Development and Evaluation of Landscape Plant Cultivars with Reduced Fertility to Minimize Potential Invasiveness[1]

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Abstract

While only a small portion of introduced species naturalize, and even fewer become invasive, those that do may alter ecosystems and disrupt natural plant communities. Recognizing that many non-native landscape plants are valuable commodities that provide important ecosystem services, enhance property values, and improve our quality of life, there is strong justification for developing cultivars with low reproductive fertility to prevent further distribution. This report reviews approaches for developing and evaluating low-fertility landscape cultivars to minimize self-sowing, weediness, range expansion, and potential invasiveness with recommended approaches, guidelines, and policy. Specific conclusions and recommendations include:

1. Selecting and developing cultivars with reduced fertility is a viable approach for maintaining economic, environmental, and aesthetic benefits of important landscape crops while minimizing potential invasiveness.
2. A $\geq$ 98% reduction in fertility, compared to fertile controls, is an achievable and practical criterion for accepting low-fertility cultivars as alternatives to potentially invasive, sexually reproducing plants.
3. Regulations of potentially invasive plants should include exclusions and provisions to allow for the continued production of cultivars with documented low reproductive fertility.

Index words: assessment, fecundity, noninvasiveness, plant breeding, reproductive biology, weediness.

Significance to the Horticulture Industry

Plant breeders continue to work on developing low fertility, seedless, non-invasive cultivars of selected taxa to minimize self-sowing and establishment of potentially weedy but valuable cultivars. Other benefits of these approaches can include enhanced flowering and re-blooming, reduced fruit litter, and reduced pollen allergens. However, specific questions often arise in this process, including: 1) what approaches can be used to develop low fertility cultivars, 2) how is reproductive fertility best evaluated for stability of expression over years and locations, 3) what level(s) of infertility are sufficient, and 4) how should policy and regulation accommodate these cultivars? This report reviews approaches for developing and evaluating low-fertility landscape cultivars to minimize self-sowing, weediness, range expansion, and potential invasiveness with recommended approaches, guidelines, and policy.

Introduction

Humans have been selecting, cultivating, and distributing plants worldwide for over 12,000 years, beginning with the Neolithic period and the dawn of civilization (Edwards 2020). The ongoing domestication of plants has transformed our crops, food supply, gardens, and landscapes, while improving our quality of life in many positive and profound ways. While most introduced plants have not been problematic, only a small portion of non-native species have naturalized (internationally about 4% of the global flora [van Kleunen et al. 2018]) and even fewer have become invasive to the point of causing economic or environmental harm (Coombs et al. 2020, Simberloff 2009, Williamson and Fitter 1996a). The presence and naturalization of a non-native species does not necessarily demonstrate harm, and in some cases introduced plants can provide positive ecosystem services (e.g., erosion control, reduced stormwater runoff, pollinator services, wildlife food, habitat, and cover, etc.) and enhanced biodiversity (species richness), particularly in urban and disturbed environments (Lefebvre et al. 2024, Sax et al. 2022, Schlaepfer et al. 2011, Sladonja, et al. 2018). In other cases, however, non-native species may have

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negative impacts on ecosystem processes, native community composition, and ecology (Mack et al. 2000, Liu et al. 2025). Beyond environmental impacts, invasive plants can cause economic harm, including agricultural losses and costs to manage invasive populations and remedy damage (Fantle-Lepczyk et al. 2022, Pimentel et al. 2005). Likewise, native species can spread to the point that they cause harm similar to non-natives and are sometimes referred to as invasive (Anderson et al. 2021), though use of this term is often reserved for non-native plants.

Reactive approaches to eradicating invasive species, such as chemical, mechanical, and biological control, are time consuming, destructive, and costly. Alternatively, preventative methods that help ensure new introductions are not at risk of becoming invasive are more efficient. In addition to more careful screening and selection of plants for sale (avoiding species and cultivars with known invasive properties), conventional and new biotechnologies can be employed to select and develop infertile cultivars (Drew et al. 2010, Ranney 2004, Ranney et al. 2010, Vining et al. 2012). In situations where economically important non-native plants are problematic, development of low fertility or sterile (seedless) cultivars can be an ideal alternative. This solution-driven approach allows for the benefits of these plants to be appreciated while minimizing potential negative impacts. Plant breeders continue to work on developing low fertility, seedless, non-invasive cultivars of selected taxa to minimize self-sowing and establishment of potentially weedy but valuable cultivars. Other benefits of these approaches can include enhanced flowering and re-blooming, reduced fruit litter, and reduced pollen allergens. However, specific questions often arise in this process, including: 1) what approaches can be used to develop low fertility cultivars, 2) how is reproductive fertility best evaluated for stability of expression over years and locations, 3) what level(s) of infertility are sufficient, and 4) how should policy and regulation accommodate these cultivars?

Approaches for Developing Low Fertility Landscape Cultivars

A. Naturally occurring, non-flowering, infertile, or fruitless/seedless plants. Infertile or sterile plants can periodically arise naturally, though the challenge is finding them as well as assuring that the infertility is not due to reproductive isolation or lack of pollen sources (Anderson and Ascher 1993). Reproduction is a complicated process, and different genetic combinations or random mutations can sometimes result in reduced fertility or sterility. Many taxa have been identified that typically either do not flower or fail to produce fruit/seeds, though not all have been formally evaluated (Table 1). In some cases, individual branches on these mostly infertile plants may sometimes produce some fruit, so stability needs to be evaluated and in most cases the mechanism(s) for infertility in these plants is not known. In dioecious species, the simple selection of males can prevent seed production (e.g., *Cortaderia selloana* Asch. & Graebn., *Ginkgo biloba* L., and *Pistacia chinensis* Bunge).

B. Flower architecture. Selection and development of plants with extra (supernumerary, petalody) petals, often referred to as “double” flowers, can result in reduced fertility. Regulatory and homeotic genes that result in additional petals often reduce the development of stamens, pistils, carpels, and ultimately reduce fertility (Pu and Xu 2022). Examples of this phenomena are evident in many horticultural crops across diverse taxonomic groups (Table 1).

C. Wide hybridization. Hybridization between distantly related taxa (e.g., interspecific, intergeneric) can result in desirable plants with a combination of valuable traits. In many cases, these wide hybrids have reduced fertility that can result from dissimilarities of the parental chromosomes, resulting in meiotic failure due to incongruity (Anderson et al. 1996). Examples of infertility within wide hybrids are found among a diverse taxa of woody landscape plants (Table 1). In rare events, some of these hybrids (e.g., *Cornus* ×*rutgersensis* Mattera, T. Molnar & Struwe) have produced infrequent, but viable seeds (Ranney, unpublished data, Mills River, NC). Genetic distance between parents is a critical factor in determining not only the compatibility of parents but also the likelihood or degree of hybrid sterility/fertility reduction in resulting progeny (Kuligowska et al., 2016).

