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Fecundity of Japanese Barberry (*Berberis thunbergii*) Cultivars and Their Ability to Invade a Deciduous Woodland

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Japanese barberry is an important landscape shrub that has a demonstrated potential to be invasive in ~30 states across the central and northern United States. Forty-six cultivars were evaluated for their potential to produce fruits and seeds in a randomized, replicated field planting. Seeds from a subset of cultivars were evaluated for their ability to germinate and survive as seedlings in a deciduous woodland. Seed production for cultivars varied from no seeds to more than 12,000 seeds plant^{-1} and the number of seeds per fruit ranged from 0.1 to 1.8. Five cultivars produced fewer than 100 seeds plant^{-1}, and two cultivars failed to produce fruit. When plants were allowed to mature for 4 to 5 yr beyond the first evaluation time, cultivars exhibited significant increases in fruits per plant, producing as much as 35,000 fruits plant^{-1} ('Sparkle'). 'Golden Devine' and 'Red Chief', fruitless cultivars at the first evaluation, produced 165 and 20 fruit plant^{-1}, respectively, at the follow-up evaluation, demonstrating that long-term evaluation of cultivars is necessary to accurately assess sterility. Between 12.5 and 31% cultivar seed sown in a deciduous woodland germinated, and seedlings survived at rates between 5.6 and 29.3%. Coupling cultivar seed-production data with germination and survival data in a deciduous woodland suggests that even cultivars producing as few as 100 seeds annually have the potential to contribute a few seedlings each year to a natural area.

Nomenclature: Japanese barberry, *Berberis thunbergii* DC.

Key words: Invasive, landscape, ornamentals.

Japanese barberry (*Berberis thunbergii* DC.) cultivars are extremely popular landscape shrubs because of their adaptability, deer resistance, ease of production, and ornamental characteristics that include purple, yellow, and variegated foliage and compact form (Dirr 2009). Barberry is worth nearly $30.5 million in annual sales in the United States, making it one of the top two ornamental shrubs, roses excluded. (U.S. Department of Agriculture [USDA] 2009). Dirr (2009) lists close to 70 cultivars of *B. thunbergii* or *B. thunbergii* hybrids, and at least 10 new cultivars have been introduced in the past 5 yr.

Since its introduction to New England in the late 1800s, Japanese barberry has naturalized in more than 30 states across the United States (Silander and Klepeis 1999; USDA NRCS 2011). Barberry spreads into unmanaged areas primarily by seed, which is dispersed by some birds, by small rodents (Decker et al. 1991; Silander and Klepeis 1999), and via water runoff and wind. Lubell et al. (2008) found genetic evidence that popular purple-leaved, cultivated forms of Japanese barberry may be introgressive with existing feral barberry populations in some locations. Seeds from *B. thunbergii* var. *atropurpurea* Chenault also germinated and survived when dispersed into five different natural environments, although survival for seedlings from var. *atropurpurea* was less than it was for *B. thunbergii* (Lubell and Brand 2011). For one feral barberry population of limited size, parentage analysis was used to show that the invasion originated with a single, large, purple-leaved, landscape individual (Lubell et al. 2009). Although it is rare to find purple-leaved plants in feral populations, seedlings derived from purple-leaved genotypes may not be purple because of sexual recombination (Lehrer et al. 2006) or because anthocyanin production is suppressed in low light levels of wooded areas (Lehrer and Brand 2010).

Concern about the detrimental ecological effects of Japanese barberry has prompted many states to consider

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Management Implications

Japanese barberry cultivars represent a substantial economic value to the nursery and landscape industries because they are popular, durable plants, widely used for landscaping. Unfortunately, Japanese barberry is also an invasive plant, and some states have imposed laws preventing the propagation and sale of the species and all cultivars. Cultivars of Japanese barberry look and behave differently from the species, with many being dwarf forms with purple or yellow foliage. The dramatic visual differences between cultivars of Japanese barberry and the species have led some to suggest that certain cultivars may be noninvasive or have a lower potential for rapid establishment in natural communities and could be exempted from species bans. The objective of this study was to evaluate the fecundity of a wide range of commercially available Japanese barberry cultivars to determine whether any could be considered noninvasive. We determined fruit production, seed production, and germination rates for 46 cultivars of Japanese barberry and its hybrids. Using seed from a representative subset of cultivars, we also determined the potential each cultivar had to germinate, survive, and grow in a deciduous woodland. Cultivars varied considerably in their seed production from more than 12,000 seeds to no seeds, and several cultivars produced fewer than 100 seeds plant^{-1}. When plants were allowed to mature for 4 to 5 yr beyond the first evaluation time, cultivars exhibited significant increases in fruits per plant. 'Sparkle' produced more than 35,000 fruits plant^{-1} and 'Golden Devine' and 'Red Chief', which initially appeared to be fruitless, produced 165 and 20 fruit plant^{-1}, respectively. To accurately assess reproductive potential of cultivars, it is necessary to conduct evaluations for durations that are longer than those typically reported and to provide ample opportunities for cross-pollination. Cultivar seed germination rates were between 12.5 and 31% in a deciduous woodland, and seedlings survived at rates between 5.6 and 29.3%. By combining seed production data with establishment data in a deciduous woodland, even cultivars producing as few as 100 seeds yr^{-1} in the landscape have the potential to contribute a few seedlings each year to a natural area. Most barberry cultivars clearly cannot be considered noninvasive, and even those that are the least fecund, can still be minimally invasive if they reach an age of 10 yr or more.

banning the sale of this species (Harrington et al. 2003). Both Massachusetts (Anonymous 2005) and New Hampshire (Anonymous 2004) have passed legislation banning the sale of all *B. thunbergii*. The two counties that comprise Long Island, NY, have legislation in place that will ban Japanese barberry and its hybrids in 2014 (Anonymous 2009a, b).

Oregon banned the sale of butterflybush (*Buddleja davidii* Franch.), including all cultivars, but then amended the ban to allow for the sale of cultivars that produce less than 2% viable seed and interspecific hybrids, which are considered to be sterile (Oregon Department of Agriculture 2010). A controlled study that documented significantly reduced seed production by the new *Buddleja* cultivar 'Blue Chip', in comparison to standard cultivars (Smith 2010), served as the impetus to amend the butterflybush ban in Oregon to allow for sale of specified noninvasive genotypes.

Cultivar evaluation for seed production can be useful to advise the green industry about particular cultivars that are prolific or to identify sterile, or near sterile, cultivars that could qualify for exemptions when plants bans are established for a species. In a limited study of landscape specimens, four cultivars of *B. thunbergii* were found to vary significantly in their fruit and seed production (Lehrer et al. 2006). In another study, where the invasive potential of a limited number of *B. thunbergii* cultivars was estimated by measuring fruit production per unit of stem length, Lovinger and Anisko (2004) found widely varying levels of fruit production.

In the present study, we compared the fruit and seed production of Japanese barberry cultivars available in the United States under identical environmental conditions. The study was conducted with opportunity for cross-pollination and with the replicates allowed to attain substantial size and become fully established to better determine the true reproductive potential of plants that are likely to remain in landscapes for decades. We also determined cultivar seed-germination and survival rates in a deciduous woodland and then coupled those data with cultivar seed production rates to predict the expected contribution of seedlings to a natural area.

