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INVASION OF TRANSITION HARDWOOD FORESTS BY EXOTIC *RHAMNUS FRANGULA*: CHRONOLOGY AND SITE REQUIREMENTS

BY

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THESIS

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ABSTRACT

INVASION OF TRANSITION HARDWOOD FORESTS BY EXOTIC *RHAMNUS FRANGULA*: CHRONOLOGY AND SITE REQUIREMENTS

by

Hanna S. Wingard

University of New Hampshire, May, 2007

The invasion chronology and site requirements of the exotic, invasive shrub, glossy buckthorn (*Rhamnus frangula*), were studied within intact transition hardwood – hemlock – white pine forests in Durham, NH. Data were collected from 63 plots (7 sites with 9 plots each). Within sites, plots were arranged over a topographic gradient with 3 plots in each of 3 topographic positions (upper, middle, and lower slope). From each plot, information on soil nutrients and texture, soil moisture, overstory community composition, and canopy openness was collected. Densities of *R. frangula* in two size classes (≥1 m in height, <1 m in height) within each plot were calculated. Morphological data (height, diameter at stem base, number of live and dead stems, and age) were collected from each individual ≥1 m tall. *R. frangula* invaded these intact, closed-canopy forests over 30 years ago and the invasion has continued, with population density increasing over time. Nominal logistic regression suggested that site, topographic position, and overstory community type played a role in whether or not *R. frangula* was present in a plot. Plots on upper slopes dominated by *Tsuga canadensis* were less likely to become invaded than other plots. Multiple linear regression showed that density of *R. frangula* (≥1 m) increased with time since invasion and increasing soil quality. Density of *R. frangula* (<1 m) was positively influenced by time since invasion, canopy openness, and density of *R. frangula* (≥1 m). Multiple regressions also showed that mean age and age of oldest *R. frangula* per plot were higher in plots with higher soil moisture content. Size of *R. frangula* individuals (i.e. height, diameter) generally increased with mean age of stems. The results show that successional, transition hardwood forests can be invaded by *R. frangula* and should not be overlooked when managing against this species. Special attention should be given to low topographic positions and areas with rich soils, while upland areas with dense hemlock canopy are much less likely to experience heavy invasion by *R. frangula.*

CHAPTER I

INTRODUCTION

Only in recent decades have exotic, invasive plants become a major ecological concern outside of agricultural systems (D'antonio et al. 2004). It is now recognized that invasive species are increasingly altering ecological communities worldwide (Gurevitch and Padilla 2004). Wilcove et al. (1998) reported that after habitat loss, invasive species are the second greatest threat to imperiled species within the United States. The invasion of exotic plants can result in changes in certain ecosystem processes, such as nutrient cycling or hydrology, that reduce the ability of native species to thrive there (Mack et al. 2000).

Invasive plants in forest ecosystems are of concern for a number of reasons. Invasive plants may compete with native tree species, reducing seedling emergence, reducing growth rates, or even increasing mortality of natives. In a 2004 study involving experimental gaps in a forest heavily invaded by *Rhamnus frangula* (taxonomy follows Gleason and Cronquist 1991), Fagan and Peart estimated that fewer than 10% of tree saplings were able to survive to maturity underneath high densities of *R. frangula*. Furthermore, they concluded that as density of *R. frangula* underneath pine canopies increases, tree regeneration within canopy gaps would be slowed. The *R. frangula* removal experiment conducted by Frappier et al. (2004) supports these findings. In this case, density of first-year tree seedlings such as *Acer rubrum, Fraxinus americana, Pinus strobus*, and *Quercus rubra* was reduced underneath ≥90% cover of *R. frangula*. Similarly, the invasive shrub *Lonicera maackii* in Ohio forests showed both above- and below-ground competition with native tree seedlings. Removal of *L. maackii* shoots increased survival of species such as *Acer saccharum* and *Quercus rubra* (Gorchov and Trisel 2003).

Herbaceous plants are also negatively affected by invasive shrubs. Experiments show that *Lonicera maackii* reduced the size and fecundity of three native herbs, *Allium berdickii*, *Thalictrum thalictroides*, and *Viola pubescens* (Miller and Gorchov 2004). *Rhamnus frangula* similarly affects herbaceous groundcover. Frappier et al. (2003a) showed that density of herb cover was inversely related to *Rhamnus frangula* basal area. Plant species richness was also reduced by increased *R. frangula* basal area.

Researchers have proposed a variety of controls on the spatial distribution of exotic, invasive plants. Dispersal is clearly important. The absence of a particular invasive plant at a site is not necessarily an indication that the site is immune to invasion. The plant's propagules may simply not have arrived yet. Propagule pressure has been suggested to be an important factor in the invasion of *Lonicera mackii* in woodlots in Ohio (Bartuszevige et al. 2006). The experiments of Von Holle and Simberloff (2005) and Rouget and Richardson (2003) also support this suggestion. The latter found that the intensity of propagule pressure was a better predictor of canopy cover of three invasive tree species than any environmental factor (i.e. altitude, proximity to cultivated fields, precipitation, temperature). Some studies have found a positive relationship between propagule availability and disturbance (Deering and Vankat 1998), both natural (i.e. streams) and anthropogenic (i.e. roads) (Parendes and Jones 2000). This is generally because the suitable habitats provided by disturbed areas provide reservoirs of propagules for future invasions. However, Johnson et al. (2006) pointed out that this trend is dependent upon the specific invasive species being studied. The abundance of disturbed areas did have this effect on *Rhamnus frangula*, but for *Berberis thunbergii* this trend was reversed.

Disturbance allows site changes that could be beneficial for exotic invasives. Whether natural or anthropogenic, disturbances allow exotic plants to overcome environmental barriers that would otherwise keep them out of an area. If dispersal is not a limiting factor, canopy gaps can allow light-limited invasives to invade. For example, removal of overstory Norway maple (*Acer platanoides*) in New Jersey resulted in the establishment of several invasive shrubs including barberry (*Berberis thunbergii*), burning bush (*Euonymus alata*), and Japanese honeysuckle (*Lonicera japonica*) (Webb et al. 2001). Several extensive landscape studies have shown that non-native plant species are associated with landscape corridors (roads and utility lines; Searcy et al. 2006) as well as areas of historic human disturbance (Lundgren et al. 2004, Von Holle and Motzkin 2007). The effects of forest edges are similar. Brothers and Springarn (1992) found that species richness of exotic plants increased sharply along the field-forest boundary. However, the difference between richness of herbs between the forest interior and forest edge was much greater than the difference in richness for woody shrubs. This suggests that woody exotics are better able to penetrate into forest interiors.

Without disturbance, poor competitive ability of invasive plants may limit their distribution. Recent experimental studies support Elton's (1958) hypothesis that high native species richness, with resulting greater efficiency of resource use, increases the competitive environment of communities and reduces the likelihood of plant invasions. Naeem et al. (2000) studied the effects of plant species richness on *Crepis tectorum*. As richness increased, available light and nutrients decreased, making the environment of diverse plant assemblages more competitive and reducing *C. tectorum* success. Also, Bartuszevige et al. (2006) found that *Lonicera maackii* density was negatively associated with higher native species richness.

Evidence also suggests that physical site factors play a role in exotic plant distributions. Searcy et al. (2006) found that introduced invasives were more frequently found in moist habitats along streams and swamps than in other habitats. Stohlgren et al. (2002) further found that invasive species richness increased as soil clay content, soil nitrogen, and precipitation increased. Non-native species richness also was higher in areas formed on glaciolacustrine deposits and in areas with high soil calcium (Von Holle and Motzkin 2007). Lundgren et al. (2004) found that soil particle size predicted both percent cover and species richness of invasive plants. Invasive species richness was further predicted by site factors such as topography, elevation, and soil wetness. Some invasive plants seem to respond more to differences in soil characteristics than others. For instance, in a landscape-scale study in southern New Hampshire, the presence of *Rosa multiflora* at a site was positively correlated with soil pH and presence of *Celastrus orbiculatus* was predicted by percent clay particles in soil, but presence of other invasive plants (i.e. *Berberis thunbergii*, *Rhamnus frangula*, *Elaeagnus umbellata*) was not predicted by any physical site factor (Johnson et al. 2006). In a fine-scale study, Frappier et al. (2003a) found that soil variables, i.e. soil clay, soil sand, or pH, were not related to *R. frangula* basal area. Instead, canopy composition and canopy openness were important predictors. Distributions of invasive plants clearly cannot be explained universally, but are dependent on the species being examined as well as the scale of the study.