D. Anisoploids/Polyploids. The selection and development of plants with an odd number of complete sets of chromosomes (anisoploids) generally results in greatly reduced fertility (Wang et al. 2016). Ploidy manipulation to reduce fertility (triploidy) is a proven technology that is cost-effective, has good public acceptance, and can be done simultaneously to develop seedless cultivars while improving pest resistance, adaptability, and overall commercial potential. This is a longstanding and common technique that resulted in seedless food crops such as *Musa* L. (Simmonds 1960), *Citrullus* Forssk. (Kihara 1951), and some cultivars of *Vitus* L. (Ji et al. 2013). However, anisoploids are not always completely infertile, require testing before introduction, and some taxa may, on occasion, produce viable offspring. This may occur through chromosome elimination, apomixis, and unreduced and/or functional aneuploid gametes (Asker and Jerling 2017, Czarnecki II and Deng 2020, Yao et al. 2024, Phillips et al. 2016, Ranney et al. 2004). In some cases, the development of induced autopolyploids with an even number of complete chromosome sets (euploid) can also compromise fertility, such as in *Berberis thunbergii* DC. autotetraploids (Brand and Durocher 2022), *Hibiscus syriacus* L. ‘DVPazurri’, which is a hexaploid compared to the standard tetraploid cytotype (Lattier and Contreras 2022), and the tetraploid cultivars *Ruellia simplex* C. Wright ‘Mayan Purple’ and ‘Mayan White’ (Freyre et al. 2012b). Some breeding has used a combination of wide hybridization and interploidy crosses to yield hybrid anisoploids (Table 1). Like infraspecific anisoploids, these hybrids with uneven ploidy also can exhibit a range of fertility, thus require testing to confirm necessary reduction in female fertility.

E. Mutagenesis. Use of chemical (colchicine, trifluralin, EMS or ethyl methanesulfonate) or physical mutagens

Table 1. Examples of plants bred, selected, or identified for reduced fertility, the method (mode of reduced fertility) used, and citations.

Taxon	Mode of reduced fertility	Citation
Acer platanoides L.	Triploid	Contreras and Hoskins 2020
Acer tataricum L.	Triploid	Contreras and Hoskins 2020
Aesculus hippocastanum L. 'Bowmanii'	Double flowers	Dirr 2009
Berberis ×*mentorensis*	Wide hybridization	Brand et al. 2012
Berberis 'NCBX1'	Wide hybridization	Ranney 2018
Berberis ×*ottawensis* 'Criruzam', 'Silver Mile'	Wide hybridization	Brand et al. 2012
Berberis thunbergii 'UCONNBTB039', 'UCONNBTB048', UCONNBTB113', 'UCONNBTCP4N'	Polyploidy	Brand and Durocher 2022
Berberis thunbergii 'Aurea', 'Bagatelle', 'Gentry Cultivar', 'Golden Devine', 'Inermis', 'J.N. Variegated', 'Lime Glow', 'Maria', 'Monlers', 'Red Chief', 'Talago'	Naturally occurring[z]	Brand et al. 2012
Berberis thunbergii 'NCBT1'	Mutation	Ranney 2019a
Bougainvillea Spach 'Mrs. McClean', 'President Roosevelt', 'Shubhra'	Wide hybridization	Zadoo et al. 1975
Buddleja 'Blue Chip', 'Blue Chip Jr.', 'Pink Micro Chip'	Wide hybridization	Renfro et al. 2007, Still and Contreras 2024, Werner and Snelling 2009, Werner 2016a, 2016b
Buddleja 'Asian Moon'	Triploid & wide hybridization	Renfro et al. 2007
Camellia L. 'Fragrant Pink'	Wide hybridization	Ackerman and Dermen 1972
Camellia japonica Wall. 'ChiDan', 'Jinpanlizhi'	Double flowers	Li et al. 2017
Campsis Lour. 'Chastity'	Triploid	Oates et al. 2014
Catalpa bignoniodes Walter 'Nana'	Naturally occurring	Dirr 2009
Catalpa ×*erubescens* Carrière 'Victoria'	Double flowers	Dirr 2009
Chaenomeles Lindl. 'Scarlet Storm', 'Orange Storm', 'Pink Storm', and 'NCCS4'	Double flowers	Ranney 2010a, 2010b, 2010c, Ranney 2019b
×*Chitalpa tashkentensis* T.S. Elias & Wisura	Wide hybridization	Olsen et al. 2006b
Cornus ×*elwinortonii* Mattera, T. Molnar & Struwe	Wide hybridization	Mattera et al. 2015
Cornus officinalis Siebold & Zucc. 'Spring Glow'	Naturally occurring	Shearer and Ranney 2013
Cornus ×*rutgersensis*	Wide hybridization	Mattera et al. 2015
Cornus sanguinea Walter 'Compressa'	Naturally occurring	Dirr 2009
×*Gordlinia grandiflora* Ranney & Fantz	Wide hybridization	Ranney and Fantz 2006
Hibiscus syriacus 'Ardens', 'Blushing Bride', 'Collie Mullins'	Double flowers	Lattier and Contreras 2022
Hibiscus syriacus 'ORSTHIB5x1' (5*x*),	Anisoploid	Contreras 2024
Hypericum androsaemum 'Matisse', 'Picasso', 'Pollock'	Triploid	Olsen, et al. 2006a, Ranney 2010d, Trueblood et al. 2010
Lagerstroemia L. 'Princess'	Wide hybridization	Pounders et al. 2007
Lantana camara 'Athens Rose'	Triploid	Czarnecki II and Deng 2020
Ligustrum sinense 'Sunshine'	Naturally occurring	Rycyna et al. 2024
Liquidambar styraciflura L. 'Rotundiloba'	Naturally occurring	Burns 1989
×*Mahoberberis aquisargenti* H. Jensen	Wide hybridization	Wyman 1958
Miscanthus ×*giganteus* J.M. Greef & Deuter ex Hodk. & Renvoize H2015-004-096[y]	Triploid & wide hybridization	Touchell et al. 2024
Miscanthus sinensis H2008-091-004[y]	Triploid	Rounsaville et al. 2011
Miscanthus sinensis 'M77'	Mutation	Hanna and Schwartz 2020
Nandina domestica 'AKA', 'Chime', 'Filamentosa', 'Firepower', Firestorm', 'Greray', 'Lemon-Lime', 'Moon Bay', 'SEIKA'	Naturally occurring	Wilson et al. 2021
Ornithogalum candicans (Baker) J.C.Manning & Goldblatt [syn. *Galtonia candicans* (Baker) Decne.][x]	Mutation	Contreras and Shearer 2020
Prunus campanulata Maxim. 'Abigail Adams'	Double flowers	Dirr and Warren 2019
Prunus caroliniana (Mill.) Aiton	Mutation	Ruter 2019
Prunus serrulata Lindl. 'Amanogawa', 'Kanzan', 'Kiku-shidare-zakura', 'Pink Perfection', 'Royal Burgundy'	Double flowers	Dirr and Warren 2019
Punica granatum L. 'Double Flower'	Double flowers	Babu 2010
Pyrus ×*triploida* Ranney 'NCPX2'	Triploid & wide hybridization	Phillips et al. 2016, Ranney 2019d
Rhododendron 'Fragrant Affinity'	Wide hybridization	Contreras et al. 2007
Rosa L. 'Mermaid', 'Pink Surprise'	Wide hybridization	Kermani et al. 2003
Ruellia simplex 'Mayan Pink', 'Mayan Purple', 'Mayan White', 'Mayan Compact Purple'	Polyploidy	Freyre and Wilson 2014, Freyre et al. 2012a, 2012b, Freyre et al. 2016
×*Schimlinia floribunda* Ranney & Fantz	Wide hybridization	Ranney et al. 2003
Spiraea japonica L.f. (syn. *S.* ×*bumalda* Burv.) 'Crispa', 'Dart's Red', 'Neon Flash'	Naturally occurring[w]	Wilson and Hoch 2009
Spiraea 'NCSX2'	Triploid[v]	Ranney 2019c
Viburnum macrocephalum Fortune	Double flowers	Dirr 2009
Viburnum opulus L. 'Sterile' (syn. 'Roseum')	Double flowers	Dirr 2009

[z] Many of these cultivars may have resulted from breeding; however, there is no information on a method commonly used to reduce fertility such as hybridization, ploidy manipulation, or mutagenesis.

