The invasion ecology of Japanese barberry (*Berberis thunbergii*) in the New England landscape

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Abstract

Japanese barberry (*Berberis thunbergii*) has been characterized as one of the most widely known and planted exotic shrubs in the United States. It was first introduced to the US in the late 1800s. By 1920 the planting of Japanese barberry was encouraged as an ornamental shrub replacing the common barberry (*Berberis vulgaris*). Japanese barberry began spreading from cultivation in suburban and selected rural retreats by the 1920s, and had dispersed rapidly throughout the northeast by the 1960s. By the 1970s it was recognized as a problematic invasive in the northeast. It is readily dispersed primarily by birds. Fruit production varies with light level, but even under very low light levels (≤ 4% full sun) some seeds are produced. Fruits are dispersed in late fall through late winter. Seed dispersal curves are highly leptokurtic; most seedling are found under or adjacent to adults, but a small number may be found tens of meters from the nearest adult. Japanese barberry thrives under a broad range of light and soil moisture conditions. Significant variation in stem growth can be explained as a function of light level. Even at less than 1% full sun, some positive stem growth can occur. Survival is quite high at intermediate to high light levels, and only under the lowest light levels (< 1% full sun) does survival drop significantly. Biomass of Japanese barberry in field plots can be largely explained as a function of light availability and soil moisture. The biomass of co-occurring species is suppressed by Japanese barberry, and recovery is slow in the first year following Japanese barberry removal except under high light levels. Glyphosate (Roundup) applied in early spring at first leaf out, when little else is in leaf, provides an effective means of eradicating Japanese barberry populations.

Introduction

Recently, conservation biologists have claimed that aggressive, exotic species may pose the greatest threat to biodiversity now and in the future (Vitousek et al. 1996). Clout (1995) states that "even if the destruction of natural habitats such as rain forests and wetlands ceases tomorrow, the insidious effects of introduced species would continue to erode the world's biodiversity." A number of these alien species are now well known, even to the general public, as aggressive weeds including the common reed (*Phragmites australis* (Cav.) Trin.), purple loosestrife (*Lythrum salicaria* L.), and kudzu (*Pueraria lobata* (Willd.) Ohwi). Others, including Japanese barberry (*Berberis thunbergii* DC) have only recently been recognized as seriously invasive (Weatherbee et al. 1998). There is little doubt that invasive plants are encroaching into native habitats, expanding ranges, displacing native species, and homogenizing ecosystems (Luken and Thieret 1997).

Historically and currently, two species of barberry have been of special concern as invasive exotics in northeastern North America: the common barberry (*Berberis vulgaris* L.) and Japanese barberry. These are closely related species that hybridize and have

been cultivated as ornamental shrubs in the US and elsewhere (Bailey 1924). These two species provide a unique contrast: the common barberry was one of the first species to be purposefully introduced to New England (Rehder 1936), it quickly became naturalized (Josselyn 1672, 1675), but soon was recognized as a noxious weed (Cronin 1983). In the early part of the twentieth century, it was finally eradicated from large parts of its range (Hutton 1928). Today in the northeast the common barberry is sporadic, infrequent or even regionally eradicated (Gleason and Cronquist 1991, personal observation). It no longer appears to display the attributes of an aggressive invader: where found, it is either as isolated individuals or small populations that do not appear to be expanding. Meanwhile, Japanese barberry has gone from an unknown escape at the turn of the century, to an aggressive invader throughout the northeast today.

Berberis thunbergii was first introduced to the US as seed sent from Russia to Boston's Arnold Arboretum in 1875 (Steffey 1985; Kyle Kelly, pers. comm.). The species was native to Japan. Specimens were planted out within a couple of years at the Arboretum and at the New York Botanic Garden in 1896 (Small 1935). Apparently, Japanese barberry was not commonly marketed as an ornamental shrub in the US before 1900 (Mack 1991), and there is little evidence of it becoming naturalized in the Northeast before 1910 (see below). Beginning at the time that *Berberis vulgaris* was being eradicated from the landscape, the USDA and others (Thompson 1926) were suggesting that *B. thunbergii* be planted as an attractive substitute for the common barberry. Japanese barberry, unlike the common barberry, was not host to black stem grain rust. Subsequently, at least 17 named cultivars of Japanese barberry have been developed (Dirr 1983). Since 1910 it has become fully naturalized throughout most of the Northeast and has been characterized as an "extremely invasive" species (Randall and Marinelli 1996; Mehrhoff 1999), often forming dense stands in deciduous forests, abandoned fields, and roadsides. Still, Japanese barberry remains "probably the most widely known exotic shrub in the United States" (Steffey 1985), and most widely planted.

In spite of its notoriety in the northeast, we know very little about the basic biology or ecology of Japanese barberry; there is very little published information on the species. Thus the objectives of this study were to: (1) document the spread of Japanese barberry throughout the northeast over the last century; (2) examine dispersal modes and dispersal characteristics; (3) characterize performance (i.e. growth, survival, and reproduction) of the species as a function of light and soil moisture conditions, both in the field and under controlled conditions; (4) examine the effects of Japanese barberry presence on the performance of other species found in the herb and shrub layers of natural communities; and (5) evaluate the effects of different eradication techniques.

Materials and methods

Historical search

As an integral part of this study, we established a historical course of spread of Japanese barberry through the northeastern United States. To do this, we collected information on dates and locations of *B. thunbergii* records (over 540 herbarium sheets) from 8 herbariums (see Acknowledgements). In addition, we examined over 60 historical and recent publications, checklists, local floras, and atlases (the full list of these sources may be obtained from the authors) for locations and dates of Japanese barberry presence in the landscape. From this information, we created a distribution map with ArcView 3.1 for the northeastern United States showing localities of the earliest dates of known occurrence as established plants in counties throughout the northeast.