While generalizations about plant invaders are valuable, it is important to gain knowledge about individual species of invaders in order to better focus management efforts. Understanding the environmental controls on a particular invasive species allows us to: a) pinpoint environments in which the species could become a pest; and b) gain insight into possible control measures.

This study focuses specifically on *Rhamnus frangula* (glossy buckthorn), a shrub that is exotic and invasive in North America. While some studies have indicated that *R. frangula* is confined to wetlands, open fields, forest edges (e.g., Catling and Porebski 1994) disturbed areas, and pond margins (Searcy et al. 2006), *R. frangula* has been observed invading intact forest ecosystems (personal observation, Fagan and Peart 2004, Frappier et al. 2003a, 2003b, Searcy et al. 2006, Webster, et al. 2006). Therefore, my goal was to determine what community and physical site characteristics, if any, were associated with *R. frangula*'s success in establishing in a given site. Also, I determined whether, once *R. frangula* had established at a site, community and site characteristics were related to *R. frangula* abundance, individual size, or amount of dieback.

CHAPTER II

METHODS

II A. Study Species

Rhamnus frangula L. (Rhamnaceae) is a non-native shrub or small tree abundant throughout New England and the Midwest. It ranges from Maryland to the south to southern Ontario to the north and Minnesota to the west (USDA 2006). Native to Europe, it is predicted that its North American range will continue to expand with time (Catling and Porebski 1994). *Rhamnus frangula* was probably introduced around 200 years ago, but did not become naturalized until after 1900 (Howell and Blackwell 1977). Although no longer in practice, *R. frangula* was once planted for hedgerows and for wildlife fodder (Wyman 1971).

R. frangula produces fruit in late summer to early fall. Fruits are small, black berries. Individual genets of *R. frangula* can produce as many as 430 to 1804 fruits (Medan 1994). The age of first reproduction is between 4 and 6 years old (Frappier et al. 2003b). Seeds are dispersed by birds, i.e., European Starlings and American Robins (Catling and Porebski 1994) as well as mice. Many of the seeds simply fall to the ground underneath the parent, allowing prolific local establishment. Godwin (1943) found that only 39% of seeds were removed by animals at Wicken Fen, England.

In some cases, seeds of *R. frangula* form single-stemmed plants; in others, a multi-stemmed plant is formed (Godwin 1943), generally with the additional stems produced from the butt of the original stem. Although literature suggests that there is no vegetative reproduction (Godwin 1943, Converse 1984), I found multiple examples of adventitious stems growing from old, toppled stems (personal observation). *R. frangula* of all ages are susceptible to dieback (Godwin 1943). In multi-stemmed individuals, whole stems can be completely dead, while other stems on the same individual are healthy and show no sign whatsoever of dieback (personal observation).

II B. Study Area and Plot Setup

Seven study sites were chosen within four woodlots in Durham, NH (Figure 1). Three sites were located in College Woods (CW1, CW2, CW3), the largest of the woodlots. Two sites were located at MacDonald Lot (MAC1, MAC 2), and one each at West Foss Farm (WFOS) and East Foss Farm (EFOS). These woodlots are managed by the Office of Woodlands and Natural Areas at the University of New Hampshire. These sites are typical of the land use and current vegetation of the region: they were cultivated or pastured after the arrival of settlers in the 1620's and abandoned after 1850 (Howard and Lee 2002). Today, they are primarily forested with pines (*Pinus strobus, P. resinosa*), birches (*Betula paperifera, B. lenta*), oaks (*Quercus alba, Q. rubra, Q. velutina*), maples (*Acer rubrum, A. saccharum*), as well as hemlock (*Tsuga canadensis*) and beech (*Fagus grandifolia*) in some areas (Howard and Lee 2002). Except for some plots at CW2, all stands originated between 1900 and 1950. Some CW2 plots were in the College Woods Natural Area, where canopy hemlocks have been dated to over 200 years (N. Henderson and T. D. Lee, unpublished data).

Most of these stands had experienced some timber stand improvement; a small number of stumps were observed at most sites. Unfortunately, records of management activities were incomplete (UNH Office of Woodlands and Natural Areas, Durham, NH).

Specifically, some removal of pine occurred in two of the College Woods sites (CW1 and CW2); the exact dates and amounts were not known. The College Woods Natural Area (which was sampled by six of nine plots in CW2) experienced canopy damage from the hurricanes of 1938 and 1954 and some timber salvage thereafter. Nothing was known about the management history at site CW3. At Macdonald lot, hardwood areas (located within site MAC1) were cut between 60-80 years ago. It is likely that this area was clear-cut. Site MAC2 was located in a pine-dominated area that experienced light thinning (specific amounts unknown) in 1980 and 1982. At East Foss Farm (EFOS), some white pine was harvested in 1978. At West Foss Farm (WFOS), minimal harvesting (unknown species or amounts) took place in 1969 and 1970. In no stand was there timber removal within the two decades preceding this study.

Upland soils in the study area were typically Hollis-Charlton fine sandy loam developed from glacial till, while lowlands were typically Buxton silt loams formed from marine sediments (NRCS 2001). Study sites were selected based on specific criteria, including presence of closed-canopy forest (sites were not located in open areas or along forest edges); presence of a slope gradient, so that plots could be set up in top-slope, mid-slope, and bottom-slope positions; and presence of buckthorn (to eliminate error due to establishment limitation).

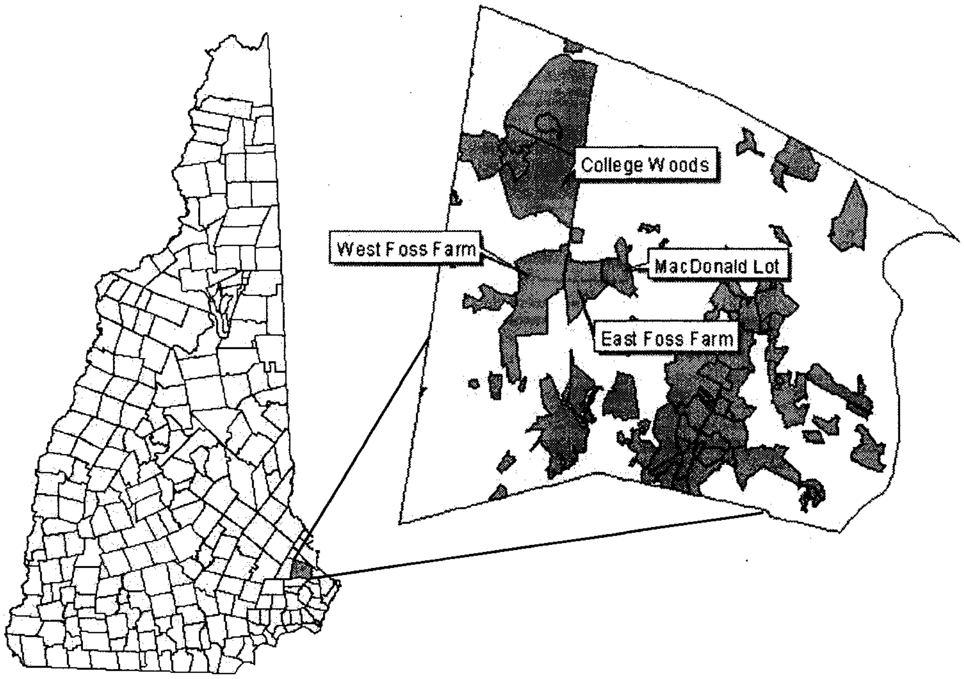


Figure 1: Map of glossy buckthorn study sites in Durham, NH.