Materials and Methods

Cultivar Fruit and Seed Production. A total of 46 barberry taxa were evaluated, which included *B. thunbergii*, *B. thunbergii* var. *atropurpurea*, 36 *Berberis thunbergii* cultivars, and 8 *B. thunbergii* hybrid cultivars (Table 1). Plants were obtained from 20 different nurseries and one arboretum. All plants were maintained at the University of Connecticut, Department of Plant Science Research Farm, Storrs, CT (latitude 41.794415°N; longitude 72.227320°W) in USDA hardiness zone 6a, in Paxton and Montauk, fine-sandy loam, with full sun exposure. The corridor between New York, NY, and Boston, MA, has been heavily invaded by *B. thunbergii*, so the study location in Storrs, CT, was ideally situated in an area where *B. thunbergii* grows well (Mehrhoff et al. 2003). Plants were installed in 2003 and 2004 from either 3.8- or 7.6-L (1- or 2-gal) containers, with three replications of each cultivar. Spacing within rows was 2.5 m on center, and spacing between rows was 3.7 m on center. Clean cultivation was maintained within rows, and grass alleyways were mowed between rows. Cultivars from 3.8-L containers were allowed to establish in the field for 3 yr before fruit and seed data collection, whereas cultivars from 7.6-L containers were allowed to establish for 2 yr. Plants were 5 to 7 yr old, from cuttings, at the point of initial data collection. Cultivars were placed into two evaluation groups based on their planting year and container size at planting (see Table 1). Evaluation group 1 was composed of plants installed in 2003 from 7.6-L containers, and evaluation group 2 comprised plants installed in 2003 as 3.8-L containers plus plants installed in 2004 as 7.6-L containers. Within each evaluation group, cultivars were arranged in a completely random design.

Table 1. *Berberis* spp. cultivars evaluated, including the source of plants, habit description, and foliage color. Cultivars were separated into two evaluation groups based on their planting date and size at planting.

Berberis species	Cultivar name	Habit	Foliage color[a]	Year planted	Size planted[b]	Year evaluated	Evaluation group[c]
koreana × *thunbergii*	'Bailsel' Golden Carousel	large	Y	2003	2	2005	1
koreana × *thunbergii*	'Tara' Emerald Carousel	large	G	2003	2	2005	1
× *mentorensis* L.M. Ames		large	G	2003	2	2005	1
× *ottawensis* Schneid.	'Concorde'	small	P	2003	2	2005	1
× *ottawensis*	'Crimson Velvet'	large	P	2003	2	2005	1
× *ottawensis*	'Criruzam' Crimson Ruby	small	P	2003	2	2005	1
× *ottawensis*	'Royal Cloak'	large	P	2003	2	2005	1
× *ottawensis*	'Silver Mile'	large	PV	2003	1	2006	2
thunbergii DC.		large	G	2003	2	2005	1
thunbergii	'Anderson' Lustre Green	medium	G	2003	2	2005	1
thunbergii	'Angel Wings'	large	P	2003	2	2005	1
thunbergii	'Antares'	large	P	2003	1	2006	2
thunbergii	'Aurea'	medium	Y	2003	2	2005	1
thunbergii	'Bagatelle'	small	P	2003	2	2005	1
thunbergii	'Bailgreen' Jade Carousel	large	G	2003	2	2005	1
thunbergii	'Bailone' Ruby Carousel	large	P	2003	2	2005	1
thunbergii	'Bailtwo' Burgundy Carousel	large	P	2003	2	2005	1
thunbergii	'Bogozam' Bonanza Gold	small	Y	2003	2	2005	1
thunbergii	'Crimson Dwarf'	small	P	2003	2	2005	1
thunbergii	'Crimson Pygmy'	small	P	2003	2	2005	1
thunbergii	'Erecta'	large	G	2003	1	2006	2
thunbergii	'Gentry Cultivar' Royal Burgundy	small	P	2003	2	2005	1
thunbergii	'Golden Devine'	small	Y	2003	1	2006	2
thunbergii	'Golden Ring'	large	P	2003	1	2006	2
thunbergii	'Green Pygmy'	small	G	2003	2	2005	1
thunbergii	'Helmond Pillar'	columnar	P	2003	2	2005	1
thunbergii	'Inermis'	medium	G	2003	1	2006	2
thunbergii	'J.N. Redleaf' Ruby Jewel	medium	P	2003	1	2006	2
thunbergii	'J.N. Variegated' Stardust	medium	GV	2003	1	2006	2
thunbergii	'Kelleriis'	medium	GV	2003	1	2006	2
thunbergii	'Kobold'	small	G	2003	2	2005	1
thunbergii	'Lime Glow'	large	YV	2003	2	2005	1
thunbergii	'Maria' Sunjoy Gold Pillar	columnar	Y	2004	2	2006	2
thunbergii	'Marshall Upright'	large	P	2003	2	2005	1
thunbergii	'Monlers' Gold Nugget	small	Y	2003	2	2005	1
thunbergii	'Monomb' Cherry Bomb	medium	P	2003	2	2005	1
thunbergii	'Monry' Sunsation	medium	Y	2003	2	2005	1
thunbergii	'Painter's Palette'	medium	GV	2004	2	2006	2
thunbergii	'Pow Wow'	medium	Y	2003	1	2006	2
thunbergii	'Red Chief'	large	P	2004	2	2006	2
thunbergii	'Red Rocket'	large	P	2004	2	2006	2
thunbergii	'Rose Glow'	large	PV	2003	2	2005	1
thunbergii	'Sparkle'	large	G	2003	2	2005	1
thunbergii	'Stan's Variegated'	medium	GV	2003	1	2006	2
thunbergii	'Talago' Sunjoy Gold Beret	small	Y	2004	2	2006	2
thunbergii	var. *atropurpurea*	large	P	2003	2	2005	1

[a] Color code: G, green; GV, green variegated; P, purple; PV, purple variegated; Y, yellow; YV, yellow variegated.

[b] Nursery containers either No. 1, 3.78-L (1 gal) or No. 2, 7.57 (2 gal) pots.

[c] Plants were separated into two evaluation groups based on the year they were planted and their size at planting time so that each evaluation group contained only plants that were of the same maturity and level of establishment in the field.

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Fruit and seed data were collected when berries ripened in October of 2005 (evaluation group 1) and 2006 (evaluation group 2). Most study plants were harvested completely by hand-removal of all fruits present. Because it was impractical to complete manual harvest for some of the largest and most prolific fruit-producing cultivars, those plants were divided into four quadrants, fruit was collected completely from two randomly selected quadrants and total production was extrapolated. Seeds were hand-extracted from 100 fruits (fewer if fruit counts were less than 100) from each replicate of each cultivar to determine the number of seeds per fruit and the number of seeds per plant. At fruit collection for cultivars in evaluation group 1, the height, width, and depth of the plants was measured. In addition, annual shoot growth was determined for each plant by randomly selecting and measuring the current season's stem length for 10 shoots plant^{-1}.

To ascertain how fruit production might change as barberry cultivars continued to mature in the field for an additional 4 to 5 yr, a follow-up assessment was completed in October 2010. These additional data were collected on a subset of 21 cultivars that included genotypes that were initially prolific fruiters, moderate fruiters, low fruiters, or had failed to fruit. Exact fruit counts were used for cultivars that produced small amounts of fruit. For plants where a visual inspection indicated fruit numbers in the thousands, it was impractical to determine exact fruit counts, and estimates were obtained by counting the number of fruits present in 25% of the plant canopy and extrapolating the total. Plant height, width, and depth were measured at the time of fruit harvest for all plants included in the 2010 follow-up fruit count.

Data for fruits per plant, seeds per fruit, and seeds per plant were subjected to ANOVA and mean separation using Fisher's Protected LSD test ($P \leq 0.05$) using SAS for Windows Version 9.2 (SAS Institute Inc., Cary, NC).