[y] Accessions of *Miscanthus* in the Mountain Crop Improvement® breeding program.

[x] Several accessions of *Ornithogalum candicans* (syn. *Galtonia candicans*) in the Oregon State University Ornamental Plant Breeding program that received 0.4% EMS (ethylmethane sulfonate) treatment have yet to set seeds. Contreras and Shearer (2020) provide means for treatments but do not reference specific accessions or any selected cultivars.

[w] All three appear to have arisen as branch sports from 'Anthony Waterer' but origins are unclear (Dirr 2009).

[v] The female parent of 'NCSX2' is an interspecific hybrid; however, the basis for seedlessness in the cultivar appears to be its triploid chromosome complement.

(gamma irradiation) are longstanding methods to induce variations that can be exploited for crop improvement (Melsen et al. 2021). Mutation breeding, particularly gamma irradiation, has been used to develop seedless *Citrus* L. (Cimen et al. 2021, Latado et al. 2006, Tang et al. 1995, Vardi et al. 2008) and *Vitis* (Tetali et al., 2020). Other studies have observed mutation treatments to reduce or potentially eliminate fertility in landscape plants, while also sometimes changing ornamental traits or performance (Table 1).

F. Biotechnology approaches. New plant biotechnology offers tremendous potential for crop improvement, including the manipulation of plant reproductive pathways (Li et al. 2004, Vining et al. 2012). These approaches include a variety of strategies to prevent flower, gamete, pollen, and/or seed development. Genetic transformation can produce genetic ablation whereby a floral promoter drives a cytotoxic protein to disrupt floral tissue development (Brunner et al. 2007). Alternatively, gene suppression can prevent the development of reproductive structures or physiological processes (e.g., meiosis). Gene editing to alter plant reproduction can use zinc finger nucleases (ZFN), transcription activator-like effector nuclease (TALEN) (Bogdanove and Voytas 2011), and more recently CRISPR (clustered regularly interspaced short palindromic repeat) with associated nucleases (e.g., Cas9) systems (Cheng et al. 2023, Nagle et al. 2023). Research is underway to use gene editing to create infertile cultivars of *Miscanthus* Andersson and *Tripidium* H. Scholz (Ranney unpublished) and related gene drive systems [genetic elements that promote spread throughout a population at greater than standard frequency (Bier 2021)] to develop a genetic biocontrol for *Tanacetum vulgare* L. (Croghan et al. 2023). Alternatively, manipulation of DNA methylation can result in floral gene silencing (Liu and Li 2011). The potential of these approaches is very appealing in that plant reproductive pathways can be suppressed with precision in elite, high-value cultivars without incurring other changes that would occur through sexual reproductive cycles or random mutagenesis. However, these approaches are technically complicated and require integrated research teams with expertise in genomics, plant transformation, biotechnology, and bioinformatics for application.

Evaluation of Plant Invasiveness and Reproductive Fertility

The propensity for plants to disperse, self-sow, establish, expand their range, and naturalize, sometimes to the point of being invasive, is dependent on complex interactions among biological, environmental, human, and ecological factors (Rejmanek 2000, Richardson et al. 2000). Historically, botanists sought to define a set of traits that improve the colonizing ability of a population. Baker (1965, 1974) conceptualized this as the "ideal weed". However, no single gene has been found for invasiveness (Anderson et al. 2006, Galatowitsch et al. 1999). While not all successful colonizers have the "ideal weed" traits, Baker's list has remained useful for generations of weed scientists and invasion biologists (Williamson and Fitter 1996b). In particular, two traits have risen to prominence as important traits in invasive plants. First, the maxim known as Baker's Law states that non-native plants will be more likely to establish if they can self-propagate (either by asexual reproduction or selfing), since newly established propagules will lack mates. Secondly, propagule pressure, often defined as the total number of individuals introduced at a given location (Williamson and Fitter 1996b), is a major determinant of invasion success.

More recently, various approaches have been utilized to A) study population dynamics and theoretically model these processes, B) develop invasive species assessments that either preemptively predict which plants might become weedy or invasive before their introduction and/or apply more regional evaluations that attempt to gauge the extent of established plants, potential to spread, and subsequent impacts, or C) evaluate infraspecific cultivars of known invasive species selected for low fertility to be exempted from the invasive standing of their wild-type resident taxon. Herein, we summarize some of these approaches to highlight how fertility reduction can complement invasive risk assessments.

A. Study of population dynamics and modeling. Since each invasion is unique, determining common biological and anthropogenic factors that lead to invasion success requires multifactor demographic models. Matrix population models are frequently used to model population dynamics and can be used to estimate population growth rate, λ (Caswell 2001). Values of λ indicate whether populations are growing (>1), static ($=1$), or declining (<1) over time. The most basic versions of these models often assume a constant environment (deterministic) independent of plant density. As such, these models are not generally suited for forecasting but have utility as a comparative tool for evaluating how changes in specific life cycle parameters, like fertility/fecundity, may impact population growth rate (Crone et al. 2011).

More elaborate models, including classic diffusion, stratified diffusion, gravity, stage-based integrodifference equation, simulation, percolation, and network models, generally broaden the scope of analysis to include components that better account for successful establishment, spread, and range expansion (Caplat et al. 2012, Hastings et al. 2005, Shigesada et al. 1995, Simberloff 2009). While there are exceptions to every rule in invasion biology, propagule pressure is widely appreciated to be a primary determinant of the successful establishment and invasion of non-native species in natural areas (Colautti et al. 2006, Lockwood et al. 2009, Martínez-Ghersa and Ghersa 2006, Pyšek et al. 2009, Simberloff 2009, Von Holle and Simberloff 2005). Jagodziński et al. (2019) and Vanhellemont et al. (2009) further found that low levels of propagule pressure were sufficient to limit the invasiveness of *Prunus serotina* Ehrh., even in disturbed, invasible plots. Not surprisingly, reducing this influx (or rain) of propagules through reduced fertility/fecundity of cultivated plants minimizes the potential for successful dispersal, establishment, and invasion.

B. Invasive species assessment systems. Invasive species assessment models assess the potential invasiveness of plant species and/or the associated environmental impact of introduced plants as they establish and spread. These systems generally utilize a series of weighted questions related to weed risk and impacts to establish recommendations. Protocols typically have a scoring system that leads to a particular recommendation for each species ranging from "not a problem", "caution", to "invasive and not recommended for use". Some assessment systems are designed to preemptively predict which plants might become weedy or invasive before their introduction (Pheloung et al. 1999, Conser et al. 2015). These predictive tools generally do not account for regionality or variation in the environment. In reality, most plant species with known human utility or value have already been distributed globally, often over decades or centuries. Hence, we are generally less concerned about predicting the potential for invasiveness and more concerned about identifying and evaluating existing problematic plants and limiting further introduction and spread in a specific region. Furthermore, most of these assessment systems were developed for species without considering the intentional selection or development of low fertility cultivars.

