2006

Regeneration Strategies of Japanese Barberry (Berberis thunbergii DC.) in Coastal Forests of Maine

Jennifer D'Appollonio

REGENERATION STRATEGIES OF JAPANESE BARBERRY (*BERBERIS THUNBERGII* DC.) IN COASTAL FORESTS OF MAINE

By

Jennifer D'Appollonio

B.S. University of Maine at Machias, 1997

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

(in Forestry)

The Graduate School

The University of Maine

August 2006

Advisory Committee:

William H. Livingston, Associate Professor of Forest Resources, Advisor

Robert G. Wagner, Henry W. Saunders Distinguished Professor in Forestry

Alison C. Dibble, Adjunct Assistant Professor, Department of Biological Sciences

LIBRARY RIGHTS STATEMENT

In presenting this thesis in partial fulfillment of the requirements for an advanced degree at The University of Maine, I agree that the Library shall make it freely available for inspection. I further agree that permission for "fair use" copying of this thesis for scholarly purposes may be granted by the Librarian. It is understood that any copying or publication of this thesis for financial gain shall not be allowed without my written permission.

Signature: _____

Date: _____

REGENERATION STRATEGIES OF JAPANESE BARBERRY (*BERBERIS THUNBERGII* DC.) IN COASTAL FORESTS OF MAINE

By Jennifer D'Appollonio

Thesis Advisor: Dr. William H. Livingston

An Abstract of the Thesis Presented
in Partial Fulfillment of the Requirements for the
Degree of Master of Science
(in Forestry)
August 2006

Japanese barberry (*Berberis thunbergii* DC.) has become invasive in forests of the northeast since its U.S. introduction as an ornamental shrub in 1875. This non-native invasive species can occupy a wide range of environmental conditions, has a longer growing season than most native species, multiple methods of reproduction, and forms thickets under which few other plants can persist. Effective control strategies and management of invaded forest stands would be improved by knowledge of how Japanese barberry regenerates in the forest, whether it forms a seed bank, and to what extent it impacts other plant species. This study focused on the following questions: 1) Which species successfully regenerate under a Japanese barberry overstory? 2) How does forest canopy cover affect the regeneration of Japanese barberry and other species? 3) Does a portion of Japanese barberry seeds from previous years remain viable in the soil for more than one growing season?

Data were collected from two coastal sites in Maine (Monhegan Island and Wells Research Reserve) that had Japanese barberry thickets under a closed tree canopy. The

Japanese barberry overstory was clipped in 1 m radius plots in fall 2004 and spring 2005. At these times and in fall 2005, data were collected in the field, soil samples were taken from the plots for soil incubation studies, and a seedling emergence test was conducted on seed from the study sites which was compared to a commercial source.

Japanese barberry seedlings were the most abundant plant group to regenerate under a Japanese barberry canopy with a maximum average 29.3 stems/m^2 at Monhegan Island, after which the next most abundant plant group, understory herbs, were 21.4 stems/m^2. At Wells Research Reserve, Japanese barberry seedlings had a maximum average of 0.4 stems/m^2 and understory herbs had a maximum of 6.8 stems/m^2. Only the Monhegan Island plots had sufficient non-barberry species regeneration to perform statistical analyses. Tree and shrub regeneration were too sparse to analyze statistically at either site; 50-80% of plots lacked seedlings. Density of understory herbs was reduced by forest canopy cover ($P = 0.003$) as was Japanese barberry sexual regeneration ($P = 0.003$) but not necessarily vegetative sprout density ($P = 0.058$). Soil incubated in a greenhouse yielded few Japanese barberry seedlings beyond those observed in the field, while a large seed bank existed for other species. A seedling emergence test showed no significant difference between 2004 commercial seed and seed from the study sites ($P = 0.218$), while mean seedling emergence of both were significantly higher than 2003 commercial seed ($P < 0.001$). Japanese barberry seed viability declined significantly in the second growing season after seed drop, indicating that Japanese barberry generally germinates the growing season following seed maturation and may not have a viable seed bank beyond that time. The lack of a seed bank will aid management of this species after removal at invaded sites.

ACKNOWLEDGEMENTS

I would like to take this opportunity to thank my advisor, Dr. William H. Livingston, for his invaluable mentoring throughout the development of this thesis, as well as committee members Dr. Robert G. Wagner and Dr. Alison C. Dibble for their guidance and professional critiques. I would also like to thank the Monhegan Associates, Inc. and the Wells National Estuarine Research Reserve for their commitment to forest health and for allowing me to conduct research on their properties. Dr. Harry and Lucia Miller, my gracious hosts on Monhegan Island and Mike Martell, my good friend and host when in Wells made research possible on a strict budget. I am deeply grateful for their generosity.

My assistants Matt Kasson, Chad Buie, Brian Curry and Mike Puleo should be commended for their hard work in the field while inundated with blackflies, mosquitoes and ticks, as well as for their help in the greenhouse. Many thanks go to Stacey Trosper, Agata Chomicz and Blanka Peridot for their assistance in the greenhouse. Thanks also go to Brad Libby (Manager, UM Horticultural Facilities) for his advice and for allowing me the use of the Roger Clapp greenhouses. For technical assistance I would like to acknowledge Dr. William Halteman (Dept. of Mathematics) for his help with statistical analysis and Dr. Mike Day (Dept. of Forest Ecosystem Science) for other technical advice. Last but not least, I wish to thank my colleagues, friends and family for their support, without which I would not have succeeded.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Chapter 1

INTRODUCTION

The following thesis is divided into two chapters. The first chapter is a literature review of the history, autecology and control of Japanese barberry (*Berberis thunbergii*) in the U.S. Chapter two describes results of a study examining regeneration of Japanese barberry in coastal forests of Maine.

JAPANESE BARBERRY LITERATURE REVIEW

Invasive Plant Species

Today's problems regarding resource conservation, management, and biodiversity stem from several anthropogenic factors, including habitat loss, inappropriate resource use, pollution, and the introduction of non-native invasive species (Coblentz 1990). Unlike the former issues, which can be corrected over a span of years, populations of non-native invasive species tend to be permanent components of habitats once they become established (Coblentz 1990). Non-native invasive plants threaten biodiversity, habitat quality, and ecosystem functions, as well as agricultural and silvicultural economics via loss of revenue and high costs of invasive control programs (Silander and Klepeis 1999; Harrington et al. 2003). On January 18, 2001, the National Invasive Species Council approved a National Invasive Species Management Plan (Harrington et al. 2003). The Council defines an invasive species as "…a species that is both not native to the region or area and whose introduction causes or is likely to cause harm to the economy, the environment, or harm to animal or human health" (Clinton 1999). The Plan is updated every two years with the last update completed in July 2005.

In forests of the Northeast, anthropogenic disturbance history may be correlated with invasion by non-native invasive species (Niering 1998). Introduced species generally follow a "Tens Rule", which states that one in ten introduced species will escape domestication, one of those ten will become naturalized, and only one of those ten will become invasive. A major exception to the rule is the introduction of species intended for cultivation, because those species are selected for their ability to perform well in the region into which they are introduced. Introduced cultivars of ornamental species are often selected for their ability to survive in adverse conditions, which means that they can grow almost anywhere they are planted (Harrington et al. 2003).

Several issues confound the identification and management of non-native invasive plant species. There are few generalities regarding reproductive, life-history, and/or physiological characteristics common to all taxa of invasive species, although these characteristics have been successful in predicting invasiveness within a taxon (Rejmánek and Richardson 1996; Ehrenfeld et al. 2001). There are also no determining habitat characteristics generally correlated with susceptibility to invasion. Furthermore, these explanations do not take into account that the complex interactions of plants and soils may influence invasiveness (Ehrenfeld et al. 2001). There are, however, some factors that have been linked to an increased possibility of a non-native invasive plant invasion. Site factors such as presence of a seed source, disturbance (including changes in type, frequency and intensity of disturbance and associated increases in light, water and nutrient availability), species richness, light availability, and overstory species composition (Hobbs and Huenneke 1992; Cassidy et al. 2004). Plant-related factors such

as a wide native range and proven invasibility elsewhere can help predict invasions in the U.S. (Harrington et al. 2003).

Invasion into intact closed-canopy forest ecosystems is typically less common than in open (e.g., grassland) or disturbed habitats (Ehrenfeld 1997; Kourtev et al. 1998). One invasive species that has successfully invaded undisturbed forest is the introduced ornamental shrub Japanese barberry (*Berberis thunbergii* DC.) in the family Berberidaceae (Fernald 1950; Ehrenfeld 1997; Kourtev et al. 1998). Although it has been identified as an immediate serious threat only within the last ten to twenty years, Japanese barberry has been spreading throughout the U.S. since the late 1800s with a drastic increase in populations since approximately 1980 (Figure 1) (Silander and Klepeis 1999). In spite of the fact that Japanese barberry was introduced over 125 years ago and is becoming a major threat to native systems, little is known or published about the basic biology or ecology of the species (Silander and Klepeis 1999). Japanese barberry continues to be one of the most widely planted non-native shrubs in the U.S., and nurseries continue to market cultivars to the public (Harrington et al. 2003).

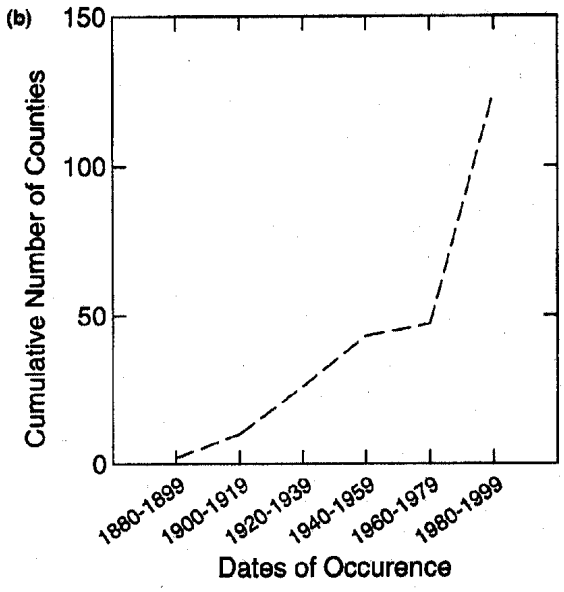

Figure 1. Spread of Japanese barberry by county in the northeast 1880-1999. (Silander and Klepeis 1999)

History of Japanese Barberry in the United States

Japanese barberry was first introduced to the United States when seed was sent from Russia to Boston's Arnold Arboretum in 1875. Specimens were subsequently planted at the Arboretum and at the New York Botanical Garden in 1896 (Ehrenfeld 1997; Silander and Klepeis 1999). Some sources list the introduction date as 1864 (Rhoads and Block 2002). The species was not marketed as an ornamental until after 1900, and did not appear to become naturalized until 1910 and later. Around 1918 the introduced common barberry (*Berberis vulgaris*) became subject to eradication efforts because it is an alternate host to stem rust of wheat (*Puccinia graminis*). This prompted the US Department of Agriculture (USDA), among others, to begin encouraging the substitution of Japanese barberry as a landscape feature as it is immune to *P. graminis* (Silander and Klepeis 1999; Mehrhoff et al. 2003). By 1920 Japanese barberry had become naturalized in several suburban and rural vacation areas. It escaped cultivation

on Nantucket and Isle au Haut before 1910 and in the Berkshires of western Massachusetts and the Mt. Monadnock region of New Hampshire before 1920. By the 1930s populations had spread in concentric circles around Boston and New York City, although it was still rare in northeast Connecticut in the 1950s (Silander and Klepeis 1999). Since the introduction of Japanese barberry many cultivars have been developed and the species is currently invasive throughout most of the northeast (Figure 2) (Silander and Klepeis 1999).

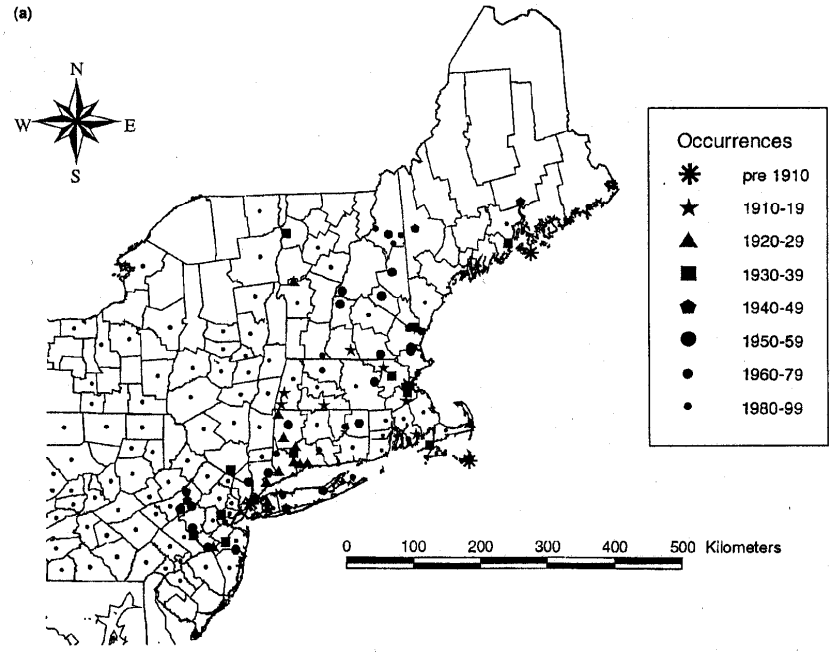

Figure 2. Distribution of Japanese barberry in the northeast pre 1910-1999.

(Silander and Klepeis 1999)

Over time Japanese barberry has spread away from sites influenced by people into intact forests (Ehrenfeld 1997). In a study conducted in Farmington, Maine (Barton et al. 2004) the authors concluded that Japanese barberry is currently naturalized but not fully invasive in the local area, and the potential for forest invasion was identified. A 2004 study by Lundgren, Small and Dreyer found that Japanese barberry in a Connecticut

forest was positively correlated with human population and road presence and size (e.g., unbroken forest vs. trail/dirt road/paved road). Japanese barberry has become widespread in the U.S. in the last thirty years and was recognized as invasive by the 1970s. Today Japanese barberry remains arguably the most widely planted non-native species in the U.S. (Kourtev et al. 1998; Silander and Klepeis 1999).

General Autecology

Description

Japanese barberry is a deciduous shrub that grows 0.5-1.5 m (3-6') high (Fernald 1950; Rhoads and Block 2002; Maine Natural Areas Program [MNAP] 2004); some accounts list the maximum height as 2.4-2.5 m (8-8.2') (Mehrhoff et al. 2003). Seedlings can grow two to four feet in one growing season (Tennessee Exotic Pest Plant Council [TNEPPC] 2004). The numerous arching branches are glabrous, brown, ridged below the node and usually have simple spines, although they can have two to three-pronged spines (Fernald 1950; Mehrhoff et al. 2003). The inner bark and wood are yellow (Fernald 1950). Leaves are alternate, entire, spatulate to narrowly ovate, and vary in color by cultivar from green to gold to reddish purple; in the fall the foliage turns orange and red (Fernald 1950; Rhoads and Block 2002). The flowers are pale yellow with six concave petals and round sepals, six stamens that spring forward when touched at the base, and a circular depressed stigma (Fernald 1950). Flowers are solitary or in sessile umbels of two to four, arranged along the upper portion of the stem, and are about 8 mm long (Fernald 1950). One or typically two seeds are contained in bright red berries which are

7-9 mm long, solid and dry, elliptic to globose, and persisting on the stem throughout winter (Davis 1927, Dirr and Heuser 1987, Mehrhoff et al. 2003).

All parts of the shrub contain the alkaloid berberine (Rhoads and Block 2002), which is an isoquinolone alkaloid found in members of the genera *Phellodendron*, *Berberis* and *Coptis*. It has been used as a dye, internally as a treatment for intestinal and lung infections, gastroenteritis, cholera, and bacillary dysentery and topically for skin diseases. Recent research has explored the potential of berberine to reduce cholesterol, blood pressure and blood sugar (Dharmananda 2005).

Japanese barberry differs from the European or common barberry (*Berberis vulgaris*) in that the latter has toothed leaves, three-pronged spines, and raceme inflorescences. The native Allegheny barberry (*Berberis canadensis*) also has toothed leaves and three-pronged spines, but has a subumbelliform raceme inflorescence (Fernald 1950; Rhoads and Block 2002). Allegheny barberry has a range extending from Pennsylvania south to Alabama and west to Missouri (USDA 2006).

Japanese barberry shrubs consist of multiple stems ranging from <50 cm long (most stems) to highly branched stems over 2 m long and over 1 cm in basal diameter (Ehrenfeld 1999; Ehrenfeld et al. 2001). Estimates of the aboveground standing-crop biomass range from 4 to 44 times the mean biomass of native *Vaccinium* understories (Ehrenfeld et al. 2001). Old stems die after a few years and are replaced by new basal sprouts; therefore, aging an individual is difficult even if it has been present for decades (Silander and Klepeis 1999). Population densities appear to vary more in size distribution rather than in the number of individuals, with higher stem densities achieved through many small plants as opposed to fewer large plants. In sparse populations plants

are distributed evenly, while in medium to dense populations plants distribute randomly or slightly clumped; stems of individuals are highly clumped except in sparse populations (Ehrenfeld 1999). Only small plants and short stems generally suffer mortality (>90% for seedlings); once a plant reaches an average of three or more stems it may decrease in volume and height but usually will not die. Most plants do not experience a net change in size from year to year, while a small fraction increase and a smaller fraction decrease in size. Thus, denser populations have a larger range of individual sizes. Differences in density are correlated to the frequency of medium and large plants (Ehrenfeld 1999).

The USDA (2006) lists the minimum rooting depth as 46 cm (18"). However, Kourtev, Ehrenfeld and Häggblom (2002a) documented that Japanese barberry has a large shallow fine root system with most roots located densely in the surface 5-10 cm of soil. Japanese barberry produces about three times as much root biomass as native *Vaccinium* (Ehrenfeld et al. 2001). Although it is able to resprout from the root collar, the species is not fire resistant (Silander and Klepeis 1999; USDA 2006).

In many invaded forests, Japanese barberry individuals are scattered, but this species can form dense thickets even under a closed canopy (Ehrenfeld 1999). No other understory shrub species and few herb species grow under the crown area of a Japanese barberry thicket (Kourtev et al. 1998; Kourtev et al. 2002a). Conversely, Silander and Klepeis (1999) found that 92% of Japanese barberry seedlings were found underneath or within a meter of the canopy of a mature shrub, while several others were found over 50 m from the parent plant.

Phenology and Reproduction

Japanese barberry is one of the first woody species to expand its leaves in spring, as much as a month or more before the canopy trees leaf out, and it retains its leaves after most of the canopy species have dropped their leaves (Silander and Klepeis 1999). Plants bloom from March to May depending on the locale (Silander and Klepeis 1999; Rhoads and Block 2002). Flowers are pollinated by small (e.g., Adrenids) and large (e.g., *Bombus* spp.) bees. Pollen is dispersed in a diminishing proportional removal pattern when a visitor stimulates the anthers to spring forward (Lebuhn and Anderson 1994). The berries mature between May and October, depending on latitude, and are persistent through the winter (Rhoads and Block 2002, Mehrhoff et al. 2003). Seeds germinate in May in the New Jersey area (Ehrenfeld 1999) and in coastal Maine (D'Appollonio, personal observation).

In addition to seed, Japanese barberry reproduces asexually from basal sprouting, rhizomes, stolons, and layering. Larger plants tend to layer more and increase their production of new shoots from year to year by virtue of size, although the contribution to population growth is about a magnitude smaller than that of seeds (Ehrenfeld 1999). Seeds require cold stratification to germinate (USDA 2006) and have a high germination rate (as high as 90%) (TNEPPC 2004). Production and mortality do not appear to be much affected by drought or extreme winters (TNEPPC 2004). Optimal germination occurs when seeds are stratified for several months at 5ºC followed by temperatures alternating between 10ºC and higher (Davis 1927, Silander and Klepeis 1999). An average of 27,040 seeds is contained per pound (USDA 2006). Berry production is higher under high and intermediate light levels than under low light levels. However, the

effect is comparatively small considering the range of light availability assessed (4%-89% light transmittance) (Silander and Klepeis 1999). Overall, the fertility requirements of Japanese barberry are low (USDA 2006).

Little is known about Japanese barberry seed dispersal and patterns, and much of the following information is anecdotal (Ehrenfeld 1999). Berries appear to be removed from Japanese barberry more rapidly under low light conditions; shrubs are mostly denuded by the end of November under low light levels as opposed to January under higher levels (Silander and Klepeis 1999). Although barberry seems to be a low priority food for birds because of its low nutritional content (Ehrenfeld 1999; Silander and Klepeis 1999), seeds are dispersed by birds such as ruffed grouse (*Bonasa umbellus*), bobwhite (*Colinus virginianus*), pheasant (*Phasianus colchicus*), thrushes (*Catharus* spp.), and eastern wild turkey (*Meleagris gallopavo silvestris*) (Ehrenfeld 1997),. Songbirds, including cedar waxwings (*Bombycilla cedrorum*), eastern bluebirds (*Sialia sialis*) and American robins (*Turdus migratorius*) eat the berries occasionally, and deer (*Odocoileus virginianus*) and chipmunks (*Tamias striatus*) may aid in dispersal (Ehrenfeld 1997; Ehrenfeld 1999; Silander and Klepeis 1999). Many berries simply drop to the ground and germinate; seed longevity in the soil bank is unknown (Ehrenfeld 1999).