Study sites varied in size, ranging from approximately 3,000 m^2 to almost a hectare in size. Each of the seven study sites contained nine, 5 m radius plots (63 plots total). Three plots were located at top-slope position and three at bottom-slope position. The middle three plots were located at half the vertical distance between the top and bottom plots. Slope length and height also varied between sites. Slope lengths ranged from approximately 60 m to 150 m in length. Vertical distances ranged from approximately 12 to 30 m. A digital altimeter was used to estimate these vertical distances. A transect was created at each slope position equal to the entire horizontal length of the slope (Figure 2). Transects ranged from approximately 60 to 140 m in length depending on terrain. Each transect was divided into three equal lengths, and a plot was randomly located in each of these subsections. This design was used because it maximized topographic variation represented at each site, and in our study area, topographic position is associated with variation in soil parent material, soil drainage, and nutrient status (Viera and Bond 1973). By maximizing topographic variation my intent was to maximize variation in edaphic and microclimatic characteristics at each site.

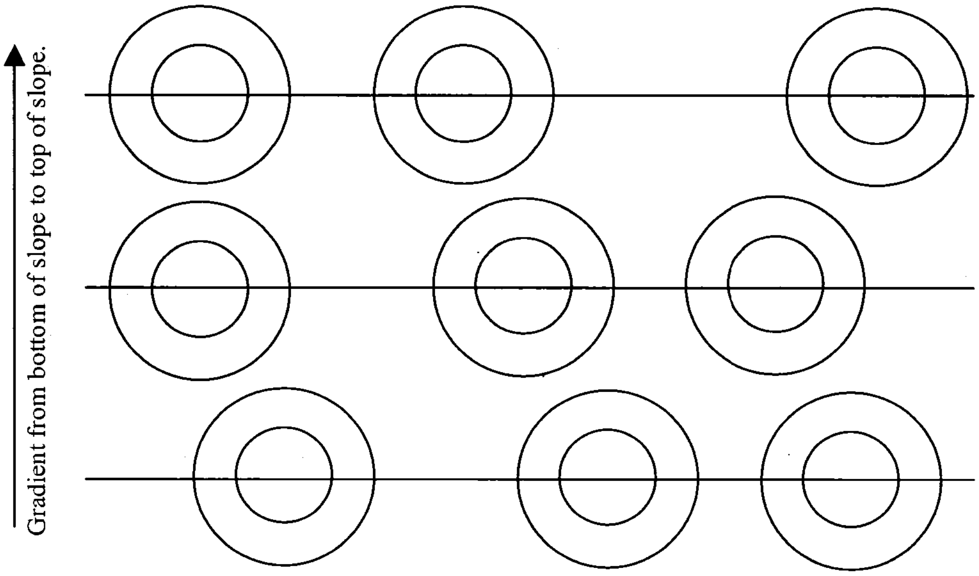


Figure 2: Example of plot (and subplot) configuration at each site. Not drawn to scale.

II C. Collection, Processing, and Analysis of Buckthorn Populations

Fieldwork was conducted in the summer and fall of 2005. Within each 5 m radius plot, the following measurements were taken on each individual (genet) of *R. frangula* ≥1 m in height: diameter at the base of the largest stem, height of tallest stem, number of living stems ≥1 m in height, number of dead stems ≥1 m in height, number of living stems <1 m in height, number of dead stems <1 m in height. Individuals were then cut at the base of the stem and a cross-section of each stem was brought back to the lab for age determination. Also within each 5 m radius plot, all individuals <1 m in height were counted. In some cases, density of *R. frangula* < 1 m in height was high enough to limit the sampling of these stems to a 2.5 m radius subplot. To standardize density, all measurements are reported in stems/100m^2. For each plot, the following were calculated: density of individuals ≥1 m, density of individuals < 1 m, average number of stems per individual, average height, average diameter at base, average percent living stems (100 times ratio of live stems to total stems per individual).

The age of each *R. frangula* stem ≥1 m was estimated by cutting cross-sections 0.5-2 cm thick of stems (within a few cm of the ground surface) and counting the annual rings underneath a dissecting scope. When a plant had multiple stems, the largest diameter stem was sectioned. For each plot, the following were calculated: mean age, modal age, and oldest individual.

II D. Collection, Processing, and Analysis of Soil Data

Soil samples were collected from within each 5 m radius plot and analyzed for pH, nutrient and particle size. Soil was collected from just underneath the organic horizons because *R. frangula* tends to be shallowly rooted (personal observation). Four soil collections, each similar in volume, were made in each plot (plot center as well as three randomly selected locations) and these were bulked. Approximately 1 kg of soil was collected per plot. Soil was sieved through a 2 mm screen. A portion of the soil was sent to the Cornell Nutrient Analysis Laboratory in Ithaca, NY (CNAL), and tested for pH as well available calcium, magnesium, potassium, and phosphorus (in ppm). 30 g of soil from each plot was reserved and analyzed (in the UNH soils lab) for particle size distribution using the hydrometer method (Moore and Chapman 1986). Percent sand, silt, and clay were recorded for each plot.

Separate soil samples were collected for soil moisture analysis. Soils were taken from just beneath the organic horizons from two random locations within each plot and placed in two separate Labelstik tins. Samples were collected three days after a moderately heavy rain and were collected within a time span of less than 30 hours. Samples were taped shut to limit moisture loss and were weighed immediately upon returning to the lab. After weighing, tins were opened and oven-dried at 105 C until constant weight was achieved. Tins were then weighed again and soil moisture was reported as grams of water/grams of dry soil (Moore and Chapman 1986).

Percent clay, percent silt, pH, and all nutrient data (concentrations of available Ca, K, Mg, P) appeared to be correlated. They were therefore condensed into a single index of soil quality in order to simplify future analyses. The above variables were analyzed using principal components analysis (PCA run on PC-ORD version 4.25). Analysis used a correlation cross products matrix and was both centered and standardized. This created a synthetic index of soil quality that was used in place of individual variables in later regression analysis.

II E. Collection, Processing, and Analysis of Community Data

To determine the effects of the local forest community on *R. frangula*, all overstory trees ≥10 cm DBH were tallied by species within a larger 10 m-radius plot with the same center as the smaller plot. The plot was larger than that used to collect buckthorn data because it is likely that the roots or canopy of overstory trees in close proximity to, but not necessarily inside, the 5 m radius buckthorn plots could influence the growth of *R. frangula* through facilitation or competition. Numbers of trees per species were reported as relative density per plot. *Pinus strobus* and *Pinus resinosa* densities were combined because they were planted together at some sites. Analysis of community data was difficult to interpret when these two species were considered separately. Forest vegetation of each plot was classified using two-way indicator species analysis (TWINSPAN; run in PC-ORD, version 4.25) using pseudospecies cut levels of 0, 0.1, 0.2, 0.3, 0.5 and maximum number of indicators per division = 5. TWINSPAN divides a group of sites into two groups based on differences in species presence and abundance. These groups can then be further divided if desired.

II F. Collection and Processing of Light Data

Canopy photos were taken to determine the percent open sky ("site openness") at each plot. Digital photos were taken with a Nikon 950 digital camera outfitted with a 180° hemispherical ("fish-eye") lens from the center of each plot after all *R. frangula* stems had been removed. The camera was positioned on a tripod 1 m above the ground. Each individual plot photo was analyzed using GAP LIGHT ANALYZER software (Frazer et al. 1999). Image pixels were classified as either "sky" or "non-sky" based on a subjective user-set tolerance level. Site openness was then the ratio of 'sky' pixels to total pixels. Tolerance for all analyses was set to 140 after analyzing one randomly selected plot photograph from each site.

II G. Data Analysis

All variables were plotted to test for normality. Only density of *R. frangula* (both height classes) was transformed onto a LOG_{10} scale. To determine what variables were associated with *R. frangula* presence in a plot, nominal logistic regression using presence/absence of *R. frangula* as the dependent variable (of either size class) was run. Presence of *R. frangula* was regressed against the independent variables: site (as a random effect variable), topographic position, canopy openness, community type, soil quality (PCA), and moisture. Backwards selection was used to remove components of the model. Akaike's Information Criterion (AIC) was used to determine how many components were removed. AIC was calculated as follows:

$$-2*\text{log-likelihood}+2*k$$

where k is the number of estimated parameters (Burnham and Anderson 2002). Only one variable, soil moisture, was removed from the model. This regression was run using JMP 6.0.

