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Will the use of Less Fecund Cultivars Reduce the Invasiveness of Perennial Plants?

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Will the Use of Less Fecund Cultivars Reduce the Invasiveness of Perennial Plants?

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*Many invasive species were originally introduced for horticultural purposes, and several continue to be profitable for the green (nursery, horticulture, and landscape) industry. Recently, some plant suppliers have marketed less fecund cultivars of several invasive species, including glossy buckthorn (*Frangula alnus*), burning bush (*Euonymus alatus*), and Japanese barberry (*Berberis thunbergii*), as "safe" alternatives to invasive relatives. We use published matrix population models to simulate the effect of reducing fecundity on the population growth rates of invasive species. We show that large changes in fecundity result in relatively small changes to the population growth rates of long-lived species, which suggests that less fecund cultivars may still provide an invasive threat. Furthermore, many cultivars are clonal selections, and if crossed with other cultivars or selfed, they produce offspring with traits and fecundities that do not resemble the parent plant. On the basis of these two lines of evidence, we suggest that only female sterile cultivars that cannot reproduce asexually should be considered "safe" and noninvasive. Marketing less fecund cultivars as "safe" is premature at this time, and further research is necessary to determine the potential invasiveness of different cultivars.*

Keywords: invasive plant, ornamental plant, cultivar, demography

Invasive woody plants pose serious threats to native species and ecosystems (Wilcove et al. 1998), and 82% of the invasive trees and shrubs in the United States were introduced through horticulture (Reichard 1997, Reichard and White 2001). The high proportion of invasive species originating from horticulture is not surprising, considering that many of the traits that we desire in ornamental plants are the same traits that are found in invasive species; for example, they are likely to form dense stands (i.e., are good for erosion control), are adaptable to a wide range of landscape conditions, have high levels of flower production and a long flowering period (i.e., they are attractive in gardens), have a high fruit set (especially of fleshy fruit, which can be attractive to bird and animal dispersers), and are able to spread on their own vegetatively or by seed (Kitajima et al. 2006).

Once a species is identified as invasive to natural areas, it is important to prevent the sale, and thus the spread, of that species. However, this effort is complicated by the high demand for the species by consumers and the high economic value of the species to the green (nursery, horticulture, and landscape) industry. For example, Japanese barberry (*Berberis thunbergii*) is considered invasive in 30 eastern and central states in the United States, and many states are considering banning, or have already banned, the sale of this species (Harrington et al. 2003). The loss of Japanese barberry is vexing to many in the green industry, since this species is a valuable commodity. In the state of

Connecticut alone, annual sales of the shrub are estimated to be $5 million (Lehrer et al. 2006).

Species sold in the green industry often have several cultivars that may vary dramatically in their seed production and viability. In most cases, these cultivars were created to provide options for landscape designs and not to create less invasive forms of the species. For example, cultivars selected to produce more petals often produce fewer seeds, and hybrid cultivars formed by crossing distantly related taxa can produce fewer seeds or can be sterile (Ramney 2004). It is only recently that many researchers are purposely creating cultivars of invasive plants that are less fecund, in an effort to reduce their invasive potential (e.g., Ranney 2004, Drew et al. 2010). Regardless of how and why the cultivar was formed, if it is unlikely to invade and harm natural areas, these cultivars should be exempt from invasive species bans. The critical question then becomes how much of a reduction in seed production or seed viability is necessary to create a cultivar that will not be invasive in natural areas. The answer depends largely on the demography of the plant across its entire life cycle, as well as the sensitivity of its population growth rate to reductions in seed production. In a worst-case scenario, large reductions in the seed production of a cultivar relative to that of the wild type would result in relatively small changes in the population growth rate of the species in the wild and therefore to the invasiveness of the plant. To date, no studies have quantified the demography of

different cultivars across their life cycle and compared their projected population growth rates.