Field experiments

Established plots

To investigate trends in Japanese barberry performance across the landscape, we selected seven permanent plots containing *B. thunbergii* in May of 1998, within the Fenton tract of the University of Connecticut Forest. This tract, adjacent to the University in Storrs, CT, is approximately 220 ha in extent and is mostly a second growth oak forest with northern hardwood elements and patches of open meadows. Japanese barberry forms dense continuous stands on the north end of the tract, becomes more patchy in distribution until there are only scattered individuals in the middle, and is locally absent at the south end of the forest. We attempted to stratify our seven plots across the full range of light and soil moisture conditions found among continuous populations of Japanese barberry in the forest. The soil conditions varied from moderately well-drained

Dystrochrepts to poorly-drained Humaquept soils. Light varied from 4% to 89% of full sun and soil moisture varied from 19% to 39% across these plots (see below). Plots were 3×5 m in size and each was divided in half. On one half (randomly selected) we cut all Japanese barberry at ground level in May 1998 and weighed all stems. In early July, we spot treated, where needed, any resprouting stems with glyphosate (Roundup – a trademark herbicide marketed by Monsanto). No Japanese barberry was removed from the second, control half of each plot. To examine effects of Japanese barberry on other plant species, we harvested all plants in each plot at the end of the growing season in September and early October 1998. Each plot half (cut and control) was harvested separately by species. We dried each sample for at least three days at 70 °C and weighed them. For the bulkier species, including Japanese barberry, we measured wet weights in the field, dried and weighed subsamples, and estimated total dry biomass from a wet/dry weight conversion.

Environmental variables

At each of the seven field plots, we selected light and soil moisture as the most likely environmental factors affecting the performance of individual Japanese barberry plants. Light was measured using two different techniques. During August and early September 1998, we took replicate hemispherical photos of the forest canopy from shrub level over the uncut portion of each plot. Using Minolta QuickScan 35, we digitized the photos and analyzed each using GLI/C 2.0 Color Fish-Eye Photo Analysis software (available from C. Canham). The percent Global Light Index (%GLI) was calculated following Canham (1988). This index integrates the solar track over the growing season and provides an estimate of the percent of open sky within the canopy structure over the growing season. This method has been used in the Northeast to accurately predict tree species growth and mortality as functions of light levels (Pacala et al. 1996; Caspersen et al. 1999).

The second technique measured the amount of PAR (photosynthetically active radiation) using quantum sensors and a Licor $21\times$ micrologger. Calculating the percent transmittance (%T) at each site relative to open sky, yielded a measurement of the light intensity penetrating the canopy at that one moment in time, at that one location (Parent and Messier 1996). The two measurements, %GLI and %T, although somewhat different in what they actually measure, tend to be correlated to the extent that a more open canopy

will allow more PAR transmittance. This correlation, however, can sometimes be weak or non-linear. For example, two sites can have the same %GLI (canopy openness), but different %T if the quality (e.g. species composition or leaf area index) of the canopy is different. This could be the case in an oak versus a sugar maple canopy forest. This justified the utility of both techniques where possible here.

The second environmental variable we measured was soil moisture. We collected soil samples over a period of a few days in September 1998, at least 10 days after the most recent rainfall event. Mineral soil samples were collected for the A and upper B horizons to approximately 15 cm depth, where the majority of rooting takes place. The organic horizon was not included. We measured fresh weight, dried the samples for three days at 70 °C, measured dry weight, and calculated percent soil moisture. Caspersen et al. (1999) found that single samples of soil moisture made at approximately the same time across a landscape provide a sufficient characterization of landscape-level soil moisture regimes to predict species-specific responses and distribution patterns.

To study the effects of varying soil moisture and light conditions on an individual's performance, we collected a sample Japanese barberry stem from each plot. A small section of the stem was used in a growth ring analysis to determine age and amount of radial growth per year. We squared and sanded an end of each stem section, counted the number of annual rings to determine age of the stem, and measured the diameter of each annual ring (two replicates each) to the nearest one hundredth of a millimeter with a digital stage micrometer. This method has been used elsewhere to relate radial stem growth of woody species to light and soil moisture conditions (Pacala et al. 1996; Capsersen et al. 1999). In this analysis we used only the most recent full season of radial growth.

Supplemental sample sites

While much of our work focused on the 7 field plots, we also designated 28 supplemental sample sites where Japanese barberry grew elsewhere in the Fenton tract. These sites were chosen to provide a broader range of light and moisture conditions in the landscape than could be encompassed in seven plots. We assessed light availability from digitized hemispherical photos (%GLI), measured percent soil moisture, and collected stem samples for ring analysis and dried biomass, using the same methods described above. For these

samples, light levels varied from 1% to 76% full sun (%GLI) and soil moisture varied from 10% to 42% (see results below). Analyses of stem growth were done on the combined data from the 7 field plots and the 28 supplemental samples.

Transplants

To study survival and performance of Japanese barberry under as full a range of environmental conditions as possible, including sites where it rarely or does not presently occur, we prepared transplants for the field. These were uniform, 8 cm stem sections taken from field accessions (5 plants), and easily rooted in standard artificial soil mixture in the greenhouse. Stem rootings were done in late winter to early spring and transplanted out in May 1998. Twelve rooted cuttings in individual peat pots were randomly selected, and transplanted out to each of twelve sites: immediately adjacent to each of the seven established field plots plus five additional sites. Four of these additional sites represented extreme local conditions for soil aridity and low light: under dark hemlock canopies (GLI < 1%), on a dry esker and a kame terrace with excessively well-drained Udipsamment or Udorthent soils, and on a dry ridge top with a thin, Lithic Dystrochrept soil. The fifth site represented more optimal conditions of an open, well-watered garden site. For all sites we measured light (%T and %GLI) and percent soil moisture as above.