Several invasive assessment systems have been developed with a broader scope that includes assessing ecological impacts of established plants, distribution and abundance, range expansion, management difficulty, economic value, and/or specific consideration of low fertility cultivars (Morse et al. 2004, Trueblood 2009). Some systems have been developed for specific states, including Arizona (AZ-WIPWG 2005), California (Cal-IPC 2024), Florida (Lieurance and Flory 2020), Michigan (Schutzki et al. 2008), North Carolina (Trueblood 2009), and Ohio (Ohio Invasive Plants Council 2020). Although these systems are useful to broadly identify potentially problematic species, unless they specifically address fertility and reproductive capacity of individual genotypes, they have little relevance or utility for evaluating the selection or development of low fertility cultivars as valuable alternatives to weedy genotypes. For example, Wilson and Deng (2023) reported on seven taxa of ornamentals with low fertility alternatives, yet the invasive ranking of the resident form (or wild-type) of these taxa are listed by the Florida Invasive Species Council (FISC), Florida Department of Agriculture and Consumer Services (FDACS), and/or the University of Florida Institute of Food and Agricultural Sciences (UF IFAS) Status Assessment without regard for cultivars and selections that have low to no fruiting. Using species assessments alone does not capture these low-fertility cultivars identified using empirical evaluation. Datta et al. (2020) propose a list of six practical questions that address specific traits of cultivars being evaluated. These questions and the general approach recommended are similar to recommendations of Chetty et al. (2024) and align with the current situation in which cultivars of a banned species are assumed invasive until evaluated and proven otherwise.

C. Empirical evaluations of reproductive fertility of individual cultivars. When intentionally selecting or developing low fertility landscape cultivars, empirically evaluating specific clones' reproductive fertility is important. Some cultivars may have traits that would suggest a reduction in fertility, such as increased petaloid stamens, alteration in ploidy level, or hybrid pedigrees. However, each of these has been found to result in variable reductions in fertility. Conversely, there are examples of species that are regarded as invasive based on species assessment systems, but specific cultivars have low fertility based on empirical data (such as *Nandina domestica* Thunb.; Wilson et al. 2021).

Various studies have evaluated the reproductive fertility of specific cultivars. Czarnecki and Deng (2020) evaluated 26 *Lantana camara* L. commercial varieties and six experimental lines exhibiting high female fertility variability among diploid, triploid, and tetraploid cytotypes. Generally, diploid and tetraploid plants were highly fertile, but some diploid plants were female sterile. Most triploid plants were female fertile due to the production of unreduced female gametes (UFG), but the two that did not produce UFG had the lowest fertility in the study, while all tetraploids were highly fertile. Triploid *Campsis* ×*tagliabueana* (Vis.) Rehder 'Chastity' produced only 0.008 seedlings per pollinated flower compared to 119 for *C. radicans* (L.) Seem., which is a 99.993% reduction (Oates et al. 2014). Phillips et al. (2016) evaluated the female fertility of hybrid flowering pears (*Pyrus* L.) and found that triploids ranged from 0% to 33.6% relative fertility compared to diploids. Interestingly, all plants, including diploids and triploids, were derived from hybrid pedigrees of varying complexities. Triploid *Miscanthus sinensis* Andersson cytotypes ranged from 0.7% to 49.2% fertility relative to the fertile diploid cultivar *M. sinensis* 'Zebrinus' (Rounsaville et al. 2011). This work demonstrates yet another taxon in which triploids show variable fertility even with the rare production of unreduced gametes. Cultivars of *Buddleja* L. with hybrid pedigrees and reportedly different ploidy levels showed highly varied seedling production (Still and Contreras 2024). Hybridity alone is a poor predictor of reduced fertility in butterfly bush, as hybrids were among the most fertile in both years of the study (e.g., 'Bosblink'). Due to varying base genome sizes, it was difficult to ascertain ploidy levels, so it remains unclear how ploidy level impacts fertility. However, breeding for reduced fertility in *Buddleja* is feasible, as 12 of 34 cultivars exhibited $\geq$98% reduction in fertility compared to the most fertile cultivar in both years. Additionally, open-pollinated seedlings derived from cultivars exhibited similar fertility to parents, with low-fertility cultivars remaining low fertility in the next generation (Still and Contreras 2024). Similar to *Buddleja*, Brand et al. (2012) evaluated 46 *Berberis* L. taxa and found that the interspecific hybrids *B. koreana* Palib. × *B. thunbergii* 'Bailsel' and 'Tara' were extremely fertile. On the other hand, *B.* ×*ottawensis* C.K. Schneid. ex Rehder 'Silver Mile' and 'Criruzam' along with *B.* ×*mentorensis* H. Schultz & Horvath ex L.M. Ames were infertile, thus providing more another example of the need for empirical study of specific cultivars (Brand et al. 2012). Their study provided an initial evaluation at three years after planting and then evaluated a subset after an additional four or five years. Ten cultivars with $\leq$ 2% fertility after the first evaluation compared to 'Sparkle' were evaluated in the extended observations. Of these, there was evidence that 'Bogozam' and 'Monry' increased slightly above the 2% threshold for fertility based on the observed fruit set and using prior data from their study, emphasizing the benefit from completing multiple evaluations over time or space (Brand et al. 2012). After 16 years of evaluation, the autotetraploid cultivars 'UCONNBTB039', 'UCONNBTB048', 'UCONNBTB113', and 'UCONNBTCP4N' did not change in fertility (Brand and Durocher 2022). This is important to note because the basis for low fertility in culitvars such as 'Bogozam' or 'Concorde' is unknown and may be tardiness to flower at their full potential due to a slow growth rate, whereas the modern cultivars referenced and introduced by Brand and Durocher (2022) were developed using ploidy manipulation. Trueblood et al. (2010) found that *Hypericum androsaemum* L. triploids had no measurable female fertility compared to highly fertile diploids. A similar conclusion was found for eight varieties of *Lantana montevidensis* Briq., which exhibited variable seed numbers and germination percentages based on ploidy level (Wilson et al. 2020). Triploid varieties of *L. montevidensis* commonly available in the US were not observed to fruit in landscape trials. However, a minimal amount of fruiting was observed when interplanted with a tetraploid variety collected from Australia. Rycyna et al. (2024) observed that *Ligustrum sinense* Lour. 'Sunshine' and *Ligustrum* L. 'NCLX1' privet cultivars produced no fruit when grown in northern and southern Florida compared to 'Variegatum', which produced nearly 3,000 fruits in northern Florida even though all cultivars are diploid. The basis for seedlessness in 'NCLX1' is hybridity, whereas 'Sunshine' generally does not flower (though rare reversions have been observed). Together, these studies emphasize the need to evaluate and document the fertility of individual cultivars to determine their actual reproductive capacity.

When a species has been banned in a state, cultivars often are treated as "guilty until proven innocent" where all entities (cultivars) of a species are banned without consideration for those that may present little or no threat of escape (Chetty et al. 2024). The burden then lies with the breeder or other interested party who is seeking exemption to prove the reduced level of fertility using robust evaluation methods such as we describe.

What Level of Fertility is Acceptable for Seedless Cultivars?

Based on theoretical models, some authors have suggested that highly infertile cultivars are not sufficient to be considered noninvasive, and only female sterile cultivars should be considered or allowed (Knight et al. 2011). Although absolute sterility is a desirable goal, this recommendation presents several problems. Although it is often possible to develop cultivars with greatly reduced fertility, the absolute lack of fertility can often be difficult to achieve due to the complexity of various reproductive pathways and mechanisms and necessitating extensive trialing over years and locations to ensure sterility expression. Also, it is challenging to prove "sterility", as it requires a negative claim based on evidence of absence and proof of non-existence, and the required burden of proof is subjective. Taking a more practical approach and knowing that propagule pressure is one of the most relevant factors driving invasion potential, a reduction in fertility and propagule pressure directly results in a reduction in self-sowing, weediness, colonization, establishment, and range expansion.