Offspring of a cultivar might perform much differently from its horticulturally produced parent plants. For taxa that do not spread vegetatively, cultivars per se do not invade: Their offspring invade. Cultivar offspring may or may not resemble the parents, because cultivars are created from sports (somatic mutations that are selected and propagated clonally) or may be clones of complex, multispecies or multicultivar hybrids. In either case, the offspring will not "breed true." Very few ornamental taxa are "seed selections" of inbred lines that will produce morphologically similar offspring when selfed or crossed with another individual of the same cultivar. Cultivars of long-lived perennial plants are not created by seed selections because the time required makes this method impractical. Furthermore, there is a financial incentive to produce clonal cultivars rather than seed selections because the clonal cultivars will not breed true, which would give the breeder built-in property rights and would secure monetary returns (Drew et al. 2010). In addition, in garden settings, there may be more than one cultivar of a species present or there may be a nearby feral population of the species. In both cases, crossing between cultivars or between a cultivar and an invasive wild type could produce offspring dissimilar from one or both parents.

We currently do not have demographic studies across the entire life cycle for species that are economically important to the green industry (e.g., Japanese barberry), and therefore, we cannot quantify how much of a reduction in seed production or seed viability is necessary to create a cultivar incapable of invading natural areas. However, we can synthesize demographic studies on wild invasive plant species as a first step in considering the degree to which reductions in seed production might result in reductions in population growth rates. In our review of the literature, we found that matrix population models have been constructed for 24 invasive plant species; these studies quantify the demography of wild invasive plant species in natural areas of their invasive ranges.

In the present article, we will first illustrate that cultivars of invasive plants are being advertised as noninvasive on the basis of limited scientific evidence. Second, we will quantitatively synthesize matrix population models parameterized for wild invasive plants and will evaluate how the population growth rates of these plants would change under a range of reductions in seed production or seed viability. Third, we will discuss the research needed to evaluate whether a cultivar is likely to be safe to natural areas. We suggest that marketing of cultivars as "safe" or "noninvasive" needs to be based on evaluations that consider the entire life cycle of the cultivar and its offspring.

Examples of three invasive species with "noninvasive" cultivars

Here, we highlight three species that (a) are popular with consumers and are therefore highly profitable for the green industry, (b) have wild types that are natural-area invaders, and (c) have cultivars with dramatically lower rates of seed production or seed viability. For each species, there is experimental evidence that some cultivars have lower fecundity than the invasive wild type. Specifically, *Frangula alnus* ('Fine Line' glossy buckthorn), *Euonymus alatus* ('Rudy Haag' burning bush), and *B. thunbergii* ('Crimson Pygmy' Japanese barberry) are cultivars with lower rates of seed production or seed viability than many available on the market. Recently, some plant suppliers have begun to market these cultivars as noninvasive. As an illustration of this, we provide examples from Web sites and other sources. We discuss the reasons for which marketing cultivars such as these as safe to natural areas is premature.

Buckthorn. *Frangula alnus* (formerly *Rhamnus frangula*; Rhamnaceae), which is originally from Europe, forms dense thickets in North American forest understories and reduces native herbaceous plant abundance and inhibits tree regeneration (Fagan and Peart 2004, Frappier et al. 2004). 'Fine Line' buckthorn originated from cross-pollination of a female 'Columnaris' cultivar and a male 'Asplenifolia' cultivar (Williams 2004); individuals have the feathery foliage of 'Asplenifolia' with the narrow upright habit of 'Columnaris.' In an experimental study, seeds of 'Fine Line' had significantly lower germination than the wild-type buckthorn (12% and 83.7%, respectively; Mark C. Starrett, Department of Plant and Soil Sciences, University of Vermont, Burlington, personal communication, 28 December 2010). Propagation of the 'Fine Line' cultivar for sale has been achieved entirely through asexual reproduction by cuttings (Williams 2004). It is unknown whether the offspring produced by seed by 'Fine Line' will have a morphology or a demographic performance similar to those of the parent plant. However, since this cultivar is of hybrid origin, it is likely that the offspring will not breed true.