Greenhouse Germination of Cultivar Seed. Ripe berries were collected in late October from barberry cultivars maintained in the previously described barberry cultivar planting at the University of Connecticut, Department of Plant Science Research Farm. Fruits were collected separately from all three individuals of each cultivar in the planting and were kept separate throughout the study. Seeds were extracted from fruit lots by maceration, and clean seeds were stored dry in polyethylene bags at 5 C (41 F). To facilitate germination, seeds were stratified for 90 d in moistened, sterilized sand, according to the protocol described by Dirr and Heuser (1987). One hundred stratified seeds of each cultivar replication were sown on May 1 in rows in heavy plastic flats (Kadon Corporation, Dayton, OH) using Metro Mix 360 Growing Medium (Scotts Company, Marysville, OH). Seed lots were randomized across all of the seed flats. The flats were placed in a greenhouse with set points of 21/17 C (70/63 F) day/night temperatures and natural lighting at the University of Connecticut Floriculture Greenhouses in Storrs, CT. Seedlings were allowed to germinate and grow for 6 wk before germination percentages were recorded. The study was repeated in time using fresh seed collected in October 2006 and October 2007. Germination data from both time replications was combined and subjected to ANOVA (PROC MIXED) and mean separation using Fisher's Protected LSD test ($P \leq 0.05$) using SAS for Windows Version 9.2 (SAS Institute).

Cultivar Seedling Growth in Containers. Fifteen seedlings (five from each of the three mother plants) from the previously described germination flats were randomly selected and potted into 1,040-ml (35-oz) black-plastic, square pots (Belden Plastics, Roseville, MN) containing Metro Mix 510 Growing Medium (Scotts) and moved to outdoor cold frames. A completely random design was used to arrange plants within the cold frames. Plants were hand-weeded, irrigated regularly, and provided soluble 20–8.74–16.6 N–P–K fertilizer (Peters 20-10-20 Fertilizer, Scotts Co.) at 200 ppmw N every 2 wk during the study. Plants grew outdoors from mid June until mid November, when they were destructively harvested. Plant width, height, and depth were measured (used to calculate plant size), and the number of branches was counted. In addition, fresh weight and dry weight were obtained for plants (shoots and roots). Data for plant size, number of branches, fresh weight, and dry weight were combined for both study years and subjected to ANOVA (PROC MIXED) and mean separation using Fisher's Protected LSD test ($P \leq 0.05$) using SAS for Windows Version 9.2 (SAS Institute).

Germination, Survival, and Growth of Seed from Barberry Cultivars in a Deciduous Woods. Seed from wild-type *B. thunbergii* and 16 barberry cultivars was evaluated for its ability to germinate, survive, and grow in a dry deciduous woods site. The goal was to determine whether there were differences in the ability of seed from different cultivars to establish in a natural environment. A dry, deciduous woods site was used because our previous research showed that this environment was the most supportive of barberry establishment of those we have studied (Lubell and Brand, 2011). The dry, deciduous woods site had 51% of full sunlight in April and 1% full sunlight by June when the deciduous canopy expanded. The primary vegetation was maple (*Acer* spp.), ash (*Fraxinus* spp., birch (*Betula* spp.), eastern white pine (*Pinus strobus* L.), and eastern hemlock [*Tsuga canadensis* (L.) Carrière]. The soil at the site was a sandy loam (52.9% sand, 34.6% silt, 12.5% clay) with a pH of 5.3, 7.3% organic matter, and 35% soil moisture (in November). Calcium, magnesium, phosphorus, and potassium levels in the soil were 610, 92, 1, and 204 kg ha^{-1} (545, 82, 1, and 183 lb ac^{-1}), respectively.

Seeds of each cultivar were sown in early November into 30 cm by 60 cm (12 in by 24 in) wooden frames that were 8 cm tall. The wooden frames were recessed halfway into the soil, and all forest floor litter was left in place. Forty seeds were sown per frame by hand-broadcasting over the plot surfaces. There were five replications of each cultivar treatment in a randomized complete-block design. Following seed sowing, frames were covered with hardware cloth with 6-mm (0.2-in) mesh openings to protect the seeds from predation by birds and small mammals. Experimental plots were harvested in late August, almost 3 yr after the seed was sowed. All seedlings present were counted, all seedlings were removed, and dry weights were determined. The study was conducted twice, with a one-time replication beginning in 2006 and the second beginning in 2007. Seeds used in this study were collected fresh each year from the replicated cultivar planting at the University of Connecticut, Department of Plant Science Research Farm.

Estimated Potential of Cultivars to Contribute Seedlings to a Deciduous Woods. Fruit and seed production data for a subset of cultivars in a research plot were coupled with seed germination and survival data from field experiments in a deciduous woodland to estimate and compare the potential for cultivars to contribute feral seedlings to natural environments. The initial evaluation period (Table 2) measured landscape plants in a stage of early maturity. Fruit and seed data collected from those plants, therefore, may be considered typical of landscape shrubs that are relatively early in the reproductive portion of their development. Data collected from these same plants 4 to 5 yr later, after significant growth, indicate the production potential of landscape specimens that have reached full maturity. Predicted establishment rates for cultivar seedlings in deciduous woods were calculated by multiplying germination percentages by survival percentages. Finally, an estimation of annual seedling contribution to deciduous woodlands was calculated by multiplying those establishment rates by the seed production of medium- and large-sized plants.

Results

Cultivar Fruit and Seed Production. Cultivars varied widely in their fruit and seed production (Table 2). The most prolific cultivar produced an average of just slightly less than 10,000 fruits following its establishment period, whereas others failed to set any fruit. The number of seeds per fruit ranged from an average of 0.1 ('Inermis') to 1.8 (Sparkle). 'Tara' Emerald Carousel® produced the greatest number of fruits of any cultivar at 9,926. Considering that this cultivar yielded an average of 1.3 seeds fruit^{-1}, Tara Emerald Carousel® was the most prolific seed producer of any cultivar tested.

Of the 46 taxa evaluated, 17 produced an average of more than 1,000 seeds plant^{-1} (Table 2). Twenty-three taxa produced more than 500 seeds plant^{-1}, and 14 taxa produced fewer than 250 seeds plant. 'Aurea', 'Bagatelle', and mentor barberry (*Berberis* × *mentorensis* L.M. Ames) produced fewer than 10 seeds plant^{-1}. Two cultivars, Golden Devine and Red Chief, did not produce any fruits or seeds following the standard establishment period. 'Crimson Pygmy', perhaps the most popular commercial *B. thunbergii* cultivar, produced moderate amounts of seeds at 558 plant^{-1}. 'Rose Glow', another popular cultivar, produced 810 seeds plant^{-1}.

The top-three seed-producing cultivars were large-growing types with green foliage (Table 2). With the exception of 'Bailsel' Golden Carousel (883 seeds plant^{-1}) and 'Talago' Sunjoy™ Gold Pillar (578 seeds plants^{-1}), the yellow-foliage cultivars produced lower numbers of seeds, generally fewer than 150 seeds plant^{-1}. Overall, cultivars with dwarf or compact habit produced fewer seeds than did standard-sized cultivars, regardless of foliage color. Although 'Monomb' Cherry Bomb™ (1,797 seeds plant^{-1}), 'Kobold' (767 seeds plant^{-1}), Crimson Pygmy (558 seeds plant^{-1}), and 'Maria' Sunjoy™ Gold Beret (322 seeds plant^{-1}) produced moderate to low quantities of seeds, the other 10 dwarf or compact cultivars all produced fewer than 300 seeds plant^{-1}. If seed production data are averaged for large-green, large-purple, small-purple, and small-yellow cultivars, some interesting trends are apparent. Large-green cultivars averaged 8,257 seeds plant^{-1}, which is significantly more than the average of 3,260 seeds plant^{-1} for large-purple cultivars. Small-purple and small-yellow cultivars produced significantly less seed than did either of the large-growing groups at 189 and 126 seeds plant^{-1}, respectively. No statistical differences were found for germination of seeds between the four different plant habits by foliage color categories. To some degree, this reduced production is a function of plant size but likely also has a genetic component. Dwarf plants may exhibit a retarded rate of maturation, and it takes longer for their reproductive potential to be realized.