Habitat and Range

Japanese barberry tolerates a wide range of light conditions. New stem growth and biomass accumulation are significantly correlated with light transmittance, but even at <1% transmittance small plants are able to survive and grow for several months, apparently because the species is able to use sun flecks. Plants capable of seed

production were not found to grow under 3% canopy light transmittance (Silander and Klepeis 1999). In western Massachusetts dense populations occur under canopies with leaf area indices of 2.9-5.5 (Cassidy 2002 as cited in Cassidy et al. 2004). The species can also tolerate a wide range of soil types and moisture conditions (Kourtev et al. 1998). Reproducing individuals are found on sites ranging from poorly drained muck soils (soil moisture >40%) to dry ridges and coarse excessively drained soils (soil moisture <10%). They are rare to absent on extremely dry soils, probably due to seedling mortality (Silander and Klepeis 1999), and tend to be less abundant on northwest facing slopes and in oak-dominated forests (Kourtev et al. 1998; Ehrenfeld 1999). The National Wetland Indicator status for Japanese barberry is UPL (<1% occurrence in a wetland) and FACU (<33% occurrence in a wetland) (USDA 2006).

Japanese barberry appears to be limited in growth and productivity by nitrogen availability but not by rock-derived nutrients such as potassium, calcium, magnesium, manganese, and phosphorous nor by soil acidity (Cassidy et al. 2004). Although Japanese barberry does not fix nitrogen, studies have shown that there is a link between presence of the species and elevated nitrogen and pH levels (Kourtev et al. 1999; Ehrenfeld et al. 2001). Japanese barberry has a pH tolerance range of 5.5-7.2 (USDA 2006), which is decidedly more basic than the levels in conifer forests such as red spruce (*Picea rubens*) (pH 4.0-5.5). Kourtev et al. (1999) found that barberry thickets are associated with fertile basic soils, although this phenomenon may be associated not with pH but with other factors such as nitrification and earthworm activity. Conversely, a study by Ehrenfeld et al. (2001) found that New Jersey sites containing Japanese barberry ranged from pH 4.8-5.8, which is within the pH range associated with conifer forests.

Cassidy (2002 as cited in Cassidy et al. 2004) also documented Japanese barberry in western Massachusetts in soils ranging from pH 4.6-5.8.

Because of the above factors, Japanese barberry can be found in a wide array of habitats. In New England they include abandoned fields, edges, meadows, pastures, railroad rights-of-way, roadsides, vacant lots, yards/gardens, early successional forests, late successional forests, floodplain forests, planted forests, and wetlands (Silander and Klepeis 1999; Mehrhoff et al. 2003). Establishment under closed canopies may be limited by seedling mortality under low (<1% transmittance) light levels (Silander and Klepeis 1999). However, invasion of undisturbed forest has become more common, and is of particular concern in open and regenerating forests in Maine as well as intact forest in Pennsylvania, New York, and New Jersey (Ehrenfeld 1997; Rhoads and Block 2002). The native range of Japanese barberry is in central and southern Japan (Mehrhoff et al. 2003). In the U.S. it is present in New York and every New England state except in the Adirondacks, northern Maine, and northern Vermont (Harrington et al. 2003; Mehrhoff et al. 2003). It has also spread south to Georgia and west to Colorado (Figure 3) (USDA 2006). Its occurrence in Maine is underreported, especially in the southern counties (Figure 4) (USDA 2006; MNAP 2004).

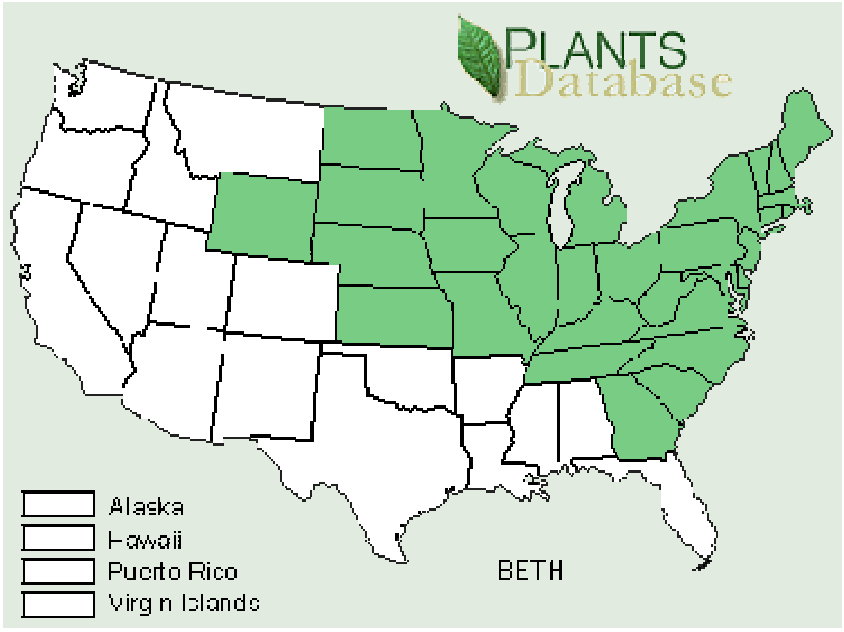

Figure 3. U.S. range of Japanese barberry.

(Shaded area denotes occurrences) (USDA 2006)

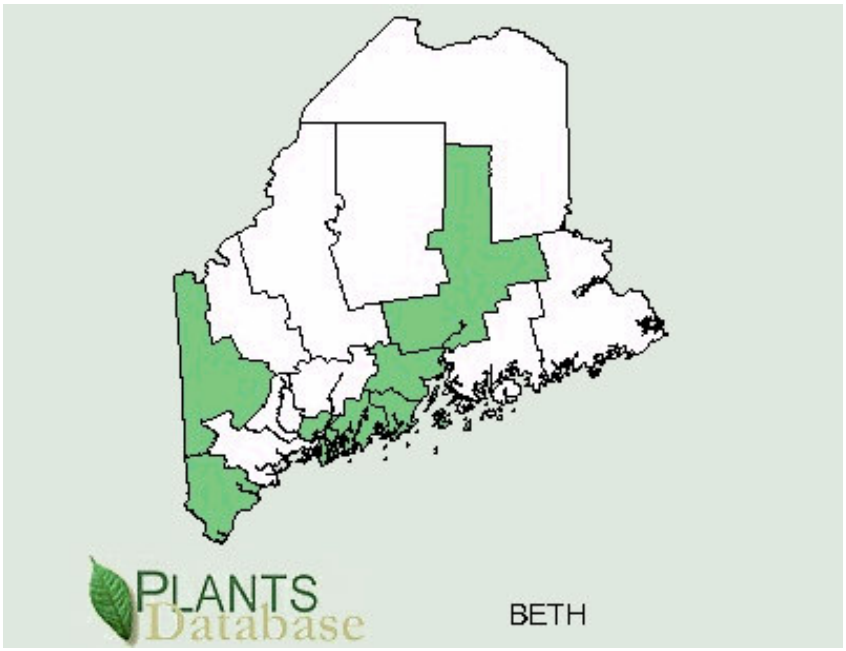

Figure 4. Range of Japanese barberry by county in Maine.

(Shaded area denotes occurrences) (USDA 2006)

Japanese barberry has a minimum temperature tolerance of -33.3°C (-28°F) and requires at least 180 frost-free days to overwinter (USDA 2006). It is hardy in USDA

zones 4-8 (Rhoads and Block 2002). The annual precipitation required for growth is 30 inches/year minimum to a maximum of 60 inches/year (USDA 2006). Although dense continuous stands can be found in the mid-Atlantic states and southern and central New England, in northern climates Japanese barberry is spreading slowly and sporadically (Silander and Klepeis 1999; Barton et al. 2004). Its northern limits in northern New England, the Midwest, Ontario, and the Canadian Maritimes appear to be constrained by its minimum temperature tolerance. Its southern limits appear to stem from the requirement of cold stratification for seed germination (Silander and Klepeis 1999). Silander and Klepeis (1999) posit that the western limits of Japanese barberry in North America may be set by low drought tolerance; this supposition is supported by the USDA (2006).

Environmental Effects

Investigators have concluded that Japanese barberry has widespread and far-reaching effects on habitats it invades. For example, the foliage is unpalatable to deer. Consequently, Japanese barberry has become a main component of the understory in forests subjected to heavy deer browsing (Rhoads and Block 2002) (see Features Contributing to Invasiveness). Japanese barberry appears to have a significant effect on regeneration of native plant species in the herb and shrub layer. Light is a significant factor driving volume of native plant biomass. When Japanese barberry was experimentally removed from forest plots the herb and shrub layers responded at the highest light level but not noticeably otherwise. Release of the native herb and shrub layers before leaf-out yielded almost no recovery in that growing season (Silander and

Klepeis 1999). Other impacts, as discussed below, appear to be less obvious and more encompassing than scientists previously recognized.

A series of studies conducted since 1997 focused on the effects of Japanese barberry upon soil properties. The initial study, which was conducted by Kourtev et al. (1998), yielded several trends. First, they found that soil pH was significantly higher under Japanese barberry (pH 4.8-5.8) than under native species such as *Vaccinium* (pH 4.3-4.8). Sites with barberry also had a significantly thinner litter layer and organic horizon, and higher total nitrogen. These alterations occurred during a relatively short period considering that the study forest was intact less than twenty years earlier. This is of concern because soil properties are normally formed over a long period, and therefore changes can last for a long time after removal of the invasive species causing the change (Kourtev et al. 1999). They followed up with an investigation of the elevated numbers of earthworms in invaded areas, a pattern observed in the initial study. The authors found significantly higher densities, specifically of introduced European earthworms, under Japanese barberry than under native species (Kourtev et al. 1999) (see Features Contributing to Invasiveness). The nitrification rate, extractable NO_3^-, and nitrate reductase activity were also higher under barberry while extractable NH_4^+ and ammonification rates were higher under native species. High nitrate levels in invaded areas have the potential to adversely affect downgradient water quality because of higher nitrate losses from leaching. The study also found that organic matter was being lost from invaded soils that could not be attributed to incorporation by earthworms or microbial respiration.

Changes in soil function after invasion by Japanese barberry were investigated by Ehrenfeld et al. (2001). They found that extractable NH_4^+ and NO_3^- were higher under Japanese barberry than under native species early in the season when Japanese barberry was the only woody plant to have leafed out. By mid-season, however, there were no differences in extractable NH_4^+. Net mineralization rates, which are the combination of net NH_4^+ and NO_3^- production, were higher under Japanese barberry early in the season but higher under the native *Vaccinium* later in the season. These changes in rates reflect a change in relative amounts of nitrogen over the growing season. Soil respiration was higher on a per-gram basis in soils under barberry grown in a greenhouse experiment. As a result, areas invaded by Japanese barberry had more total nitrogen transferred from soil pools to standing vegetation and ultimately to leaf litter. Japanese barberry leaf litter was found to decompose much more quickly than litter of native plants.

Pursuant to the previous studies, two studies were carried out examining the effects of Japanese barberry on microbial structure and function in invaded soils in the forest (Kourtev et al. 2002a; Kourtev et al. 2002b). The following effects were observed by Kourtev et al. (2002a): Higher rhizosphere bacterial to fungal ratios in invaded soils than native *Vaccinium* soils; higher N-related rhizospheric enzyme activities in invaded soils as opposed to higher cellulolytic and phosphatase activities in *Vaccinium* soils; and a higher response to carboxylic acids in invaded soils. These differences in structure and enzymatic function were greater in the respective rhizospheres than in rhizospheres vs. deeper soils, suggesting that microbial community structure and function are related to the growth (through root activity or litter deposition) and composition of the plants. The higher relative activities of N-related enzymes in invaded soils suggest that microbes may

be competing with Japanese barberry for nitrogen, or the microbes may be limited by low available nitrogen to available carbon ratio (Kourtev et al. 2002a). Kourtev et al. (2002b) found that microbial communities rapidly altered patterns of enzyme activity in response to barberry litter, even when the litter was placed on uninvaded soil. Although litter quality seemed to be the major determinant of enzyme activity, activity was also tied to site soil conditions. These alterations may have an effect at the ecosystem level.

Kourtev et al. (2003) examined effects on soil microbial structure and function in a controlled greenhouse setting. Soil was collected from an uninvaded habitat, Japanese barberry and native *Vaccinium* were planted separately, and the responses of the microbial community were assessed. In short, within three months the microbial community altered in the same way as the previous field studies in regard to pH, nitrification, nitrogen levels, microbial functions, and microbial structure.

Features Contributing to Invasiveness

There is no single factor that enables an introduced species to invade alien habitats, but rather a suite of complementary features. Some known and possible invasive features of Japanese barberry are listed below.

The success of a non-native invasive species such as Japanese barberry is due in part to life-history characteristics such as the ability to use NO_3^-, the ability to efficiently use high resource availability, colonization of disturbed and undisturbed habitats, multiple methods of reproduction, formation of thickets, and vertebrate seed dispersal (Rejmánek and Richardson 1996; Ehrenfeld 1999; Kourtev et al. 1999; Harrington et al. 2003; Barton et al. 2004). In Japanese barberry the combination of abundant seed set, asexual reproduction via layering and sprouting, growth by multiple new stems, and low

mortality of stems and established individuals contribute to the formation of dense thickets that exclude other competitors (Ehrenfeld 1999). Kourtev et al. (1998) found that areas invaded with Japanese barberry contained almost no other shrubs because deer had browsed them heavily while avoiding Japanese barberry. This appears to be due to high concentrations of alkaloids which deter mammalian browsing. Consequently, a competitive advantage arises in areas of heavy deer browsing (Silander and Klepeis 1999; Cassidy et al. 2004). On the other hand, Japanese barberry is not immune to deer browse as they will eat Japanese barberry when there is little food available (Dibble, A.C., University of ME, message dated 4/20/06).

The dispersal of Japanese barberry berries by birds and possibly by deer and small mammals contributes to its success as an invader. In fact, almost all highly invasive shrubs and vines in the Northeast are dispersed by birds (Silander and Klepeis 1999). Birds feed directly on berries and discard seeds locally or ingest the berries and defecate seeds elsewhere, providing dispersal into uninvaded areas. Recent increases in frugivorous bird populations like ruffed grouse and eastern wild turkey in the Northeast may have contributed to the recent rapid spread of Japanese barberry (Silander and Klepeis 1999).

Japanese barberry is also successful because it tolerates wide ranges of soil and light (Silander and Klepeis 1999; Harrington et al. 2003) (see Habitat and Range). In full sun the species competes successfully with other fast-growing woody species, and it dominates the understory under a tree canopy or when exposed to light grazing. It can persist in poor, saturated, dry, and thin soils. Its early leaf-out and late leaf drop

compared to native species in the same habitat is also a characteristic observed in other invasive shrubs (Silander and Klepeis 1999).

Kourtev et al. (1998), in their initial study on soil property effects, were unable to determine whether soil changes (i.e., elevated pH and nitrogen, thinner litter and organic layers) preceded invasion by Japanese barberry or were an effect of the invasion. In a follow-up study, Kourtev et al. (1999) were unable to determine whether the invasion of Japanese barberry caused higher non-native earthworm densities or vice versa. They posited the notion of a positive feedback loop. Earthworms native to North America were eliminated from the study area in New Jersey during the last glacial period and European earthworms were most likely reintroduced with colonial agriculture. Because the study area was never tilled the worms presumably moved in from adjacent cultivated areas and were historically present in low numbers in the intact forest. Therefore, Japanese barberry invasions may have created more favorable conditions for increased earthworm populations. Conversely, earthworms are known to incorporate leaf litter into the soil, increase pH, and increase nitrification, which may have facilitated invasion by Japanese barberry.

The high levels of nitrogen reductase in Japanese barberry suggest that the species is better able to use NO_3^- than most native species and thus has a competitive edge in areas of high earthworm densities (Kourtev et al. 1999). Significantly higher nitrate uptake per gram of root biomass, and elevated pH levels when compared to native *Vaccinium* in a greenhouse experiment, imply that Japanese barberry has a higher relative nitrate uptake capacity and support the evidence that nitrogen cycling and pH are affected by Japanese barberry (Ehrenfeld et al. 2001). As was previously mentioned, Japanese

barberry produces large amounts of nitrogen-rich aboveground and belowground biomass. This nitrogen-rich litter decomposes within a year and is taken up again by the plant, promoting a positive feedback loop where the plant increases net nitrification and preferentially uses the resulting nitrates to support a larger biomass than native shrubs, thereby enhancing the spread of the species while reducing the fitness of competitors (Ehrenfeld et al. 2001). Increased production of biomass in response to increased soil N appears to be a combination of higher leaf biomass/area and higher foliar [N]/photosynthesis; N uptake efficiency in the Northeast does not appear to vary with N availability (Harrington et al. 2004). In addition, high concentrations of soil nitrogen have been shown to facilitate additional invasions by other non-native invasive species, as was observed in barberry-invaded areas in New Jersey (Kourtev et al. 1999).

Kourtev et al. (2002a, 2002b) provide evidence that Japanese barberry alters microbial soil function and structure. Microbes in invaded soils respond more to amino acids such as carboxylic acid (see Effects on Environment) that are apparently made more available in soil by Japanese barberry. Litter from Japanese barberry causes a microbial community to quickly shift enzyme activity patterns, completely decomposing cellulose over the course of a year. Any benefit to Japanese barberry was not examined.

A non-native invasive species like Japanese barberry may confer advantage to itself by altering the root biomass of native species. As was mentioned in the Description subsection, Japanese barberry has a dense mat of fine roots in the first 5-10 cm of soil. Native tree and shrub species coexisting with Japanese barberry have significantly lower root biomass than they would otherwise such that the bulk biomass of Japanese barberry

was found to almost offset the reduction in biomass of native species (Ehrenfeld et al. 2001).

Japanese barberry hybridizes with common barberry to yield the hybrid *Berberis* x *ottawensis* (Silander and Klepeis 1999; Mehrhoff et al. 2003). Such hybrids are dangerous if they demonstrate increased hybrid vigor, growth, tolerance, and/or plasticity; they may be able to invade habitats that each parent species could not (Vilà et al. 2000). The primary cause of such hybridizations is species dispersal via breakdown of natural ecological species barriers by disturbance, habitat fragmentation, and intentional crossbreeding (Vilà et al. 2000). Although *B.* x *ottawensis* has been identified, there do not appear to be any studies assessing the invasive potential of the hybrid at this time. An indirect mechanism of success is linked to the hybrid issue – a lack of recognition of the problem by forest managers and a dearth of scientific reporting (Ehrenfeld 1997). Simply stated, if an invasion is not recognized and understood it cannot be stopped.

Management

If Japanese barberry is to be controlled effectively, several approaches must be considered. Eradication may not be feasible in some situations. Control methods for Japanese barberry in the U.S. vary according to region, the extent and density of populations, limitations regarding management activities allowable on a given property (e.g., prescribed burning and herbicide may not be options) and surrounding site conditions. Not all management methods pertain directly to Japanese barberry, however, but rather to the perceptions of society regarding invasive species.

The species does not appear to be fire resistant (USDA 2006), and control by prescribed fire in fire-adapted habitats can effectively kill the plant (Connecticut

Department of Environmental Protection [CTDEP] 1999). Prescribed fire has reduced some populations in the Midwest (Richburg et al. 2001). Richburg et al. (2004) tested the response to cutting and burning treatments for Japanese barberry populations in Massachusetts. Although the authors found that burning of cut stems and standing vegetation were more successful during the dormant season, dormant season treatments (i.e., cutting and/or burning) had little effect on the carbohydrate reserves of Japanese barberry and vigorous sprouting ensued during the next growing season. Carbohydrate reserves were also replenished by the end of the next growing season. Growing season treatments were more effective in reducing carbohydrate reserves, which led to less vigorous sprouts. One treatment per growing season for multiple years reduced the vigor of Japanese barberry, but multiple treatments per growing season over multiple years were even more effective. The authors recommended that treatment commence when carbohydrate reserves are lowest, for example just after leaf out or regrowth of sprouts following a disturbance or previous treatment. Japanese barberry leafs out earlier than most native woody species, so an early season burn can be accomplished with fewer effects on other dormant species which have not yet tapped their carbohydrate reserves. If multiple treatments are planned for one growing season, the shrubs should be allowed to resprout between treatments, further depleting reserves. Japanese barberry will not burn during the growing season without first cutting it because of the lack of fine fuels on the forest floor to carry the fire (see Ehrenfeld et al. 2001 under Environmental Effects). Ideally, Japanese barberry should be treated mechanically at first, with a prescribed burn for the slash; additional treatment during the growing season should be mechanical.

The Maine Natural Areas Program (2004) recommends manual control of Japanese barberry because it is effective and "may cause the least disturbance". Mowing and cutting will reduce seed formation, but the plants will resprout (Rhoads and Block 2002). Regular mowing may or may not prevent resprouting (MNAP 2004; TNEPPC 2004). Hand pulling is effective for small populations and can be done most of the year; smaller plants pull up easily from forest soils (Rhoads and Block 2002, TNEPPC 2004). Removal of as much root mass as possible is recommended (MNAP 2004), and any berries should be bagged and disposed of to prevent dispersal (TNEPPC 2004). At the least, berries should be removed from plants before they mature.