Various studies have attempted to model and estimate how reductions in fertility/fecundity might impact population dynamics. Knight et al. (2011) used data from published matrix population models to simulate how reducing fecundity could reduce population growth rates in established populations. Life history played an important role in how much fertility reduction may be required to facilitate population reduction. For most of the studied monocarpic herbs and grasses, the simulations predicted a reduction in fecundity of 30% to 95% would drive a population decline. In contrast, perennial plants required 75% or higher reductions to reduce population growth rate significantly. Shea and Kelly (1998) studied the biocontrol of *Carduus nutans* Boiss. ex Nyman, which is a monocarpic species but produces seeds that survive in the seed bank for up to 13 years, and found that in New Zealand, reducing viable seeds up to 69% would result in a reduced population growth rate. However, they cited studies in which population sizes were reduced when seed losses were as low as 35% (Shea and Kelly 1998). *Cytisus scoparius* (L.) Link is a long-lived, polycarpic perennial that can have many reproductive cycles over its lifetime and has persistent seeds. Sheppard et al. (2002) predicted the potential efficacy of biological control by seed-feeding insects for *C. scoparius* using a simulation model. In natural settings of New South Wales, Australia, they predicted a reduction in fertility of only 62% would be sufficient to suppress population growth over time. In contrast, populations in disturbed areas would require more than 97% reduction in viable seeds to facilitate management. To invade new areas, their simulations estimated that it would require a seed rain of 497 seeds$\cdot$m^{-2} for *C. scoparius* to invade disturbed exotic pastures and an astounding 2,360 seeds$\cdot$m^{-2} to invade native ecosystems. Using multiple models, Rees and Paynter (1997) estimated that a reduction of 75% in seed production would dramatically reduce the abundance of *C. scoparius*. In contrast, Parker (2000) constructed a simulation model for the west coast of North America that predicted it would take a 99.9% reduction in viable seeds in prairies to reduce population growth of *C. scoparius*. In contrast, a 70% reduction was sufficient to induce a population decline in urban settings. Invasion of the woody perennial *Rubus discolor* Weihe & Nees is often driven by clonal sprouting. However, Lambrecht-McDowell and Radosevich (2005) estimated that a 70% or more reduction in seedling establishment would lead to population decline.

Although many of these studies have researched how reducing fertility/fecundity may impact population growth rates, it is important to recognize that most of these studies are simulations that estimate what reductions would be required to reverse the growth rates of established populations. As stated previously, it is difficult to reduce established populations, and the goal of developing low-fertility landscape cultivars is to minimize seed production in cultivated plants to preemptively avoid self-sowing and potential spread to other areas. Any reduction in the fertility of landscape cultivars will similarly reduce the number of seedlings that might become established outside of cultivated areas and reduce the likelihood of colonization. Even if a small number of viable seeds are produced, the likelihood that they will be dispersed, germinate, and survive is exceedingly low (Williamson and Fitter 1996a). Evaluating the survival of viable seeds in natural settings is challenging and highly dependent on environmental conditions. As such, when evaluating cultivars, breeders typically use optimal artificial environments to evaluate germination potential that vastly overestimate survival under natural conditions. Still and Contreras (2024) in a *Buddleja* study estimated many millions of viable seedlings in greenhouse studies but field observations of natural sites and attempts to replicate in managed field plots have not shown nearly the same fecundity levels. Based on these ecological studies, empirical evidence, and practical applications, a reduction in female fertility of $\geq$ 98%, compared to fertile controls, is proposed as a reasonable and achievable goal that would severely reduce reseeding and establishment of potentially invasive, sexually reproducing plants.

Although any future offspring's fertility cannot necessarily be predicted, there is evidence in butterfly bush (Still and Contreras, 2024) that the rare progeny produced from low fertility cultivars generally remains low in the subsequent generation. This is particularly true with triploid-derived aneuploids that often have low fertility and fitness (Phillips et al. 2016, Rounsaville et al. 2011, Ramsey and Schemske 1998). However, over multiple generations, fertility could potentially increase. For example, triploids can sometimes produce a mix of gametes (including x, $2x$, and $3x$) that can produce diploid or tetraploid offspring, especially when crossed with diploid progenitors (Li et al. 2022). While this phenomenon is typically rare, these offspring may have greater fertility.

When is Male Fertility Also Important?

In the development of seedless cultivars of invasive species, it sometimes may be desirable to reduce pollen viability. Male fertility could be an issue if an introduced plant readily hybridizes with closely related native species such that the resulting hybrids exhibit greater fitness over the native species to the point of outcompeting, though one could argue that this does not necessarily result in a loss of genetic- or bio-diversity and could benefit inbred populations. Regardless, some projects have addressed male fertility. For example, due to the invasive nature of *Stachytarpheta cayenennsis* (Rich.) Vahl, Wilson et al. (2009) and Qian et al. (2021), examined plant morphology, seed viability, ploidy levels, and pollen viability of commercially available porterweed selections. They found specific selections to be female sterile but not pollen sterile. As a result, new hybrid cultivar development was directed at not only improving ornamental traits but ensuring plants were incapable of spreading by seed and unlikely to cross-pollinate with the Florida native *S. jamaicensis* (L.) Vahl (Parrish et al. 2025). Similar circumstances have been observed for other new cultivar development for ornamentals that share invasive and native genera, such as *Lantana* L. (Deng et al., 2020), and *Ruellia* L. (Freyre et al. 2012a). However, in cases where there is no native congener with which to hybridize, male fertility is of little importance compared to reducing female fertility. Propagule pressure is the driving force for range expansion, so reduced female fertility is paramount in minimizing plants' escape. Cultivars with sufficiently low female fertility will minimize potential invasiveness regardless of male fertility. This also applies to dioecious species. Based on the evidence, the introduction of male cultivars presents little or no ecological threat. Recently, *Ilex crenata* Thunb. was proposed for regulation in New England. This is a dioecious species introduced from Japan. While there are native congeners in the US, they are distantly related (Yao et al. 2021), with no spontaneous hybrids with native species reported even though it was introduced into the United States in 1898 and many millions of an array of cultivars have been produced and planted since that time (Dirr 2009). So, while the idea of gene flow from cultivated male selections to wild females should not be completely dismissed, male fertility is of relatively little importance in reducing the escape of plants from cultivated areas compared to reducing female fertility.

Regulation

The United States Department of Agriculture (USDA) Animal Plant Health Inspection Service (APHIS) maintains the federal noxious weed list prohibiting the planting of listed species. In 2001, the National Invasive Species Council was established and included a management plan that has since been updated for 2008-2012 and 2016-2018. Each state maintains its own list of noxious weeds in addition to those identified by APHIS, each of which is regulated within the state. However, each state may have different bodies or organizations involved in classifying and regulating species. There can be conflicting information provided by non-governmental organizations (NGOs) that may confuse growers and consumers (Anderson et al. 2021, Drew et al. 2010).

Additionally, it can be difficult to know where to get information or understand which body regulates cultivars. In California, the Invasive Species Council of California (ISCC), an interagency council, appointed the California Invasive Species Advisory Committee (CISAC) to make recommendations for action plans. In its by-laws, the ISCC appears tasked with recommendations and action plans, but it is unclear what regulatory authority it holds. It is unclear if any cultivar exemptions are in place in CA, but if so, they will presumably be determined by the California Department of Food and Agriculture (CDFA). Connecticut and other New England states have been proactive in regulating nursery crops that have escaped cultivation. Connecticut has a provision in their list of invasive species (https://cipwg.uconn.edu/invasive_plant_list/) for non-invasive cultivars that states "that the species, although shown by scientific evaluation to be invasive, has cultivars that have not been evaluated for invasive characteristics. Further research may determine whether individual cultivars are potentially invasive." This language provides no clear threshold for growers or breeders to meet. Some states have dedicated advisory groups that may work directly with states' departments of agriculture, such as the Massachusetts Invasive Plant Advisory Group (https://massnrc.org/mipag/) and Oregon in which a new committee has been assembled that includes staff from the Oregon Department of Agriculture, scientists from Oregon State

University (both breeders and ecologists), an ecologist from the NGO Institute for Applied Ecology (https://applieddeco.org/), and representatives from the Oregon Association of Nurseries (https://www.oan.org/). Some states have acted to regulate species based on empirical data, such as the case with *Berberis thunbergii* in Minnesota and Wisconsin, where they banned the species and 25 cultivars found to produce large amounts of fruit; however, their regulations allowed for low fruiting cultivars (Brand 2016).