Seed production and dispersal

An important component to understanding the spread of Japanese barberry involves characterizing seed production and dispersal. Japanese barberry flowers from mid April to May in the northeast and pollination is effected by small and large bees (e.g. Adrenids and *Bombus* spp., respectively (Lebuhn and Anderson 1994)). Fruits mature from July to October. In October 1998 we marked and counted fruits on five branches (on separate individuals) each in high, medium and low light sites, (respectively 89%, 44% and 4%T). The selected bushes were within 1 m of our study plots so that we could use the same light measurements. We counted the number of mature (red) fruit, immature (non-red) fruit, and the likely number of fruit already dispersed (estimated from remaining peduncles with no fruit attached) in October, November, January and February to assess the fruit loss over the winter. To estimate the total number of fruits per bush conservatively, we used only the initial October counts of observed

fruits to calculate a number of fruits per branch. We estimated the number of branches per bush (identical in length to our sample) and estimated the total number of fruits per bush. We used a mean of four independent branch count estimates to calculate the number of branches per bush.

To assess effective seed dispersal, we censused the occurrence of seedlings throughout the University of Connecticut forest. Across the Fenton tract, Japanese barberry distribution is quite heterogeneous with areas of continous coverage to areas with only a few isolated individuals or none. Ten kilometers of trail system crisscross the tract allowing easy access to many sites. We sampled for seedling occurrence in a continuous 1 m belt adjacent to 2804 m of the trail system. We included trail sections that extended from areas of continuous coverage of Japanese barberry to isolated individuals. For each seedling encountered, we measured the distance to the canopy of the closest adult Japanese barberry plant. In cases where the seedlings were found under the canopy of the adult plant, the distance was recorded as 0 m.

Greenhouse studies

To supplement our growth studies in the field, we grew transplants in the greenhouse under four different controlled light conditions. Uniform stem cuttings from the same source as above were transplanted individually to pots with a standard greenhouse artificial soil mixture. The plants were arranged in random arrays in each treatment, watered regularly, and rotated regularly to avoid positional effects and spatial variation in soil moisture regimes. To test varying light conditions, we grew transplants under different levels of Aluminet R 50% I shade screen (available from commercial greenhouse supply companies). We grew one group of transplants as a control with no screen (highest light level (33%T). Over another group we placed one layer of Aluminet screen yielding 15%T. The third group had two layers (9%T), and the fourth group was grown under the greenhouse bench (but elevated) to simulate the lowest light conditions (0.8%T). Since the greenhouse is fan regulated and no other plants were on top of the bench covering the fourth treatment, we assume that any confounding effects of variation in temperature and moisture differences were small relative to light effects. Of course under lower light levels evapo-transpiration will necessarily be lower. We assessed each light condition in October 1998 using only quantum sensors

(%*T*), since canopy photographs were of no value here. As was the case for the field experiments, we did not assess variation in light spectral quality. In December all plants were harvested. We counted the number alive, noting deaths, and measured the length of the total new growth from the original stem. We cut all new growth from the original stem, dried and weighed each sample separately.

Results and discussion

Distribution patterns

Changes in the distribution of Japanese barberry in the Northeastern United States over the past century are shown in Figure 1a. The cumulative spread of Japanese barberry by county from 1880 to the present is shown in Figure 1b. This reflects the 'J' shaped or sigmoidal pattern of increase in population occurrence that others have found for invasive exotic species (e.g. Forcella 1985; Mack 1985; Nuzzo 1991).

The map is based on herbarium records, published accounts, regional or local floras, checklists, and atlases of various sorts (a complete list is available from the authors). As a consequence there are certain inherent limitations to this data set. The occurrences and spread of Japanese barberry across the Northeastern landscape are probably underestimated for period 1950–1980. In the early stages of the spread of any exotic species, individuals are often collected when encountered as a novelty. As the exotic species becomes more common, they are inherently less interesting botanically and often are under-collected. It was during this time (1950–80) that the perception of Japanese barberry changed from simply an exotic element in the landscape, to a serious invader of natural communities.

With efforts over the past two decades to publishing complete distribution atlases and checklists for various regions in the Northeast (including Campbell et al. 1995; George 1998; Hough 1983; New York Flora Association 1990; Rhoads and Klein 1993; Tucker 1995) we now have a fairly accurate account of the current distribution of Japanese barberry on a county by county basis. However, this information provides little or no quantitative or qualitative information on the distribution or abundance within counties.

After its introduction as an ornamental shrub to Boston and New York in the late 1800s, Japanese barberry had become naturalized in selected suburban and rural retreats by 1920 (Figure 1). It turned up as a garden escape on Nantucket and Isle au Haut before 1910, and in the Berkshires of western Massachusetts and in the Mt. Monadnock region of southern New Hampshire before 1920. These were areas typically frequented by individuals from Boston and New York on extended summer holidays. The implication is that Japanese barberry was being planted around vacation homes owned by city dwellers or resorts and it was subsequently becoming naturalized in the rural landscape. Even in the early 1910s, Manning (1913), a botanist and plant collector, mentions after finding it near Mt. Monadnock, that "it is likely to be introduced in many places in a few years, because I am constantly finding seedlings at some distance from the original plants in private places". By the 1920s and 1930s Japanese barberry had spread in concentric circles around Boston and New York. Even by the late 1950s it was still considered rare in northeastern Connecticut (Upham 1959), half way between Boston and New York. By the 1960s and 1970s it had become recognized as a serious invader of many natural communities in the landscape (e.g. closed forests, woodlands, wetlands, meadows, pastures, fence rows, waste places, etc.), often forming dense continuous stands especially in the middle Atlantic states, and southern and central New England.