The data suggest that hybridity between *B. thunbergii* and another *Berberis* species may influence the reproductive potential of a genotype. The two Korean barberry (*B. koreana* Palib. × *B. thunbergii*) cultivars (Bailsel Golden Carousel® and Tara Emerald Carousel®) appeared to be more prolific than comparable yellow- and green-foliage cultivars of pure *B. thunbergii* (Table 2). Bailsel Golden Carousel® produced the most seeds of any yellow-foliage cultivar, whereas Tara Emerald Carousel® produced more seeds than any green *B. thunbergii*.

The *Berberis* × *ottawensis* C. K. Schneid. taxa [European barberry (*Berberis vulgaris* L. × *B. thunbergii*)] did not appear any more or less prolific than pure *B. thunbergii* cultivars. *Berberis* × *ottawensis* cultivars such as 'Crimson

Table 2. Fruit production per plant, number of seeds per fruit, number of seeds per plant, seed germination rates, and plant size measurements for *Berberis* spp. cultivars. Cultivars are separated into two evaluation groups based on their planting date and size at planting.[a]

Evaluation group 1[b]

Taxa	Fruits $plant^{-1}$	Seeds $fruit^{-1}$	Seeds $plant^{-1}$	% germination	Plant size[c] Height	Width	Depth	Annual shoot length
					cm			
'Tara' Emerald Carousel	9,926 a	1.3 cd	1,2419 a	77.5 abcde	92	189	162	23.6
'Sparkle'	5,543 bc	1.8 a	9,917 b	89.7 a	87	184	156	18.5
'Anderson' Lustre Green	4,257 cd	1.6 abcd	6,768 c	76.5 abcde	88	184	165	13.8
'Bailone' Ruby Carousel	4,063 cd	1.6 abcd	6,422 c	85.8 ab	162	262	241	18.4
'Crimson Velvet'	6,675 b	1.0 ef	6,311 c	71.2 abcdefg	147	235	213	20.4
'Marshall Upright'	3,249 de	1.4 abcd	4,362 cd	67.6 abcdefg	122	160	107	16.3
'Bailgreen' Jade Carousel	2,267 de	1.7 ab	3,925 de	75.3 abcde	68	142	123	11.0
'Angel Wings'	1,847 def	1.6 abcd	2,999 def	70.5 abcdefg	83	172	150	18.5
'Bailtwo' Burgundy Carousel	1,377 def	1.7 abc	2,309 defg	70.3 abcdefg	104	170	166	21.2
'Monomb' Cherry Bomb	1,225 def	1.5 abcd	1,797 efgh	73.0 abcde	72	131	111	10.2
var. *atropurpurea*	1,045 ef	1.2 de	1,179 fgh	70.8 abcdefg	131	171	146	17.8
'Bailsel' Golden Carousel	681 ef	1.3 cd	883 fgh	58.0 cdefgh	83	81	73	16.2
'Rose Glow'	939 ef	0.9 ef	810 fgh	77.8 abcd	95	139	124	23.3
'Kobold'	842 ef	0.9 ef	767 gh	76.0 abcde	40	72	64	6.5
'Crimson Pygmy'	429 ef	1.3 cd	558 gh	66.0 abcdefg	65	138	130	11.2
thunbergii	1,105 ef	0.7 f	478 gh	61.5 bcdefg	109	179	139	15.9
'Royal Cloak'	504 ef	0.9 ef	467 gh	44.5 g	155	182	165	13.9
'Helmond Pillar'	209 f	1.7 abcd	366 gh	71.3 abcdefg	81	38	30	14.5
'Lime Glow'	333 f	0.9 ef	294 gh	50.5 efg	59	125	113	15.0
'Crimson Dwarf'	191 f	1.4 abcd	261 gh	79.3 abcd	62	119	108	17.4
'Green Pygmy'	556 ef	0.4 g	220 gh	83.7 abc	27	58	51	4.7
'Concorde'	254 f	0.9 ef	214 gh	47.8 fg	44	69	62	6.4
'Criruzam' Crimson Ruby	523 ef	0.4 g	166 gh	n/a	52	90	62	8.4
'Bogozam' Bonanza Gold	108 f	1.3 bcd	141 gh	55.3 defg	37	66	60	4.9
'Monry' Sunsation	222 f	0.6 fg	140 gh	63.0 acdefg	58	85	75	6.1
'Gentry Cultivar' Royal Burgundy	106 f	0.7 f	61 h	n/a	38	86	79	7.8
'Monlers' Gold Nugget	22 f	1.4 abcd	29 h	n/a	32	53	38	4.1
'Aurea'	7 f	0.7 ef	8 h	n/a	52	73	64	8.4
'Bagatelle'	5 f	0.5 g	5 h	n/a	25	38	32	5.5
× *mentorensis*	1 f	0.4 g	1 h	n/a	44	50	32	8.6

Evaluation group 2

Taxa	Fruits $plant^{-1}$	Seeds $fruit^{-1}$	Seeds $plant^{-1}$	germination %
'Red Rocket'	1,332 b	1.4 a	1,918 a	64.0 ab
'Erecta'	2,912 a	0.6 c	1,411 ab	55.8 ab
'Painter's Palette'	1,177 b	1.1 ab	1,295 ab	50.2 ab
'Golden Ring'	954 b	1.3 a	1,209 abc	77.2 a
'Pow Wow'	1,004 b	1.2 a	1,205 abc	38.8 b
'J. N. Redleaf' Ruby Jewel	998 b	1.0 b	1,010 bcd	44.8 b
'Kelleriis'	855 b	1.1 ab	927 bcde	63.2 ab
'Talago' Sunjoy Gold Pillar	525 b	1.1 b	578 cde	n/a

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Table 2. Continued.

Evaluation group 2				
Taxa	Fruits plant^{-1}	Seeds fruit^{-1}	Seeds plant^{-1}	germination %
'Stan's Variegated'	432 b	0.9 b	394 cde	74.5 a
'J. N. Variegated' Stardust	768 b	0.6 c	348 de	50.5 ab
'Maria' Sunjoy Gold Beret	358 b	0.9 b	322 de	n/a
'Antares'	620 b	0.6 c	302 de	62.0 ab
'Silver Mile'	638 b	0.3 c	206 de	60.8 ab
'Inermis'	1,152 b	0.1 d	125 e	56.8 ab
'Golden Devine'	0 c	n/a	n/a	n/a
'Red Chief'	0 c	n/a	n/a	n/a

[a] Abbreviation: n/a, not available.

[b] Plants were separated into two evaluation groups based on the year they were planted and their size at planting time, so that each evaluation group contained only plants that were of the same maturity and level of establishment in the field.

[c] Within an evaluation group, mean separation in columns by Fisher's Protected LSD test. Means followed by the same letter are not significantly different at $P \leq 0.05$.