It is concerning that there are cases in which evidence is strong for cultivars with low fertility, yet underlying reasons specific to the growth habit of their parents or the random occurrence of small amount of seeds prevent their recommended use and/or release (Wilson and Deng 2023). This may be related to the problem identified by Brand (2016) that we have observed in many states – that when there are existing plant bans, reversal can be more challenging than the original regulation, especially in cases where rules were legislatively imposed. Proactive and reasonable regulation or legislation based on data can streamline the process.

Even though plants may be uniquely problematic to a particular region, the same concerns and questions arise across all states grappling with this issue. As more seedless or low fertility cultivars are introduced, we need a common language and assessment tools to use across state lines. The nursery industry is one of interstate commerce. For example, the State of Oregon ships nearly 80% of its nursery stock out of state, including the entire continental US. Therefore, regulation in a single state may impact many economically. This has led to confusion for breeders, growers, consumers, and regulators. During our discussions, common questions arise, including “How do you evaluate invasiveness?”, “How do you evaluate fertility?” “What are the criteria for making decisions?”, and “Are there any recommended guidelines for doing this?”. These and similar questions require standardization across the US to allow breeders, growers, retailers, regulators, and consumers to have confidence in how the issue of nursery crops bred for low fertility is handled. A wide range of invasive plant risk assessment protocols has been developed. However, these often differ considerably in what criteria they evaluate, what stage of the invasion process they focus on, and how risks are weighted. In the United States, differences in subjective risk assessments often produce different results for the same taxa (Bradley et al. 2022). We do not propose a single one-size-fits-all style regulation. However, we hope to establish practical guidelines that allow plants of different functional types in different regions to be evaluated for fertility in a cost effective and timely manner.

Policy Recommendations Related to Potentially Invasive Nursery Crops

1. The goal of relevant policy or regulation should be to minimize the future introduction of weedy and invasive species while not impacting the production and sale of plants for which sufficient reduction in fertility has been documented or are otherwise deemed to present little or no environmental or economic harm.
2. Any restrictions on potentially invasive species should allow for low fertility, seedless cultivars. Compared to fertile cultivars, we recommend that a $\geq$98% documented reduction in female fertility is a practical and achievable threshold for accepting low fertility cultivars of potentially invasive, sexually reproducing plants. Plants known to or observed to invade through vegetative means should be considered separately.
3. Consider exemptions based on data gathered as outlined below and have a panel to evaluate data for scientific rigor. We recommend that the panel be diverse in composition and include geneticists, horticulturists, and ecologists with government, university, industry and regulatory representatives.
4. Review lists annually and maintain a single web-based source for information that clarifies the state policy for these crops.

Recommended Protocols for Evaluating Plant Fertility

Although there are various approaches for selecting and developing low-fertility cultivars, it is important to quantify and document relative fertility. For example, while some interspecific hybrids exhibit virtually no fertility (Contreras et al. 2007, Olsen et al. 2006b), others may exhibit little or no reduction in seed and seedling production (Still and Contreras 2024). Similarly, triploids or plants exhibiting other uneven ploidies (e.g., pentaploid) frequently have greatly reduced fertility, but this varies, even within a species or genus (Phillips et al. 2016; Rounsaville et al., 2011). In other cases, misinformation or confusion has led to the suggestion that some plants were seedless when they were not. For instance, when *Pyrus calleryana* Decne. ‘Bradford’ was initially introduced, it rarely produced fruit when isolated from other pear trees due to reproductive self-incompatibility, leading some people to believe it was sterile. Over time, when other genotypes were introduced, allowing for cross pollination, ‘Bradford’ trees produced viable seeds, escaped and have naturalized extensively in the eastern US. However, it should be made clear that ‘Bradford’ was never developed, selected, or introduced as a seedless cultivar. On the contrary, the original release notice and subsequent articles referenced its fruit and fertility (Ackerman and Creech 1966, Parker 1960, Vincent 2005, Whitehouse et al. 1963). Unfortunately, this type of confusion erodes confidence in modern breeding methods. However, these examples illustrate the need for valid testing of low-fertility cultivars of weedy species.

Although many researchers and private breeders have evaluated reproductive fertility in specific cultivars, no standardized protocols or recommendations exist. Evaluating fertility should include a sound experimental design, with replication, appropriate controls, and suitable pollination conditions including cross pollination. The overall goal is to evaluate fertility under favorable conditions for pollination and reproduction. Specific recommendations for plants may vary in methods, duration, or location based on life cycle or other factors. However, some factors described below apply across plant types.

Experimental Conditions and Procedures

Studies should have a valid experimental design that aims to test the likelihood that new cultivars have less than 98% reduction in fertility over fertile cultivars. In most cases, a simple completely randomized design or randomized complete block design with a minimum of 5-6 replications across years and locations is sufficient. As weather and environment can be factors in pollination and fruit set, it is desirable to repeat the experiment over at least two years of flowering or, alternatively, in two different locations in the same year. In addition to natural pollination, supplemental hand pollination can be done, particularly if an experiment is done in a greenhouse. Hand pollinations can use a mixture of pollen from multiple male parents to ensure good cross pollination and avoid issues of incompatibility due to shared *S*-alleles, for example. Suitable, fertile cultivars should be included as controls or market comparisons. We recommend selecting controls that represent the industry standards found in commerce and are known to be male and female fertile. Such controls confirm that studies were completed in an environment and under conditions favorable for pollination and reproduction of the taxon under investigation by producing viable seeds in sufficient amounts. Environmental variability is a proven factor in evaluating fertility. However, this can be reduced by using common garden studies as comparisons. Whereas it may take decades and unreasonable expense to evaluate the fertility of a tree species among all environments where it may be produced and distributed for planting, common garden studies using putative seedless cultivars alongside noted fertile selections can be used to establish how fertile a cultivar is in a shorter time and at less cost. While the absolute value of seedlings produced may vary among environments, the relative fertility will provide a relative comparison. For example, a study on *Acer ginnala* Maxim. conducted in Oregon with proper controls may have different absolute fertility levels than a comparable study in Minnesota, but the relative fertility of plants is comparable. Finally, if plants are self-infertile, at least two highly fertile cultivars/genotypes should be included as pollenizers that have overlapping bloom times (phenology) to flower simultaneously, with cultivars being tested to ensure the presence of fertile and compatible pollen. In situations where study plants have different euploid levels (e.g., diploid, tetraploid), pollenizers with the same ploidy should be included.

Data Collection

To measure floriferousness, a researcher may count the number of flowers or compound inflorescences on each plant, or a subsample of branches, representing the greatest flower density on that plant. If measuring the number of flowers or inflorescences per plant, the evaluators can measure an index of plant size or approximate volume (e.g., cylinder: plant height × π × radius^2; dome: (π × base radius^3 × 2/3). If measuring the number of flowers on a subsample of branches, evaluators can measure the total length of the subsample of branches for that plant.

When fruit is ripe, it should be collected and counted from the entire plant or subsample of marked branches or inflorescences, then the total number of seeds can be extracted and counted from either the entire plant or subsample of marked branches or inflorescences. For some plants, like *Rhododendron* L., *Buddleja*, and *Spiraea* L., counting all the seeds may not be feasible. In cases like this, fertility can be expressed as the number of germinated seedlings per plant, subsample, or inflorescence compared to controls.