To determine what ecological variables affected *R. frangula* characteristics, multiple linear regressions were used. Dependent variables describing *R. frangula* characteristics that were tested were: log (density of stems ≥1 m in height), log (density of stems <1 m in height), mean number of stems per plant, mean percent of dead stems per individual, mean diameter of stems, mean height per plant, mean age, and oldest individual per plot. Six variables, referred to hereafter as the "**site-related independent variables**" were included in each linear regression. These were site (as a random effect variable), topographic position, soil quality (PCA), soil moisture, canopy openness, and community type. In addition, for each dependent variable, other potentially influential independent variables were included in the predictive model.

Specifically, the model describing log (density of stems ≥1 m in height) included the six site-related variables and also the age of the oldest individual. The model describing log (density of stems <1 m in height) included the six site related variables, age of the oldest individual, and log (density of stems ≥1 m in height). The models describing mean number of stems per plant and mean percent of dead stems per individual both included the six site-related variables, age of the oldest individual, mean age, log (density of stems ≥1 m in height) and log (density of stems <1 m in height). The models describing mean height and mean diameter per plant both included the six site-related variables as well as age of the oldest individual, mean age, log (density of stems ≥1 m in height), log (density of stems <1 m in height), and mean number of stems per plant. Only the six site-related variables were included in the models describing mean age per plot and oldest individual per plot. Backwards selection using AIC was again used to determine which components remained in each model. All regressions were run using JMP 6.0.

CHAPTER III

RESULTS

III A. Synthetic Indices of Soil Quality and Tree Community Composition

Only the first PCA axis, which represented 62% of variation (per Jackson1993), was used (Kaiser-Guttman method, Cliff 1988). This axis appeared to be associated with soil fertility (Table 1). Loadings (correlations of individual variables with the axis) of calcium, magnesium, and potassium concentrations were negative and had a magnitude over 0.4. Silt and clay content, as well as pH, were also negatively related to the axis, but had lower magnitudes. Phosphorus concentration showed a weak and positive relationship to this axis. Thus, plots with negative axis 1 scores had more fertile soils than those with positive values.

Table 1: Results of principal components analysis: loadings of individual soil variables on the first principal component. Loadings indicate the relative contribution of each variable to an eigenvector.

Soil Variable	Axis 1 Loading
% Clay	-0.3979
% Silt	-0.3803
pH	-0.2973
Log (Ca)	-0.4208
Log (Mg)	-0.4476
Log (K)	-0.4061
Log (P)	0.2577

Based on overstory tree species composition, TWINSPAN classified plots into three community types. Type "A" was characterized by a dominance of *Quercus rubra,* *Pinus spp., Carya ovata, and Juniperus virginiana.* Type "B" was characterized by a dominance of *Pinus strobus* and *Pinus resinosa.* Type "C" was characterized by a dominance of *Tsuga canadensis and Quercus rubra* (Table 2).

Table 2: Mean and standard deviation of relative abundances of the 9 most common tree species for all plots within each community type. Highest abundances in each community are bolded.

Species	Community A	Community B	Community C
Juniperus virginiana	0.14 (0.17)	-	-
Carya ovata	0.14 (0.17)	0.01 (0.04)	0.01 (0.02)
Fraxinus americana	0.09 (0.11)	0.01 (0.02)	0.01 (0.03)
Acer rubrum	0.12 (0.15)	0.11 (0.19)	0.08 (0.11)
Quercus rubra	**0.16 (0.23)**	0.08 (0.12)	0.19 (0.17)
Pinus spp.	**0.16 (0.16)**	**0.62 (0.30)**	0.14 (0.10)
Fagus grandifolia	-	0.07 (0.11)	0.04 (0.06)
Betula lenta	-	0.01 (0.02)	0.13 (0.14)
Tsuga canadensis	-	0.01 (0.3)	**0.27 (0.22)**

III B. Variables Affecting *Rhamnus frangula* Presence

Of 63 total plots, 46 had *R. frangula* in both sizes classes (< and ≥ 1 m in height). Eight plots had no *R. frangula* ≥1 m in height, but at least one *R. frangula* <1 m in height. Nine plots had no stems of *R. frangula* at all.

Presence of *R. frangula* was regressed against the six independent site-related variables. Presence of *R. frangula* (regardless of size class) in plots was predicted by site, topographic position, and overstory community, all of which had P-values lower than 0.05 (Table 3). Canopy openness and soil quality were also included in the model, but had much higher P-values (Table 3). *Rhamnus frangula* was present at all seven sites but three sites had at least one plot that lacked *R. frangula* (Table 4). All of the 21 plots in the lower topographic position contained *R. frangula*, while 4 plots in the top topographic position and 5 plots in the middle topographic position contained no stems of *R. frangula* (Table 4). All 9 of the plots that lacked any stems of *R. frangula* were classified as community type C, dominated by *Tsuga canadensis* and *Quercus rubra*, and had only positive PCA scores with a mean of 1.58, representing low soil fertility. In contrast, plots that did contain *R. frangula* occurred in all three community types and had both positive and negative PCA scores with a mean of -0.26. Mean canopy openness for plots where *R. frangula* was not present and those that did contain *R. frangula* were very similar; 15.4% and 15.0% respectively. However, plots that did contain *R. frangula* did have a wider range of canopy openness, from 9.8% to 22.5%, compared to a range of 11.0% to 22.2% for plots that lacked *R. frangula.*

Table 3: Results of logistic regressions of *R. frangula* presence/absence (either size class) on site, topographic position, canopy openness, community type, soil quality, and soil moisture.
* Indicates significant value.

Response	R^2	Chi Sq.	Parameter	DF	L-R ChiSq.	Prob>ChiSq
Presence/absence of *R. frangula*	0.9123	67.025				
			Site	6	19.7446	0.0031*
			Topo position	2	14.4764	0.0007*
			Canopy Openness	1	3.3341	0.0679
			Community Type	2	7.4260	0.0244*
			Soil Quality (PCA)	1	2.6943	0.1007

Table 4: Distribution of plots containing *Rhamnus frangula* across sites and topographic positions.

Site	Bottom	Middle	Top	Total
CW1	3	3	3	9
MAC1	3	3	3	9
MAC2	3	3	3	9
CW2	3	0	0	3
WFOS	3	2	3	8
EFOS	3	3	3	9
CW3	3	2	2	7