Foliar herbicidal sprays containing a 2% solution of glyphosate or triclopyr plus 0.5% non-ionic surfactant have proved effective for control of large thickets where non-target species effects are minimal. Triclopyr is recommended in locations where desirable grasses are in proximity to target plants (Rhoads and Block 2002) or early in the spring when barberry is actively growing but most other species remain dormant. Foliar glyphosate application early in the growing season can eradicate barberry populations (Silander and Klepeis 1999), but cut stump treatment is recommended in areas where foliar application is not feasible (TNEPPC 2004). Cut stems horizontally at or near ground level. Immediately apply a 25% glyphosate or triclopyr solution to the cut surface of the stump. This method may be used whenever the ground is not frozen (Rhoads and Block 2002). Many homeowners and woodlot owners prefer to minimize or avoid the use of herbicides by implementing Integrated Pest Management (IPM). To date, the U.S. does not have a standard for IPM regarding control of non-native invasive plants, but there are alternatives that may be available in the future. There are no known

biological control methods at this time (Rhoads and Block 2002), but tephritid flies have shown promise for control of common barberry in Europe (Huppman 1986 as cited in Silander and Klepeis 1999). Sterile cultivars of Japanese barberry are currently being developed but are not yet available to the public (Brand, M.H., University of CT, message dated 3/14/06).

Ehrenfeld (1999) concludes that herbicidal treatment of short stems is crucial to management because the bulk of stem density in all populations is made up of these short stems. She also suggests that even small or isolated plants must be removed or they will persist indefinitely. Finally, when constrained by limited resources or when facing a large area of infestation, large plants should be targeted with the aim of preventing the formation of thickets. Silander and Klepeis (1999) consider the most effective landscape-level control strategy over time to be a focus of efforts on small expanding populations, thereby limiting species recruitment.

Another high priority for Japanese barberry control is sites in the northeast where eastern hemlock (*Tsuga canadensis*) populations are being devastated by the hemlock woolly adelgid (Cassidy et al. 2004). After a stand of hemlock dies, nitrogen availability in the soil increases. There is a possibility that established Japanese barberry populations under the forest canopy will spread into these nitrogen-rich gaps as well as into harvested or thinned forest stands where nitrogen is also more available. Therefore, Cassidy et al. (2004) believe that control efforts should be primarily directed at rich mesic forests and dying hemlock stands.

Educating the public and encouraging them to buy native ornamental shrubs is another important component of management. Approximately 85% of the woody

invasive species in North America were introduced by the landscape industry to satisfy public demand (Harrington et al. 2003). Barton et al. (2004) found that invasive species abundance, including Japanese barberry, was negatively correlated to distance from the center of their study town, which suggests a close relationship between local planting and invasive spread. However, the only attention paid thus far to this problem on a national level has been the development of a "Voluntary Code of Conduct for Nursery Professionals" by the American Nursery and Landscape Association regarding the phasing out of non-native invasive plants (Harrington et al. 2003). This lack of national standards highlights the dire need for education of industry personnel as well as the institution of industry standards. The general preferences of both industry and non-industry groups are for implementation of voluntary standards and continuous education of green industry personnel and clients (Harrington et al. 2003).

The public plants Japanese barberry because of the colorful foliage and bright red berries that persist throughout winter. The following native shrubs may be considered alternatives to Japanese barberry because they have similar characteristics: serviceberry or shadbush (*Amelanchier* spp.), winterberry holly (*Ilex verticillata*), inkberry holly (*Ilex glabra*), New Jersey tea (*Ceanothus americanus*), bayberry (*Myrica pensylvanica*), wild hydrangea (*Hydrangea arborescens*), silky dogwood (*Cornus racemosa*) (which is considered a native invasive when managing for early successional breeding bird habitat [Dibble, A.C., message dated 4/20/06]), red chokeberry (*Aronia arbutifolia*), and black chokeberry (*Aronia melanocarpa*) (Rhoads and Block 2002). Finally, the effects that Japanese barberry has on ecosystems, namely pH elevation and changes in nitrogen dynamics, should be considered when making a management plan (Kourtev et al. 2003).

Conclusion

> "Eradication of exotic organisms…is an opportunity to simultaneously do good science and good conservation; it is one of relatively few areas to actually combine the two into functioning conservation biology."
>
> Bruce E. Coblentz (*Conservation Biology* 1990:264)

Because Japanese barberry remains one of the most popular ornamentals sold today, without restriction, the potential for this non-native invasive species to invade additional natural areas will increase. Japanese barberry was not adequately recognized and studied as a problem at the time it should have been, namely the period between 1950 and 1980. By 1980 the species was perceived as a serious threat (Silander and Klepeis 1999), yet today relatively little is known about Japanese barberry. At the same time Japanese barberry populations are increasing rapidly (Kourtev et al. 1998; Silander and Klepeis 1999). An issue common to all invasive species is the under-collection of specimens during the intermediate phase of invasion after its novelty has worn off (Silander and Klepeis 1999). As information for this paper was reviewed, a common theme emerged. Scientists investigating Japanese barberry are decrying the lack and uncertainty of current information and are advocating the need for additional research (Coblentz 1990; Ehrenfeld 1997; Kourtev et al. 1998; Ehrenfeld 1999; Silander and Klepeis 1999; Vilà et al. 2000; Kourtev et al. 2002a and 2002b; Barton et al. 2004; Cassidy et al. 2004).

In 1999 the trade magazine *American Nurseryman* conducted a roundtable to gather views about invasive plants (Harrington et al. 2003). Several common themes emerged, most notably the need for objective data to support listing a species as invasive,

the need to educate industry personnel and clients, and minimal disruption to the nursery industry. Green industry personnel are concerned that broad-brush national mandates would unnecessarily restrict the sale of introduced non-invasive species or species that are invasive only in certain regions, and they would prefer regional plant lists and solutions. They also feel that green industry involvement is vital to the development of policies regarding invasive plants.

Chapter 2

INTRODUCTION

Japanese barberry (*Berberis thunbergii*) has become an increasingly severe threat to forests in the northeast. It has life-history characteristics which provide it with a competitive advantage over many native species, but how it regenerates in native ecosystems is poorly understood. Overall fertility requirements are low, seed production increases with light and most seeds germinate under or near the parent plant (Silander and Klepeis 1999, Ehrenfeld 1999, USDA 2006). Regeneration is mainly by seed as opposed to asexual means (Ehrenfeld 1999), but the longevity of viable seed in forest soils is unknown. Dirr and Heuser (1987) state that dry Japanese barberry seeds can remain viable under artificial storage conditions for up to four years (Dirr and Heuser 1987), which conflicts with older research stating that seeds should be stored moist to maintain viability (Davis 1927). Previous research also indicates that Japanese barberry does not contain a germination inhibitor in the fleshy seedcoat (Dirr and Heuser 1987). Germination of seeds within berries was retarded by one to two weeks compared to naked seeds, but overall germination success was not significantly different (Davis 1927).

Once a forest stand is invaded by Japanese barberry, vegetation succession may be altered in the understory and/or the overstory because the non-native invasive species can out-compete native species. In full sunlight Japanese barberry competes with other fast-growing tree and shrub species, while under light grazing conditions or a tree canopy it can dominate the understory, affecting herb and shrub biomass (Silander and Klepeis 1999). In invaded areas, root biomass of woody plants may be significantly reduced compared to uninvaded sites (Ehrenfeld et al. 2001). In invaded areas that support high

deer populations, deer preferentially browse native shrubs before Japanese barberry because of the bitter tasting alkaloid berberine contained in the latter, resulting in a competitive advantage for Japanese barberry (Silander and Klepeis 1999, Cassidy et al. 2004). However, there is no known literature regarding effects of Japanese barberry invasion on advance tree regeneration in forests of the northeast or any other U.S. region. Because of its ability to invade and dominate fields or closed canopy forest understories, Japanese barberry may affect tree regeneration to the point of failure to re-establish tree canopies on released sites. Furthermore, if Japanese barberry has a seed bank, merely removing established plants or killing them to the roots would not prevent re-establishment of new plants in a short period of time.

Because Japanese barberry remains one of the most popular ornamentals sold today, the potential for this non-native invasive species to invade additional natural areas will increase. An understanding of how Japanese barberry affects other plant species, how it regenerates in the forest and how long viable seeds persist in forest soils are crucial to implementation of effective control strategies and management of forest stands invaded by Japanese barberry. Therefore, this study focused on the following questions and hypotheses:

1. Which species successfully regenerate under a Japanese barberry overstory?

   Hypothesis 1a: Few other plants will be present under the Japanese barberry understory.

   Hypothesis 1b: Japanese barberry will regenerate in higher numbers than other species.

2. How does forest canopy cover affect the regeneration of Japanese barberry and other species?

   Hypothesis 2: Japanese barberry and other regeneration will be inversely proportional to tree canopy shading.

3. Does a portion of Japanese barberry seed from previous years remain viable in the soil for more than one growing season?

   Hypothesis 3a: There will be a viable Japanese barberry seed bank beyond one growing season.

   Hypothesis 3b: Viability of Japanese barberry seed is not affected by its berry.

MATERIALS AND METHODS

In order to assess the questions stated above, this study was divided into three components: Field studies, soil incubation studies, and a seedling emergence test.

Field Studies

The field studies were designed to evaluate Hypotheses 1a, 1b, and 2. Data were collected from study sites in fall 2004, spring 2005 and fall 2005.

Study Sites

The field studies were conducted on two study sites: Monhegan Island, ME and the Wells National Estuarine Research Reserve in Wells, ME. The sites were chosen because they were both coastal, contained a forest stand and were in an advanced state of invasion by Japanese barberry.

Monhegan Island (43°46'56" N, 69°18'45" W) is located at the outer limit of Muscongus Bay in the Gulf of Maine (Figure 5). It was discovered by the European

explorer John Smith in 1614, and has been an artists' colony as well as a local fishery for over 100 years. The island is approximately 2.7 km long by 1.1 km wide with an area totaling approximately 202 ha; most of the land beyond the village and harbor is protected by Monhegan Associates, Inc. The study site on Monhegan Island was located on the southeast slope of the islands tallest hill (Lighthouse Hill, denoted by star on Figure 5) and is owned by the Monhegan Associates. This portion of forest was chosen due to its advanced stage of Japanese barberry invasion. Soils at the study area are in the Lyman-Peru-Scantic association, which are shallow or deep, gently sloping to steep, moderately well drained to excessively drained soils formed in glacial till (Hedstrom 1987). The nearest weather station is at Port Clyde, ME (43°55'38" N, 69°15'12" W), where the average annual temperature is 7.6°C (45.6°F) with temperatures ranging from an average high of 22.1°C (71.7°F) in August to an average low of -7.8°C (17.9°F) in January. The average annual precipitation is 112.9 cm (data range 1989-2005 from the National Climatic Data Center [NCDC] 2006). The upper strata of the overstory at the Monhegan Island study site were dominated by American mountain ash (*Sorbus americana*), white spruce (*Picea glauca*) and balsam fir (*Abies balsamea*), while the lower stratum was dominated by choke cherry (*Prunus virginiana*).

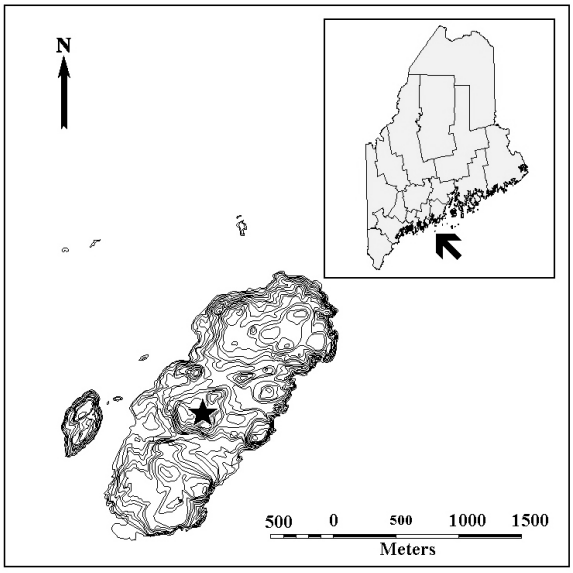

Figure 5. Location map of the Monhegan Island study site.

(Study site denoted by star)

Laudholm Farm/Wells National Esturarine Research Reserve (43°20'15" N 70°33'10" W) is located in Wells, ME (Figure 6). It was established by European settlers in 1643 on what became Laudholm Farm. In 1986 the farm became part of the National Estuarine Research Reserve System, and it now protects over 1600 acres of uplands, marshes, estuary, and shoreland. Soils at the study area belong to the Sulfihemists-Udipsamments association near the shore phasing to the Naumberg-Croghan association further inland. The former are deep, level very poorly drained soils formed in organic deposits and/or deep, rolling excessively drained/moderately well drained soils formed in eolian deposits. The latter are deep, nearly level poorly drained/moderately well drained soils formed by glacial meltwater deposits (Flewelling and Lisante 1982). Based on records from the nearest weather station in Kennebunkport, ME (43°23'32" N, 70°28'22" W), the average annual temperature is 7.2°C (45.0°F) with temperatures ranging from an average high of 24.6°C (76.2°F) in July to an average low of -11.1°C (12.1°F) in January. The average annual precipitation is 121.9 cm (data range 1989-2005

from NCDC 2006). The Wells Research Reserve study site was chosen due to its advanced stage of Japanese barberry invasion and flat terrain (denoted by the star in Figure 6), and was dominated by gray birch (*Betula populifolia*) in the upper strata and choke cherry in the lower stratum.

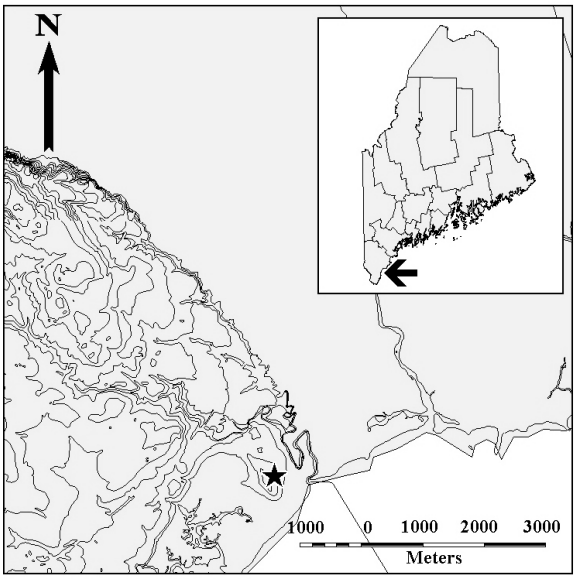

Figure 6. Location map of the Wells Research Reserve study site.

(Study site denoted by star)

August/September 2004

Monhegan Island. Because the Japanese barberry was too dense to permit passage, two parallel transects just wide enough for foot traffic were cut through the understory using a brush saw in late August 2004. The head of the transects (Transect 1 43°45'51" N, 69°18'51" W and Transect 2 20 m southwest of this point) were at the southern boundary of a field at the crest of Lighthouse Hill, followed a bearing of 140° and measured 120 m and 100 m respectively. The Japanese barberry study stand was approximately 110 m by 55 m bounded on the north by the field, the south by a steep topographic break, the east by the Whitehead Trail and the west by a Japanese barberry study site previously manipulated by the Monhegan Associates. The transects were wide enough to allow

passage through the understory, and all cut brush was piled along the sides. Both transects ran through a forest canopy gap; the canopy closed in again just prior to the end of each transect.

Twenty 1 m radius plots were created and sampled in late August 2004. The plot centers were spaced 10 m apart and 2 m perpendicular to the southwestern edge of each transect. Japanese barberry cover was assessed by standing at plot center and sweeping a meter stick 360°; percent cover within a meter was estimated to the nearest 5% by ocular estimation and always by the same person. For each plot, all Japanese barberry stems within a meter radius were clipped at ground level using hand loppers. If a barberry stem originated outside one meter but the branch arched into the plot it was cut within 20 cm of ground level. All other herbs, shrubs and trees within the plot were left intact. All cutting was performed either by standing at plot center or beyond a meter from the center as to minimize disturbance within the plots. Plots 1-11 were located along Transect 1 and plots 12-20 along Transect 2, with plots 1 and 12 located 20 m from the edge of the field (Figure 7).

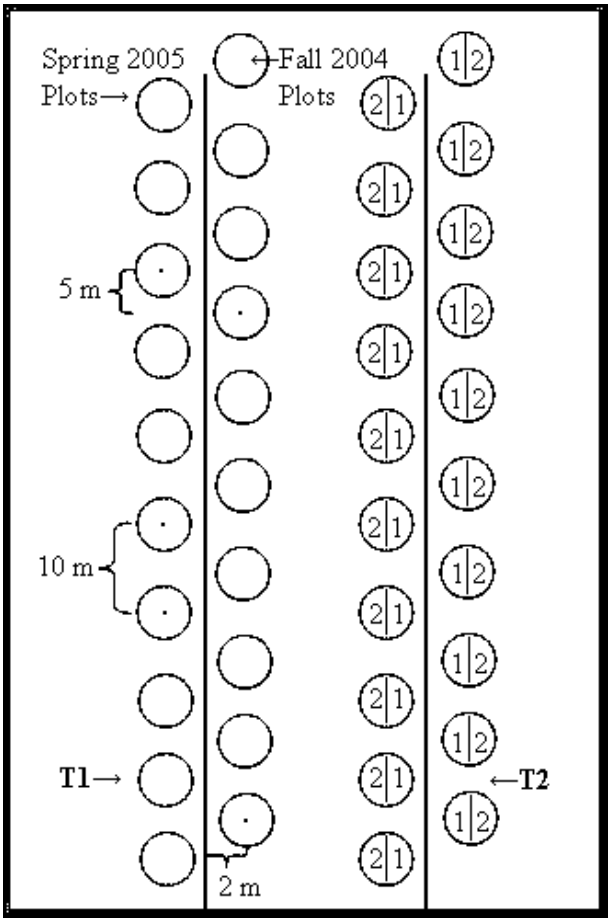

Figure 7. Diagram of typical experimental design for plot placement.

T1 = Transect 1 T2 = Transect 2
1 = initial observation fall 2004/spring 2005 2 = observation fall 2005

Wells Research Reserve. Two transects were also laid in an area of high barberry population in early September 2004 using the same methodology as at Monhegan Island. The head of each transect (Transect 1 43°19'56" N, 70°32'55" W and Tranect 2 10 m north of that point) was at a straight north-south section of the Pilger Trail just west of the Beach Road, had a bearing of 280° and was approximately 100 m long. Both transects traversed a wetland. Because of standing water which precluded walking Transect 2, the bearing had to be sighted across the wetland and picked up on the western side (there was no barberry in the wetland). The plots were located and clipped using the same methodology as at Monhegan Island. Plots 21-30 were located along Transect 1, while

plots 31-40 were located along Transect 2; plot locations began 10 m from the transect's east boundary on the Pilger Trail (Figure 7).

Forest Canopy Cover. Forest canopy cover was measured at each site using a Canon EOS Rebel digital camera fitted with a fisheye camera lens. After each plot was clipped a tripod was set up with its center over plot center. The camera was mounted on the tripod at an average height of 140 cm with the lens leveled facing upward towards the forest canopy and the camera top facing north. Photos were ideally taken during cloudy days or when the sun was low in the sky to prevent glare. In those cases where sun glare was a problem, the camera was raised or lowered no more than 15 cm to take advantage of blockage of the sun by tree trunks or foliage. The photos were later analyzed using Gap Light Analyzer v.2 software (Frazer et al. 1999).

Vegetation Sampling. After each plot was clipped, stem counts were conducted within one day to quantify initial conditions upon removal of the Japanese barberry understory. Each plot was split into two halves with the dividing line running parallel to the bearing of the transect. The half closer to the transect was sampled, while the further half was left completely untouched until fall 2005. A meter-long stick was placed with one end at plot center and rotated around the plot half in order to prevent double-counting or omission of plants.

All herbs, shrubs, and trees were quantified by stem counts and were left intact in the plots. If a species was too abundant to feasibly allow stem counts then percent cover of the plot half was estimated. This technique applied to the species listed in the Appendix (Table A1). Each species count of herbs was separated by mature plants ("understory") and seedlings ("regeneration"). An herb was considered regeneration if it

had cotyledons or only 2-3 true leaves. When only cotyledons were present, a seedling was considered "unknown". A shrub was considered regeneration if it was below 30 cm (12") or less, placing it below the Japanese barberry canopy. A tree was considered regeneration in two categories: <30 cm and 30-100 cm. Identifications were to species when possible, to genus or recorded as "unknown" (Newcomb 1977, Maine Forest Service Department of Conservation [MFS] 1995, Chambers et al. 1996).

Percent cover of mature Japanese barberry plants was quantified when plots were established. Smaller stems, considered "Japanese barberry regeneration", were quantified destructively. Seedlings were pulled as they were counted. Vegetative sprouts, defined here as one or two stems less than 1 m high, were cut below the soil surface to avoid significant soil disturbance.

Soil Sampling. Two soil samples were collected from each sampled plot half described above, each approximately 15 cm across by 10 cm deep (excluding litter). The soil samples, including the litter layer, were transported and stored in Tupperware as intact cubes until processing occurred. The soil samples were taken to the University of Maine as soon as possible; one sample from each plot was immediately processed, while the other was placed in cold storage at 5°C until spring 2005 (see Soil Incubation Study under Materials and Methods).