Velvet' (6,311 seeds plant^{-1}) were very prolific, whereas others, such as 'Concorde' (214 seeds plant^{-1}), Silver Mile (206 seeds plant^{-1}) and 'Criruzam' Crimson Ruby™ (116 seeds plant^{-1}) were low seed producers. *Berberis* × *mentorensis*, the result of a cross between *B. thunbergii* and wintergreen barberry (*Berberis julianae* C. K. Schneid.), exhibited very low seed set, producing only 16 seeds plant^{-1} even when allowed to establish for 8 yr (Tables 2 and 3).

Following maturation in the field for 4 to 5 additional yr after initial evaluation of reproductive capacity, all cultivars saw an increase in fruit production with the exception of Crimson Velvet (Table 3). The fruit production of this cultivar decreased by 21%, from 6,675 to 5,270 fruits plant^{-1}. Increase in fruit production across all cultivars ranged from a low of 90% for Concorde to a high of 5,860% for Bagatelle. The average percentage of increase for all cultivars was 1,365%. Barberry cultivars 9 to 12 yr old and established in the field for 6 to 8 yr were capable of producing as much as 35,000 fruits plant^{-1} (Sparkle) (Table 3). The popular Crimson Pygmy and Rose Glow produced 7,970 and 4,400 fruits plant^{-1}, respectively.

Golden Devine and Red Chief cultivars that failed to produce any fruit when first evaluated, produced 165 and 20 fruits plant^{-1}, respectively, when examined 4 to 5 yr later (Table 3). Other cultivars that initially exhibited very modest fruit production ('Bogozam' Bonanza Gold™ 108 fruits; 'Monry' Sunsation™ 222 fruits; 'Helmond Pillar' 209 fruits plant−1) yielded thousands of fruits (Bogozam Bonanza Gold™ 1,870 fruits; Monry Sunsation™ 4,330 fruits; Helmond Pillar 6,550 fruits plant−1) following sufficient time to develop and mature.

Greenhouse Germination of Cultivar Seed. Germination in the greenhouse among group 1 cultivars ranged from a high of 89.7% for Sparkle to a low of 44.5% for 'Royal Cloak' (Table 2). *Berberis thunbergii* had a germination rate of 61.5% ,which was not statistically different from the cultivars in this group, with the exception of Sparkle. In group 2, germination ranged from a high of 77.2% for 'Gold Ring' to a low of 38.8% for 'Pow Wow' (Table 2). The two best-germinating cultivars (Gold Ring and 'Stan's Variegated') were statistically higher than the two worst-germinating cultivars (Pow Wow and 'J. N. Redleaf' Ruby Jewel™). Overall, most barberry cultivars can be expected to germinate at 60% or higher under optimum germination conditions.

Cultivar Seedling Growth in Containers. *Berberis thunbergii* seedlings produced the greatest plant size, number of branches, fresh weight, and dry weight in comparison to 17 cultivars of barberry when grown in container culture under optimum conditions (Table 4). Seedlings of the cultivars Rose Glow and 'Monlers' Gold Nugget™ grew statistically as well as *B. thunbergii* seedlings, but seedlings of several other cultivars, including Aurea, Bailsel Golden Carousel®, Bogozam Bonanza Gold™, Concorde, Crimson Pygmy, Gentry Cultivar Royal BurgundyTM, Helmond Pillar and Kobold grew less vigorously than *B. thunbergii* seedlings. Although seedlings in this group of less vigorous growers did not grow as large as *B. thunbergii* seedlings, they were healthy and did not appear in any way to be likely to fail.

Germination, Survival, and Growth of Seed from Barberry Cultivars in a Deciduous Woods. All barberry cultivars and the species exhibited some germination in the deciduous woods site in the first year following sowing and significant additional germination in the second year

Table 3. Fruit production per plant, number of seeds per fruit, number of seeds per plant and plant size measurements for selected *Berberis* spp. cultivars four to five years after initial data collection.[a]

	Fruit production			Plant size			
Taxa	Beyond initial comparison	Fruits[b]	Change over time[c]	Height	Width	Depth	Change over time[d]
	yr	No. plant^{-1}	%	cm	cm	cm	%
'Sparkle'	4	35,300 a	537	92	189	162	13
'Tara' Emerald Carousel	4	25,300 b	155	139	241	219	160
'Crimson Pygmy'	5	7,970 c	1,758	108	239	217	380
B. thunbergii	5	7,100 cd	543	199	268	258	407
'Helmond Pillar'	4	6,500 cde	3,010	162	115	101	1,938
'Crimson Velvet'	4	5,270 cdef	−21	311	330	319	345
'Royal Cloak'	5	4,930 defg	878	283	277	255	329
'Rose Glow'	5	4,400 defgh	369	163	225	188	321
'Monry' Sunsation	5	4,330 defgh	1,850	132	136	122	492
'Bailsel' Golden Carousel	4	3,730 efgh	448	148	146	135	494
'Green Pygmy'	5	2,430 ghi	337	55	113	102	694
'Kobold'	5	2,020 hi	140	69	124	112	420
'Bogozam' Bonanza Gold	5	1,870 hi	1,631	62	105	103	358
'Gentry Cultivar' Royal Burgundy	5	767 i	624	65	155	140	446
'Monlers' Gold Nugget	5	717 i	3,159	59	94	84	623
'Concorde'	4	483 i	90	69	114	102	326
'Bagatelle'	5	298 i	5,860	46	59	58	418
'Golden Devine'	3	165 i	n/a	38	50	46	n/a
'Aurea'	5	123 i	1,657	115	129	115	602
'Red Chief'	2	20 i	n/a	160	172	166	n/a
× *mentorensis*	4	16 i	1,500	131	155	145	4,082

[a] Abbreviation: n/a, missing initial measurement data.

[b] Mean separation by Fisher's Protected LSD test. Means followed by the same letter are not significantly different at $P \leq 0.05$.

[c] Change in number of fruits in comparison to the initial evaluation time 4 or 5 yr earlier.

[d] Change in plant size in comparison to the initial evaluation time 4 or 5 yr earlier.

following germination (Table 5). Two-year cumulative germination in the woodland site was less than one-third of that under greenhouse germination conditions. Barberry cultivar seeds can be expected to germinate between 12.5 and 31% in deciduous woods depending on the cultivar, with an average germination rate for all cultivars tested of around 20%. The cultivars Royal Cloak and Concorde had seed germination percentages that were statistically lower than for *B. thunbergii* seed, but all other cultivars had germination percentages that were statistically similar to the species.

Survival of *B. thunbergii* seedlings was 40.4%, whereas survival of cultivar seedlings ranged from a low of 5.6% for Bailsel Golden Carousel® to a high of 29.3% for 'Green Pygmy' (Table 5). Six cultivars had seedling survival rates that were statistically similar to *B. thunbergii* seedlings, whereas 10 cultivars had seedling survival rates less than *B. thunbergii* seedlings. Based on our observations, seedlings that survive in the woods until they are 2 to 3 yr old have a very low attrition rate as they grow older. Most seedling losses occur in the first growing season and overwintering period. There were no differences in seedling dry weight between any of the cultivars or *B. thunbergii* (Table 5). Seedlings that germinated in the deciduous woods averaged less than 0.1 g (0.004 oz) dry weight seedling^{-1}, whereas similar seedlings grown in containers under optimal conditions averaged more than 4.5 g dry weight seedling^{-1} (Tables 4 and 5).