'Fine Line' buckthorn is advertised as a noninvasive by several Web sites. For example, this cultivar was featured as an "Indiana Plant Pick" in the November–December 2009 issue of the Indiana Nursery and Landscapers Association Journal (see Jacquart and Knight 2010 for a response to this choice). Furthermore, one Web site claims that "It has been proven to be an environmentally friendly plant that is not invasive like other types of buckthorn" (7 April 2010; *www.colorchoiceplants.com/fine_line.htm#ixzz0htbHfEgz*).

Burning bush. *Euonymus alatus* (Celastraceae), which is native to East Asia, forms dense thickets and displaces native plant species in forest understories of the United States (Marinelli and Hanson 1996). The 'Rudy Haag' cultivar is a more compact form of the popular 'Compactus' cultivar. The origin of 'Rudy Haag' has not been documented, but it likely resulted from a seedling or a sport from 'Compactus' (Mark Brand, Department of Plant Science and Landscape Architecture, University of Connecticut, Storrs, personal communication, 24 May 2011).

Table 1. Invasive plant species in which matrix population models have been parameterized.

Life form category	Species	Plant family	Population growth rate (λ)	Reduction in fecundity for $\lambda \leq 1$ (percentage)	Location of study	Citation
Monocarpic	*Alliaria petiolata*	Brassicaceae	1.42	55–60	Compiled from multiple sites in the United States	Davis et al. 2006
	Carduus nutans	Asteraceae	1.80	60–65	New Zealand	Shea and Kelly 1998
	Cirsium vulgare	Asteraceae	1.54	65–70	Nebraska	Tenhumberg et al. 2008
	Dipsacus sylvestris	Dipsacaceae	2.33	90–95	Michigan	Werner and Caswell 1977
	Echium vulgare	Boraginaceae	2.28	75–80	Canberra, Australia	Grigulis et al. 2001
	Heracleum mantegazzianum	Apiaceae	1.21	55–60	Czech Republic	Nehrbass et al. 2006
	Polygonum perfoliatum	Polygonaceae	1.56	60–65	Pennsylvania	Hyatt and Araki 2006
	Setaria faberi	Poaceae	1.51	30–35	Iowa	Davis et al. 2004
Perennial herb or grass	*Centaurea maculosa*	Asteraceae	1.33	75–80	Michigan	Emery and Gross 2005
	Molinia caerulea	Poaceae	1.86	95–100	Belgium	Jacquemyn et al. 2005
Shrub or tree	*Ardisia elliptica*	Myrsinaceae	1.16	95–100	Florida	Koop and Horvitz 2005
	Clidemia hirta	Melastomataceae	1.78	95–100	Hawaii	DeWalt 2006
	Cytisus scoparius	Fabaceae	1.40	95–100	Washington state	Parker 2000
	Gleditsia triacanthos	Fabaceae	2.03	95–100	Cordoba Province, Argentina	Marco and Páez 2000
	Parkinsonia aculeata	Fabaceae	1.53	95–100	Central Australia	Raghu et al. 2006
	Pinus nigra	Pinaceae	1.96	95–100	New Zealand	Buckley et al. 2005
	Rubus armeniacus	Rosaceae	1.15	n/a	Oregon	Lambrecht-McDowell and Radosevich 2005
	Syzygium jambos	Myrtaceae	1.16	95–100	Puerto Rico	Brown et al. 2008

Note: λ was based on the average matrix for studies in which multiple populations and years were considered.
n/a, not applicable.

(Caswell 2001). The asymptotic population growth rate, λ, is the dominant eigenvalue of *A*. In order to quantify how reductions in fecundity would affect λ, we multiplied all fecundity matrix elements by $(1 - p)$, where *p* is the proportion by which fecundity is reduced. We reduced fecundity in increments of .05 across a range of 0 (no reduction) to 1 (completely sterile).