The viability of seeds should be assessed. In some cases, as with fertile controls, this can be a subsample, such as 100-300 seeds per experimental unit. As opposed to tetrazolium staining, the percentage germination of seedlings is a preferred method for evaluating viability after providing any necessary stratification or scarification treatments. In the case of triploids, if seedlings are obtained, it is desirable, but not essential, to test the genome sizes of the parents and seedlings to determine if the seedlings are euploid (and potentially apomictic) or aneuploid (often highly abnormal).

For situations where it is desirable to measure male fertility, such as in cases where there are native congeneric species for which outcrossing is a concern, pollen germination percentage and pollen staining (Contreras et al. 2007, Olsen et al. 2006b) can give an indication of pollen viability but may overestimate viability. Using test plants as pollen parents in controlled crosses with fertile female parents can provide a more accurate estimate of potential male fertility (Still and Contreras 2024).

Data Reporting

It is generally desirable to present a relative female fertility (%) measure compared to a fertile control. To better understand what factors contribute to relative female fertility, it is recommended to present a measure of floriferousness (e.g., flowers per unit branch length or flowers/inflorescences per unit plant size) and individual metrics of fertility including fruit set per flower/inflorescence (%), seeds per fruit/inflorescence (#), seed germination (%), and seedlings per plant/branch length/inflorescence (#), and relative female fertility (%) compared to a fertile control. Providing these individual data points can better equip regulating bodies to more fully evaluate cultivars being proposed for exemptions.

Case Studies

Berberis fertility assessment

Materials and methods. The experimental design was completely randomized, n = 5 with 12 accessions/genotypes of *Berberis*, including the *B. thunbergii* cultivars Tara and Golden Devine as controls. Well-rooted Trade #2 (Nursery Supplies Classic C600) container grown plants were planted into a raised-bed, plasticulture, nursery crop production system on January 27, 2021. Fertility data was collected over the 2021 and 2022 growing seasons.

Table 2. Sample data sheet.

Accession	Replicate	Total Marked Branch Length/plant	Total Number of Flowers on Marked Branches	Date of Peak Bloom	Total Number of Fruit on Marked Branches	Total Number of Seeds from Marked Branches	Total Number of Seedlings from Marked Branches

A. Data Collection. A sample data sheet is provided in Table 2. Details of data collection include:

1. Flowers:
   1.1 Two or three branches (∼20-30 cm long) with the greatest number of flowers found on that plant were selected and labeled.
   1.2 The total number of flowers on the combined marked branches per plant was counted and recorded.
   1.3 The total length of the combined marked branches per plant was counted and recorded.
   1.4 The date of peak bloom for each plant was recorded.
2. Fruit:
   2.1 The total number of fruit from the combined marked branches (keeping the fruit from each plant separate from the total fruit harvested in preparation for Step 3.) on each plant was harvested and counted. If there was no fruit on any of the marked branches, the total number of fruit on the entire plant was counted.
3. Seeds:
   3.1 The total number of seeds from the fruit harvested from each plant was counted.
   3.2 Seeds from each plant were separated and stratified for 90 days at 6.1 C (43F).
4. Seedlings:
   4.1 Containers were moved to a heated greenhouse with a minimum temperature of 18.3°C (65F). The number of seedlings were counted after 90 days.

B. Results. 'Tara' had the greatest number of seedlings per unit branch length for both years (Tables 3 and 4). Three cultivars, 'NCBX1', 'NCBT1', and 'NCBX2', had less than 2% relative fertility of 'Tara', the fertile control, over both years, and would therefore be considered sufficiently infertile to meet our criterion as a seedless cultivar.

Terminology

To provide effective communication and messaging regarding invasive species, the consistent use of terminology across research, teaching, and extension disciplines is necessary. For example, recent efforts were made to create a standardized set of terms to distinguish introduced, established, invasive, and nuisance species, among others (Iannone et al., 2020). Specific to the contents of this review paper, the following definitions of important and relevant terms are provided as:

- Non-native species – An organism, including its seeds, eggs, spores, or other biological material capable of propagating that species, that occurs outside of its natural range (Executive order 13751 2016, Invasive Species Advisory Committee 2006).

Table 3. Replicated *Berberis* fertility field trial completed in 2021 at the Mountain Horticultural Crops Research Station, Mills River, NC, evaluating accessions, peak bloom date, floriferousness, fruit set per flower, seeds/fruit, seed germination, seedlings per unit branch, and relative female fertility^{z}.

Accession	Peak bloom date	Floriferousness (flowers/branch length) #/cm	Fruit set per flower (%)	Seeds/fruit (#)	Seed germination (%)	Seedlings per unit branch length (#/cm)	Relative female fertility (%)
'Tara'	4/13	4.91 ± 0.5^{a}	33.5 ± 6.2^{abc}	1.1 ± 0.1^{bc}	71.6 ± 4.7^{ab}	1.15 ± 0.2^{a}	100.0 ± 13.8^{a}
'Golden Devine'	4/10	0.22 ± 0.1^{d}	18.8 ± 10.8^{def}	1.6 ± 0.1^{a}	42.8 ± 22.8^{bcd}	0.03 ± 0.02^{c}	2.8 ± 1.8^{c}
'NCBX1'	4/20	1.04 ± 0.2^{c}	0.0 ± 0.0^{ef}	-	-	0.0 ± 0.0^{c}	0.0 ± 0.0^{c}
'NCBT1'	4/12	1.04 ± 0.2^{c}	1.2 ± 0.4^{ef}	0.5 ± 0.2^{de}	88.9 ± 11.1^{a}	0.008 ± 0.004^{c}	0.7 ± 0.3^{c}
'NCBT2'	4/14	1.04 ± 0.2^{c}	12.2 ± 3.8^{def}	1.4 ± 0.2^{ab}	23.8 ± 9.2^{cde}	0.04 ± 0.01^{c}	3.1 ± 0.9^{c}
'NCBT9'	4/10	0.94 ± 0.1^{c}	6.8 ± 1.5^{ef}	1.41 ± 0.2^{ab}	21.7 ± 16.2^{cde}	0.01 ± 0.01^{c}	1.1 ± 0.8^{c}
'NCBT3'	4/14	1.2 ± 0.1^{bc}	25.4 ± 3.8^{bcd}	1.6 ± 0.0^{a}	21.6 ± 5.7^{cde}	0.1 ± 0.04^{bc}	9.3 ± 3.0^{bc}
'NCBT4'	4/18	1.32 ± 0.2^{bc}	25.0 ± 5.9^{bcd}	1.5 ± 0.0^{ab}	10.9 ± 2.7^{de}	0.04 ± 0.005^{c}	3.7 ± 0.5^{c}
'NCBX9'	4/15	0.35 ± 0.1^{d}	39.6 ± 5.4^{ab}	1.2 ± 0.1^{abc}	7.8 ± 6.8^{de}	0.02 ± 0.02^{c}	2.0 ± 1.8^{c}
'NCBX2'	No Bloom	0.00 ± 0.0^{d}	-	-	-	$0 .0 \pm 0^{c}$	0.0 ± 0.0^{c}
'NCBT12'	4/12	1.04 ± 0.1^{b}	48.9 ± 6.8^{a}	1.6 ± 0.1^{a}	28.6 ± 4.6^{cde}	0.23 ± 0.06^{b}	19.6 ± 16.1^{b}
'NCBT14'	4/13	0.20 ± 0.1^{d}	14.7 ± 4.3^{def}	1.6 ± 0.3^{ab}	50.8 ± 13.8^{bc}	0.02 ± 0.01^{c}	2.0 ± 12.8^{c}

^{z}Values are means, n = 5, ± standard error of the mean. Values sharing common letters are not significantly different at $P \leq 0.05$. Relative female fertility was calculated as: (Seedlings per unit branch length/Seedlings per unit branch length of the control) * 100. The overall least significant difference ($P \leq 0.05$) for relative female fertility was 13.5%.