Estimated Potential of Cultivars to Contribute Seedlings to a Deciduous Woods. By coupling data about barberry cultivar establishment in a deciduous woodland with data about cultivar seed production, it is possible to gain some insight into how quickly different barberry cultivars in landscapes may be able to spread into adjacent unmanaged areas (Table 6). Of course, these calculated

Table 4. Growth measurements for seedlings of *Berberis* spp. cultivars grown under container culture for a single growing season.[a]

Taxa	Size	No. branches	Fresh wt	Dry wt
	cm^3		g	
'Aurea'	2189 bc	4.5 cde	15.5 cdef	4.5 cde
'Bailsel' Golden Carousel	1485 c	3.3 de	9.0 f	2.3 e
'Bogozam' Bonanza Gold	1514 c	4.1 cde	10.1 ef	2.8 de
'Concorde'	1736 bc	5.4 bcde	12.7 ef	3.3 de
'Crimson Pygmy'	2470 bc	4.1 cde	13.3 ef	3.6 de
'Crimson Velvet'	5801 ab	4.2 cde	16.2 cdef	4.7 cde
'Gentry Cultivar' Royal Burgundy	3972 bc	6.3 bcd	16.8 cdef	4.4 cde
'Green Pygmy'	3151 bc	6.6 bc	20.9 bcde	5.8 bcd
'Helmond Pillar'	831 c	2.9 e	7.3 f	2.1 e
'Kobold'	2216 bc	5.8 bcde	15.4 def	4.0 cde
'Monlers' Gold Nugget	5811 ab	8.0 ab	25.0 abcd	6.8 abc
'Monry' Sunsation	3537 bc	6.0 bcd	15.3 def	4.1 cde
'Rose Glow'	8288 a	6.3 bc	26.7 abc	7.8 ab
'Royal Cloak'	3782 bc	4.0 cde	14.2 def	3.8 de
'Sparkle'	4918 abc	5.9 bcd	21.0 bcde	5.6 bcd
'Tara' Emerald Carousel	3626 bc	5.4 bcde	29.6 ab	8.4 ab
B. thunbergii	8283 a	9.9 a	33.2 a	8.8 a

[a] Mean separation in columns by Fisher's Protected LSD test. Means followed by the same letter are not significantly different at $P \leq 0.05$.

Table 5. Germination, seedling survival, and average seedling weight for seeds of *Berberis* spp. cultivars sown in a deciduous woods.[a]

Cultivar	First-yr germination[b]	Second-yr cumulative germination	Seedling survival	Seedling dry wt
	%			g
'Aurea'	8.0 bcd	15.0 cd	22.0 abcd	0.06 a
'Bailsel' Golden Carousel	10.0 abcd	18.0 bcd	5.6 d	0.08 a
'Bogozam' Bonanza Gold	3.5 d	21.0 abcd	14.1 bcd	0.04 a
'Concorde'	6.0 cd	12.5 d	15.5 bcd	0.03 a
'Crimson Pygmy'	6.5 cd	15.0 cd	17.5 bcd	0.07 a
'Crimson Velvet'	10.5 abcd	18.5 bcd	20.0 bcd	0.05 a
'Gentry Cultivar' Royal Burgundy	12.0 abc	16.0 cd	19.4 bcd	0.09 a
'Green Pygmy'	15.0 ab	28.0 ab	29.3 ab	0.11 a
'Helmond Pillar'	6.5 cd	17.5 bcd	20.7 abcd	0.06 a
'Kobold'	15.5 ab	30.5 a	23.3 abcd	0.07 a
'Monlers' Gold Nugget	6.5 cd	20.5 abcd	7.2 cd	0.04 a
'Monry' Sunsation	10.0 abcd	19.5 abcd	25.7 abc	0.07 a
'Rose Glow'	12.5 abc	23.0 abcd	28.4 ab	0.14 a
'Royal Cloak'	5.0 cd	12.5 d	10.5 bcd	0.04 a
'Sparkle'	17.0 a	31.0 a	16.6 bcd	0.10 a
'Tara' Emerald Carousel	9.0 abcd	26.2 abc	15.4 bcd	0.08 a
B. thunbergii	10.0 abcd	25.0 abc	40.4 a	0.11 a

[a] Mean separation in columns by Fisher's Protected LSD test. Means followed by the same letter are not significantly different at $P \leq 0.05$.

[b] Total of 200 seeds, 40 seeds sown, 5 replications.

Table 6. Predicted contribution of established seedlings to a deciduous woodland from adjacent medium and large plants of *Berberis* spp. cultivars.

Cultivar	Predicted seeds produced from early maturity plant[a]	Predicted seeds from fully mature plant[b]	Predicted seedlings establishing[c]		
			Establishment rate[d]	Early maturity plant	Full maturity plant
	No. yr^{-1}				
'Aurea'	8	123	0.033	0.3	4.1
'Bailsel' Golden Carousel	883	3,730	0.010	8.9	37.6
'Bogozam' Bonanza Gold	141	1,870	0.030	4.2	55.4
'Concorde'	214	483	0.019	4.1	9.4
'Crimson Pygmy'	558	7,970	0.026	14.6	209.2
'Crimson Velvet'	6,311	5,270	0.037	233.5	195.0
'Gentry Cultivar' Royal Burgundy	61	767	0.031	1.9	23.8
'Green Pygmy'	220	2,430	0.082	18.0	199.4
'Helmond Pillar'	336	6,500	0.036	13.3	235.5
'Kobold'	767	2,020	0.071	54.5	143.6
'Monlers' Gold Nugget	29	717	0.015	0.4	10.6
'Monry' Sunsation	140	4,330	0.050	7.0	217.0
'Rose Glow'	810	4,400	0.065	52.9	287.4
'Royal Cloak'	467	4,930	0.013	6.1	64.7
'Sparkle'	9,917	35,300	0.051	510.3	1,816.5
'Tara' Emerald Carousel	12,419	25,300	0.040	501.1	1,020.8
B. thunbergii	478	7,100	0.101	48.3	717.1

[a] Values for seed for early maturing plants were from the first fruit and seed evaluation time. Data from Table 2.

[b] Values for seed for fully mature plants were from the second evaluation time when plants were 4–5 yr older and assumed an average of 1 seed $fruit^{-1}$. Data from Table 3.

[c] Values for predicted seedlings establishing per year were calculated as predicted seeds produced per year × predicted establishment rate.

[d] Values for predicted establishment rate were calculated as the second-year cumulative-germination rate × the seedling survival rate. Data from Table 5.

estimates are limited by many factors, such as local environmental conditions, ability of cultivars to cross-pollinate, health and vigor of particular landscape plants, and how well seeds can move from the landscape to the adjacent woodland. Nonetheless, such estimates may provide useful information about the potential that exists for barberry cultivars to invade.

In looking at plants that would be considered medium-sized landscape plants, cultivars such as Tara Emerald Carousel® and Sparkle could contribute around 500 seedlings $plant^{-1}$ to an adjacent woodland each year (Table 6). This is substantially more than the approximately 50 seedlings $plant^{-1}$ that the species is likely to contribute per year. On the other end of the spectrum, the cultivars Aurea and Monlers Gold Nugget™ would contribute less than 1 seedling yr^{-1} landscape $plant^{-1}$. Eleven out of 16 cultivars evaluated would likely contribute fewer seedlings to a woodland than would *B. thunbergii*, whereas five would contribute as many or more seedlings than the species. Larger, more mature specimens of landscape plants could be expected to contribute very significant numbers of seedlings to an adjacent woodland (Table 6). A large, mature plant of Sparkle could contribute more than 1,800 seedlings yr^{-1} to an adjacent natural area. Furthermore, plants of 9 out of the 16 cultivars evaluated could contribute more than 100 seedlings yr^{-1} to a deciduous woodland.