May/June 2005

Monhegan Island. During a revisit in early June 2005, plots 61-80 were established and clipped on the northeast side (bearing 50°) of each transect. Because of the 20 m strip of recently disturbed land between the edge of the field and intact forest, plots 61-70 were clipped and numbered starting at the far extent of Transect 1 and 71-80 continued at the

far extent of Transect 2. Plot 61 was offset 5 m so as to be between plots 11 and 10, an exception to the typical experimental design, while plot 71 was located 5 m beyond plot 20 (Figure 7).

Wells Research Reserve. During a revisit in late May 2005, plots 41-60 were set up with centers located 2 m from the south edge of each transect (bearing 190°) with plots 41-50 located along Transect 1 and plots 51-59 along Transect 2 (Figure 7). Plots 41 and 51 were placed 5 m from Pilger Trail and therefore each subsequent plot was offset 5 m from the plots cut in 2004. Placement of plot center and plot clipping were conducted using the same methodology as in September 2004. Due to an unusually wet spring the water level in the wetland was high. Therefore, plots 47, 56 and 57 could not be set or clipped and data were not gathered from these plots. Because of heavy rains during the initial site visit, a follow-up site visit was conducted in June 2005 to finish data collection in plots 41-60; at this time plots 21-40 were checked again for new Japanese barberry seedlings.

Forest Canopy Cover, Vegetation and Soil Sampling. Forest canopy cover was estimated as in fall 2004. Vegetation cover data for plots 41-80 were collected using the same methodology as in fall 2004. The same plot halves of plots 1-40 were also resampled to assess effects of overwintering on Japanese barberry regeneration and native species once Japanese barberry had been removed. Herbs, shrubs, and trees were non-destructively quantified while Japanese barberry seedlings and vegetative sprouts were destructively sampled. One soil sample each was collected from plots 41-80 as were previously described in fall 2004.

August 2005

Vegetation Sampling. In August 2005 both sites were revisited to assess effects of Japanese barberry removal on forest regeneration after one growing season. Data were gathered from the previously unsampled halves of all plots using the same methodology as previously described. Plots 12-15 at the Monhegan Island study site were excluded as the unsampled halves had been disturbed in May 2005. Data were not gathered from plots 47, 56 and 57 at the Wells Research Reserve since they had not been clipped in the spring.

Soil Sampling. One soil sample each was collected from plots 41-80. The samples were collected in the same manner as in spring 2005 but from the other half of each plot.

Soil Incubation Studies

As a follow-up to the three field studies, soil incubation studies were designed to evaluate whether a portion of Japanese barberry seeds from previous years remains as a viable soil seed bank (Hypothesis 3a). The soil samples previously collected during the site visits were processed and seedling emergence was quantified as described below.

Soil Samples Collected in Fall 2004

One soil sample from each of plots 1-40 were immediately processed in the Roger Clapp Greenhouses upon returning to University of Maine. Each soil sample was divided into three layers: Litter, 0-5 cm, and 5-10 cm depth. Each subsample was spread out evenly on a standard perforated plastic tray (25.4 cm by 52.1 cm) to which had been added approximately 0.6 cm fine sand over 2.5 cm peat moss (Chadwick 1935, Gough 1996). A sample was divided into subsamples by first removing the litter layer, and then

by dividing the soil in half by depth. Because the storage containers were 10 cm deep and the litter layer was thin it was assumed that halving the soil cube would result in 0-5 cm and 5-10 cm depths. The soil at both sites was relatively rich in humus and the bulk of Japanese barberry roots held the soil cubes together so that the soil samples were still intact upon processing. Roots were removed to prevent the possibility of root sprouts, along with sticks and stones.

Subsamples were labeled and distributed randomly on wire-topped benches in a greenhouse. Sand was used to separate the subsample from the peat moss. Six flats of commercial seed were interspersed regularly along each bench. Seedling emergence from these flats was used to confirm that light, moisture and temperature conditions in the greenhouse were within parameters for germination of a Japanese barberry seed bank if one was present. Each commercial seed flat consisted of approximately 3.8 cm peat moss and 100 commercially collected Japanese barberry seeds (Mistletoe-Carter Wholesale Seeds in Goleta, CA collected by F.W. Shumacher, Inc. in fall 2003). Sand was not used in the commercial seed flats because any seeds contained in the forest soil samples would be in a matrix of soil, not sand; therefore, because peat is more similar to the forest soils at the study sites the commercial seed was sown directly on peat. The only commercial seed available was a purple variety called 'atropurpurea', for which germination is similar to feral green-leaved populations in the field (9% and 4.5%, respectively) but was higher under greenhouse conditions (99% and 49%, respectively) (Brand, M.H., University of CT, message dated 3/14/06). The commercial seed was stratified prior to shipping. A float test was conducted in order to ensure maximum

viability of the commercial seed (Gough 1996). Seeds were placed in a glass jar filled with distilled water. All floating seeds were discarded as not viable.

All flats were monitored daily for emergence of germinants. Germinants were counted weekly to daily depending on overall emergence rates. The germinants were divided into three categories: Japanese barberry, other, and unknown. If a germinant was unknown, a colored plastic ring was placed around it to mark it, and the plant was monitored until identification could be made. If a germinant was identified as Japanese barberry a ring was placed around it and it was left intact. If a germinant was identified as non-barberry it was immediately removed. Grasses were not counted because of time constraints and were not removed.

All flats were rearranged on the benches every two weeks to account for microclimatic variation in the greenhouse. The maximum and minimum greenhouse temperatures were recorded daily and ranged from 8-36 °C. The flats were also watered as necessary to keep the soil moist but not saturated. After the point at which commercial seedling emergence significantly slowed or ceased and most subsamples had no germinants all samples were discarded.

On November 24, 2004 most of the commercial germinants were killed by a fungal infection. At this point emergence had slowed to where approximately half of the subsamples had no new germinants. Those flats with new germinants had no new Japanese barberry. Monitoring continued for another three weeks, and no additional live or dead Japanese barberry germinants were observed.

The soil samples that had been collected in fall 2004 and placed in cold storage over the winter were incubated for percent Japanese barberry seedling emergence in the

spring 2005. Due to excessive heat in the greenhouse, all emerging germinants died and the samples were discarded; no data were collected.

Soil Samples Collected in Spring 2005

The forest soil samples collected in May/June 2005 were immediately processed in a nursery pad near Nutting Hall. The nursery pad was covered by 30% shade cloth and watered daily by an automatic overhead misting system. The daily temperatures were monitored and remained within an acceptable range for germination and growth of Japanese barberry (7-36°C).

Soil samples were processed as above. Five commercial seed flats containing *Berberis thunbergii* 'atropurpurea' were dispersed evenly among the subsample flats. To ensure viability of the commercial seed, seed collected in fall 2004 was ordered from Mistletoe-Carter Wholesale Seeds and used in both 2005 trials. All flats were placed on the graveled surface of the nursery pad floor. The flats were rearranged at random every two weeks. When seedling emergence became sporadic and the majority of flats had no germinants, a final stem count was taken on August 26 and all samples were discarded.

Soil Samples Collected in Fall 2005

Soil samples collected in August 2005 were immediately processed as previously described, along with five commercial seed flats of *Berberis thunbergii* 'atropurpurea'. The maximum and minimum temperatures were monitored daily and remained within acceptable limits (7-36°C). A final stem count was taken on October 21 and the samples were discarded.

Seedling Emergence Test

A seedling emergence test was also conducted on Japanese barberry seeds collected from the study sites. This study complements the soil incubation studies above and evaluates Hypotheses 3a and 3b.

Seed Collection

In fall 2005 seedling emergence rates were estimated for (1) 2003 commercial 'atropurpurea' seed from Carter-Mistletoe Wholesale Seeds, (2) 2004 commercial 'atropurpurea' seed from Carter-Mistletoe Wholesale Seeds, (3) seeds from undispersed berries collected on October 1 (Wells Research Reserve) and October 2 (Monhegan Island), 2004, and (4) seeds extracted from those berries. All plants had produced berries, which were ripe but still attached. Berries were collected randomly along the transects and obviously diseased or damaged berries were immediately discarded. Because berries along transects had high incidence of insect damage compared to berries on shrubs along the Whitehead Trail on Monhegan Island and the Beach Road at the Wells Research Reserve, additional berries were collected from these paths to prevent possible seed loss from additional insect damage during storage.

The berries were stored in airtight containers at 5°C in the same storage unit as commercial seed collected in 2003 or 2004 to provide cold stratification requirement at 0-5°F for at least 15-60 days (Dirr and Heuser 1987, Gough 1996). They were checked periodically and any newly insect-damaged or rotted berries were discarded. In June 2005 a portion of the berries were macerated in a blender with distilled water to extract seeds from the pulp without damaging them (Gough 1996). A subsample of ca. 30 berries was opened to confirm the literature which states an average of two seeds per

berry (Dirr and Heuser 1987). The seeds were then rinsed with distilled water to remove all pulp and were tested for viability using the float method (Gough 1996). All floating or damaged seeds were discarded. The berries could not be tested for viability because the integrity of the pulp could not be compromised. At this time the 2003 and 2004 commercial seed were also tested for viability using the same procedure. The extracted seeds, commercial seeds, and berries were then sterilized by soaking in a 3% hydrogen peroxide solution for twenty minutes (Riley 1981; Schmidt 2002), after which they were stored in glass jars at 5°C until used.

Seedling Emergence Test

The experimental design consisted of 25 multi-celled flats with 32 cells 6 cm x 6 cm x 5.7 cm. Each cell contained an approximately 1:1 ratio of sand over peat moss and (Gough 1996). Four cells constituted a block of a certain seed type, with two blocks of each seed type per flat. Four seeds of extracted seed, 2003 commercial seed, 2004 commercial seed, or two berries were placed in each cell for a total of 32 seeds each per flat. The seeds were covered by a 0.3-0.6 cm layer of sand (Chadwick 1935). The flats were placed in the nursery pad with 30% shade cloth and an automatic watering system on June 24, 2005. They were monitored for seedling emergence and moisture, and were supplemented by hand watering as needed. Flats were randomly shuffled every two weeks to account for microclimatic differences. The cells were checked regularly for evidence of predation by birds or rodents, of which none was found. Daily to weekly seedling counts (depending on emergence rate) spanned from July 20 to September 28, 2005 by which time no additional emergence was observed.

Analyses

Analysis of Forest Canopy Photos

All forest canopy photos were analyzed using Gap Light Analyzer (GLA) software version 2.0 (Frazer et al. 1999). One photo from each plot was chosen based on whether it was under a cloudy sky. If a suitable photo was not available, one was corrected to eliminate false canopy readings from sunglare or deep blue sky. The digital photo was edited by applying gray pixels to sky portions of the photo to simulate cloud cover. The photo was then saved and processed using GLA in the same manner as uncorrected photos.

Plot photos were analyzed in GLA by first setting the boundaries of the area to be analyzed. Because plot photo area exceeded the extent of the fisheye camera lens, when a photo was opened in GLA the upper (north) and lower (south) extents of the photo were truncated. Therefore, each photo was cropped during registration so that it was analyzed as a circular photo. The total amount of cropped area was negligible in terms of canopy area lost. Once a photo was registered, it was assigned a threshold. All photos were assigned a threshold of 170 on a scale of 0 to 255 (Frazer et al. 1999). Once the threshold was assigned, the canopy structure was analyzed and total percent canopy openness was calculated. The percent openness values were subtracted from 100 to calculate percent shade.

Statistical Analysis of Field Studies

The field data were analyzed as a repeated measures ANOVA using SYSTAT version 11.00.01 (SYSTAT 2004). The main factor was season of clipping (fall 2004 or spring 2005) and the repeated measure was time of observation ("first" = fall 2004 or

spring 2005, "second" = fall 2005). The response variable was plant group density (Japanese barberry seedlings, Japanese barberry vegetative sprouts, understory herbs, herb regeneration, shrub regeneration, and tree regeneration). A dataset was analyzed if the plant group had a frequency of at least 80% or sufficient to result in residual spreads no more than two standard deviations away from the mean. Forest canopy cover and Japanese barberry cover could have influenced plant group densities. Therefore, they were added into the repeated measures ANOVA model as covariates (ANCOVA). The natural log+1 of stem counts were used to account for unequal variance. Significance was assessed at $\alpha=0.05$.

Analysis of Soil Incubation Studies

Three analyses were conducted: 1.) Incidence of Japanese barberry seedling emergence in the soil samples collected from the plots clipped in fall 2004 were compared to the number of new germinants found in the same plot halves in spring 2005. Because both sets of data originated from the same plots and overwintered without a Japanese barberry canopy the two could be used to estimate viable seed older than 12 months. 2.) The incidence of Japanese barberry seedling emergence in the soil samples collected from the plots clipped spring 2005 were compared to the number of new germinants found in the same plot halves in spring 2005. These samples included seed from previous years including the 2004 crop. The greenhouse trial would indicate whether there was additional ungerminated seed in the field. 3.) The incidence of Japanese barberry seedling emergence in the soil samples collected in fall 2005 from the plots clipped in spring 2005 were compared to the number of new germinants found in the same plot halves sampled in fall 2005. These samples would indicate if viable,

ungerminated seed remained in the soil over the summer. The surface areas of each set of soil samples collected at the respective sites and times were summed to generate seedling densities in the greenhouse. The densities of Japanese barberry seedlings were also compared to the respective total densities of non-barberry species at each site and time.

Statistical Analysis of Seedling Emergence Test

Data collected from the seedling emergence test were analyzed using a one-way ANOVA. The response variable was mean percent emergence of Japanese barberry seedlings (x out of 32 seeds per flat). A square root transformation of the data was taken to adjust for non-homogeneous variances.

RESULTS

Field Studies

Native species regenerated poorly under Japanese barberry cover with frequencies and densities presented for the Monhegan Island study site in Table 1 and the Wells Research Reserve study site in Table 2. Frequencies and densities of each species contributing to Tables 1 and 2 are presented in the Appendix (Tables A2-A5). Mean forest canopy cover at the Monhegan Island site was 46±7% for plots clipped in fall 2004 and 55±5% for plots clipped in spring 2005 (Figure 8). Mean forest canopy cover at Wells Research Reserve was 68±4% for plots clipped in fall 2004 and 70±3% for plots clipped in spring 2005 (Figure 9). Mean Japanese barberry cover for fall 2004 plots at Monhegan Island was 67±7% (range 5-100%) while spring 2005 plots averaged 78±6% (range 5-100%) (Figure 10). Mean Japanese barberry cover at Wells Research Reserve

was 98±1% (range 80-100%) in fall 2004 and 82±5% (range 25-100%) in spring 2005 (Figure 11).

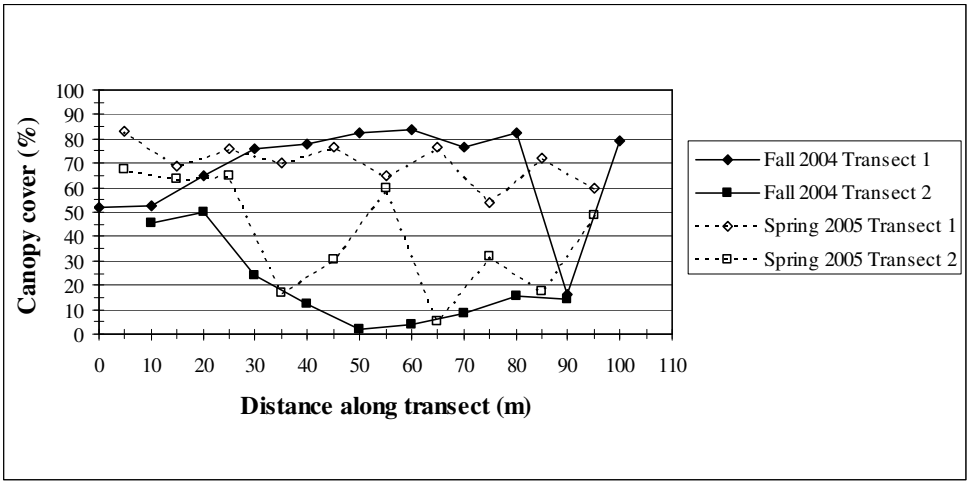

Figure 8. Plot position vs. forest canopy cover at the Monhegan Island study site.

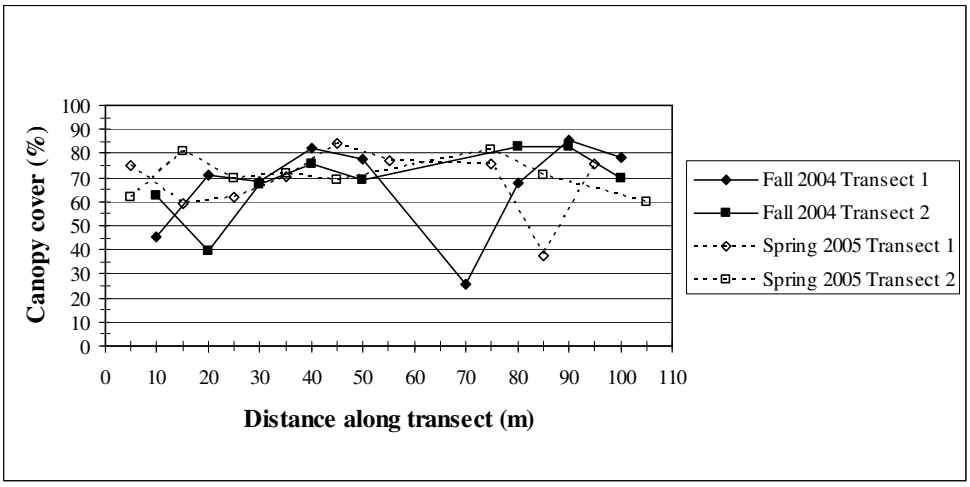

Figure 9. Plot position vs. forest canopy cover at the Wells Research Reserve study site.

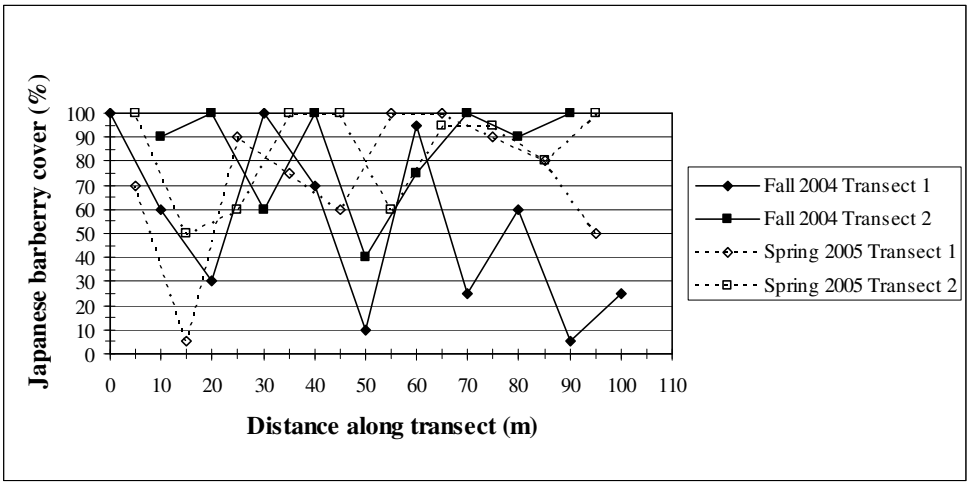

Figure 10. Plot position vs. Japanese barberry cover at the Monhegan Island study site.

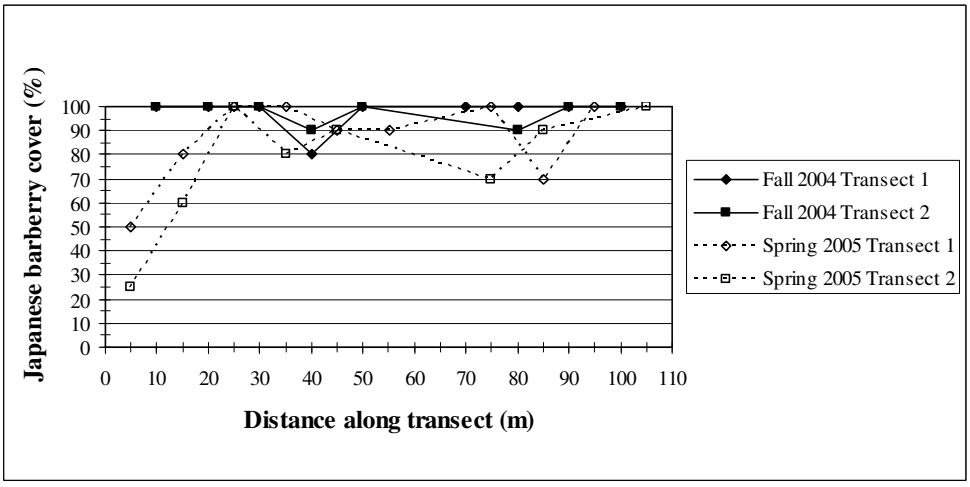

Figure 11. Plot position vs. Japanese barberry cover at the Wells Research Reserve study site.

Plant groups with enough non-zero data to be statistically analyzed consisted of Japanese barberry seedlings, Japanese barberry vegetative sprouts and understory herbs. Herb, shrub and tree regeneration data at Monhegan Island could not be analyzed due to low frequencies; an average of 50% of plots lacked seedlings. Data from Wells Research Reserve could not be analyzed due to a lack of variation in forest canopy cover (60-90%) (Figure 9), the high number of plots with 100% barberry cover (Figure 11) and the low frequencies of plant groups overall.