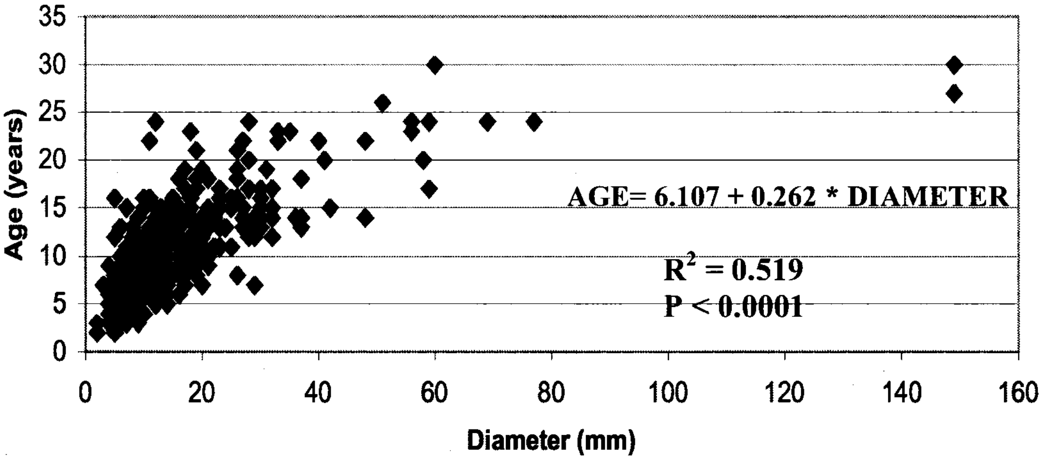
III C. Age and Age Structure

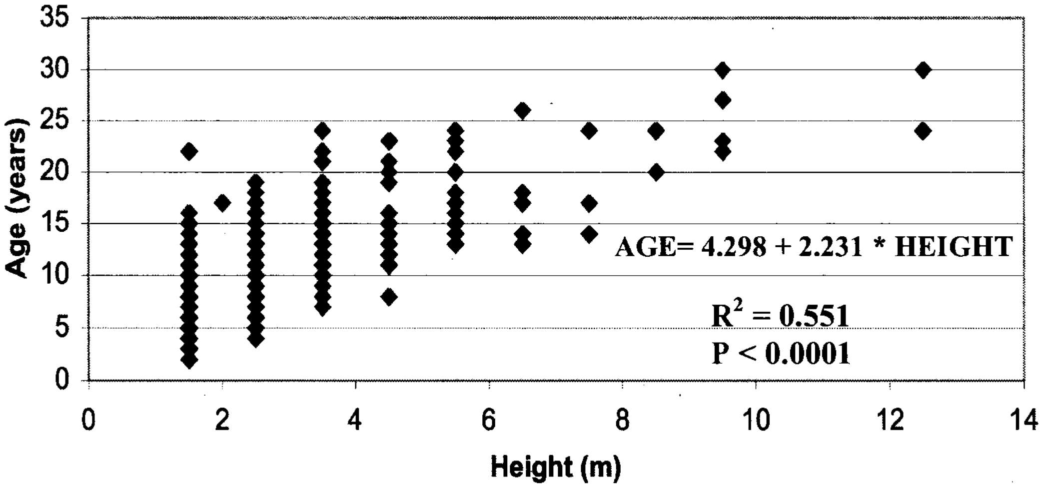
Age of individual *R. frangula* (≥ 1 m) across all 63 plots ranged from 2 to 30 years (n=502) and averaged 9.72 years. Only 3 individuals were over 25 years old. In those plots that contained buckthorn, the time since first invasion (age of the oldest stem) ranged from 6 to 30 years ago. When age of oldest stem (per plot) was regressed against the six site-related independent variables; topographic class and soil quality were dropped from the model; while site, community type, soil moisture, and canopy openness were retained. Site accounted for 31.03% of the total residual variance. Age of the oldest stem showed a strong positive relationship with soil moisture. The Akaike criterion dictated that community type and canopy openness remain in the regression model, but these variables had very high P-values. Age of the oldest stem was positively associated with both community types A and B. Canopy openness had a negative relationship with age of the oldest stem (Table 5).

Mean age was also regressed against the six site-related independent variables. Of these, site, soil quality (PCA), soil moisture, canopy openness, and overstory community type were retained in the model. Site accounted for 13.16% of the total residual variance. As with maximum age, multiple linear regression showed a strong, positive correlation of mean age with soil moisture. The other variables that remained in the model had high P-values. These were: soil quality and both community types A and B, which were positively correlated with mean age. Canopy openness showed a negative relationship with mean age (Table 5).

All sites but one had oldest individuals > 20 years of age; the exception was College Woods 3, where the oldest individual was only 12 years old (Figure 4). Across all the site/topo classes with one exception, there were fewer stems ≥1 m in height than stems <1 m in height. That this ratio is less than 1 suggests that there were more juveniles than adults (Table 6). The exception was the *R. frangula* population within the plots at the bottom topographic positions at the College Woods 1 site. Here the density of stems ≥1 m in height was greater than the density of stems < 1 m in height. On a per-plot basis, 6 plots had more stems ≥1 m in height than stems <1 m in height, two at each topographic position within site CW1. In these cases, the ratios were greater than one, meaning that there were more large than small stems.

Age of individual plants ≥1 m in height was significantly related to both basal diameter of the largest stem and to plant height (Figures 3a and 3b). Plants 5 mm and 60 mm in diameter were estimated to be 7 and 22 years of age, respectively. Plants 1-2 m in height and 7-8 m in height were estimated to be 8 and 21 years of age, respectively.





Figures 3a and 3b: The relationship between stem size and stem age. Stem age can accurately be predicted by both stem diameter (top diagram) and stem height (lower diagram).

Table 5: Results of linear regressions using plots with *R. frangula* present. *Indicates significant value.

Response Variable	R^2	R^2 Adj.	Effects	Parameter Estimate	DF	SE	f-ratio	p>ChiSq.
Log (density of *R. frangula* >1m)	0.738	0.728						
			Soil quality (PCA)	-0.1023	1	0.0332	9.4888	0.0033*
			Age of oldest individual	0.0387	1	0.0090	18.6561	<0.0001*
Log (density of *R. frangula* <1m)	0.791	0.779						
			Log (density of R.f. >1m)	0.723	1	0.1794	16.2441	0.0002*
			Age of oldest individual	0.0365	1	0.0138	7.0116	0.011*
			Canopy openness	5.9757	1	3.4589	2.9846	0.0904
Mean diameter at base of *R. frangula*	0.769	0.722						
			Topographic position	B: -2.3418 M: 0.7477	2	B: 1.3146 M: 0.7476	1.6497	0.2043
			Soil quality (PCA)	-0.6701	1	0.4921	1.8543	0.1810
			Canopy openness	-32.3321	1	26.8553	1.4495	0.2383
			Community type	A: 2.0580 B: -1.5236	2	A: 0.9760 B: 1.0113	2.7583	0.1042
			Log (density of *R. frangula* <1m)	2.0300	1	0.7668	7.0084	0.0128*
			No. stems per plant	0.4475	1	0.2726	2.6954	0.1082
			Mean age	0.9483	1	0.1681	31.8242	<.0001*
Mean no. stems per plant	0.530	0.502						
			Community type	A: -0.1635 B: 1.0692	2	A: 0.6020 B: 0.5822	1.7568	0.1887
			Mean age	0.3284	1	0.0778	17.8147	0.0001*
Mean % dead branches per indiv.	0.067	0.049						
			Mean age	0.0049	1	0.0050	0.9559	0.3347

Table 5 (cont.)

Response Variable	R^2	R^2 Adj.	Effects	Parameter Estimate	DF	SE	f-ratio	p>ChiSq.
Mean height	0.800	0.788						
			Mean age	0.1499	1	0.0315	22.5811	<.0001*
			Age of oldest individual	0.0404	1	0.0185	4.7985	0.0333*
			Site openness	-4.1614	1	3.8509	1.1678	0.2851
Mean age	0.392	0.329						
			Soil quality (PCA)	0.6388	1	0.4467	2.0454	0.1625
			Soil moisture	14.8084	1	7.1705	4.265	0.0454*
			Canopy openness	-18.6767	1	28.3033	0.4354	0.5135
			Community type	A: 1.0556	2	A: 2.0459	2.1889	0.1444
				B: 1.6350		B: 1.0929		
Age of oldest individual in plot	0.520	0.481						
			Community type	A: 0.8067	2	A: 2.0459	0.7648	0.4730
				B: 1.6914		B: 1.8322		
			Soil moisture	25.0234	1	8.1805	9.3569	0.0036*
			Canopy openness	-12.4314	1	44.8203	0.0769	0.7827

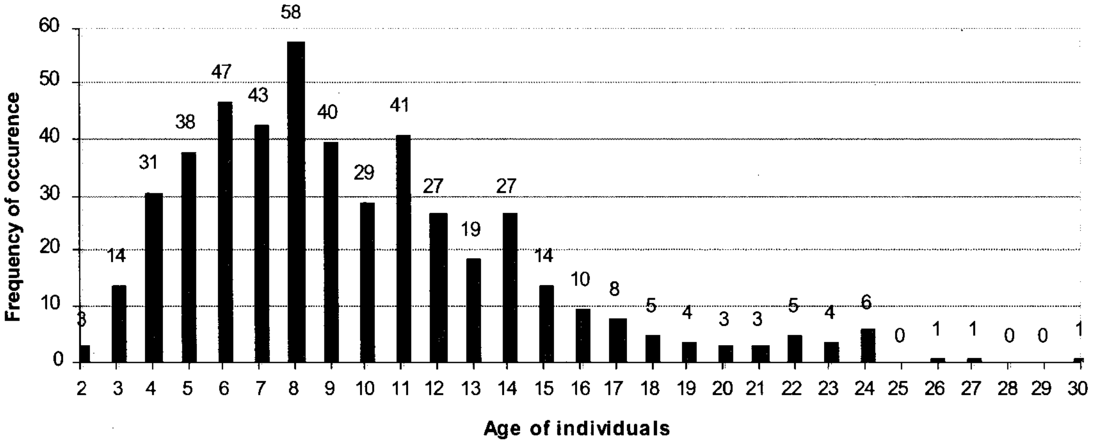


Figure 4: Age structure of *Rhamnus frangula* in 63, 78.5m^2 plots in Durham, NH.