Table 4. Replicated *Berberis* fertility field trial completed in 2022 at the Mountain Horticultural Crops Research Station, Mills River, NC, evaluating accessions, peak bloom date, floriferousness, fruit set per flower, seeds/fruit, seed germination, seedlings per unit branch, and relative female fertility[z].

Accession	Peak bloom date	Floriferousness (flowers/branch length) #/cm	Fruit set per flower (%)	Seeds/fruit (#)	Seed germination (%)	Seedlings per unit branch length (#/cm)	Relative female fertility (%)
'Tara'	4/13	4.1 ± 0.7^{a}	46.3 ± 2.8^{cde}	1.2 ± 0.1^{bcde}	78.1 ± 3.1^{a}	1.80 ± 0.3^{a}	100.0 ± 18.0^{a}
'Golden Devine'	4/25	0.4 ± 0.1^{de}	30.5 ± 10.8^{ef}	1.1 ± 0.3^{de}	87.4 ± 12.7^{a}	0.15 ± 0.1^{e}	8.6 ± 6.0^{c}
'NCBX1'	4/27	4.3 ± 1.0^{a}	0.0 ± 0.0^{g}	-	-	0.00 ± 0.0^{e}	0.0 ± 0.0^{e}
'NCBT1'	4/18	0.7 ± 0.1^{de}	9.2 ± 3.0^{fg}	0.2 ± 0.1^{f}	75.0 ± 19.4^{a}	0.01 ± 0.0^{e}	0.4 ± 0.1^{e}
'NCBT2'	4/27	1.2 ± 0.3^{d}	35.7 ± 4.2^{cde}	1.5 ± 0.1^{ab}	86.4 ± 4.3^{a}	0.60 ± 0.1^{cde}	31.8 ± 8.1^{cde}
'NCBT9'	4/19	1.4 ± 0.1^{cd}	35.7 ± 2.1^{cde}	1.4 ± 0.0^{abcde}	70.6 ± 7.2^{a}	0.50 ± 0.1^{cde}	27.6 ± 5.5^{cde}
'NCBT3'	4/26	1.2 ± 0.1^{de}	54.8 ± 9.5^{bcd}	1.5 ± 0.1^{abc}	88.8 ± 1.6^{a}	0.84 ± 0.2^{cd}	47.1 ± 15.7^{cd}
'NCBT4'	4/27	2.7 ± 0.3^{b}	33.8 ± 7.5^{de}	1.5 ± 0.0^{abc}	80.1 ± 3.5^{a}	1.00 ± 0.1^{bc}	55.3 ± 7.3^{bc}
'NCBX9'	4/30	2.5 ± 0.4^{bc}	6.9 ± 2.6^{g}	1.4 ± 0.1^{abcd}	71.6 ± 4.3^{a}	0.20 ± 0.1^{e}	10.1 ± 4.34^{e}
'NCBX2'	No Bloom	0.0 ± 0.0^{e}	-	-	-	0.00 ± 0^{e}	0.0 ± 0.0^{e}
'NCBT12'	4/23	1.3 ± 0.1^{d}	95.7 ± 12.3^{a}	1.5 ± 0.1^{abcd}	86.2 ± 1.5^{a}	1.74 ± 0.5^{a}	97.3 ± 26.2^{a}
'NCBT14'	4/21	0.4 ± 0.1^{de}	56.5 ± 9.5^{cd}	1.1 ± 0.2^{cde}	92.7 ± 2.5^{a}	0.23 ± 0.1^{de}	13.1 ± 4.5^{de}

[z] Values are means, n = 5, ± standard error of the mean. Values sharing common letters are not significantly different at $P \leq 0.05$. Relative female fertility was calculated as: (Seedlings per unit branch length/Seedlings per unit branch length of the control) * 100. The overall least significant difference ($P \leq 0.05$) for relative female fertility was 35.1%.

- Anisoploid – Plants or cells with an odd (uneven) number of complete chromosome sets (e.g., 3, 5, 7…; triploid, pentaploid, heptaploid…).
- Aneuploid – Cells, or individuals comprised of cells, with an incomplete or extra number of chromosomes compared to a complete set or sets for that organism.
- Apomixis (agamospermy)– Asexual seed formation.
- Colonization rate – Rate of successful establishment of long-distance propagules (i.e. not near the mother plant).
- Cytotype – Cell, or an individual comprised of cells, with a characteristic number and type of chromosomes.
- Euploid – Cells with an even number of complete chromosome sets (e.g., 2, 4, 6…; diploid, tetraploid, hexaploid…).
- Fecundity (syn. reproductive capacity) – The biological capacity or potential to produce offspring. For example, the greatest number of viable seeds or seedlings a plant can produce per unit of time.
- Fertility – The actual ability to reproduce or produce progeny in a given environment. This can include female fertility (e.g., the ability to produce viable seeds) or male fertility (e.g., the ability to produce viable pollen). Fertility is quantitative (e.g., low fertility or high fertility). Relative fertility is in comparison to a benchmark or control, e.g., % relative fertility.
- Floriferousness - Number of flowers produced per unit of plant size or branch length.
- Infertility/Infertile/Low Fertility - Limited ability to reproduce; can refer to reduced female fertility (viable seed production) or reduced male fertile (pollen viability) compared to a benchmark.
- Intrinsic rate of growth – The rate at which a population increases or decreases in size under ideal conditions with no limiting factors. Often represented by the constant "r" and calculated as the birth rate – death rate.
- Invasive (species) –

  A) A non-native organism whose introduction causes or is likely to cause economic or environmental harm, or harm to human, animal, or plant health. (Executive order 13751, 2016).

  B) Species that establish and spread outside their native range or management area and degrade the environment (Mack et al. 2000).

  C) Any species that is not native to that ecosystem and is capable of propagating itself, whose introduction causes or is likely to cause harm to the environment, economy, or human health (Pejchar and Mooney 2009).

- Naturalized – A non-native species that establishes self-perpetuating populations (Richardson et al. 2000). This does not indicate if plants that have naturalized are causing negative impacts on the native environment.
- Ploidy – Number of complete sets of chromosomes in an organism's cells. Diploids have two, triploids three, and so on. Polyploids are any plant with more than two complete sets of chromosomes.
- Propagule pressure – The total number of individuals introduced into a surrounding area.
- Propagule rain – The extent to which established individuals of a species add offspring to the exotic environment.
- Population growth rate (λ) – the actual rate at which a population size changes over time often assumed to be in a constant environment (deterministic), independent of plant density.
- Relative fertility – percent fertility (male or female) compared to a fertile standard. For example, 50% relative female fertility would mean a plant produced half as many viable seeds or seedlings compared to a control.
- Seedless – Condition where seed production is greatly reduced or rare, but not necessarily zero.
- Self-sowing (self-seeding) – To reproduce and spread by the dispersal of its own seeds.
- Sterility – Absolute inability to reproduce sexually.
- Triploid – A plant with three complete sets of chromosomes.
- Weed – An undesirable plant, especially one with broad adaptability that spreads aggressively and is well adapted to environmental disturbances. Weeds may be native or non-native and may or may not have negative effects on ecosystems.
- Weediness – The propensity to be a weed.

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