal area†				**<0.001**	-0.1000	135.708			
site age†	1b (tie)	14.29	0	**0.009**	-18.5292	97,257.023	1	0.37	1.38
hemlock basal area†				**<0.001**	-0.6281	3,286.019			
red oak basal area†				**<0.001**	+0.5290	2,771.188			
site age * red oak basal area†				**0.008**	+0.0006	3.804			
site age	3	14.94	0.65	**0.005**	-0.6035	1.004	0.72	0.27	1
hemlock basal area				**<0.001**	-0.0232	0.036			
red oak basal area				**0.001**	+0.0193	0.031			

Table 2.5. *Results of multiple linear regression on log-transformed (ln+1) abundance of glossy buckthorn density at 22 sites in Durham, New Hampshire sampled in 1998. ΔAICc = corrected Akaike Information Criterion differences. Bold p-values indicate significance at α = 0.05. Positive or negative (+ / -) signs on parameter estimates indicate parameter's direction of influence on buckthorn abundance. Asterisk (*) indicates an interaction.*

Model parameters	**Rank**	**AICc**	**∆ AICc**	**Adj. r²**	**Parameter estimate p-value**	**Parameter estimate**	**Standard error**	**Log likelihood**	**Akaike weight**	**Evidence ratio**
site age	1	87.92	0	0.49	**0.034**	-0.0152	0.007	1	0.14	2.13
tolerance index					0.057	-1.2101	0.596			
site age	2	88.02	0.10	0.54	**0.008**	-0.0182	0.006	0.95	0.13	2.02
tolerant spp. basal area					**0.034**	-0.0002	<0.001			
site age * tolerant spp. basal area					0.054	>-0.0001	<0.001			
site age	3	88.22	0.30	0.53	**0.002**	-0.0269	0.008	0.86	0.12	1.83
intolerant spp. basal area					0.497	+0.0004	0.001			
site age * intolerant spp. basal area					0.077	>-0.0001	<0.001			
site age	4	88.71	0.79	0.58	**0.036**	-0.0144	0.006	0.67	0.09	1.43
intolerant spp. basal area					0.123	+0.0007	<0.001			
tolerant spp. basal area					**0.044**	-0.0002	<0.001			
site age * tolerant spp. basal area					0.066	<+0.0001	<0.001			
site age	5	88.75	0.83	0.47	**0.010**	-0.0178	0.006	0.66	0.09	1.40
intolerant spp. basal area					0.086	+0.0009	0.001			
site age	6	88.76	0.84	0.52	**0.015**	-0.0182	0.007	0.66	0.09	1.40
tolerance index					0.080	-1.0826	0.584			
site age * tolerance index					0.154	+0.0109	0.007			
site age	7	89.22	1.30	0.41	**0.001**	-0.0231	0.006	0.52	0.07	1.11
site age	8	89.30	1.38	0.46	**0.017**	-0.0173	0.007	0.50	0.07	1.07
tolerant spp. basal area					0.116	-0.0002	<0.001			
site age	9	89.35	1.43	0.51	**0.003**	-0.0204	0.006	0.49	0.07	1.04
hemlock basal area					0.063	-0.0002	<0.001			
site age * hemlock basal area					0.096	<+0.0001	<0.001			
site age	10	89.37	1.45	0.51	0.070	-0.0130	0.007	0.48	0.07	1.03
intolerant spp. basal area					0.104	+0.0009	0.001			
tolerant spp. basal area					0.138	-0.0001	<0.001			
site age	11	89.43	1.51	0.46	**0.007**	-0.0187	0.006	0.47	0.06	1
hemlock basal area					0.124	-0.0002	<0.001			

Table 2.6. *Results of multiple linear regression on log-transformed (ln+1) abundance of glossy buckthorn density at 20 sites in Durham, New Hampshire sampled in 2015. ΔAICc = corrected Akaike Information Criterion differences. Bold p-values indicate significance at α = 0.05. Positive or negative (+ / -) signs on parameter estimates indicate parameter's direction of influence on buckthorn abundance. Asterisk (*) indicates an interaction.*

Model parameters	Rank	AICc	∆ AICc	Adj. r^2	Parameter estimate p-value	Parameter estimate	Standard error	Log likelihood	Akaike weight	Evidence ratio
site age	1	79.81	0	0.67	**0.043**	-0.0158	0.007	1	0.35	2.59
tolerance index					**0.007**	-2.3123	0.746			
site age * tolerance index					**0.006**	+0.0270	0.008			
site age	2	79.85	0.04	0.72	0.147	-0.0109	0.007	0.98	0.34	2.53
intolerant spp. basal area					**0.023**	+0.0017	0.001			
tolerant spp. basal area					**0.012**	-0.0002	<0.001			
site age * tolerant spp. basal area					**0.033**	<+0.0001	<0.001			
site age	3	81.14	1.33	0.65	**0.015**	-0.0265	0.010	0.51	0.18	1.33
intolerant spp. basal area					0.755	-0.0005	0.002			
site age * intolerant spp. basal area					0.054	>-0.0001	<0.001			
site age	4	81.71	1.90	0.69	0.077	-0.0191	0.010	0.39	0.13	1
intolerant spp. basal area					0.896	-0.0002	0.002			
site age * intolerant spp. basal area					0.074	>-0.0001	<0.001			
tolerant spp. basal area					0.105	-0.0001	0.000			

Table 2.7. *Results of multiple linear regression on log-transformed (ln+1) abundance of glossy buckthorn density at 16 sites with less than 10 m^2 ha^{-1} of hemlock BA in Durham, New Hampshire sampled in 1998. ΔAICc = corrected Akaike Information Criterion differences. Bold p-values indicate significance at α = 0.05. Positive or negative (+ / -) signs on parameter estimates indicate parameter's direction of influence on buckthorn abundance.*

Model parameters	**Rank**	**AICc**	**∆ AICc**	**Adj. r²**	**Parameter estimate p-value**	**Parameter estimate**	**Standard error**	**Log likelihood**	**Akaike weight**	**Evidence ratio**
site age	1	67.67	0	0.40	**0.005**	-0.0270	0.008	1	0.42	0.40
site age intolerant spp. basal area	2	67.72	0.05	0.48	**0.029** 0.094	-0.0206 +0.0010	0.008 <0.001	0.98	0.41	0.41
site age tolerance index	3	69.49	1.82	0.42	**0.020** 0.234	-0.0229 -1.1831	0.009 0.948	0.40	0.17	1

Table 2.8. *Results of multiple linear regression on log-transformed (ln+1) abundance of glossy buckthorn density at 14 sites with less than 10 m^2 ha^{-1} of hemlock BA in Durham, New Hampshire sampled in 2015. ΔAICc = corrected Akaike Information Criterion differences. Bold p-values indicate significance at α = 0.05. Positive or negative (+ / -) signs on parameter estimates indicate parameter's direction of influence on buckthorn abundance.*

Model parameters	**Rank**	**AICc**	**∆ AICc**	**Adj. r²**	**Parameter estimate p-value**	**Parameter estimate**	**Standard error**	**Log likelihood**	**Akaike weight**	**Evidence ratio**
intolerant spp. basal area	1	59.73	0	0.59	**<0.001**	+0.0030	<0.001	1	0.62	0.62
tolerance index	2	60.70	0.97	0.56	**0.001**	-6.8172	1.618	0.62	0.38	1