Today Japanese barberry can be found throughout the northeast, except the Adirondaks, northern Maine, and parts of northern Vermont. Apparently, over much of its northern range, Japanese barberry appears to be less invasive, is only spreading slowly, and is sporadic in its distribution. From a regional perspective, the northern limits of Japanese barberry in northern New England, the Canadian Maritimes, Ontario, and the upper Midwest are probably set by low temperature tolerance limits. Its expansion to the south may be limited by its specific cold stratification requirements for germination. Optimal germination occurs following seed statification for several months at 5 °C, followed by alternating temperatures between 10 °C and higher (Davis 1927, Nikoleava and Alekseeva 1984). Expansion to the west may be set by drought tolerance.

Fruiting and dispersal

We evaluated fruit production in Japanese barberry as a function of light availability for replicate sample bushes
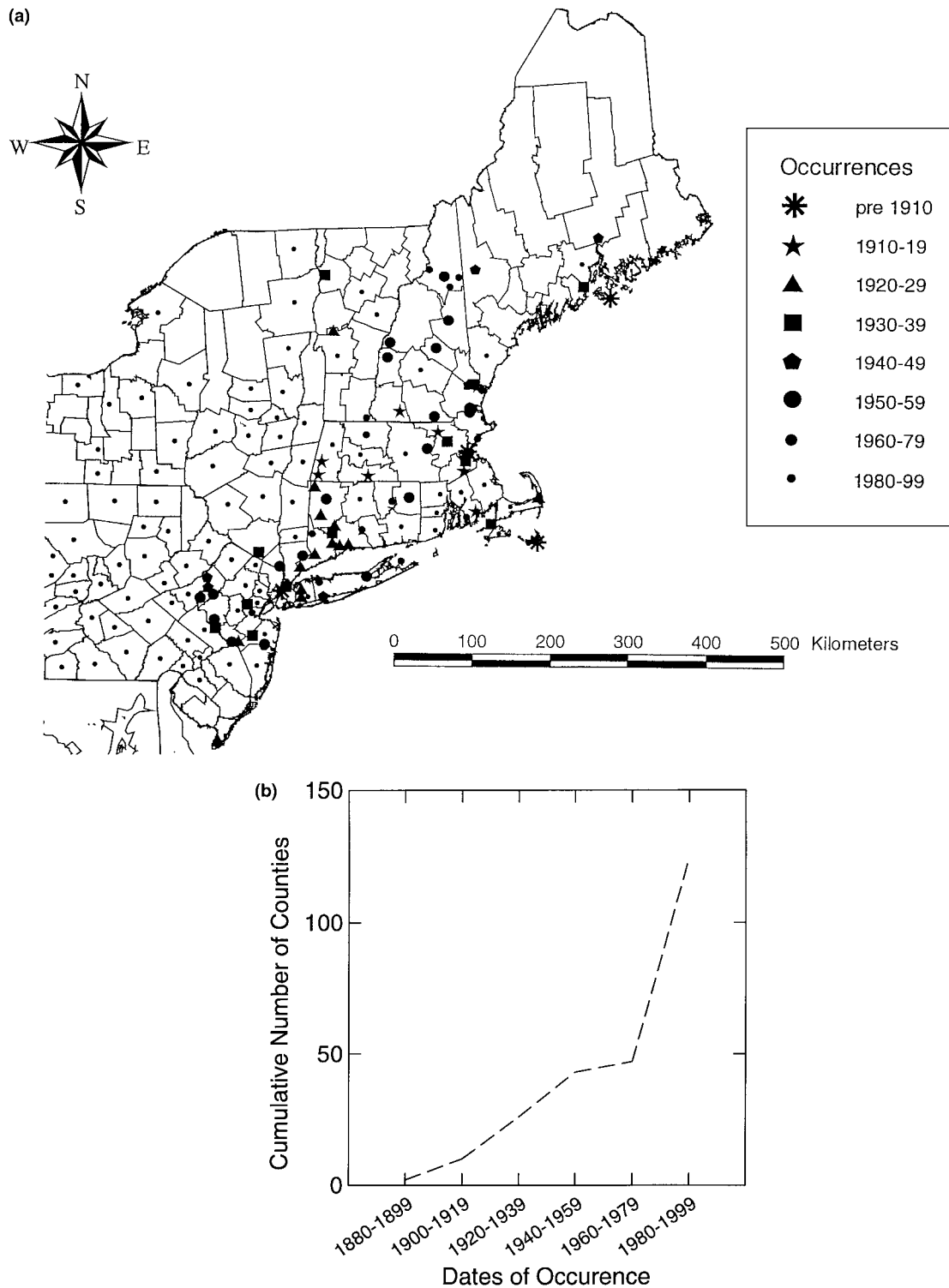
(a)

(b)

Figure 1. (a) The distribution of Japanese barberry in the northeastern United States from the nineteenth century to the present. Occurrences are shown by decade with unique symbols; the occurrences from 1960 to the present are shown in twenty year increments. To minimize clutter on the map, we have indicated only county presence for dates from 1960 to 1999. (b) The cumulative spread by county of Japanese barberry in northeastern United States is shown over the period from 1880 to 1999.

located in high (89%T), medium (44%T) and low (4%T) light conditions. Fruit production was assessed on the basis of fruits per cm of branch and total fruits (estimated) per individual shrub. The trend, given a small sample size ($n = 15$), was for more fruit production per plant under high and intermediate light, than under low light conditions: 1500 ± 550 (s.e.m), 1800 ± 600, and 200 ± 20 respectively ($P = 0.08$, $r^2 = 0.4$, ANOVA). Similar results are seen when fruit production is expressed per cm of branch. Under high, intermediate and low light conditions fruit production was 0.141 ± 0.072, 0.215 ± 0.027, and 0.104 ± 0.022 respectively. The effect of low light on fruit production was small, considering that light levels varied from almost full sun to heavy shade (4%T).