We conducted an elasticity analysis of each unaltered matrix ($p = 0$) to determine the proportional sensitivity of λ to changes in the matrix element a_{ij}:

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}} = \frac{\partial (\log \lambda)}{\partial (\log a_{ij})}.$$

For each species, we summed the elasticity values across all matrix elements associated with fecundity and used an ANOVA (analysis of variance) and Tukey's HSD (honestly significant difference) test to determine whether plants in each of the three life history categories described above differ in the sensitivity of λ to changes in fecundity.

This quantitative synthesis demonstrates that there are generalities in the relationship between fecundity and population growth rate attributable to plant life history. The population growth rate drops dramatically with reductions in fecundity for short-lived plant species (e.g., monocarpic species) but not for longer-lived species of herbs, shrubs, and trees (figure 1). It typically takes reductions in fecundity

between 95%–100% to reduce the population growth rates of shrubs and trees to 1 (figure 1, table 1). The population growth rates of shorter-lived species are more sensitive to changes in fecundity than those of longer-lived species (figure 2; $F(2,19) = 12.022$, $p < .001$). This result is not surprising, and several plant demography reviews have pointed out the negative relationship between life span and the sensitivity of the population growth rate to changes in fecundity (e.g., Silvertown et al. 1993), including a review focused on invasive plant species (Ramula et al. 2008). Our review highlights that reductions in seed production or seed viability alone are likely not sufficient to create a "safe" cultivar for an invasive long-lived perennial or woody plant (e.g., *F. alnus*, *E. alatus*, *B. thunbergii*) and also highlights the importance of considering the entire plant life cycle in evaluations of demographic performance and invasive potential. Our goal in these analyses was not to identify an exact magnitude by which reductions in seed production can lead to a safe cultivar but, rather, to make the point that it is difficult to decrease the population growth rate of long-lived species by reducing seed production and that one should not assume that dramatic reductions in seed production will result in similarly dramatic reductions in population growth.

In the studies reviewed here, density-independent matrix population models were employed, and thus population growth in the absence of density-dependent regulation was projected. However, invasive plants reach high densities

a Monocarpic herbs and grasses

1. *Alliaria petiolata*
2. *Carduus nutans*
3. *Cirsium vulgare*
4. *Dipsacus sylvestris*
5. *Echium vulgare*
6. *Heracleum mantegazzianum*
7. *Polygonum perfoliatum*
8. *Setaria faberi*

b Polycarpic herbs and grasses

1. *Centaurea maculosa*
2. *Molinia caerulea*

c Shrubs and trees

1. *Ardisia elliptica*
2. *Clidemia hirta*
3. *Cytisus scoparius*
4. *Gleditsia triacanthos*
5. *Parkinsonia aculeata*
6. *Pinus nigra*
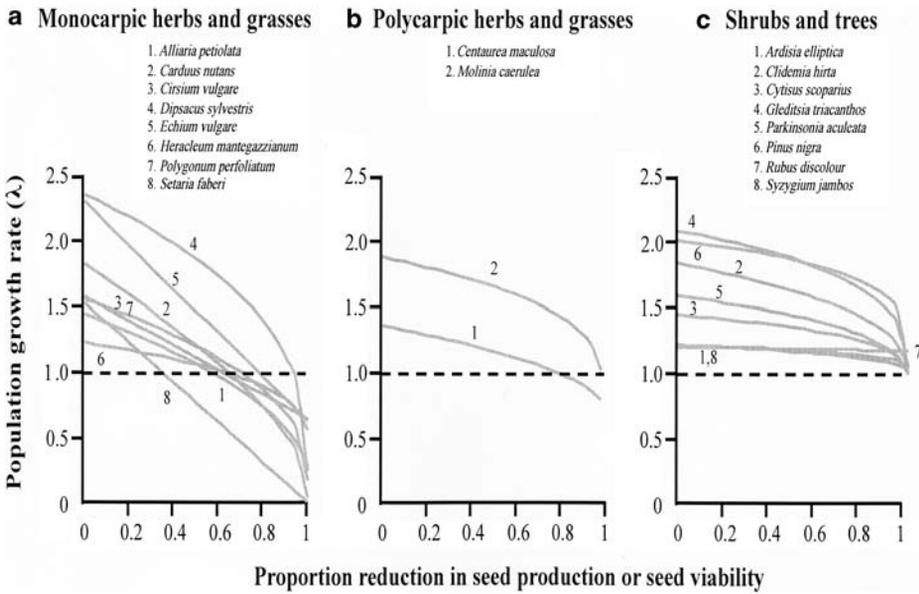7. *Rubus discolour*
8. *Syzygium jambos*