Discussion

We found that *B. thunbergii* cultivars varied widely in their fruit and seed production. These observations on cultivar differences concur with similar studies of other woody landscape species including butterflybush, Norway maple, and alder buckthorn (*Frangula alnus* P. Mill.) (Anisko and Im 2001; Conklin and Sellmer 2009; Wheeler and Starrett 2001). Lovinger and Anisko (2004), who evaluated fruit set on barberry cultivars by counting fruits per length of stem, found that Tara Emerald Carousel® was the most prolific cultivar studied. This finding was confirmed by our study. Sparkle, the second most prolific cultivar in our trial, was also one of the more prolific cultivars in the Lovinger and Anisko (2004) study. Although cultivars examined in our work and by Lovinger and Anisko (2004) generally produced similar findings there are exceptions. Concorde was identified as not producing any fruits in the Lovinger and Anisko (2004) research; however, we found that Concorde produced 254 fruits plant^{-1}. So, although this cultivar it is not highly prolific, it is also not sterile. Lovinger and Anisko (2004) also categorized Kobold as having low fruit set, but we found it to produce relatively high amounts of fruit (842 plant1), especially for a dwarf cultivar. Lovinger and Anisko (2004) may not have allowed enough time for their plants to become fully reproductively mature.

Cultivars with yellow foliage and dwarf, purple-foliage plants appear to be the least-prolific seed producers in comparison to standard-sized, purple-foliage cultivars or any green-foliage cultivars. Numerous new *Berberis thunbergii* cultivars have recently been introduced that have dwarf or columnar forms with purple or yellow foliage, and there is a desire to consider these plants as having a low potential for rapid reproduction and establishment in natural communities. Although they may be less potent than the more-prolific, full-sized, and green-leaved cultivars, dwarf-purple and yellow-foliage cultivars will probably just take longer to become invasive.

Several popular barberry cultivars are actually interspecific hybrids between *B. thunbergii* and other *Berberis* species. *Berberis* × *mentorensis*, which produced very little seed in our study, is a wide, interspecific hybrid between the deciduous, red-fruited *B. thunbergii* and the evergreen, black-fruited *B. julianae*. Wide interspecific hybridization may be a breeding avenue to develop noninvasive landscape cultivars of barberry that are sterile because of chromosomal dissimilarities between the two taxa resulting in meiotic failure. Some important landscape plants that are sterile because of wide hybridization include *Prunus* × *cistena* (Hansen) Koehne [*Prunus pumila* L. var. *besseyi* (Bailey) Gleason crossed with *Prunus cerasifera* Ehrh. 'Autropurpurea'] and *Cornus* × *rutgersensis* [*Cornus kousa* (Buerger ex Miq.) Hance × *Cornus florida* L.] (Dirr 2009). Breeding work to develop sterile forms of invasive butterflybush has used wide or complex hybridization successfully. The *Buddleja* 'Asian Moon' is a sterile, interspecific hybrid (Renfro et al. 2007), whereas the *Buddleja* 'Blue Chip', which exhibits 100-fold reduced seed production, resulted from very complex parentage (Smith 2010; Werner and Snelling 2009).

Interspecific barberry hybrids between the closely related, red-fruited *B. thunbergii* and *B. vulgaris* exhibited fruit and seed set similar to that observed for many *B. thunbergii* cultivars. *B. thunbergii* and *B. koreana* hybrid cultivars were very prolific seed producers, suggesting that certain barberry hybrids may present a high invasive risk. Hybridization has been suggested to be a stimulus for the development of invasiveness in some plants because of heterosis resulting from genotypic novelty, increased genetic variation, or reduction of accumulated deleterious alleles (Ellstrand and Schierenbeck 2000). Tamarisk (*Tamarix* spp.) (Gaskin and Schaal 2002) and rhododendron (*Rhododendron* spp.) (Milne and Abbott 2000) are two woody genera in which interspecific hybridization has been documented among invasive populations. To counter this risk, careful selection of breeding parents should be exercised when undertaking a hybridization program with barberry and other crops with invasive potential.

Lehrer et al. (2006) found that landscape plants of Aurea, Crimson Pygmy, and Rose Glow barberry, most of which were between 10 and 20 yr old, produced approximately 100, 100, and 800 fruits plant^{-1}, respectively. Similar-aged plants in this study produced 123 (Aurea), 7,970 (Crimson Pygmy), and 4,400 (Rose Glow) fruits plant^{-1} (Table 4). Although the Aurea landscape plants and the plants in the experimental planting produced similar numbers of fruits, the Crimson Pygmy and Rose Glow landscape plants produced many fewer fruits than their counterparts in the experimental planting. The discrepancy between fruit production in a landscape setting and fruit production in an experimental setting may be explained by suboptimal growing conditions for many plants in landscape situations. Another factor that may contribute to reduced cultivar fruit set in landscape situations is limited opportunities for cross pollination among various Japanese barberry genotypes. Many landscape plantings use only a single cultivar to achieve the desired landscaping result, thereby eliminating or significantly reducing cross-pollination. In the absence of cross-pollination, poor seed set may result. Experimental plantings used to evaluate cultivar reproductive potential of a species typically bring together many diverse genotypes, which leads to substantial cross-pollination and a tendency for higher seed set. Even though overall fruit and seed production may be elevated in diverse experimental plantings, relative differences in fecundity between genotypes will still be present, and useful trends may be observed.

Most studies examining cultivar fruit and seed production collect data from plants that are relatively young and have not been allowed sufficient time to establish. This study clearly demonstrated that plants must become fully established and mature in study plantings if accurate data about reproductive potential is to be obtained. When comparing fruit production in the first comparison year to follow-up data collected 4 or 5 yr later, we saw very large increases in fruit production. The cultivars Golden Devine and Red Chief did not produce any fruit the first comparison year but did produce some fruits when rechecked a few years later. In addition, Lovinger and Anisko (2004) did not observe fruit set on Concorde, whereas we recorded 254 fruits plant^{-1} in the first comparison year and 483 fruit plant^{-1} in the follow-up count. There is a real risk that cultivars may be deemed sterile prematurely if sufficient time is not allotted for long-term evaluation.

Fruit and seed production data are often used to make judgments about the invasive risks of using specific cultivars. Researchers have suggested that certain cultivars of *Acer platanoides* L., burningbush [*Euonymus alatus* (Thunb.) Siebold], and *Frangula alnus* may be less invasive because of reduced seed set (Conklin and Sellmer 2009; Ranney et al. 2007; Wheeler and Starrett 2001). For *Berberis*, it has been recommended that cultivars producing three or more fruits per 2.54 cm (1 in) of stem should be avoided, whereas those producing fewer fruits pose a reduced invasive threat (Lovinger and Anisko 2004). Lehrer et al. (2006) found that landscape plants of Aurea and Crimson Pygmy were less prolific than landscape plants of *B. thunbergii* var. *atropurpurea* and Rose Glow and suggested that they may be less invasive. The Connecticut Nursery and Landscape Association used some of the seed production data presented in Table 2 to approve a voluntary ban on 25 cultivars or hybrids of Japanese barberry that are the most-prolific seed producers (Connecticut Nursery and Landscape Association 2010).

We currently do not have demographic studies across the entire life cycle for Japanese barberry, so it is difficult to know how much of a reduction in seed production is necessary to prevent invasion into natural areas. Knight et al. (2011) used matrix-population models to simulate the effect of reducing fecundity on population growth rates of long-lived species, such as Japanese barberry. They concluded that large changes in fecundity result in relatively small changes in population growth rates of long-lived species. Our work certainly shows that most popular barberry cultivars produce sufficiently high numbers of seeds, which have ample capacity to germinate and survive in natural areas. Even use of the least-fecund cultivars may still contribute to population growth. Japanese barberry plants typically live for multiple decades, and they are often planted in groupings or mass plantings, so the actual number of seedlings contributed to a natural area from a typical landscape installation of a barberry cultivar with low fecundity could still be significant. Another complicating factor is that Japanese barberry invades through the spread of sexual seed, and seedlings do not necessarily resemble the maternal parent (Lehrer et al. 2006). Every cultivar we evaluated produced some proportion of seedlings that had foliage color that was different from the maternal parent and variable growth habits (data not shown). As Knight et al. (2011) accurately point out, secondary generations from cultivars may bear little resemblance to the original cultivar of origin and may express different levels of fecundity.