We followed fruit loss in the same marked Japanese barberry branches from October 1998 to late February 1999. There was rapid removal of ripe fruits in only the low light conditions (about 30% remaining by the second month), but by January most of the fruit were gone across all light levels (Figure 2). Although there was a tendency for more fruit to remain on bushes in intermediate light levels, this was significant only for November ($P < 0.05$).
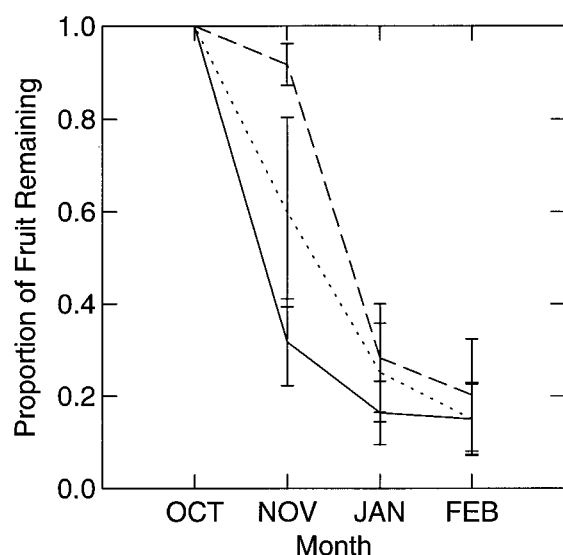

Figure 2. Japanese barberry fruit loss per marked branch is shown over a 5 month period beginning in October 1998. Fruit loss is expressed as a proportion of the fruit present in October. Results are shown for three contrasting light levels observed in the field: high (89%T, dotted line), intermediate (44%T, dashed line), and low light (4%, solid line). The vertical lines express standard errors of the mean.

We have no direct observations on the explicit dispersal agents for these populations, but birds are known to be the dominant natural dispersers of barberries. At least 10 species have been observed consuming the seeds of *Berberis* spp. (Kern 1921; McAtee 1918) including: Cedar Waxwing, Ruffed Grouse, Eastern Bluebird, American Robin, and various other thrushes (Turdidae). Generally barberries are low priority food items for most birds, often consumed late in the season (Kern 1921). Other vertebrate dispersal agents are probably minor, but we know of no reports to substantiate this.

Our mapping of seedling occurrences along almost 3 km of a belt transect yielded 525 first year seedlings. The vast majority (92%) of these were underneath or within 1 m of the canopy of a Japanese barberry shrub. But several were at a greater distance (50+ m) from the nearest adult. The farthest seedling was over 80 m from the nearest adult. Clearly the dispersal pattern for Japanese barberry is highly leptokurtic. We fitted a variety of exponential functions (cf. Kot et al. 1995) to the observed dispersal profile, all of which provide good fits. In Figure 3, we show the raw data and one form of a two parameter exponential function ($r^2 = 0.868$). This works well for characterizing short dispersal distances. But, rare, persistent long distance dispersal events, which are critical to understanding and predicting migration patterns, are not well modeled by these exponential functions; they are not sufficiently fat in the tail of the distribution while also being sufficiently leptokurtic (see Clark 1998 for a discussion of this problem). This is a sufficiently complex issue that we are modeling dispersal in a separate study.

The effective spread of Japanese barberry across the landscape is undoubtedly a function of its dispersal characteristics – large numbers of bird dispersed fruits. This is a characteristic of many important invasive species (Mack 1996). Indeed virtually all of the most aggressive invasive shrubs and vines in the Northeast are bird dispersed. For listed invasive species in Connecticut, 9 of 9 shrubs are bird dispersed, for woody vines 3 of 3 species, but none of 16 herbaceous species are bird dispersed (Mehrhoff 1999). Some examples of the most aggressive bird dispersed invasives are Asiatic Bittersweet (*Celastrus orbiculatus* L.) Autumn Olive (*Elaeagnus umbellata* Thunb.), Buckthorn (*Rhamnus cathartica* L.), Multiflora Rose (*Rosa multiflora* Thunb.), and the various Eurasian Honeysuckles (*Lonicera* spp. and hybrids), in addition to Japanese barberry. Why bird dispersal as a syndrome
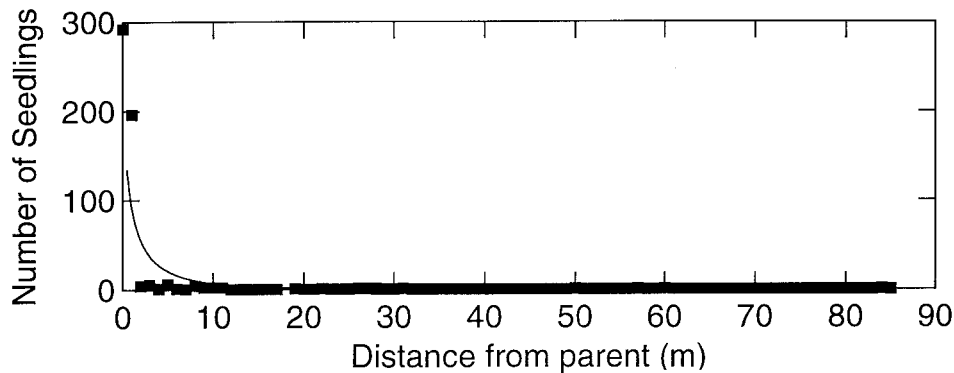
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Figure 3. Effective seed dispersal curves for Japanese barberry, expressed as the number of first year seedlings (filled squares) found at varying distances for the nearest adult. A two parameter exponential function was fitted to the observed data: Number of seedlings = exp(5.7 – 1.2 square root(distance)). The r^2 for the non-linear regression was 0.868. The regression line is shown.

is particularly associated with aggressively invasive shrubs and vines versus trees and herbaceous plants is unknown.