The results of the repeated measures ANCOVA for Japanese barberry seedlings, Japanese barberry vegetative sprouts and understory herbs are presented in Table 3. The results apply to count data only. Species assessed as percent covers were solely understory herbs. These data could not be estimated precisely enough and had frequencies too low to permit analysis, and were of sufficiently low cover values as to be considered unimportant in their contribution to the herb understory (Appendix, Table A1).

The season of clipping did not have a significant effect on the density of any of the above plant groups. There were significant negative relationships between forest canopy cover and density of Japanese barberry seedlings ($P = 0.003$) (Figure 12) and understory herbs ($P = 0.003$) (Figure 13) The relationship between forest canopy cover and Japanese barberry vegetative sprouts showed a trend of decreasing density with increasing forest canopy cover, but had marginal significance ($P = 0.058$) (Figure 14). Maximum understory herb density was approximately half that of Japanese barberry seedlings, while Japanese barberry vegetative sprout density was an order of magnitude lower.

		Clipped Fall 2004				Clipped Spring 2005			
		N=20		N=20 (N=16 JB seedlings & sprouts)		N=20		N=20 (N=14 understory herb)	
		Observed Fall 2004		Observed Fall 2005		Observed Spring 2005		Observed Fall 2005	
Plant Group	**Stratum**	**Stems/m^2**	**Frequency**	**Stems/m^2**	**Frequency**	**Stems/m^2**	**Frequency**	**Stems/m^2**	**Frequency**
JB seedling	reg	17.7	17	17.9	14	29.3	18	11.6	19
JB vegetative	reg	1.3	13	4.8	16	1.7	13	7.1	19
herb	und	5.2	20	24.5	17	21.4	19	13.5	19
herb	reg	0.4	7	2.3	12	1.0	13	1.0	7
shrub	reg	0.0	0	6.0	17	2.3	14	1.5	6
tree	reg	2.5	11	3.8	18	1.1	6	1.6	5

Table 1. Density and frequency of plant groups at the Monhegan Island study site.

JB = Japanese barberry reg = regeneration und = understory

		Clipped Fall 2004				Clipped Spring 2005			
		N=17				N=17			
		Observed Fall 2004		Observed Fall 2005		Observed Spring 2005		Observed Fall 2005	
Plant Group	**Stratum**	**Stems/m^2**	**Frequency**	**Stems/m^2**	**Frequency**	**Stems/m^2**	**Frequency**	**Stems/m^2**	**Frequency**
JB seedling	reg	0.2	4	0.4	4	0.4	5	0.2	2
JB vegetative	reg	0.03	1	2.0	15	0.1	2	0.8	10
herb	und	1.2	9	6.8	13	6.7	11	3.9	16
herb	reg	3.6	12	3.2	9	0.2	3	0.9	6
shrub	reg	0.5	5	0.7	6	0.3	4	0.03	1
tree	reg	0.0	0	1.6	9	0.2	2	0.7	5

Table 2. Density and frequency of plant groups at the Wells Research Reserve study site.

JB = Japanese barberry reg = regeneration und = understory

Source	JB seedlings		JB vegetative		Understory herbs	
	F (P-value)	**error MS (df)**	**F (P-value)**	**error MS (df)**	**F (P-value)**	**error MS (df)**
Season of clipping	0.11 (0.740)	243.94 (1)	1.58 (0.218)	43.36 (1)	1.67 (0.206)	1818.61 (1)
Forest canopy cover	10.00 ***(0.003)***	21762.66 (1)	3.86 **(0.058)**	105.67 (1)	10.75 ***(0.003)***	11721.25 (1)
JB cover	2.34 (0.136)	5090.40 (1)	3.97 **(0.055)**	108.90 (1)	0.00 (0.998)	0.01 (1)
Between subjects error MS		2176.71(32)		27.41 (32)		1090.31 (30)
Observation time	0.83 (0.370)	575.14 (1)	2.31 (0.138)	60.88 (1)	5.19 ***(0.030)***	2494.23 (1)
Observe*clipped	4.55 ***(0.041)***	3162.24 (1)	1.19 (0.284)	31.33 (1)	5.43 ***(0.027)***	2608.44 (1)
Within subjects error MS		695.25 (32)		26.34 (32)		480.61 (30)

Table 3. Repeated measures Analysis of Covariance (ANCOVA) for selected plant groups at the Monhegan Island study site.

JB = Japanese barberry MS = mean squared df = degrees of freedom

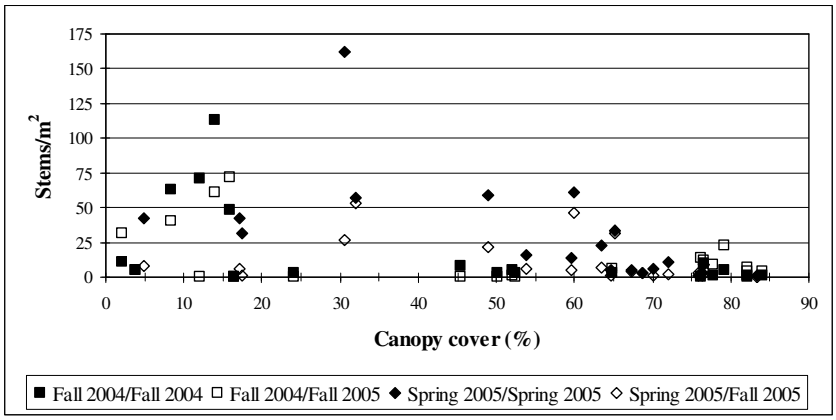

Figure 12. Forest canopy cover vs. density of Japanese barberry seedlings at the Monhegan Island study site.

(P = 0.003).

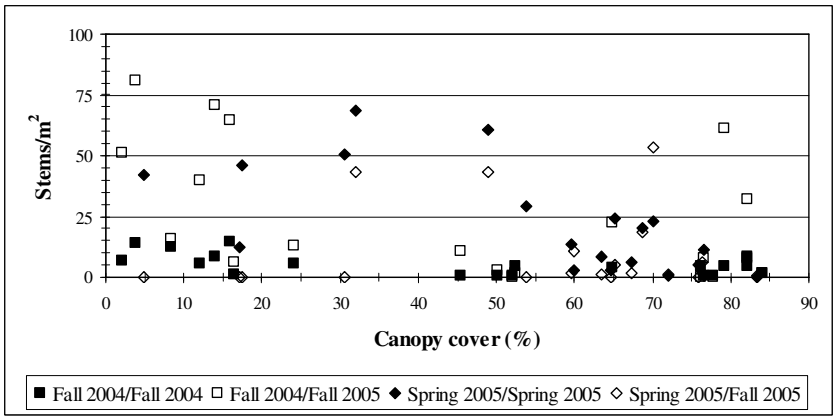

Figure 13. Forest canopy cover vs. density of understory herbs at the Monhegan Island study site.

(P = 0.003)

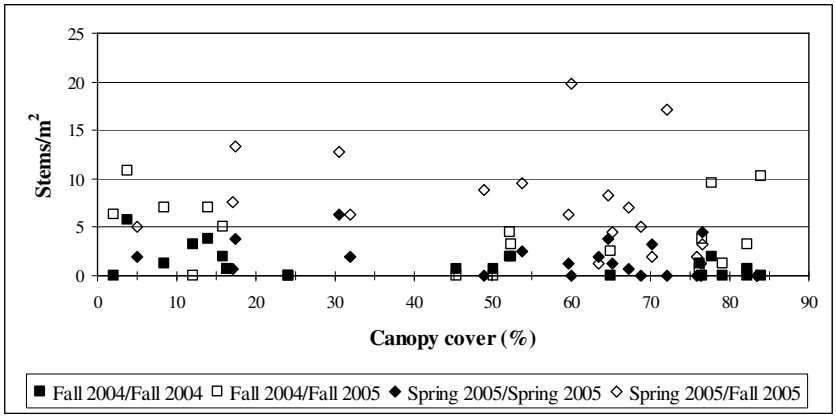

Figure 14. Forest canopy cover vs. density of Japanese barberry vegetative sprouts at the Monhegan Island study site.

(P = 0.058).

There was a marginally significant trend of increasing Japanese barberry sprouts with increasing Japanese barberry cover (P = 0.055) (Figure 15) but no relationship between Japanese barberry cover and Japanese barberry seedlings (Figure 16) or understory herbs (Figure 17). Again, maximum understory herb abundance was approximately half that of Japanese barberry seedlings, while Japanese barberry vegetative sprout density was an order of magnitude lower.

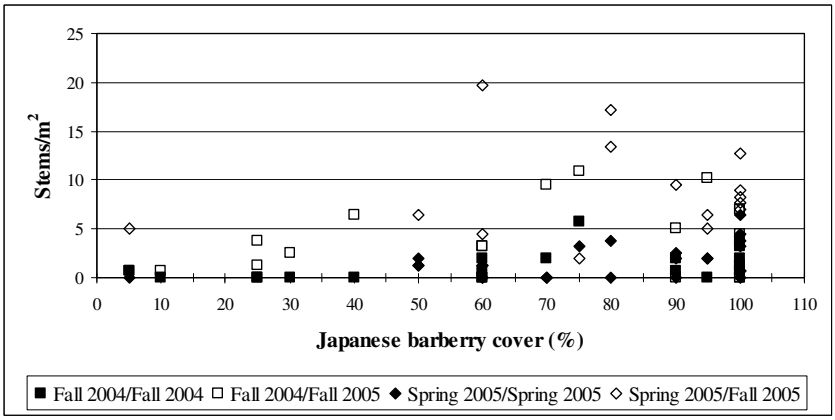

Figure 15. Japanese barberry cover vs. density of J. barberry vegetative sprouts at the Monhegan Island study site.

(P = 0.055).

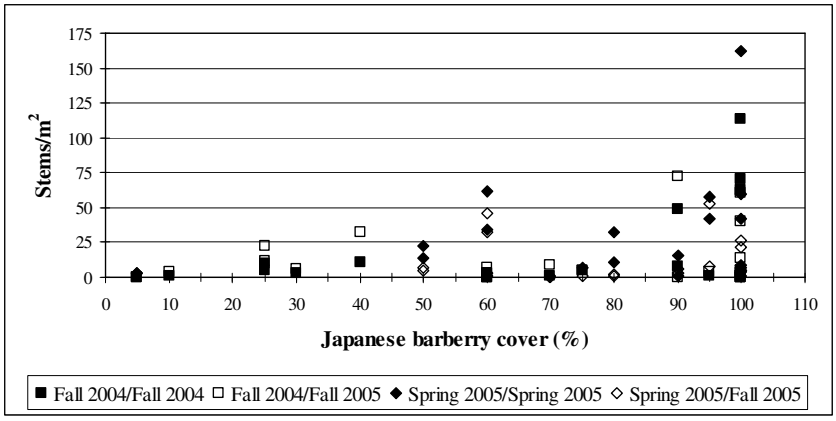

Figure 16. Japanese barberry cover vs. density of J. barberry seedlings at the Monhegan Island study site.

(P = 0.136).

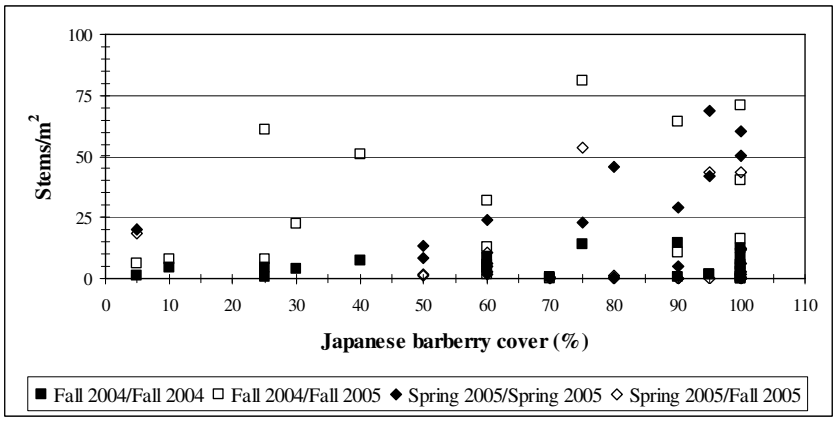

Figure 17. Japanese barberry cover vs. density of understory herbs at the Monhegan Island study site

(P = 0.998).

The interaction between season of clipping and time of observation (e.g., first or second) was significant for Japanese barberry seedlings (P = 0.041) (Figure 18a) and understory herbs (P = 0.027) (Figure 19a). The high initial Japanese barberry seedling density in the spring 2005 clipped plots was reduced in fall 2005 to a level below the first and second counts for the fall 2004 clipped plots. The significant interaction for understory herbs is due to low mean density in fall 2004 which increased by fall 2005 to a level above mean densities of the first and second observations for the spring 2005

plots. Japanese barberry vegetative sprout abundance increased at the second observation on both clipping treatments, but the increase was not statistically significant (P = 0.138) (Figure 20a).

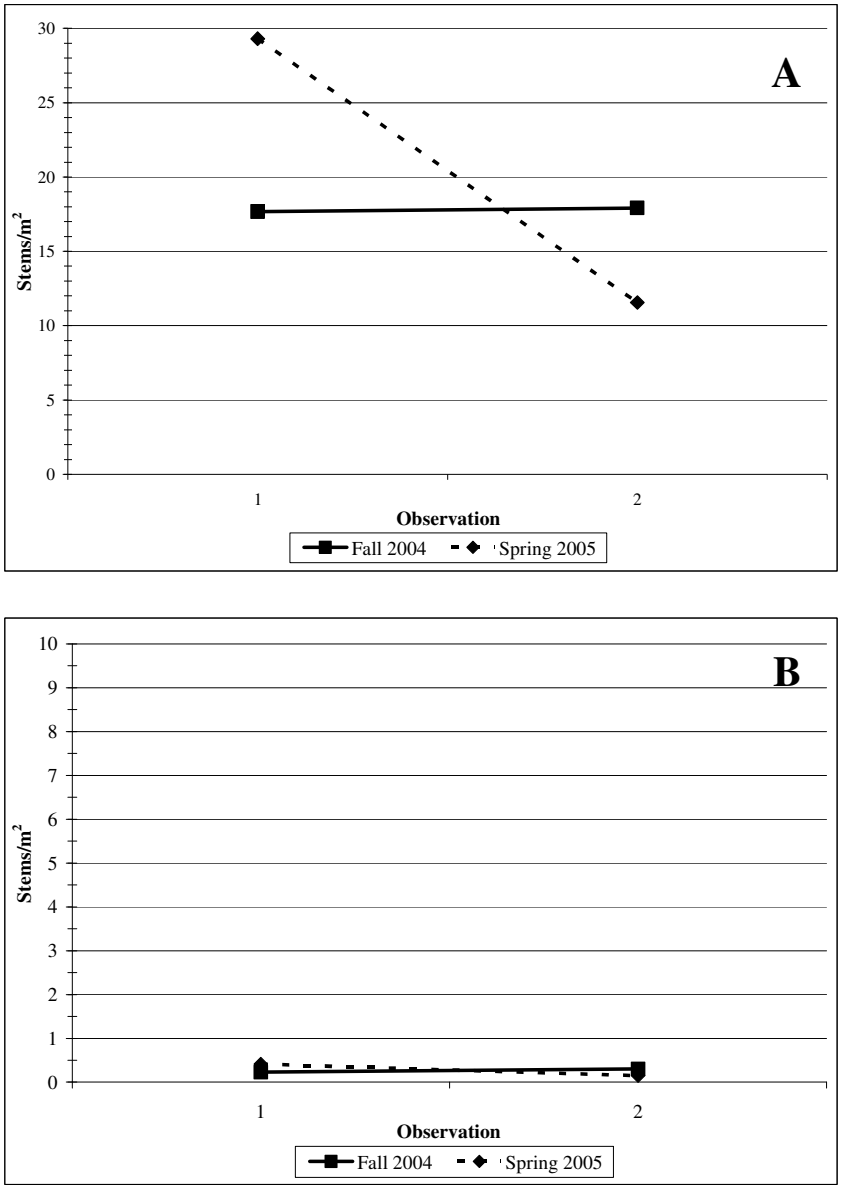

Figure 18. Changes in Japanese barberry seedling density over one growing season.

A = Monhegan Island (P = 0.041)
B = Wells Research Reserve
1 = season of clipping/initial observation
2 = observation fall 2005

Mean densities at the Wells Research Reserve study site were lower than those at Monhegan Island for all plant groups. Changes in mean densities of Japanese barberry seedlings at Monhegan Island (Figure 18a) were similar to those at Wells Research Reserve for plots clipped in fall 2004 (Figure 18b). Mean abundance of the spring 2005 clipped plots decreased slightly in fall 2005 at Wells Research Reserve but at Monhegan Island density was highest in spring 2005 and decreased sharply over the growing season. There was a similar relationship for understory herbs at both Monhegan Island (Figure 19a) and the Wells Research Reserve (Figure 19b). Changes in mean densities of Japanese barberry vegetative sprouts at the Wells Research Reserve (Figure 20b) also supported the trend found at Monhegan Island (Figure 20a). Mean densities of tree regeneration appeared similar at both sites with four or fewer seedlings/m^2 and a slight increase after one growing season (Figure 21a and b). However, trends in mean density changes for shrub regeneration (Figure 22a and b) and herb regeneration (Figure 23a and b) were not consistent between sites.

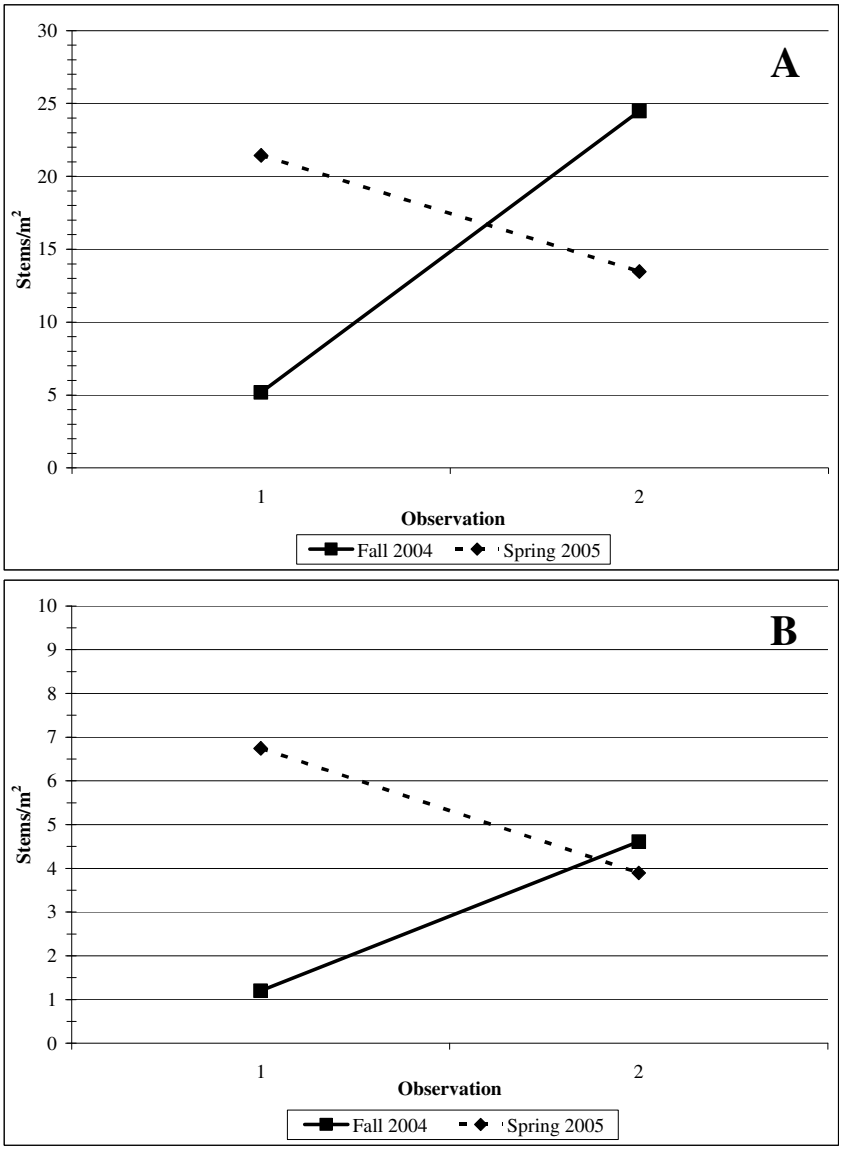

Figure 19. Changes in density of understory herbs over one growing season.