Our research cannot be used to define a specific reproductive threshold beyond which Japanese barberry cultivars will be problematic, but it demonstrates that even cultivars that produce relatively small numbers of seeds are likely to contribute seedlings to natural areas. The nursery and landscape industries, as well as invasive plant regulation entities, should exercise caution in deeming specific barberry cultivars as noninvasive. Truly female-sterile genotypes of barberry may represent the best option in moving forward with this important ornamental shrub.

Literature Cited

Anisko, T. and U. Im. 2001. Beware of butterfly bush. Am. Nurseryman 194:46–49.

Anonymous. 2004. Chapter Agr 3800: Invasive Species. Adopted Rule. http://www.gencourt.state.nh.us/rules/state_agencies/agr3800.html. Accessed: April 4, 2012.

Anonymous. 2005. Massachusetts Prohibited Plants. http://mass.gov/agr/farmproducts/Prohibited_Plant_Index2.htm. Accessed: April 4, 2012.

Anonymous. 2009a. Resolution No. 645: 2009, Adopting Local Law No. 27-2009, A Local Law Amending Chapter 278a of the Suffolk County Code Addressing Invasive Non-native Plant Species. http://cyrus4.lightlink.com/guests/nyis_new/pdf/LIISMA_PDF/Suffolk_Co_LocalLaw_27-2009.pdf. Accessed: April 4, 2012.

Anonymous. 2009b. Local Law 22-2009: A Local Law to Amend Title D15 of Chapter 21 of Chapter 272 of the Laws of 1939, Constitution the Nassau County Administrative Code, in Relation to Preventing the Spread of Invasive Species in Nassau County. http://cyrus4.lightlink.com/guests/nyis_new/pdf/LIISMA_PDF/Nassau_Co_LocalLaw_22-2009.pdf. Accessed: April 4, 2012.

Conklin, J. and J. C. Sellmer. 2009. Flower and seed production of Norway maple cultivars. Horttechnology 19(1):91–95.

Connecticut Nursery and Landscape Association. 2010. Three years to phase-out 25 barberry cultivars. Conn. Nursery Landsc. Mag. (2):3–8.

Decker, S. R., P. J. Penkins, and W. M. Mautz. 1991. Nutritional evaluation of winter foods of wild turkeys. Can. J. Zool. 69: 2128–2132.

Dirr, M. A. 2009. Manual of Woody Landscape Plants. 6th ed. Champaign, IL: Stipes. 1325 p.

Dirr, M. A. and C. W. Heuser. 1987. The Reference Manual of Woody Plant Propagation. Athens, GA: Varsity. 239 p.

Ellstrand, N. C. and K. A. Schierenbeck. 2000. Hybridization as a stimulus for the evolution of invasiveness in plants? Proc. Natl. Acad. Sci. U. S. A. 97(13):7043–7050.

Gaskin, J. F. and B. A. Schaal. 2002. Hybrid *Tamarix* widespread in U.S. invasion and undetected in native Asian range. Proc. Natl. Acad. Sci. U. S. A. 99:11256–11259.

Harrington, R. A., R. Kujawski, and H.D.P. Ryan. 2003. Invasive plants and the green industry. J. Arboric. 29:42–48.

Knight, T. M., K. Havens, and P. Vitt. 2011. Will the use of less fecund cultivars reduce the invasiveness of perennial plants? Bioscience 61(10):816–822.

Lehrer, J. M. and M. H. Brand. 2010. Purple-leaved Japanese barberry (var. *atropurpurea*) genotypes become visually indistinguishable from green-leaved genotypes (*Berberis thunbergii* DC.) at low light levels. J. Environ. Hortic. 28:187–189.

Lehrer, J. M., M. H. Brand, and J. D. Lubell. 2006. Four cultivars of Japanese barberry demonstrate differential reproductive potential under landscape conditions. Hortscience 41:762–767.

Lovinger, S. and T. Anisko. 2004. Benign *Berberis*. Am. Nurseryman December 1:36–39.
Lubell, J. D. and M. H. Brand. 2011. Germination, growth and survival of *Berberis thunbergii* DC. (Berberidadceae) and *Berberis thunbergii* var. *atropurpurea* in five natural environments. Biol. Invasions 13:135–141.
Lubell, J. D., M. H. Brand, J. M. Lehrer, and K. E. Holsinger. 2008. Detecting the influence of ornamental *Berberis thunbergii* var. *atropurpurea* in invasive populations of *Berberis thunbergii* (Berberidaceae) using AFLP. Am. J. Bot. 95:1–7.
Lubell, J. D., M. H. Brand, J. M. Lehrer, and K. E. Holsinger. 2009. Amplified Fragment Length Polymorphism and parentage analysis of a feral barberry (*Berberis thunbergii* DC.) population to determine the contribution of an ornamental landscape genotype. Hortscience 44:1–4.
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. Storrs, CT: Department of Ecology and Evolutionary Biology, University of Connecticut. http://www.ipane.org. Accessed: April 4, 2012.
Milne, R. I. and R. J. Abbott. 2000. Origin and evolution of invasive naturalised material of *Rhododendron ponticum* L. in the British Isles. Mol. Ecol. 9:541–556.
Oregon Department of Agriculture. 2010. Butterfly Bush Cultivar Approval Process. http://www.oregon.gov/ODA/PLANT/NURSERY/buddleja_process.shtml. Accessed: April 4, 2012.
Ranney, T. G., T. A. Eaker, and J. A. Mowrey. 2007. Assessing fertility among cultivars of winged euonymus. Pages 352–354 *in* B. James, ed. Proceedings of the 52nd Southern Nurseryman Association Research Conference. Acworth, GA: Southern Nurseryman Association.
Renfro, S. E., B. M. Burkett, B. L. Dunn, and J. T. Lindstrom. 2007. 'Asian Moon' *Buddleja*. Hortscience 42:1486–1487.
Silander, J. A. and D. M. Klepeis. 1999. The invasion ecology of Japanese barberry (*Berberis thunbergii*) in the New England landscape. Biol. Invasions 1:189–201.
Smith, W. A. 2010. Development of novel breeding stock in *Buddleja davidii* through mutation breeding and haploid induction. Ph.D. dissertation. Storrs, CT: University of Connecticut. 163 p.
[USDA] U.S. Department of Agriculture. 2009. Census of horticultural specialties (2007). Washington, DC: U.S. Department of Agriculture.
[USDA, NRCS] U.S. Department of Agriculture, National Resources Conservation Service. 2011. The PLANTS Database. National Plant Data Team, Greensboro, NC 27401-4901 USA. http://plants.usda.gov. Accessed April 4, 2012.
Werner, D. J. and L. K. Snelling. 2009. 'Blue Chip' and 'Miss Ruby' *Buddleja*. Hortscience 44:841–843.
Wheeler, A. R. and M. C. Starrett. 2001. Determining the invasive potential of *Rhamnus frangula* 'Asplenifolia' and 'Columnaris' based on seed germination. Pages 397–400 *in* the C. W. Heuser, Jr., ed. Combined Proceedings of the 51st International Plant Propagation Society. Carlisle, PA: IPPS.

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