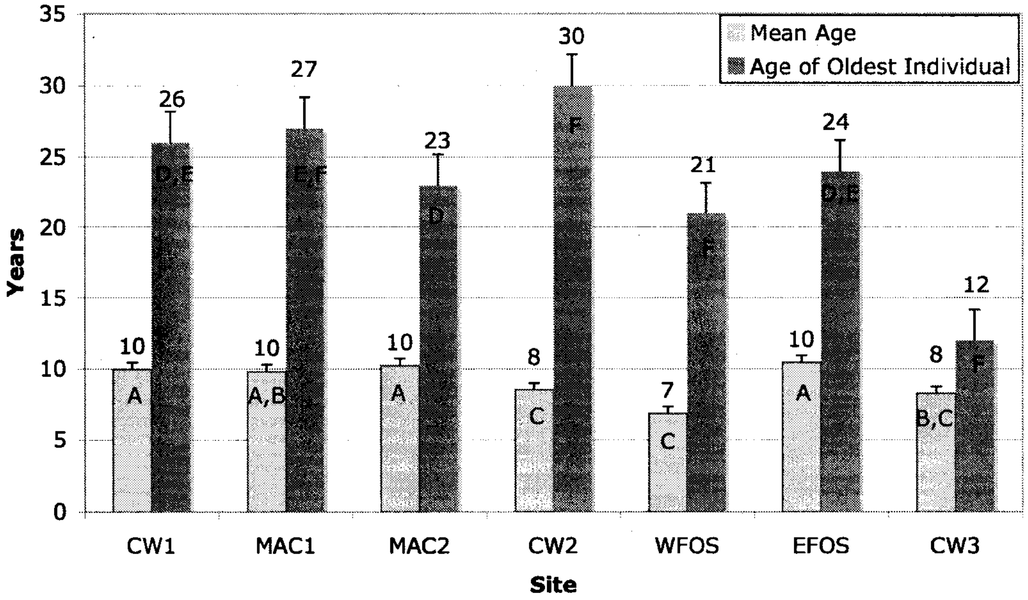


Figure 5: Mean age and age of oldest individual at each site. Error bars indicate standard error. Similar letters signify no significant difference between sites. The letters seem misleading due to the large variation in ages found at all of the sites.

Table 6: Comparison of growth patterns of *R. frangula* across sites and topographic positions. Ratios <1 indicate growing populations.

Site	Topo	Avg. #stems ≥1 m per 100 sq.m	Avg. #stems <1 m per 100 sq.m	≥1 m:<1 m	Age of oldest stem ≥1 m
CW1	Top	12	14	0.857	24
	Middle	14	16	0.875	17
	Bottom	95	65	1.462	26
MAC1	Top	4	45	0.088	10
	Middle	6	38	0.157	19
	Bottom	104	10029	0.010	27
MAC2	Top	166	705	0.235	21
	Middle	151	1655	0.091	23
	Bottom	189	7353	0.026	23
CW2	Top	0	0	0	-
	Middle	0	0	0	-
	Bottom	891	2801	0.318	30
WFOS	Top	4	123	0.033	9
	Middle	0	19	0	-
	Bottom	18	1645	0.011	21
EFOS	Top	14	6854	0.002	23
	Middle	106	3028	0.035	23
	Bottom	56	2488	0.022	24
CW3	Top	4	7	0.571	11
	Middle	0	6	0	-
	Bottom	23	45	0.511	12

III D. Variables Affecting RF Abundance and Morphological Characteristics

In those plots that contained *R. frangula,* density of stems ≥1 m in height ranged from 1 individual per 100 m^2 to 477 individuals per 100 m^2 and averaged 29 individuals per 100 m^2. Log (density of stems ≥1 m in height) was regressed against the six site-related independent variables as well as mean age and age of oldest individual. The best fitting model included a positive correlation with both soil quality and age of the oldest individual (Table 5, Figure 5). Site accounted for 45.6% of the total residual variance in this model. Stems of *R. frangula* <1 m in height ranged in density from 1 individual to 9454 individuals per 100 m^2. Log (density of stems <1 m in height) was regressed against the six site-related independent variables along with mean age, age of oldest individual, and log (density stems ≥1 m) (Table 5). Of these, log (density stems ≥1 m) and age of oldest individual showed strong positive correlations with log (density of stems <1 m in height) (Figure 5). A positive correlation was also found between log (density of stems <1 m in height) and canopy openness; however, this relationship had a P-value of greater than 0.05 (Table 5). Site accounted for 51.3% of the total residual variance in this model.

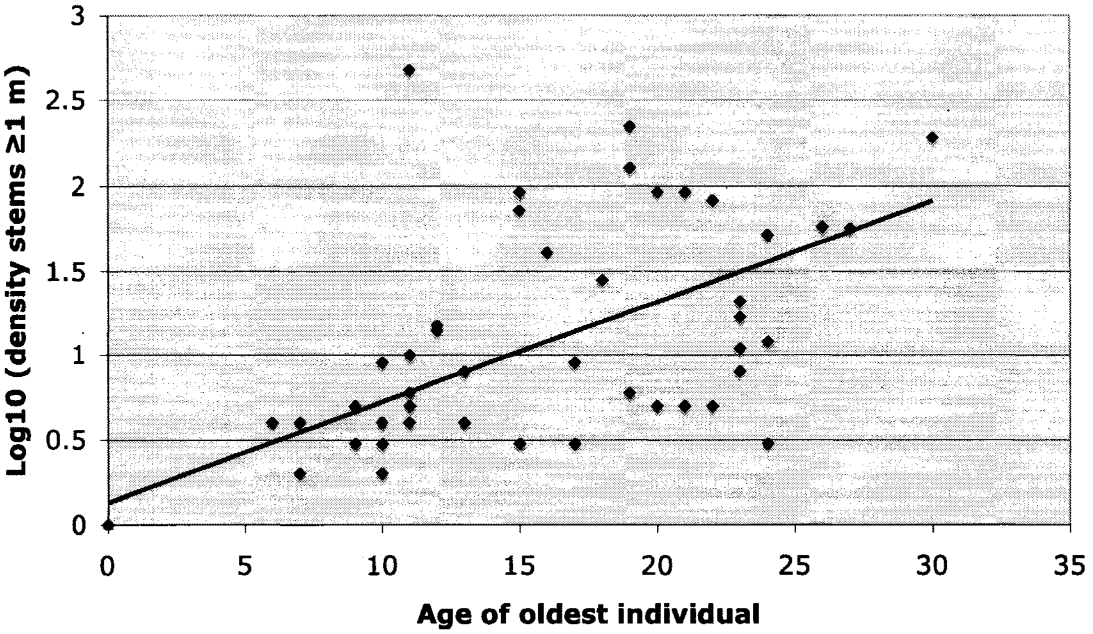


Figure 6a: Comparison of R. frangula ≥1 m density (log_{10} scale) and time since plots were invaded. Plots in which R. frangula arrived earlier (i.e. have higher ages for their oldest individuals) also have higher stem densities.