Individual Japanese barberry shrubs can produce huge numbers of bright red fruits under a full range of light and soil conditions. The birds that disperse barberry display a range of feeding behaviors: feeding directly on the fruit pulp and locally discarding the seeds, or ingesting the entire fruit and defecating the seeds. The former may provide effective local dispersal, and the latter effective long distance dispersal. Increases in frugivorous game bird populations (ruffed grouse, turkeys, etc.) over the past few decades in the Northeast may have enhanced the spread of Japanese barberry.

Growth and survival performance of Japanese barberry

Of the 43 stems we sampled to assess radial growth, 81% were 2 or 3 years old. Fewer than 7% were more than four years old and only one stem was as old as seven years. There appears to be a high and continuous stem turn over; old stems die after a few years and are replaced by new stems sprouting from the base. Thus there is no easy way to estimate that age of individual shrubs, some of which have persisted in the forest for several decades.

When we examined radial stem growth as a function of light for the most recent complete years growth (1997), we found a significant linear relationship (Figure 4) ($P < 0.002$). Influence Plot analyses (SYSTAT 7.0) revealed relatively little
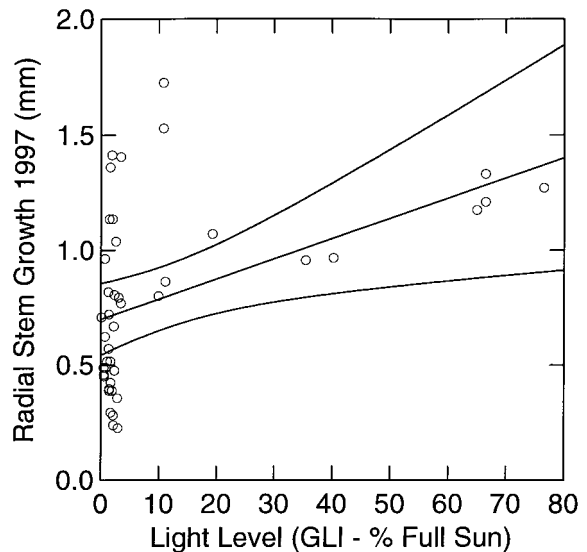

Figure 4. Radial stem growth during 1997 in 43 samples as a function of light availability. The fitted linear regression is shown along with the 95% confidence intervals. Individual sample points are shown as open circles ($r^2 = 0.3$, intercept = 0.7 ± 0.06 (se) and slope = 0.009 ± 0.003).

disproportionate effects of samples at intermediate to high light levels on the relationship. A stepwise regression showed that soil moisture was not a significant explanatory variable ($P = 0.3$). The strength of the regression is dependent on performance of stem samples from intermediate and high light conditions. Considerable variation in radial stem growth can be observed at low light levels. This may reflect the ability of Japanese barberry to utilize sun flecks at low light levels. However, sun flecks can be extremely variable
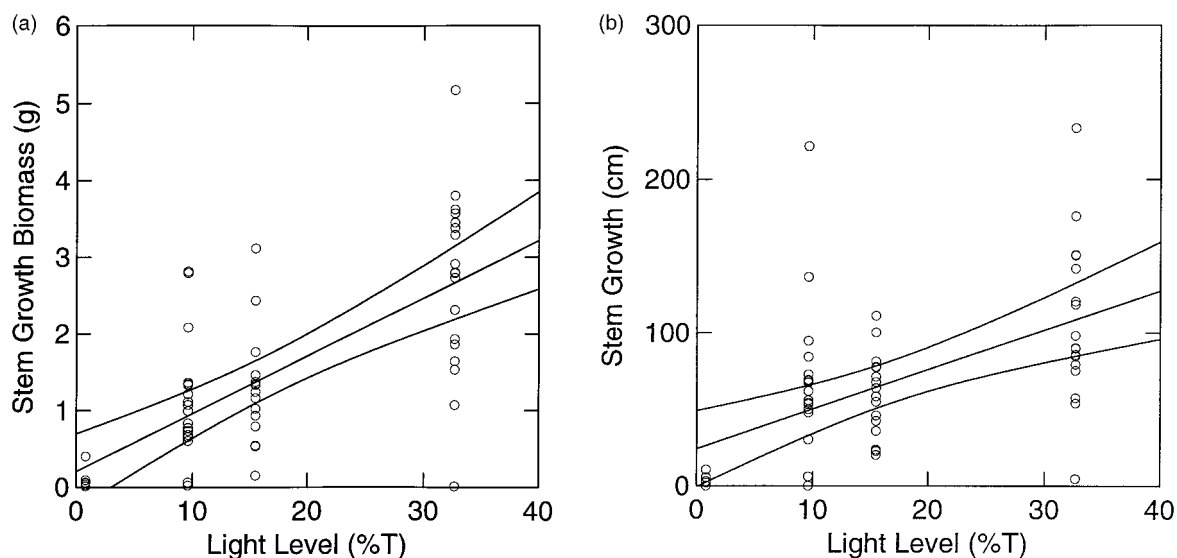
Figure 5. (a) Japanese barberry stem growth as a function of light levels under controlled conditions in the greenhouse. Growth response is expressed as total length of new stem per individual. The linear regression line is shown with 95% confidence intervals ($r^2 = 0.35$, intercept $= 24.1 \pm 9.8$, slope $= 2.6 \pm 0.494$). (b) stem growth as a function of light levels under the same conditions. Growth response is expressed as total biomass of new stem per individual. The linear regression line is shown with 95% confidence intervals ($r^2 = 0.51$, intercept $= 0.21 \pm 0.2$, slope $= 0.08 \pm 0.01$).

under dense canopies, and this may explain the high variability observed at light levels below 4% full sun.