A = Monhegan Island (P = 0.027)
B = Wells Research Reserve
1 = season of clipping/initial observation
2 = second observation fall 2005

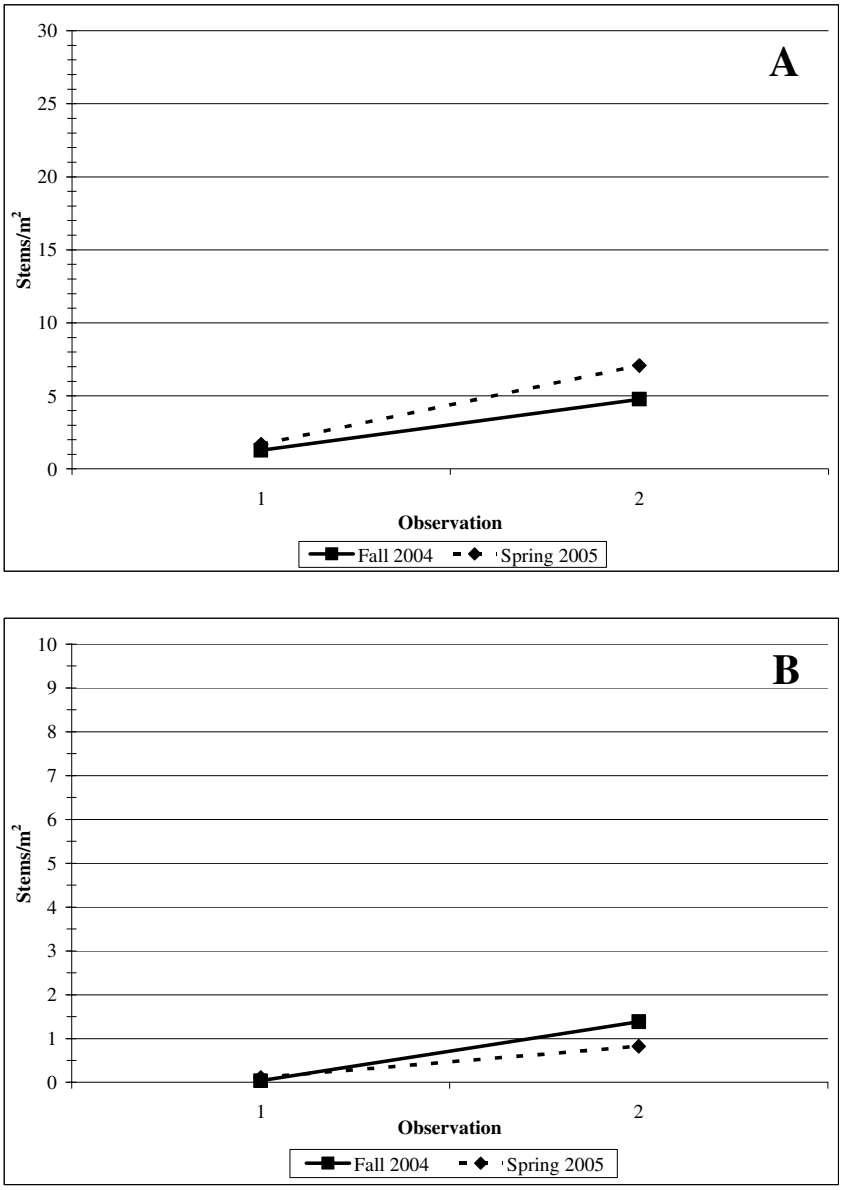

Figure 20. Changes in Japanese barberry vegetative sprout density over one growing season.

A = Monhegan Island (P = 0.284)
B = Wells Research Reserve
1 = season of clipping/initial observation
2 = observation fall 2005

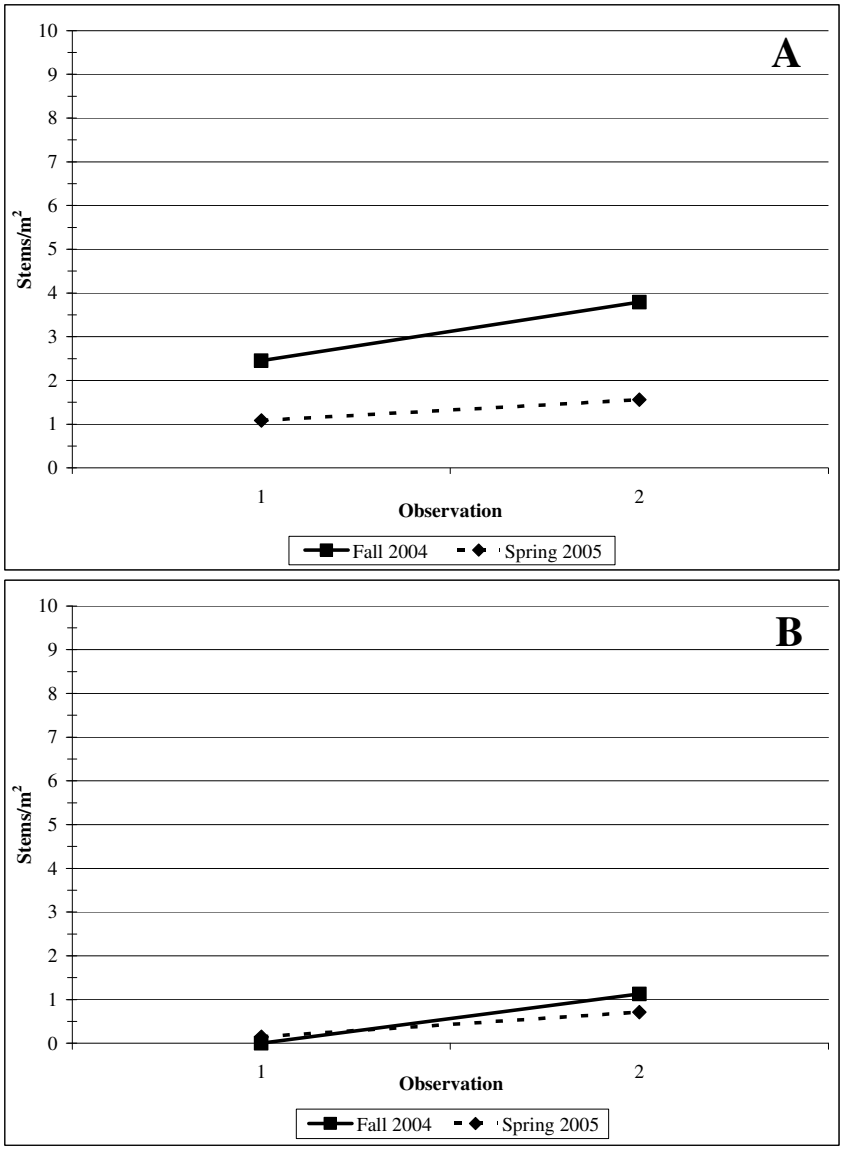

Figure 21. Changes in density of tree regeneration over one growing season.

A = Monhegan Island B = Wells Research Reserve
1 = season of clipping/initial observation
2 = observation fall 2005

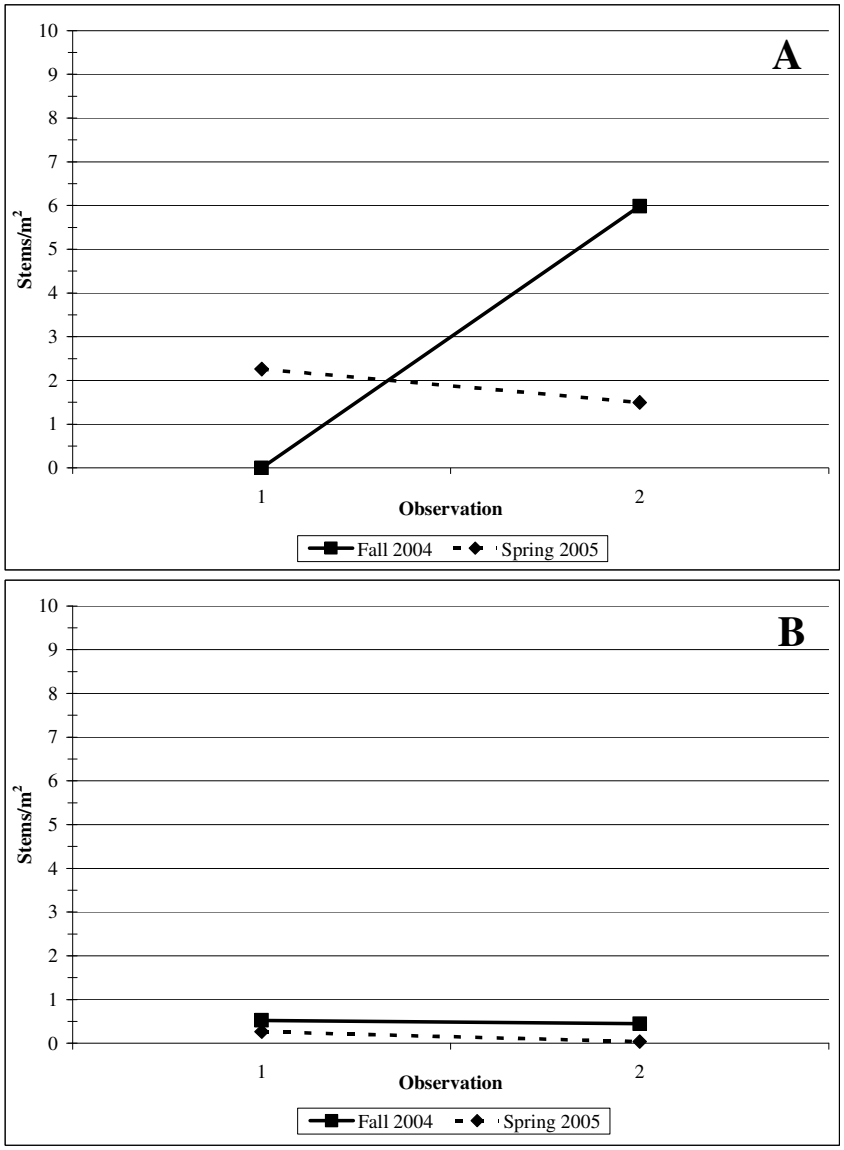

Figure 22. Changes in density of shrub regeneration over one growing season.

A = Monhegan Island B = Wells Research Reserve
1 = season of clipping/initial observation
2 = observation fall 2005

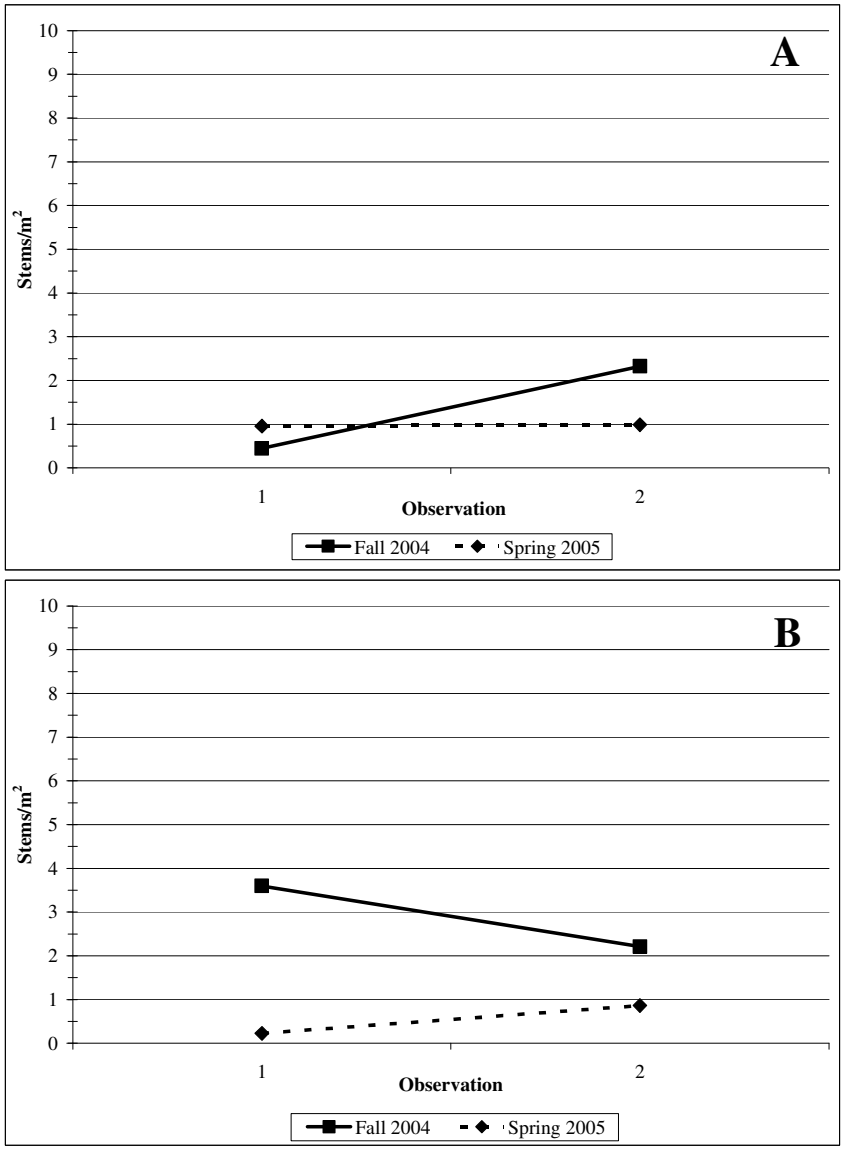

Figure 23. Changes in density of herb regeneration over one growing season.

A = Monhegan Island B = Wells Research Reserve
1 = season of clipping/initial observation
2 = observation fall 2005

Soil Incubation Studies

The results for data collected during the soil incubation studies were compared to the respective results for the field data. However, due to low incidence of seedlings in plots, statistical analyses were not calculated. Field observations confirmed that Japanese

barberry at both study sites produced seeds such that they likely contribute seed to a soil seed bank.

Incubating soil from the field sites in a greenhouse resulted in a lower Japanese barberry seedling density (4.5 stems/m^2) than what was measured in the field (11.8 stems/m^2) at the Monhegan Island study site for fall 2004. Conversely, density of non-barberry species was much higher in the greenhouse (15,669.8 stems/m^2 vs. 4.4 stems/m^2) (Table 4). Japanese barberry seedling densities at Wells Research Reserve were similar for the field and greenhouse (2.7 and 2.6 stems/m^2, respectively) but density of non-barberry species was much higher in the greenhouse. Emergence of commercial seed was 34.5%. In spring 2005 Japanese barberry seedling density on the nursery pad (16.1 stems/m^2) was lower than that in the field (29.3 stems/m^2) for Monhegan Island. However, seedling density at Wells Research Reserve rose from 0.4 stem/m^2 in the field to 6.3 stems/m^2 on the nursery pad. Once again, the densities of non-Japanese barberry seedlings (5,886.7 stems/m^2 Monhegan and 2,713.0 stems/m^2 Wells) were magnitudes higher than field densities (25.7 stems/m^2 and 7.4 stems/m^2 respectively) for both study sites. Emergence of commercial seed was 10.2%. In fall 2005 Japanese barberry seedling density at Monhegan Island dropped from 11.6 stems/m^2 in the field to 9.2 stems/m^2 in the greenhouse. At Wells Research Reserve, however, seedling density went from 0.2 stem/m^2 in the field to 4.7 stems/m^2 in the greenhouse. The large increase in density of non-Japanese barberry species in incubated soil (11,973.9 stems/m^2 and 3.054.3 stems/m^2, respectively) compared to the field (Table 1, Table 2) remained consistent with the 2004 results for both sites. Emergence of commercial seed was 28.2%.

			Clipped Fall 2004 Observed Spring 2005			Fall 2004 Soil Samples			Spring 2005 Soil Samples			Fall 2005 Soil Samples		
Site	**Plant Group**	**N***	**Stems/m^2**	**SE**	**Freq.**	**Stems/m^2**	**SE**	**Freq.**	**Stems/m^2**	**SE**	**Freq.**	**Stems/m^2**	**SE**	**Freq.**
Monhegan	JB seedling	20	11.8	2.1	20	4.5	NA	2	16.1	NA	8	9.2	NA	3
	JB vegetative	20	7.5	1.1	20	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Other	20	4.4	2.3	13	15669.8	NA	20	5886.7	NA	20	11973.9	NA	20
Wells	JB seedling	17	2.7	1.6	8	2.6	NA	1	6.3	NA	2	4.7	NA	1
	JB vegetative	17	2.0	0.4	16	NA	NA	NA	NA	NA	NA	NA	NA	NA
	Other	17	25.0	4.3	17	7064.0	NA	17	2713.0	NA	16	3054.3	NA	17

Table 4. Spring 2005 Japanese barberry field counts of fall 2004 plots and seedling emergence of Japanese barberry versus other species for fall 2004, spring 2005 and fall 2005 soil samples incubated in the greenhouse/nursery pad.

*N=16 Wells Research Reserve soil samples spring 2005.
JB = Japanese barberry SE = standard error Freq. = frequency

In the forest, many of the seeds present deeper in the soil could not germinate but could do so when exposed to light during soil incubation. Therefore, in order to confirm the results shown in Table 4, the emergence of Japanese barberry seedlings versus other seedlings was compared for the litter layer only (Table 5). The results in Table 5 show the same trends as those in Table 4.

		Fall 2004 Soil Samples	Spring 2005 Soil Samples	Fall 2005 Soil Samples
Site	**Plant Group**	**Stems/m^2**	**Stems/m^2**	**Stems/m^2**
Monhegan	JB seedling	0.0	10.0	6.9
	Other	2494.4	353.5	3320.4
Wells	JB seedling	2.6	0.0	0.0
	Other	1080.2	172.9	448.2

Table 5. Seedling emergence of Japanese barberry versus other species in the litter layer only for fall 2004, spring 2005 and fall 2005 soil samples incubated in the greenhouse/nursery pad.

JB = Japanese barberry

Seedling Emergence Test

The one-way ANOVA was performed for the extracted seed, 2004 commercial seed and 2003 commercial seed only because the emergence success of seed contained in berries was too low to allow analysis. Pairwise mean differences were compared using a post-hoc Tukey's test. Treatment was a significant source of variation ($P < 0.001$). The emergence success of the extracted seed (12.8%) and 2003 commercial seed (1.8%) were significantly different ($P < 0.001$), as were the 2004 commercial seed (9.4%) and the 2003 commercial seed ($P < 0.001$). Emergence success of the extracted seed and 2004 commercial seed were not significantly different ($P = 0.218$). Mean percent emergence of Japanese barberry seedlings is presented in Table 6, and the ANOVA results are presented in Table 7.

Storage Type	Seed Type	N	Mean % emergence/flat*	SE
berry	berry	25	0.3	0.2
	extracted	25	12.8	1.5
seed	2003 commercial	25	1.8	0.6
	2004 commercial	25	9.4	1.3

Table 6. Seedling emergence averages of Japanese barberry under four seed conditions.

*out of 32 seeds/flat.
N = number of flats SE = standard error

Source	MS	df	F-ratio	P-value
Treatment*	0.44	2	29.40	<0.001
Error	0.02	72		

Table 7. One-way ANOVA of seedling emergence test.

*excludes berry/berry due to low frequency
MS = mean squared df = degrees of freedom

DISCUSSION

Field Studies

Native plants regenerated poorly under a Japanese barberry canopy (Table 1, Table 2). Others (Kourtev et al. 1998 and 2002a, Ehrenfeld 1999) have also found that Japanese barberry can form thickets under closed canopies under which few herb species and no shrub species grow. In this study, seedlings of Japanese barberry were more abundant than any other plant group found in the Monhegan Island study site plots (162.4 stems/m^2) at twice the maximum density of understory herbs (80.9 stems/m^2). Tree, shrub and herb regeneration at Monhegan Island were so sparse that the data could not be

statistically analyzed using parametric techniques, as were all plant groups at Wells Research Reserve.

The percent cover of Japanese barberry had little effect on the number of stems of plants growing underneath. Percent Japanese barberry cover was not correlated with density of Japanese barberry seedlings or understory herbs (Figure 16, Figure 17), and there was a marginally significant trend of increasing vegetative sprouts with increased initial Japanese barberry cover over one growing season (Figure 15). Ehrenfeld (1999) found a higher density of Japanese barberry sprouts associated with larger plants after two growing seasons (1994 $r^2 = 0.456$, $P < 0.001$; 1995 $r^2 = 0.508$, $P < 0.001$), but the relationship varied with population and year. I speculate that the abundance of vegetative Japanese barberry sprouts on plots with high Japanese barberry cover at my study sites will likely increase with additional growing seasons.

Density of Japanese barberry seedlings was not correlated with percent cover of Japanese barberry cover (Figure 16), but the lack of a relationship here may be due to the ability of seedlings to persist under a Japanese barberry overstory with low light transmittance, even 1% (Silander and Klepeis 1999). Ehrenfeld (1999) also found that seedling density and mortality were variable among populations and years (although mortality was generally <15%), but she did find a correlation between number of seedlings and initial stem densities of reproductive individuals ($r^2 = 0.466$, $P < 0.001$). Ehrenfeld did not remove the Japanese barberry overstory and sampled more plots in seven stands over two growing seasons. Therefore, her results are not directly comparable to the results presented here.

Where percent cover of forest canopy cover was high, I found an associated lower density of Japanese barberry seedlings and understory herbs (Figure 12, Figure 13). These findings are supported by Silander and Klepeis (1999) who state that growth of herbs and shrubs in a Japanese barberry thicket are positively correlated with light (4-89% light transmittance in the field over two growing seasons: no removal of Japanese barberry $r^2 = 0.87$, $P = 0.002$; removal $r^2 = 0.65$, $P = 0.030$). Silandar and Klepeis (1999) also found more barberry sprouts with increasing light (0.8%, 9%, 15%, and 33% light transmittance in the greenhouse; $r^2 = 0.350$, $P < 0.001$) while I found a marginally significant relationship ($P = 0.058$). If observations at the study sites had continued over additional growing seasons, I would expect that a stronger relationship between increasing canopy light and vegetation growth would be evident.