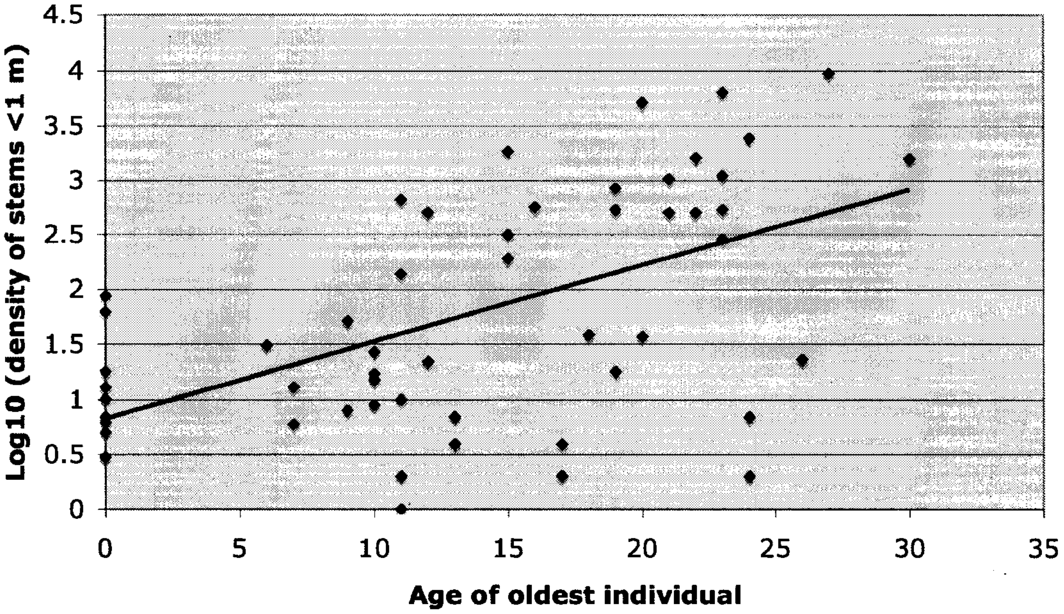


Figure 6b: Comparison of R. frangula <1 m density ($\log_{10}$ scale) and time since plots were invaded. Plots in which R. frangula arrived earlier (i.e. have higher ages for the oldest individuals also have larger density of stems. Plots that only contained R. frangula <1 m appear to have an oldest age of zero. This is because the ages of stems <1 m were not determined.

Diameter of *R. frangula* ranged from 2 mm to 149 mm. Mean diameter was 13.4 mm. Mean diameter of *R. frangula* was regressed against the six site-related independent variables along with log (density stems ≥1 m), log (density stems <1 m), number of stems per individual, mean age, and age of the oldest individual. Only log (density stems ≥1 m), age of oldest individual, and soil moisture were removed from the model. Site accounted for 2.9% of the total residual variance. Multiple linear regression showed positive associations between diameter and the middle topographic position, community type A, log (density stems <1 m), number of stems per plant, and mean age. Negative associations were found between diameter and the bottom topographic position, soil quality, canopy openness, and community type B (Table 5). In this model, only two variables, log (density stems <1 m) and mean age, had P-values of less than 0.05.

The tallest stem of *R. frangula* was between 12-13 m tall. Mean height of individuals ≥1 m tall was 2.39 m. Mean height was regressed against the six site-related independent variables along with log (density stems ≥1 m), log (density stems <1 m), number of stems per individual, mean age, and age of the oldest individual. Site accounted for 24.8% of the total residual variance. The best fit regression model included a strong, positive relationship between height and mean age and age of the oldest individual (in both cases, $P<0.05$). A negative correlation between height and site openness was also shown in the model, however this correlation had a very high P-value (Table 5).

Individuals of *R. frangula* in this study had anywhere from 1 to 130 stems per individual plant, with a mean of 3.83 stems. Mean number of stems was regressed against the six site-related independent variables as well as log (density stems ≥1 m), log (density stems <1 m), mean age, and age of the oldest individual. Only site, overstory community type and mean age were retained in the final model. Site accounted for 17.1% of the total residual variance. The results of multiple linear regression showed a significant positive correlation with mean age ($P<0.05$) (Table 5). A positive correlation was also found between number of stems and community type B. Community type A was negatively correlated with number of stems per plant. Although it remained in the model, community type had a high p-value (Table 5).

Percent dead branches per individual varied from 0% to 50%. The mean was 9.65%. Mean percent dead branches per individual was regressed against the six site-related independent variables along with log (density stems ≥1 m), log (density stems <1 m), mean age, and age of the oldest individual. The adjusted R^2 for this model was extremely small (0.049), and although the best fit regression model showed a positive correlation between percent dead branches and mean age, the P-value for this relationship was very high (Table 5). In this model, site accounted for 3.2% of the total residual variance.

CHAPTER IV

DISCUSSION

Based on maximum stem ages, invasion by *R. frangula* into the study area probably occurred more than 30 years prior to sampling (i.e., before 1975), assuming that the oldest individual did not occur within one of the study plots. Frappier et al. (2003b), working in College Woods close to my site CW2, estimated that *R. frangula* first invaded about 43 years prior to my sampling (ca. 1962). If we assume a low rate of mortality for buckthorn, then because the number of stems increased from older to younger age classes (from about the 20 yr class to the 8 yr class), one might infer a growing population of *R. frangula* over this time. Although the age structure diagram infers that the population of *R. frangula* under the age of 8 is declining, this is likely an artifact of my sampling scheme. Many of the individuals under age 8 probably fell into the < 1 m height class where ages were not determined. While I did not age stems < 1 m, the significant height-age relationship in Figure 3b suggests that short plants would generally be younger than tall ones. Moreover, T. Lee (personal communication) has aged stems 0.5 -1.0 m in height at two sites on nearby UNH properties. He found that stems < 1 m averaged 4.0-6.5 years in age, and that plants < 1 m in height were significantly younger than those ≥ 1 m. If plants < 1 m tall in my sites are in fact younger than taller plants, then the continued growth of the *R. frangula* population in my study sites is suggested by the fact that the ratio of small stems (< 1 m) to large stems (≥ 1 m) was > 1 in most plots.

It is difficult to evaluate the effect of the silvicultural activities that took place in these stands several decades ago. It is possible that the opening of the forest canopy by selective harvesting or thinning encouraged the colonization and establishment of *R. frangula*. Vague and imprecise harvesting records, combined with the inability of my age data to provide exact dates for the origin of populations, make it impossible to associate *R. frangula* establishment with time of disturbance. However, today these sites are located within forest ecosystems that have forest canopies that are continuous and have been for some time. The age structure data strongly suggest that, *R. frangula* has continued to recruit over the years. In heavily disturbed ecosystems such as a clear cut, large patch cut, or old field, we would be more likely to see a pulse of recruitment followed by little or no recruitment (Hunter and Mattice 2002, Yates et al. 2004). Some of the prior cutting in my study sites may have provided a beneficial disturbance for *R. frangula*, but it is important to note that recruitment is *still* occurring, despite the fact that these forest canopies are now nearly closed.

The implication of the observed invasion pattern for management is that, while invasion is occurring more slowly in intact forests, it is nonetheless occurring in places that have not traditionally been monitored for *R. frangula* by land managers. Few other invasives have the ability to invade intact forests (Webster et al. 2006); most remain more conspicuously in disturbed areas or forest edges (e.g., Searcy et al. 2006). Searcy et al. (2006) found only two other invasive plants with higher proportions of their total populations found in undisturbed forested habitats than *R. frangula*. Fourteen percent of *R. frangula* individuals were found in undisturbed forests, the remaining 86% were located in disturbed areas or pond margins. *Eleagnus umbellata* and *Euonymus alatus* were also found in undisturbed forest, with 32% and 20% of their total populations found within them, respectively.

That site was a significant factor associated with presence of *R. frangula* was difficult to interpret. Site was considered a random effect in this study, so it was of little help in predicting the likelihood or timing of future *R. frangula* invasions. The most likely explanation for the significance of site in predicting the presence of *R. frangula* in some plots but not others is dispersal. Seeds were perhaps available in some plots, but had not yet arrived at others; some sites (e.g., CW2, Table 4) had more of the latter than others. Plots in which *R. frangula* arrived earlier also had higher densities than those that were more recently invaded (Figure 5). Without further investigation, it is unclear whether this 'site effect' was due to growing local populations, an influx of dispersing propagules from outside the site, or a combination of both.