To investigate the relationship between light environment and plant growth further we examined stem growth under more controlled conditions in the greenhouse. We controlled four light levels. We measured total new stem growth of live individuals, and found a highly significant relationship with light level ($P < 0.001$) (Figure 5a). At the very lowest light levels ($<1\%T$) individuals were barely growing. There were no differences in growth at the two intermediate light levels.

Biomass provided another measure of performance. New biomass accumulation under the controlled greenhouse conditions directly paralleled stem growth (Figure 5b). There were highly significant differences in biomass production across light levels ($P < 0.001$).

We also measured Japanese barberry biomass harvested from the seven field plots, for which we had measured light and soil moisture. A stepwise regression (plot not shown) showed that both soil moisture and light contributed significantly ($P = 0.009$, $r^2 = 0.58$) as explanatory variables for Japanese barberry biomass per unit area. Slope parameter estimates for light and soil moisture effects were respectively 78 ± 23 and 419 ± 117.

We examined survival of transplanted individuals both in the field and under controlled conditions in the greenhouse. At least some individuals survived in all transplants monitored in the 12 field sites (data not shown). These sites spanned light levels from < 1 to $90\%T$, and from 17–40% soil moisture. After initial loss or mortality within a week of transplanting, primarily resulting from animals excavating the peat pots, little or no further deaths occurred through late fall. Survival of transplants in the greenhouse under four controlled light conditions is shown in Figure 6 as a bar chart. Very few deaths occurred under high or intermediate to low light levels. Only at the very lowest light levels $< 1\%$ T, did survival drop to about 40%.

An important key to the success of Japanese barberry is that it tolerates a very wide range of soil and light conditions. Once established it can persist under dense canopies ($< 1-2\%$ full sun). Even when light levels are less than 1% full sun, small individuals can grow and survive at least for many months. However, one rarely finds Japanese barberry under such dark canopy positions. The darkest conditions under which we found any naturally established adults was about $3\%T$ or 1%GLI. Seedling establishment may be the critical filtering phase that limits Japanese barberry from becoming established in the darkest canopy locations. Under
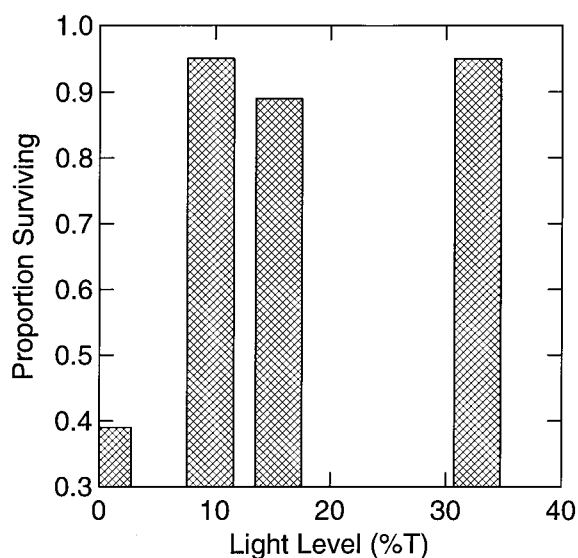
Figure 6. Survival of barberry under controlled conditions, expressed as the proportion of individuals surviving after 9 months at each of 4 light levels.

full sun Japanese barberry effectively competes with other fast growing woody species (*Rosa multiflora, Rhus toxicodendron* L., *Rubus* spp., *Celastrus orbiculatus*, and various tree seedling and saplings), but it does not dominate the system as it can under a tree canopy, or with persistent light grazing in pastures. Another advantage for *B. thunbergii* is that it is one of the first woody plants to leaf out in the spring, perhaps a month or more before the tree canopy is fully leafed out. It also retains its leaves after most of the canopy leaves have dropped in the autumn. This longer growing season undoubtedly gives Japanese barberry an advantage over native competitors in the shrub or herb layer. This longer photosynthetic season is also found in other, invasive shrubs (e.g. Eurasian honeysuckles (*Lonicera* spp.) and buckthorn (*Rhamnus cathartica*) (Harrington et al. 1989).

Japanese barberry also tolerates a full range of soil moisture regimes from very poorly-drained muck soils (soil moisture > 40%) to dry ridge tops with thin soils, or coarse textured, extremely well-drained soils (soil moisture < 10%). Established adults are rare or absent from the driest extremes, especially under shade. Again this probably reflects a critical and more sensitive seedling establishment phase. But once established, it can apparently persist under these extreme conditions.

The success of Japanese barberry today contrasts with the much less invasive nature of the common barberry. We know that *Berberis vulgaris* was invasive across the Northeastern landscape in the nineteenth century (Dwight 1821; Stakman 1919; Cronin 1983). A likely explanation for why it does not seem to be invasive today, is that it differs from Japanese barberry in light tolerance, and there have been dramatic changes in the landscape over the past century. A study that compared *Berberis vulgaris* with other shrub species in Europe (Kohlman and Reiner 1996), demonstrated that survival and growth of the common barberry were poor under low light conditions, and that this barberry displayed the photosynthetic characteristics of a light demanding species. The landscape in the Northeast was mostly open agricultural lands until the twentieth century (Foster 1992). The common barberry would be naturally adapted to the open landscape then. What is left of the natural Northeastern landscape today is mostly forested (Foster 1992), conditions that apparently do not favor the spread of the common barberry. We know of no comparative ecophysiological studies that have focused on photosynthetic characteristics of Japanese barberry, but we predict a lower light compensation point than for the common barberry.

Deer are an increasingly pervasive element of the landscape today. There is growing evidence that under high deer browse, less palatable species, including Japanese barberry, are given a competitive advantage (Tilghman 1989). The consequence of this is a dramatic change in the composition of the forest understory. There will be positive reinforcement of this to the extent that unpalatable species like Japanese barberry are also highly invasive.