There was a significant interaction between season of clipping and time of observation for Japanese barberry seedlings (Figure 18a) and understory herbs (Figure 19a). At the Monhegan Island study site Japanese barberry seedling density dropped sharply from spring 2005 to fall 2005 but there was little change from fall 2004 to fall 2005. Change in seedling density at Wells Research Reserve was similar for plots clipped in fall 2004 only (Figure 18b). By waiting to clip the Japanese barberry in some plots until spring 2005, the 2004 seed crop was able to mature and fall to the ground during the winter and likely explains the higher seedling density (30 stems/m^2) at this time. However, the decrease in density observed in fall 2005 (12 stems/m^2) could be due to mortality over the summer. There was little change in Japanese barberry seedlings densities on the fall-clipped plots. Because these plots also had almost no new seedlings in spring 2005 (Table 4), seedling mortality at Monhegan Island may have occurred

mostly in the first growing season. Also, the lack of a significant increase in Japanese barberry seedling density from the first observation in fall 2004 to the second observation in fall 2005 when released from Japanese barberry canopy shading indicates that Japanese barberry does not have a seed bank at these locations.

The lowest density of herbs was found after clipping the barberry in the fall (Figure 19). The increase in herb density after one growing season and the high levels of herbs in the spring-clipped plots were likely responses to having enough light in early spring and through the summer to allow strong growth. At Monhegan Island, many species with relatively high densities in spring 2005 (e.g., bunchberry [*Cornus canadensis*], buttercups [*Ranunculus* spp.], starflower [*Trientalis borealis*], violets [*Viola* spp.], strawberries [*Fragaria* spp.]) were either absent or at lower densities in fall 2005 (see Appendix). These species all flower in May and June (Chambers et al. 1996). Species found in fall 2004 typically had increased density in fall 2005 with the notable exception, rough-stemmed goldenrod (*Solidago rugosa*), which was not found in fall 2004 but was the most abundant understory herb in fall 2005. The Wells Research Reserve plots also contained many species in fall 2005 that were absent in fall 2004. The overall higher density in spring 2005 was due to high densities of two spring flowering species, wood anemone (*Anemone quinquefolia*) and starflower.

Mean densities of tree regeneration were similar at each site (Figure 21). Both sites had consistently low densities with little short-term recovery after release from the Japanese barberry overstory. For example, a coastal forest in mid- to downeast Maine would normally be dominated by balsam fir and spruce (*Picea* spp.) (Davis 1966) and so one would expect to see seedlings of these species in the understory. Although balsam fir

was the most abundant regenerating tree species at Monhegan Island, it had low frequencies in the study area. The spruces also had low frequencies and changes in density after release from Japanese barberry canopy shading were inconsistent over the 2005 growing season, but this study was not long enough to determine an overall growth response.

The increase in shrub regeneration at the Monhegan Island study site from fall 2004 to fall 2005 after clipping (Figure 22a) is due to regeneration of mainly northern wild raisin (*Viburnum nudum* var. *cassinoides*), an unknown shrub, and winterberry holly (*Ilex verticillata*). Winterberry holly is more typical of wet sites, but northern wild raisin inhabits a wide range of habitats (Chambers et al. 1996) and should have been able to regenerate at this site. Winterberry holly was also the most common regenerating species observed at Wells Research Reserve along with speckled alder (*Alnus incana* ssp. *rugosa*), both of which should have thrived in the swampy conditions at this study site. As Figure 22b shows, however, shrub regeneration was almost nonexistent.

Soil Incubation Studies

The higher density of non-barberry species and seedling emergence of the commercial seed indicate that there is virtually no Japanese barberry seed bank, because if viable Japanese barberry seed were present in the forest soil samples taken in fall 2004, more than two seedlings should have germinated. At eight total seedlings, emergence of Japanese barberry seedlings in soil sampled in spring 2005 at Monhegan Island were higher than that in fall 2004 because the spring samples presumably had ungerminated seed from the 2004 seed crop (Table 4). In fall 2005 emergence of viable seed fell to four seedlings (9.2 stems/m^2) from three plots. Soil samples collected in fall 2005

approximated the 2004 soil results; there was virtually no viable Japanese barberry seed remaining in the soil after one growing season.

Japanese barberry seedling emergence in soil from the Wells Research Reserve study site yielded only one seedling in fall 2004, two in spring 2005, and two in fall 2005. In addition, germination observed in the field was also extremely low (2.7 stems/m^2 maximum). Japanese barberry probably had low seedling densities at the Wells Research Reserve study site because of an unusually wet spring (57 cm precipitation March-May) coupled with greater forest canopy shading (canopy shading averaged 70% for spring 2005 clipped plots at the Wells Research Reserve site as opposed to 55% at the Monhegan Island site) and a site that was already wetter than Monhegan Island. . Evidently, the wet conditions at the Wells site were detrimental to viability of Japanese barberry seed. Silander and Klepeis (1999) state that Japanese barberry can survive a wide range of soil moisture, including soils with over 40% soil moisture. They do not clarify whether establishment was via seed or vegetative means. It may be that Japanese barberry can spread itself vegetatively at wet sites but not sexually, but more research is needed to determine whether this is true.

The results of my soil incubation studies support the preliminary results of Brand (University of CT, message dated 3/14/06). Brand found that 'atropurpurea' seed greenhouse germination was two times that of seed collected from feral green-leaved Japanese barberry. The soil samples I processed resulted in emergence of one to eight seedlings. By contrast, 'atropurpurea' germination success averaged 10.2%, 28.2% and 34.5%. Although the total number of seeds in the soil samples was unknown and percent emergence could not be calculated, it is clear that 'atropurpurea' seed was more

successful than the feral green-leaved Japanese barberry at the study sites. Brand believes that this is due to inbreeding depression in some feral populations of Japanese barberry, but research to confirm this is in progress.

At both locations for all three greenhouse trials, emergence of seedlings of non-barberry species was magnitudes higher than emergence in the field (Table 1, Table 2, Table 4). The incidence of both Japanese barberry seedlings and those of other species were overrepresented in the greenhouse because the soil was spread out on flats. Even when data for the litter layer only was evaluated (Table 5), there were still much higher counts of non-barberry seedlings in the greenhouse than what was observed in the field. These results indicate the presence of a large non-barberry seed bank, which could germinate after a disturbance exposing the seed bank to light. Therefore, current low numbers of native plants on the study sites may not be due to the lack of seed but to lack of light suppressing their regeneration. Once released from a Japanese barberry canopy, native species should be able to re-establish themselves in the study areas if forest canopy cover is not limiting.

The seedling emergence of my commercial seed for fall 2004, spring 2005 and fall 2005 was 34.5%, 10.2% and 28.2%, respectively. The fall 2004 soil samples had the highest emergence rate despite fungal infection appearing approximately 12 weeks into incubation; apparently the fungus was not a factor in emergence success. Davis (1927) had emergence rates of 49-78% for seeds planted in cold frames. An explanation for my lower rates could be differences in incubation temperature; Rohde (1984) found that germination of a related species, *Berberis* x *hybridogagnepainii*, varied from approximately 10% to 90% depending on incubation temperature. Therefore, lower

emergence rates in my study could be due to temperature conditions, but Davis (1927) did not report her incubation temperatures for comparison. Despite the range in emergence rates of the commercial seed, emergence densities remained very low for all field trials. Although the spring 2005 trial had the lowest emergence rate of commercial seed, it had the highest emergence density of Japanese barberry seed in the subsample flats, indicating that the reduced densities from the fall soil samples were due to reduced seed viability and not poorer incubation conditions (Figure 18). Extracted seed from both study sites had higher emergence rates than the commercial seed (Table 6), indicating that viable seed contained in the soil samples was detected. However, temperature conditions probably resulted in lower densities in the soil incubation studies versus densities in the field.

Seedling Emergence Test

The results of the seedling emergence test also indicate that Japanese barberry has virtually no viable seed bank beyond one growing season. The berries collected in the field were gathered approximately the same time as the 2004 commercial seed and were stored for approximately the same length of time. There was no significant difference in mean percent emergence between the extracted seed (12.8%) and the 2004 commercial seed (9.4%) ($P = 0.218$). The 2003 commercial seed was collected during approximately the same time frame the previous year, and its mean percent emergence (1.8%) was significantly lower than that of the 2004 extracted and 2004 commercial seed. This indicates that after two growing seasons of storage, seed viability had significantly dropped which supports the findings of the soil incubation studies. It is not known why the seeds in berries showed such poor germination because the seedcoat does not have a

germination inhibitor (Dirr and Heuser 1987). In spring 2005 I observed both naked seeds and berries on the forest floor. Davis (1927) found that germination of seeds immediately sowed in berries was delayed by a few weeks but overall emergence (52-96%) was similar to extracted seeds (49-78%). However, she recommended that seeds not be stored in the berry because significant or total seed loss could occur due to fungal infection, a finding also recommended in Piotto and Di Noi (2001). I did not observe any obvious fungal infection in my study, but no attempts were made to isolate potential pathogens.

As previously explained, the low seedling emergence for commercial seed (1.8% and 9.4%) could be due to suboptimal conditions. Therefore, results of this study are limited in application; more research is needed assessing a range of seedling emergence test conditions to further evaluate the trends found in this study.

MANAGEMENT CONSIDERATIONS

An invasion of Japanese barberry is detrimental to native systems and should be of concern not only to homeowners or scientists, but also to woodlot owners and managers. Japanese barberry thickets may be detrimental to tree regeneration so that even if a woodlot owner controls this invasive shrub, he or she may still have to plant trees to regenerate a forest canopy on the site. A partial harvest may be needed for light to reach the forest floor and aid tree regeneration. Therefore, to promote natural regeneration of trees on a woodlot, it is highly recommended that the woodlot owner commence control efforts prior to thicket formation or any harvesting of trees. Keep in mind that germination success of tree and other seed also depends on seed source, shade, soil, moisture and other site conditions subsequent to release from Japanese barberry.

At this point the most effective control method for Japanese barberry in forests of the northeast appears to be herbicide application (Ehrenfeld 1999, Silander and Klepeis 1999). To minimize non-target impacts, apply herbicide early in the growing season just after Japanese barberry has leafed out and before leaf-out of other native shrubs and trees. In areas with desirable grasses triclopyr should be used instead of glyphosate (Rhoads and Block 2002). If spring application is not feasible, plants should be sprayed before the seeds mature and drop in the fall. For small or sparse populations, cut stump treatment is recommended so that reproductive individuals are removed before treatment and do not become a fire hazard or interfere with harvesting equipment. When treatment of individual stumps is not feasible, removal of dead shrubs after foliar herbicide application is recommended so that as much light as possible reaches the forest floor. Removal of dead shrubs will also greatly aid in moving through the understory, because follow-up removal of seedlings will most likely be necessary at least in the growing season directly after removal. Seedlings can be killed with herbicide or can be easily pulled up. As long as the species is not allowed to reinvade from surrounding locales, Japanese barberry should be suppressed or eradicated within three growing seasons of annual treatments.

In areas where herbicide is prohibited, not feasible or not desired, merely clipping shrubs to ground level is not recommended. If the root system is not killed, the shrubs will resprout from the root collar and may still spread vegetatively until new branches set seed. In those cases, manual or mechanical removal of the entire root system is recommended. The resulting soil disturbance may stimulate germination of viable seed from the previous year (D'Appollonio, personal observation), so follow-up removal of

seedlings is key. If soil disturbance is not desired, the woodlot owner must clip branches to ground level annually to biannually.

Prescribed fire is also a management tool for Japanese barberry, but it is often impractical or prohibited in heavily populated areas of the Northeast. The most effective treatment regime is multiple treatments per growing season over multiple growing seasons (Richburg et al. 2004). Cut stems to the ground just after Japanese barberry leafs out. Allow time for resprouting and then burn the slash. Additional treatments during the same growing season should be mechanical (e.g., cutting or mowing). Burning of cut stems and standing vegetation is more successful during the dormant season, but it does little to reduce the vigor of Japanese barberry in the long-term.

Follow-up control methods may vary by site, because Japanese barberry may regenerate via different means under different site conditions. For example, Silander and Klepeis (1999) believe that seedling establishment may be the critical component in limiting establishment of Japanese barberry at locations with dense canopies; pulling seedlings or herbicide treatments could stop establishment in these cases. At other locations invasion and/or reinvasion may be primarily via vegetative means if neighboring thickets exist, and follow-up control may mean herbicidal cut stump treatment of sprouts or prescribed fire as opposed to pulling seedlings by hand.

CONCLUSION

Although the relationships between Japanese barberry cover and other plants were not always consistent among plant groups, Japanese barberry appears to have a detrimental effect in suppressing regeneration of other species in two coastal forests of Maine, as was evidenced by the scarcity of non-barberry plant seedlings overall. Forest

canopy cover was negatively correlated with density of Japanese barberry sexual regeneration but not necessarily vegetative sprout density. Higher forest canopy cover was associated with low understory herb density, but regeneration of other herbs, shrubs and trees were too sparse to analyze in regard to a relationship with forest canopy shading. Japanese barberry seed viability appears to drop off significantly in the second growing season after seed drop, indicating that Japanese barberry generally germinates the growing season following seed maturation and does not have a viable seed bank beyond that time; more research is needed to confirm this. So, although Japanese barberry reproduces mainly by seed, reinvasion of a compromised site can be avoided or minimized by preventing seedling establishment over the span of a few years. This translates into long-term cost savings for woodlot owners.

The key to eradicating Japanese barberry in coastal forests stems from early detection and control efforts. Once Japanese barberry forms thickets, eradication quickly becomes difficult to impossible, and preventing the spread of existing populations becomes critical. Eradication efforts should begin while a population is sparse and plants are small, so that all plants can be removed and follow-up monitoring and removal of seedlings is manageable. In populations approaching the thicket phase, control efforts should focus on the larger plants because they produce more seed, the primary source of reproduction, and seedlings (especially those at the fringe of the population) so that the population can at least be contained. If herbicide is not used on a thicket, the population can also be contained by prescribed fire and/or regular clipping of branches and pulling of seedlings. Removal of branches prior to seed maturation will help to prevent germination of new plants. An effective strategy for protecting uninvaded natural areas is

to alert resource managers and visitors to watch for the spread of Japanese barberry and then eliminate small populations promptly when they are first noticed.

The considerations and conclusions discussed above should be viewed in context with the limitations of this study, i.e. two study sites and one growing season. While my results were consistent in many ways with previous studies, more research in more locations over multiple growing seasons is needed to investigate how Japanese barberry regenerates under an array of site conditions.

Future autecological research should focus on filling the gaps of knowledge pertaining to this species. Vertebrates and invertebrates must be studied as short- and long-distance seed dispersal vectors so that we better understand how Japanese barberry escapes from cultivation. The effects of deer browsing pressure and how it aids Japanese barberry populations while detrimentally affecting other woody species must be quantified. Regeneration strategies in response to environmental factors should also be examined; for example, the notion of asexual regeneration on wet sites as opposed to sexual regeneration on drier sites. Therefore, further research on population dynamics is required to determine if there are critical factors determining the rate at which isolated foci expand to become thickets.

REFERENCES

Barton, A.M., L.B. Brewster, A.N. Cox and N.K. Prentiss. 2004. Non-indigenous woody invasive plants in a rural New England town. *Biological Invasions* 6:205-211.

Brand, M.H. Personal communication with Jennifer D'Appollonio in emails dated March 14 and 17, 2006. Professor, Ornamental Horticulture and Co-Head, Plant Biotechnology Facility, Department of Plant Science, University of Connecticut, 1376 Storrs Rd. Storrs, CT 06269.

Cassidy, T.M. 2002. Effects of soil acidity and resource availability on the growth of Japanese barberry (*Berberis thunbergii*). MS thesis, Department of Natural resources Conservation, University of Massachusetts at Amherst, 49 pp.

Cassidy, T.M., J.H. Fownes and R.A. Harrington. 2004. Nitrogen limits an invasive perennial shrub in forest understory. *Biological Invasions* 6:113-121.

Chadwick, L.C. 1935. Practices in propagation by seed. *American Nurseryman* 62(12): 3-9.

Chambers, B., K. Legasy and C.V. Bentley. 1996. Forest plants of central Ontario. Edmonton, Alberta, Canada: Lone Pine Publishing & Queen's Printer for Ontario. 448 pp.

Clinton, W.J. 1999. Executive order 13112: invasive species. *Federal Register* 64(25): 6183-6186.

Coblentz, B.E. 1990. Exotic organisms: a dilemma for conservation biology. *Conservation Biology* 4(3):261-265.

Connecticut Department of Environmental Protection (CTDEP). 1999. Japanese barberry *Berberis thunbergii* Barberry family (Berberidaceae). Department of Environmental Protection Environmental and Geographic Information Center, 79 Elm St. Hartford, CT 06106. www.hort.uconn.edu/cipwg/art_pubs/DEP/pdf/p_japbarb.pdf

Davis, O.H. 1927. Germination and early growth of *Cornus florida*, *Sambucus canadensis*, and *Berberis thunbergii*. *The Botanical Gazette* 84(3):225-263.

Davis, R. B. 1966. Spruce-fir forests of the coast of Maine. *Ecological Monographs* 36(2):79-94.

Dharmananda, S. 2005. New uses of berberine: a valuable alkaloid from herbs for "damp-heat" syndrome. Institute for Traditional Medicine, 2017 SE Hawthorne Ave. Portland, OR 97214. www.itmonline.org/arts/berberine.htm.

Dibble, A.C. Personal communication with Jennifer D'Appollonio in an email dated April 20, 2006. Adjunct Assistant Professor, Department of Biological Sciences, 5722 Murray Hall, University of Maine, Orono ME 04469.

Dirr, M.A. and C.W. Heuser, Jr. 1987. The reference manual of woody plant propagation – from seed to culture. Athens, GA: Varsity Press, Inc. pp. 94-95.

Ehrenfeld, J.G. 1997. Invasion of deciduous forest preserves in the New York metropolitan region by Japanese barberry (*Berberis thunbergii* DC.). *Journal of the Torrey Botanical Society* 124(2):210-215.

Ehrenfeld, J.G. 1999. Structure and dynamics of populations of Japanese barberry (*Berberis thunbergii* DC.) in deciduous forests of New Jersey. *Biological Invasions* 1:203-213.

Ehrenfeld, J.G., P. Kourtev and W. Huang. 2001. Changes in soil functions following invasions of exotic understory plants in deciduous forests. *Ecological Applications* 11(5):1287-1300.

Fernald, M. L. 1950. Gray's Manual of Botany, 8th ed. A handbook of the flowering plants and ferns of the central and northeastern United States and Adjacent Canada, Volume 2. Portland, OR: Dioscorides Press. 1632 p. (1987 reprint with corrections by R.C. Rollins).

Flewelling, L.R. and R.H. Lisante. 1982. Soil survey of York County, Maine. USDA Soil Conservation Service in cooperation with the Maine Agricultural Experimental Station and Maine Soil and Water Conservation Commission. Sheet 50.

Frazer, G.W., C.D. Canham and K.P. Lertzman. 1999. Gap Light Analyzer (GLA): Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. Copyright ©1999: Simon Fraser University, Burnaby, British Columbia and the Institute of Ecosystem Studies, Millbrook, New York.

Gough, R.E. 1996. Growing trees and shrubs from seed. Colorado State University, Fort Collins. Montguide 9604. www.colostate.edu/Depts/CSFS/growseed.pdf.

Haines, A. and T.F. Vining. 1998. Flora of Maine: a manual for identification of native and naturalized vascular plants of Maine. Bar Harbor, ME: V.F. Thomas Co. 847 pp.

Harrington, R.A., R. Kujawski and H.D.P. Ryan. 2003. Invasive plants and the green industry. *Journal of Arboriculture* 29(1):42-48.

Harrington, R.A., J.H. Fownes and T.M. Cassidy. 2004. Japanese barberry (*Berberis thunbergii*) in forest understory: leaf and whole plant responses to nitrogen availability. *American Midland Naturalist* 151:206-216.

Hedstrom, G.T. 1987. Soil survey of Knox and Lincoln Counties, Maine. USDA Soil Conservation Service in cooperation with the Maine Agricultural Experimental Station and Maine Soil and Water Conservation Commission. Sheet 79.

Hobbs, R.J. and L.F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology* 6:324-337.

Huppmann, U. 1986. Investigations of the biology of *Rhagoletis berberidis* and *Rhagoletis meigeni* Diptera Tephritidae [abstract translated from German]. Pflanzenschutzberichte 47:45-64.

Kourtev, P.S., J.G. Ehrenfeld and W.Z. Huang. 1998. Effects of exotic plant species on soil properties in hardwood forests of New Jersey. *Water, Air, and Soil Pollution* 105:493-501.

Kourtev, P.S., W.Z. Huang and J.G. Ehrenfeld. 1999. Differences in earthworm densities and nitrogen dynamics in soils under exotic and native plant species. *Biological Invasions* 1:237-245.

Kourtev, P.S., J.G. Ehrenfeld and M. Häggblom. 2002a. Exotic plant species alter the microbial community structure and function in the soil. *Ecology* 83(11): 3152-3166.

Kourtev, P.S., J.G. Ehrenfeld and W.Z. Huang. 2002b. Enzyme activities during litter decomposition of two exotic and two native plant species in hardwood forests of New Jersey. *Soil Biology & Biochemistry* 34:1207-1218.

Kourtev, P.S., J.G. Ehrenfeld and M. Häggblom. 2003. Experimental analysis of the effect of exotic and native plant species on the structure and function of soil microbial communities. *Soil Biology & Biochemistry* 35:895-905.

Lebuhn, G. and G.J. Anderson. 1994. Anther tripping and pollen dispersal in *Berberis thunberii*. *American Midland Naturalist* 131:257-265.