Figure 1. Population growth rate of invasive plant species as a function of reductions in fecundity (seed production or seed viability), shown separately for species with different life forms: (a) monocarpic herbs and grasses, (b) short-lived herbs and grasses, and (c) woody shrubs and trees. The dotted line is shown for a population growth rate of $\lambda = 1$ (see the text for a discussion of population growth rate*).*
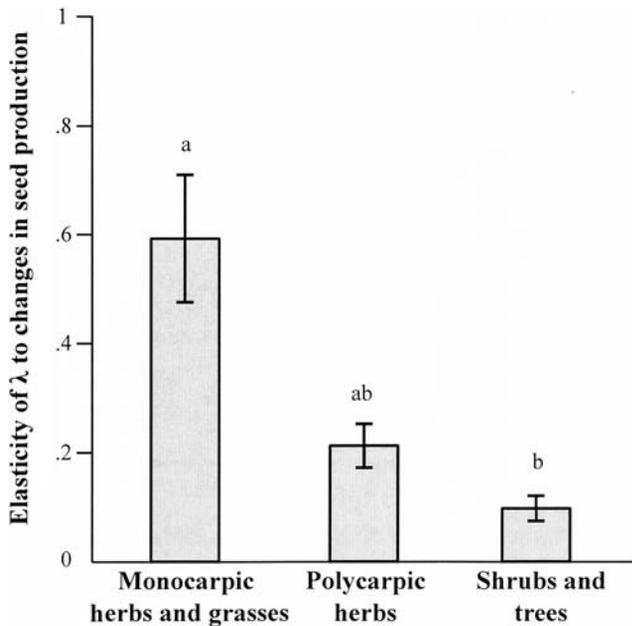
Figure 2. Mean elasticity (see the text for a discussion of elasticity*) of the population growth rate to changes in fecundity matrix elements, shown separately for species with different life forms. The error bars represent one standard error. The letters over the bars indicate significant pairwise differences between the groups based on Tukey's HSD (honestly significant difference) test.*

where lower vital rates due to density dependence would be expected (Pardini et al. 2009). If density dependence in plant establishment is strong, higher fruit and seed production will result in higher rates of density-dependence-related death of seedlings and will not result in more established plants. This provides another mechanism by which reductions in seed production and seed viability in cultivars may not result in a less invasive phenotype: Cultivars that produce fewer viable seeds may have recruited offspring similar to those producing more seeds if their offspring suffer less from density-dependent mortality.

In our synthesis, we considered only how reductions in seed production influence the population growth rates of invasive plants. In reality, cultivars may differ in a variety of demographic vital rates (e.g., adult survivorship, seedling growth rates), all of which might affect their invasive potential. For example, the time to reproductive maturity can vary among cultivars for many species. In *Ardisia crenata*, artificial selection for denser foliage resulted in a cultivar for which individual plants grow more slowly than the wild type. However, this ecotype is not necessarily less invasive, since plants with this denser foliage were found to be stronger competitors for light (Kitajima et al. 2006).