Site accounted for a large proportion of the total residual variance in some of the linear regression models, but a very small percent in others. Site accounted for less than 3% of the residual variance in the model describing diameter. In the models describing age of the oldest individual, and densities of both size classes, site accounted for at least 30% of the residual variance. In these latter cases, it is possible that site might be representing some unmeasured factor in the environment, such as soil nitrogen concentration or seed rain.

Community type also predicted the presence or absence of *R. frangula* within a plot, but did not predict density. Specifically, community type C, dominated by *Tsuga canadensis* and *Betula lenta*, generally seemed impervious to *R. frangula* invasion. Many studies have shown reduced plant diversity beneath *T. canadensis* (Beatty 1984, Woods 1984, Howard and Lee 2003), and this may be the result of more than one mechanism. The high concentrations of tannins in *T. canadensis* bark slow the rate of litter decomposition allowing for the formation of a thick and highly acidic forest floor (Finzi et al. 1998) and inhibiting seedling establishment. In addition, *T. canadensis* dramatically lowers light levels beneath it (Beatty 1984, Howard and Lee 2002). All of this might seem promising for old-growth *T. canadensis* stands; however, the decline of *T. canadensis* throughout the east due to hemlock woolly adelgid (*Adelges tsugae*) infestation will likely make these plots susceptible to *R. frangula* invasion in the future. If *T. canadensis* in Durham, NH declines, it will most likely be replaced by *Betula lenta* along with *Acer rubrum* and *Quercus* species (Orwig 2002). Although this community type was not encountered during this study, Orwig and Foster (1998) found that an increase in exotic species occurred following *T. canadensis* mortality due to hemlock wooly adelgid in forest stands in Connecticut.

Topographic position also predicted the presence or absence of *R. frangula.* Fruits not carried away by birds will likely fall and germinate very near the parent (Frappier et al. 2003b), or directly downhill from the parent. Hampe (2004) showed that secondary dispersal of *R. frangula* fruits occurred via seasonal flooding. Although this theory was not tested in this study, it could explain the increased presence of *R. frangula* in lower topographic positions. Inventories or control efforts can be focused on *R. frangula* populations at lower topographic positions.

Both presence of *R. frangula* and density of *R. frangula* ≥1 m in height could be explained by soil quality. *R. frangula* were more likely to be found, and at higher densities, in richer soils with higher clay and nutrient contents. Similarly, Von Holle and Motzkin (2007) found a positive relationship between soil calcium levels and invasive species richness and Greenberg et al. (1997) found a connection between finer textured soils and species richness of invasive plants. Lundgren et al. (2004) extended this finding to include both richness and percent cover of invasive plants. However, the association of *R. frangula* with fertile soils contradicts the findings of Frappier et al. (2003a) who found that neither soil texture nor pH related significantly to *R. frangula* basal area. This difference in results is most likely attributed to the difference in scale between the two studies. Frappier et al. studied within-site predictors of *R. frangula* basal area (including soil variables). In contrast, my study studied *R. frangula* characteristics across the landscape, and thus aimed to maximize variation in physical factors.

Density (of either size class) was explained by time since invasion (age of the oldest stem in each plot); as the age of the oldest individual in a plot increases, the density of large and small stems will increase. Moreover, the density of small stems (< 1 m) was predicted by the density of large stems (≥ 1 m). These relationships are likely due to local population dynamics. Hampe (2004) found that *R. frangula* seedfall density at a given sampling point was positively correlated with distance to the nearest tree as well as that tree's crop size. Thus, in my study, a progression occurred: the longer *R. frangula* was present in a plot, the number of large stems had increased, which produced more seeds, which resulted in a greater the number of small stems that were present. Densities of *R. frangula* do not seem to reach a plateau as time since invasion increases (Figure 5) and this suggests that maximum *R. fragula* densities have yet to be reached on these sites. Thus, when both size classes are accounted for, *R. fragula* may be capable of reaching densities that exceed of 9510 individuals per 100 m^2 (Figure 5).

Both mean age of *R. frangula* per plot and age of the oldest *R. frangula* individual were most strongly predicted by soil moisture. A number of invasives show preference for moister habitats. Lundgren et al. (2004) found that invasive species richness increased as soil moisture increased. Stohlgren et al. (2002) found higher numbers of invasive species in riparian areas as well as areas with higher amounts of precipitation. Thus, it is likely that upon arrival, *R. frangula* germinated first in wetter areas, accounting for the higher ages in plots with higher soil moisture. Soil moisture did not, however, predict the presence of *R. frangula*. While dry soils do not preclude invasion, they may delay it for sometime, perhaps until an adequate seed source is established at a more favorable site nearby (Von Holle and Simberloff 2005).

It should be noted that canopy openness remained in several of the regression models [presence of *R. frangula*, log (density of *R. frangula* <1m), mean diameter, mean height, mean age, and age of oldest individual]. With the exception of log (density of *R. frangula* <1 m), canopy openness had a negative relationship with the other variables. The negative association with diameter and height along with its positive association with log (density of *R. frangula* <1m) suggests that larger canopy openings will promote not the growth of existing plants, but large numbers of juvenile *R. frangula*. The negative association with mean age and age of oldest individual suggest the opposite. In addition to this disagreement, the P-value was quite high in all models, ranging from 0.09 to 0.78. While AIC calculations deem that this variable improves each of these models enough for it to remain, it should not be over-interpreted. In each model, there were better predictors than canopy openness. It is possible that canopy openness is too strongly related to another independent variable to appear as a strong predictor on its own; however, this is unlikely as no other single variable consistently appears in the models in which canopy openness remains. Another possibility is that there simply was not a wide enough range in the canopy openness data.

The morphological characteristics of *R. frangula* plants (height, diameter at base, number of stems, percent of dead stems) were all positively correlated with age. As individuals age, they are more likely to be larger be taller, with larger diameters, more stems per plant, and more likely to exhibit dieback. It is important to note, however, that the model describing mean percent dead branches per individual had an extremely low adjusted R^2 (0.049). We can therefore safely assume that percent dead branches per individual cannot be predicted by any of the variables that were measured in this study.

With the exception of mean diameter, soil quality was not associated with any of the morphological characteristics of *R. frangula*. As mean diameter was shown to decline with soil fertility (while plant density tended to increase), one might infer that R. frangula will tend to produce more individuals on high quality soils, rather than fewer, more robust individuals.

A single individual of *Rhamnus frangula* is able to produce as many as 1804 fruits in a single growing season, each containing 2-3 seeds (Godwin 1943). This is concerning in light of Von Holle and Simberloff's (2005) recent findings that propagule pressure from invaders is able to overwhelm whatever ecological resistance a forest has to invasion. In tandem with the ability of *R. frangula*'s tendency to form very dense stands in a variety of site conditions, the future of these study sites appears bleak. The continuing growth of *R. frangula* within these study sites could mean changes in forest composition, suppression of native tree and herb species (Frappier et al. 2003a, 2004) or alteration of successional patterns (Collier 2002). Additionally, Webster et al. (2006)

speculate that the simplification of natural plant communities due to dense stands of woody invasives could have unforeseen cascading effects that compromise the ability of forests to provide ecological services.

V. CONCLUSION

Rhamnus frangula is capable of invading and forming dense populations in white pine-hardwood forests of southeastern New Hampshire. While disturbance may or may not be critical to initial stand entry, *Rhamnus frangula* can apparently continue to recruit even with a high degree of forest canopy closure. Although relatively intact forests may not be as susceptible to invasion as heavily disturbed (i.e., clear-cut) stands they are nonetheless worth monitoring for invasives such as *Rhamnus frangula* that are able to recruit without major disturbance. Within these forested ecosystems, certain attributes of the physical environment can give clues to the likelihood or intensity of *R. frangula* invasion. Lower topographic positions within the landscape are significantly more likely to be or become invaded by *R. frangula.* The more fertile and moist soils that are generally associated with lower slopes favor establishment of *R. frangula,* so populations in these areas tend to be older and more dense, with larger individuals, and therefore more likely to be problematic for managers. In contrast, buckthorn may be excluded from hemlock-oak stands on uplands and these stands may require less attention from managers. In general, however, because densities of all size classes increased with time since invasion, we can assume that, without intervention, populations of *R. frangula* in the study area will continue to grow over time.

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