Effect of Japanese barberry presence on the performance of other species

To examine the influence of Japanese barberry on other understory herbs and woody perennials, we compared total biomass of non-Japanese barberry species across the seven plots, each with cut (Japanese barberry removed at the beginning of the growing season) and uncut (control) treatments. We found that there was a parallel light response signal for both treatment series (Figure 7). The effect of light as an explanatory variable of plant biomass, for both cutting treatment was quite significant (respectively $P = 0.03$ and $P = 0.002$ for cut and control plot sections). Soil moisture was not a
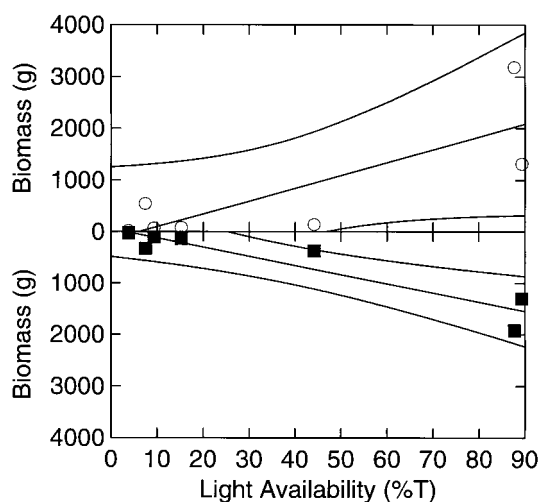
Figure 7. A mirror regression plot of total non-barberry biomass expressed as a function of light availability in the two portions of the field plots: the portion on which barberry had been removed at the beginning of the growing season (top, circles), and the controls (bottom, filled squares). Linear 95% confidence intervals are shown in both cases. For the control plots $P = 0.002$, $r^2 = 0.87$, slope $= 17.8 \pm 3.1$ (se), and for the plots with barberry removed $P = 0.03$, $r^2 = 0.65$, and slope $= 24 \pm 8.1$.

significant explanatory variable ($P > 0.6$, $r^2 = 0.7$). The treatment effects of Japanese barberry removals versus controls with light as a co-variate were not significant ($P = 0.6$) however. Only at the highest light levels was there any noticeable response over the growing season to Japanese barberry removal. At low and intermediate light levels, we found no, or variable growth responses by other species to the removal of Japanese barberry. Soil moisture used as a co-variate was also not significant ($P = 0.7$).

These slow or failed recovery responses to Japanese barberry removel paralleled similar observations we made in a pilot study on controlling Japanese barberry in woodlands with the herbicide glyphosate (Roundup). We were able to achieve 100% Japanese barberry mortality in treatment plots (data not shown) when glyphosate was applied in early April 1998 at first leaf out, while little or nothing else was in leaf. We could detect no effect on any other vegetation present, but there was virtually no recovery (i.e. recruitment and growth) of species in the herb and shrub layer over one growing season. Light conditions here were not available at the time we did the pilot study, but we estimated these to be in the range of 10–30% *T*.

Control and eradication of Japanese barberry

Control of Japanese barberry has been little studied, but there is an extensive list of control methods for the common barberry (Andersson 1969; Cloutire 1972; Thompson 1926). The most common method suggested for the control of barberry species has been simply pulling it out. This was the most universal method used to eradicate the common barberry in the 1910s, during 'Barberry Days' (Kern 1921). It is less likely to be widely effective today for Japanese barberry. It is difficult, time consuming, and not particularly effective, as individuals easily resprout from stem fragments left in the ground.

Glyphosate can provide an effective means of controlling barberry in forest systems and elsewhere, if appropriately applied. Glyphosate Roundup is a non-selective herbicide that can kill any plant that is green and actively growing. It quickly degrades to non-toxic materials over a few days. If glyphosate is applied to Japanese barberry populations in early spring at leaf out, when little else is in leaf, it can be 100% successful in eradication. The physiological irony of Japanese barberry's successful carbon gain strategy with early leaf out is that it can be easily controlled with herbicides. Our pilot trials in Connecticut woodlands showed that there were no apparent negative effects on other species present in the community. Thus glyphosate can effectively be used in either spot treating to kill individuals, or in broadcast treatment to kill large populations.

There may be some potential for biological control of Japanese barberry by tephritid flies. For example, *Rhagoletis* ssp. seem to be partially effective as a bio-control agent in Europe, severely reducing seed production (Huppmann 1986). The possibilities for bio-control have not been studied for this species here. But, there is always the risk with an introduced bio-control agent that it too can become a serious invasive (Simberloff and Stilling 1996).

The most effective landscape-level control for Japanese barberry may be to focus on small newly expanding populations. A modeling study published by Moody and Mack (1988) showed that focusing eradication on small, marginal populations or 'nascent foci' of an invading weedy species may provide the most effective control over time. Such foci otherwise quickly expand and coalesce forming dense populations and give rise to new 'nascent foci'. Clearly Japanese barberry is a recruitment limited species

(*sensu* Ribbens et al. 1994) both locally and regionally. By recruitment limitation, we mean that the species has not become established either locally or regionally in all of the places in which it is capable of thriving; it is simply limited by time and its ability to disperse and recruit into all suitable habitats. Japanese barberry appears to be continuing to moving north and east, local populations are continuing to expand, and we are still discovering new, founding populations in the landscape. By limiting further recruitment, the species may be controlled. A control route for Japanese barberry that Canada has chosen is the prohibition of its commercial sale and planting, an option that may help stop new 'nascent foci' from establishing in Canada. If Japanese barberry remains "the most widely known exotic shrub in the United States" (Steffy 1985), and most widely planted, we may be destined to eventually find it everywhere that it is capable of surviving and reproducing.

Acknowledgements

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