Future research priorities

We are concerned that the marketing of cultivars as "safe to natural areas" has advanced much faster than the research evaluating those cultivars. We recommend two additional lines of study that would advance our ability to evaluate whether a cultivar is likely to threaten natural areas. First, significant demographic differences must exist between cultivars. Studies in which significant differences are found between cultivars in a few vital rates (e.g., the seed production of cultivars) should not be sufficient evidence to justify marketing a cultivar as noninvasive. Our review highlights this point by showing that, in many cases, large reductions in fecundity are inadequate to reduce population growth, particularly for invasive woody plants. Ideally, field trials in which the demography of cultivars is compared would be conducted in all growing zones in which the species is sold. Second, it must be demonstrated that cultivars do not revert to "wild-type" or more weedy forms, either because their offspring do not breed true or through crossing with other cultivars or wild-type individuals. If focal cultivars are capable of hybridizing with other cultivars or wild-type individuals, the fecundity of the offspring may be significantly higher than that of the parent plant. For example, there is evidence that intraspecific hybridization in the

Callery pear (*Pyrus calleryana*), including between different cultivars, can increase invasiveness (Culley and Hardimann 2008). It is possible that some cultivars truly are less invasive than the wild type of the species, and if this is the case, the diversity that can exist among cultivars must be recognized with respect to species bans, and exceptions should be made for those that are highly unlikely to form viable populations in natural areas. However, to date, the research does not exist that would place any nonsterile cultivar in this category.

To our knowledge, these lines of evidence have not been investigated through thorough experimentation on any cultivars of invasive species. An important first step for research is to consider the simplest scenario: If all cultivars of a species except the least fecund one are banned from sale, will the species still pose a significant risk of forming new populations in natural areas and becoming invasive? The answer to this question lies in measuring the vital rates of outcrossed offspring of the cultivar. Only when cultivars do not revert and when their population growth rate is low (close to or less than 1) should they be considered "safe." We note that completely sterile (female sterile) cultivars can be considered safe without any further investigation. However, we would urge caution in describing self-incompatible cultivars or cultivars that are male but not female sterile as safe. As has been demonstrated in purple loosestrife (*Lythrum salicaria*), these cultivars can set copious seed if they are planted in proximity to other cultivars or feral populations (Anderson and Ascher 1993).

Whenever it is possible, efforts should be focused on creating completely sterile cultivars. Such efforts are underway for some taxa, including *B. thunbergii* and *E. alatus* (Mark Brand, Department of Plant Science and Landscape Architecture, University of Connecticut, Storrs, personal communication, 24 May 2011). Li and colleagues (2004) described a transgenic approach to create "supersterile" cultivars that are both male and female sterile and parthenocarpic. Such molecular approaches to sterility have been applied to many crop plants but, to date, have not been developed for horticultural shrubs. Li and colleagues (2004) argued that supersterile cultivars are highly unlikely to ever reproduce sexually and that the risk of escape of transgenes is greatly reduced as well. Although developing sterility is time consuming and expensive, it provides an alternative to taking a species off the market that it difficult to replace.

Conclusions

We are concerned by the advertisement and marketing of "safe" cultivars of some of the most invasive woody plant species. These claims of their environmental safety are based on very limited demographic evidence that was focused on horticulturally produced plants rather than on their offspring. This article is intended to serve as a thought piece to present this problem to invasive species biologists, as well as to scientists and practitioners in the green industry. Our article highlights that even dramatic changes in some demographic vital rates—particularly, seed production—may be insufficient to reduce the population growth rate and therefore the invasive potential of a species. Furthermore, offspring of a horticulturally produced plant might look very different from their parent, either because they cross with other cultivars or a wild plant or because they do not breed true. We hope that this article will encourage researchers to consider all demographic vital rates and offspring combinations and will encourage a greater focus on the development of completely sterile plants or on emphasizing native species in horticulture.

Acknowledgments

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