Lundgren, M.R., C.J. Small and G.D. Dreyer. 2004. Influence of land use and site characteristics on invasive plant abundance in the Quinebaug Highlands of southern New England. *Northeastern Naturalist* 11(3):313-332.

Maine Forest Service Department of Conservation (MFS). 1995. Forest Trees of Maine, 12th ed. Maine Forest Service Department of Conservation Appropriation no. 014-04A-1111-122. 113 pp.

Maine Natural Areas Program (MNAP). 2004. 93 State House Station, Augusta, ME 04333. ww.state.me.us/doc/nrimc/mnap/factsheets/invasivefacts/bthunbergii.pdf.

Mehrhoff, L. J., J. A. Silander, Jr., S. A. Leicht, E. S. Mosher and N. M. Tabak. 2003. IPANE: Invasive Plant Atlas of New England. Department of Ecology & Evolutionary Biology, University of Connecticut, Storrs, CT, 06269. www.ipane.org.

National Climatic Data Center (NCDC). 2006. Data compiled from 1989-2005 weather station records. National Climatic Data Center, Federal Building, 151 Patton Ave., Asheville NC 28801. www.ncdc.noaa.gov/oa/climate/stationlocator.html.

Newcomb, L. 1977. Newcomb's wildflower guide. Boston, MA: Little, Brown and Company. 490 pp.

Niering, W.A. 1998. Forces that shaped the forests of the northeastern United States. *Northeastern Naturalist* 5(2):99-110.

Piotto, B. and A. Di Noi, ed. 2001. Fact sheets on the propagation of Mediterranean trees and shrubs from seed. Chapter 12 *in* Propagation of Mediterranean trees and shrubs from seed. Rome, Italy: I.G.E.R. srl - Viale C. T. Odescalchi, 67/A - 00147. p. 19. (translated from Italian by John Cullum, Writtle College, UK for the Agency for the protection of the environment and for technical services)

Rejmánek, M. and D.M. Richardson. 1996. What attributes make some plant species more invasive? *Ecology* 77(6):1655-1661.

Rhoads, A.F. and T.A. Block. 2002. Japanese barberry *Berberis thunbergii* DC. barberry family (Berberidaceae). Morris Arboretum of the University of Pennsylvania, 100 Northwestern Ave. Philadelphia, PA 19118.
www.paflora.org/Berberis%20thunbergii.pdf.

Richburg, J.A., A.C. Dibble and W.A. Patterson III. 2001. Woody invasive species and their role in altering fire regimes of the Northeast and Mid-Atlantic states. pp. 104-111 *in* K.E.M. Galley and T.P. Wilson (eds.) Proceedings of the invasive species workshop: The role of fire in the control and spread of invasive species. Fire conference 2000: The first national conference on fire ecology, prevention, and management. Miscellaneous publication No. 11, Tall Timbers Research Station, Tallahassee, FL.

Richburg, J.A., W.A. Patterson III and M. Ohman. 2004. Fire management options for controlling woody invasive plants in the northeastern and mid-Atlantic U.S. Department of Natural Resources Conservation, University of Massachusetts, Amherst, MA 01003. 63 pp.
www.umass.edu/nrc/nebarrensfuels/publications/pdfs/Richburg_Ohman-Invasives_Fire_final_report.pdf

Riley, J.M. 1981. Growing rare fruit from seed. *California Rare Fruit Growers Yearbook* 13:1-47. excerpted at www.crfg.org/tidbits/seedprop.html.

Rohde, J. 1984. Einfluβ der temperatur auf die kiemung von Berberis x hybridogagnepainii Suring. *Gartenbauwissenschaft* 49(5/6): 238-244.

Schmidt, L. 2002. Phytosanitary problems and seed treatment. Chapter 7 *in* Guide to handling of tropical and subtropical forest seed. Denmark: Danida Forest Seed Seed Centre. p. 25.

Silander, J.A. Jr. and D.M. Klepeis. 1999. The invasion ecology of Japanese barberry (*Berberis thunbergii*) in the New England landscape. *Biological Invasions* 1: 189-201.

SYSTAT Software, Inc. 2004. SYSTAT for Windows, Version 11.00.01. Systat Software, Inc., 501 Canal Blvd, Suite E. Point Richmand, CA 94804.

Tennessee Exotic Pest Plants Council (TNEPPC). 2004. Japanese barberry *Berberis thunbergii* DC. www.tneppc.org/Manual/Japanese_Barberry.htm.

U.S. Department of Agriculture (USDA), NRCS. 2006. The PLANTS Database, (http://plants.usda.gov). National Plant Data Center, Baton Rouge, LA. 70874-4490.

Vilà, M., E. Weber, and C.M. D'Antonio. 2000. Conservation implications of invasion by plant hybridization. *Biological Invasions* 2:207-217.

APPENDIX

		Clipped Fall 2004				Clipped Spring 2005			
		N_{Mon}=20 N_{Wells}=17				N_{Mon}=20 N_{Wells}=17			
		Observed Fall 2004		Observed Fall 2005		Observed Spring 2005		Observed Fall 2005	
Site	**Species**	**% cover/m²**	**Frequency**	**% cover/m²**	**Frequency**	**% cover/m²**	**Frequency**	**% cover/m²**	**Frequency**
Monhegan	*Carex* spp.	0.1	2	0.1	2			0.03	6
	Fragaria spp.	0.1	2	0.1	1				
	Galium spp.	0.03	1						
	grass/sedge	0.2	6	0.3	4	0.2	3		
	Maianthemum canadense Desf.					0.1	1		
	Potentilla simplex Michx.	0.05	2	0.1	1				
	Trifolium spp.			0.1	1				
	unknown herb	0.3	1	0.3	2				
	Viola spp.	0.03	1						
Wells	*Carex* spp.	0.03	4	0.1	7			0.02	8
	Fragaria spp.								
	grass/sedge	0.03	6			0.03	1	0.01	5

Table A1. Frequency and density of percent cover of understory herb species by study site.

(Haines and Vining 1998)

		Clipped Fall 2004				Clipped Spring 2005			
		N=20				N=20		N=20 (N=14 und herbs)	
		Observed Fall 2004		Observed Fall 2005		Observed Spring 2005		Observed Fall 2005	
Plant Group	**Species**	**Stems/m^2**	**Frequency**	**Stems/m^2**	**Frequency**	**Stems/m^2**	**Frequency**	**Stems/m^2**	**Frequency**
tree	*Abies balsamea* (L.) P. Mill.					1.3	1	1.3	7
tree	*Acer rubrum* L.					1.6	2		
tree	*Picea glauca* (Moench) Voss	2.1	3	0.6	1	0.8	4		
tree	*Picea rubens* Sarg.	0.6	2			1.3	2	1.1	3
tree	*Picea* spp.	0.6	1					4.2	5
tree	*Prunus* spp.							0.6	1
tree	*Prunus virginiana* L.	1.9	15	1.5	7	2.5	17	2.4	12
tree	*Sorbus americana* Marsh.	1.1	4	0.6	2	1.4	10	1.5	5
shrub	*Alnus incana* (L.) Moench ssp. *rugosa* (Du Roi) Clausen	0.6	1			0.6	1	3.8	2
shrub	*Amelanchier* spp.			1.3	2	0.8	4	1.0	5
shrub	*Cornus alternifolia* L.f.	1.3	1			1.3	1	1.3	1
shrub	*Diervilla lonicera* P. Mill.	3.8	1	7.6	1			0.6	1
shrub	*Ilex verticillata* (L.) Gray			0.6	1				
shrub	*Juniperus communis* L. var. *depressa* Pursh	0.6	2	0.6	1				
shrub	*Kalmia angustifolia* L.			5.7	1				
shrub	*Lonicera canadensis* Bartr. *ex* Marsh.	2.8	10	1.9	7	2.5	15	2.3	5
shrub	*Lonicera* spp.	0.6	1	1.9	3			2.2	7
shrub	*Rosa multiflora* Thunb. *ex* Murr.	0.6	1	1.5	7	0.6	1	2.5	2
shrub	*Rosa rugosa* Thunb.	2.5	1						
shrub	*Rubus flagellaris* Willd.	0.6	1						
shrub	*Rubus idaeus* L.	1.4	6	1.3	4			2.6	8
shrub	*Rubus* spp.	0.8	4	3.3	8	1.8	8	2.4	6
shrub	unknown shrub	0.6	2	0.6	1	3.6	12	1.1	3

		Clipped Fall 2004				Clipped Spring 2005			
		N=20				N=20		N=20 (N=14 und herbs)	
		Observed Fall 2004		Observed Fall 2005		Observed Spring 2005		Observed Fall 2005	
Plant Group	**Species**	**Stems/m^2**	**Frequency**	**Stems/m^2**	**Frequency**	**Stems/m^2**	**Frequency**	**Stems/m^2**	**Frequency**
shrub	*Viburnum nudum* var. *cassinoides* (L.) Torr. & Gray	7.6	1	6.4	2			4.9	14
herb	*Achillea millefolium* L.			1.3	1	7.0	1	9.5	1
herb	*Aralia nudicaulis* L.					0.6	1		
herb	*Campanula rotundifolia* L.					2.6	7		
herb	*Carex* spp.	0.6	7	0.6	2	1.0	2		
herb	*Celastrus orbiculata* Thunb.	1.3	1						
herb	*Cerastium* spp.			0.6	2	0.6	3		
herb	*Cornus canadensis* L.	3.0	3	8.0	2	3.8	2		
herb	*Doellingeria umbellate* (P. Mill.) Nees	1.1	3						
herb	*Fragaria* spp.	0.8	6	8.6	9	8.7	5	5.7	2
herb	*Galium palustre* L.			1.6	2				
herb	*Galium* spp.	0.6	2	4.5	4	1.0	2	3.8	1
herb	*Geranium* spp.			1.9	1				
herb	grass	0.6	2			1.1	6		
herb	*Hieracium* spp.	1.7	3	2.2	4				
herb	*Maianthemum canadense* Desf.	1.5	7	2.9	13	8.7	15	11.1	8
herb	*Medeola virginiana* L.					0.6	1		
herb	*Oxalis* spp.			1.3	2	0.6	2		
herb	*Potentilla simplex* Michx.	0.8	5	5.3	8	2.8	7	0.8	3
herb	*Prenanthes* spp.	1.9	1	1.0	4	1.3	1		
herb	*Pyrola elliptica* Nutt.							3.2	2
herb	*Pyrola* spp.	0.6	1	3.2	1	1.3	2		
herb	*Ranunculus* spp.					11.5	1		
herb	*Solidago bicolor* L.			6.4	1				
herb	*Solidago rugosa* P. Mill.			12.7	1				

		Clipped Fall 2004				Clipped Spring 2005			
		N=20				N=20		N=20 (N=14 und herbs)	
		Observed Fall 2004		Observed Fall 2005		Observed Spring 2005		Observed Fall 2005	
Plant Group	**Species**	**Stems/m^2**	**Frequency**	**Stems/m^2**	**Frequency**	**Stems/m^2**	**Frequency**	**Stems/m^2**	**Frequency**
herb	*Solidago* spp.	1.1	5	2.8	5			6.4	2
herb	*Streptopus lanceolatus* (Ait.) Raf.							0.6	1
herb	*Symphotrichum cordifolium* (L.) Nesom	1.3	2	0.6	1				
herb	*Symphotrichum* spp.	1.4	4	6.9	9			2.3	7
herb	*Symphotrichum/Solidago* spp.			3.8	3	2.3	9		
herb	*Taraxacum* spp.	0.6	1	3.8	2	1.1	3	1.3	1
herb	*Thalictrum dioicum* L.			1.3	1	0.6	1		
herb	*Thelypteris* spp.	4.5	1			0.6	1		
herb	*Toxicodendron radicans* (L.) Kuntze			0.6	1				
herb	*Trientalis borealis* Raf.	1.4	8	4.4	10	7.2	13	3.8	7
herb	*Trifolium* spp.	3.2	1						
herb	*Trillium* spp.							0.6	1
herb	unknown herb	1.8	10	7.8	10	2.8	17	0.9	5
herb	*Veronica offinalis* L.	1.0	2	2.4	6			1.9	2
herb	*Viola* spp.	0.8	3	2.2	8	3.2	2		

Table A2. Frequency and density of understory species present at the Monhegan Island study site.

(Haines and Vining 1998)

		Clipped Fall 2004				Clipped Spring 2005			
		N=17				N=17			
		Observed Fall 2004		Observed Fall 2005		Observed Spring 2005		Observed Fall 2005	
Plant Group	**Species**	**Stems/m^2**	**Frequency**	**Stems/m^2**	**Frequency**	**Stems/m^2**	**Frequency**	**Stems/m^2**	**Frequency**
tree	*Acer rubrum* L.					4.5	1	0.6	1
tree	*Betula papyrifera* Marsh.	0.6	1						
tree	*Betula populifolia* Marsh.							2.5	2
tree	*Malus* spp.							1.3	1
tree	*Prunus* spp.	0.6	1						
tree	*Prunus virginiana* L.							0.6	2
shrub	*Alnus incana* (L.) Moench ssp. *rugosa* (Du Roi) Clausen	2.2	2	1.4	5	0.8	4	1.3	2
shrub	*Ilex verticillata* (L.) Gray			1.8	10			1.4	8
shrub	*Lonicera canadensis* Bartr. *ex* Marsh.			4.0	4			0.8	4
shrub	*Lonicera* spp.	1.4	6			1.0	6		
shrub	*Rosa multiflora* Thunb. *ex* Murr.			1.3	1				
shrub	*Rubus flagellaris* Willd.							3.2	1
shrub	*Rubus hispidus* L.			0.6	1				
shrub	*Rubus idaeus* L.			1.1	3	1.3	2	2.2	4
shrub	*Rubus* spp.	1.0	4	0.6	3	2.5	2	3.2	2
shrub	unknown shrub	0.6	1	3.8	8			1.1	5
herb	*Anemone quinquefolia* L.					13.6	3		
herb	*Carex* spp.	0.6	1	0.6	2	4.1	2		
herb	*Cerastium fontanum* Baumg. ssp. *vulgare* (Hartman) Greuter & Burdet	0.6	1						
herb	*Cerastium* spp.	0.6	1	2.2	2			0.6	1
herb	*Clematis* spp.	0.6	1	0.6	2	0.6	1		
herb	*Clinopodium vulgare* L.					0.6	1		

		Clipped Fall 2004				Clipped Spring 2005			
		N=17				N=17			
		Observed Fall 2004		Observed Fall 2005		Observed Spring 2005		Observed Fall 2005	
Plant Group	**Species**	**Stems/m^2**	**Frequency**	**Stems/m^2**	**Frequency**	**Stems/m^2**	**Frequency**	**Stems/m^2**	**Frequency**
herb	*Fragaria* spp.			1.6	2	2.2	2	2.5	2
herb	*Geranium* spp.			1.9	1				
herb	grass					1.8	5		
herb	*Impatiens capensis* Meerb.			3.2	2				
herb	*Lycopus uniflorus* Michx.			0.6	1			1.6	2
herb	*Maianthemum canadense* Desf.	2.5	1	1.9	1	2.5	1		
herb	*Oenothera* spp.			5.7	1				
herb	*Onoclea sensibilis* L.	1.6	2	2.4	4	0.8	3	3.6	3
herb	*Oxalis* spp.			2.1	3				
herb	*Penstemon* spp.							0.6	1
herb	*Persicaria hydropiperoides* (Michx.) Small			0.6	1				
herb	*Persicaria sagittata* (L.) H. Gross			1.1	3			0.6	1
herb	*Potentilla simplex* Michx.	0.6	1	1.1	3				
herb	*Pyrola* spp.			0.6	1				
herb	*Scutellaria lateriflora* L.			0.6	1				
herb	*Solidago* spp.			1.9	1			7.3	2
herb	*Symphotrichum* spp.	1.9	2					1.3	1
herb	*Symphotrichum/Solidago* spp.			0.6	3	4.9	3	1.7	5
herb	*Thalictrum dioicum* L.					1.3	1		
herb	*Thalictrum* spp.							2.5	1
herb	*Thelypteris* spp.	1.1	3	0.6	2	1.5	3	1.0	8
herb	*Trientalis borealis* Raf.			1.9	1	10.5	2	1.3	3

		Clipped Fall 2004				Clipped Spring 2005			
		N=17				N=17			
		Observed Fall 2004		Observed Fall 2005		Observed Spring 2005		Observed Fall 2005	
Plant Group	**Species**	**Stems/m^2**	**Frequency**	**Stems/m^2**	**Frequency**	**Stems/m^2**	**Frequency**	**Stems/m^2**	**Frequency**
herb	*Trillium* spp.	1.3	2	0.6	1	0.6	1	1.0	2
herb	unknown fern			0.6	1	0.6	1		
herb	unknown herb	1.0	2	2.5	7	3.2	1	0.6	2
herb	*Veronica officinales* L.			0.6	1			3.2	1

Table A3. Frequency and density of understory species present at the Wells Research Reserve study site.

(Haines and Vining 1998)

		Clipped Fall 2004				Clipped Spring 2005			
		N=20				N=20			
		Observed F'04		Observed F'05		Observed Spring 2005		Observed Fall 2005	
Plant Group	**Species**	**Stems/m^2**	**Frequency**	**Stems/m^2**	**Frequency**	**Stems/m^2**	**Frequency**	**Stems/m^2**	**Frequency**
tree	*Abies balsamea* (L.) P. Mill	2.1	6	1.9	9	3.6	5	6.0	2
tree	*Acer rubrum* L.	0.6	1	0.6	4			3.8	2
tree	*Betula papyrifera* L.			1.6	2				
tree	*Picea glauca* (Moench) Voss	3.3	4			0.9	1		
tree	*Picea rubens* Sarg.	1.3	1	2.5	1	1.9	4	0.6	1
tree	*Picea* spp.	0.6	1	2.7	8			7.0	1
tree	*Prunus virginiana* L.	7.0	1	1.5	8	5.6	1	1.3	2
tree	*Sorbus americana* Marsh.	1.9	7	1.4	12			1.3	1
shrub	*Amelanchier* spp.			1.3	2				
shrub	*Ilex verticillata* (L.) Gray			1.9	1	4.1	12		
shrub	*Lonicera canadensis* Bartr. *ex* Marsh.			1.8	4			0.6	1
shrub	*Lonicera* spp.			0.6	1				
shrub	*Ribes/Viburnum* spp.							0.6	1
shrub	*Rubus* spp.							3.2	1
shrub	unknown shrub			2.5	19	2.8	6	8.3	1
shrub	*Viburnum nudum* var. *cassinoides* (L.) Torr. & Gray			4.6	13			4.3	4
shrub	*Viburnum* spp.			0.6	1				
unknown	unknown	1.3	7						
unknown	unknown			3.1	15				
unknown	unknown					2.2	13		
unknown	unknown							2.8	7

Table A4. Frequency and density of regenerating species present at the Monhegan Island study site.

(Haines and Vining 1998)

		Clipped Fall 2004				Clipped Spring 2005			
		N=17				N=17			
		Observed Fall 2004		Observed Fall 2005		Observed Spring 2005		Observed Fall 2005	
Plant Group	**Species**	**Stems/m^2**	**Frequency**	**Stems/m^2**	**Frequency**	**Stems/m^2**	**Frequency**	**Stems/m^2**	**Frequency**
tree	*Acer rubrum* L.			0.6	3			0.8	4
tree	*Betula papyrifera* Marsh.			0.9	5			1.9	2
tree	*Betula populifolia* Marsh.			1.9	3				
tree	*Craetagus* spp.			2.9	2			3.8	1
tree	*Malus* spp.			1.3	1			0.6	1
tree	*Prunus virginiana* L.					1.3	1	0.6	1
tree	unknown tree					1.3	1		
shrub	*Alnus incana* (L.) Moench ssp. *rugosa* (Du Roi) Clausen	0.6	1	2.5	1	1.3	1		
shrub	*Ilex verticillata* (L.) Gray							0.6	1
shrub	*Lonicera* spp.					0.6	1		
shrub	unknown shrub	1.7	5	1.0	5	1.3	2		
unknown	unknown	5.1	12	3.8	10	1.3	3	2.4	6

Table A5. Frequency and density of regenerating species present at the Wells Research Reserve study site.

(Haines and Vining 1998)

BIOGRAPHY OF THE AUTHOR

Jennifer D'Appollonio was born in Hartford, CT on October 13, 1974. She was reared in a historic colonial in Coventry, CT until she left for college. In the late 1700s her childhood home belonged to the Strongs, cousins to the Revolutionary War spy hero Nathan Hale who was born and reared a few miles away. Jennifer learned to appreciate the natural world around her as she grew up amongst orchards and livestock, her favorites of which were her goats and her beloved cow Norman. She graduated valedictorian of the class of 1992 from the Cornerstone Christian School in Manchester, CT. She attended the University of Maine at Machias, during which time she joined Kappa Delta Phi National Affiliated Sorority, Kappa Eta chapter, and graduated in 1997 with a Bachelor's degree in Environmental Studies – Conservation Biology. Jennifer then worked for an environmental consulting firm in NH, during which time she conducted environmental inspection and monitoring of industrial and construction sites, stormwater pollution prevention monitoring, underground storage tank removal, and monitoring of impacted wetlands. Medical conditions then kept her out of the workforce for almost two years, after which she decided she had better use her eyes and mind before she lost one or both of them. She then returned to Maine and entered the Forest Ecosystem Sciences graduate program at UMaine in the fall of 2003. Jennifer is currently a student member of the Ecological Society of America and is a candidate for the Master of Science degree in Forestry from the University of Maine in August 2006.