Are sterile *Buddleja* cultivars really sterile and "environmentally safe"?

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Abstract: Native to China, the ornamental *Buddleja davidii* (Scrophulariaceae) and its many cultivated varieties have become problematic alien plants in many countries. While their sale has been prohibited or discouraged, horticultural breeders have developed sterile or almost sterile cultivars sold as "environmentally safe", raising discussions about how "safe" they really are. This study revisited the literature on this kind of *B. davidii* cultivars and discusses the characteristics that make them supposedly "environmentally safe". Most *Buddleja* cultivars considered sterile or with reduced fertility derive from complex breeding programs. No publication quantifies "reduced fertility" or guarantees female and male sterility in the long term. What is mainly meant is reduced or no fruit and/or seed production, i.e. stamens can still release viable pollen that can reach stigmas of normally fertile *B. davidii* naturalized taxa, and stigmas can receive pollen from these wild individuals. Then, genetic recombination could pass on characteristics of "environmentally safe" cultivars to plants in the wild, contributing to originate more resilient invasive *B. davidii* lineages, and/or could lead to fertility restoration in seedlings from "environmentally safe" cultivars. Fertility restoration could also occur spontaneously. Because no evidence was found that sterile cultivars or with reduced fertility can be considered environmentally safe, they should be subjected to the same legal bases of normally fertile *B. davidii* taxa.

Le cultivar sterili di Buddleja sono davvero sterili e "sicure per l'ambiente"?

Riassunto esteso

Introduzione: La buddleja, *Buddleja davidii* (Scrophulariaceae), è un'apprezzato arbusto ornamentale dei giardini e parchi, con oltre due centinaia di varietà botaniche e coltivate. Originaria della Cina, *B. davidii* è considerata una pianta esotica problematica (neofita invasiva) in Svizzera e in molti altri paesi, dove è stata introdotta e dove la sua vendita è stata vietata o scoraggiata. Per aumentarne l'accettazione, il settore verde ha sviluppato cultivar con una fertilità ridotta che sono state vendute sul mercato come "sicure per l'ambiente", sollevando discussioni su quanto queste cultivar fossero realmente "sicure". Motivati inizialmente dalle preoccupazioni delle autorità competenti svizzere, in questo studio abbiamo rivisitato la letteratura disponibile sulle cultivar di *B. davidii* presumibilmente sterili e quelle a fertilità ridotta per indagare e discutere le caratteristiche che rendono queste cultivar apparentemente "sicure per l'ambiente".

Metodi: La ricerca bibliografica è stata effettuata in Google e Google Scholar, in inglese, tedesco, francese e italiano, e consultando anche la letteratura citata in pubblicazioni rilevanti. Oltre ai nomi di cultivar note, come 'Blue Chip', le parole chiave utilizzate di partenza sono state "*Buddleja davidii*" o "esotica invasiva" da sole e in diverse combinazioni con "cultivar sterili", "fertilità ridotta" o "ambientalmente sicuro".

Risultati: La maggior parte delle cultivar di *Buddleja* considerate sterili o a fertilità ridotta emerse dalla nostra indagine sono ibridi stabili derivati da complessi programmi di ibridizzazione, nel Regno Unito e soprattutto negli Stati Uniti, in cui sono coinvolti *B. davidii* e un certo numero di altre specie e varietà botaniche. Sebbene siano disponibili informazioni dettagliate su queste ibridizzazioni, nessuna pubblicazione presenta dei valori per quantificare la "fertilità ridotta". Le parole "fertilità ridotta" o "sterilità ridotta" sono usate per indicare "produzione di frutti e/o semi ridotta o nulla"; in altre parole, i loro stami possono ancora rilasciare polline vitale che può raggiungere gli stimmi di taxa selvatici normalmente fertili di *B. davidii*, e i loro stimmi possono ricevere polline da questi individui selvatici. Da un lato, la ricombinazione genetica potrebbe trasmettere le caratteristiche delle cultivar "ambientalmente sicure" alle piante di *Buddleja* in natura, contribuendo a dare origine a discendenti di *B. davidii* invasivi più resistenti. D'altra parte, la ricombinazione genetica potrebbe portare al ripristino della fertilità nelle piantine delle cosiddette cultivar "ambientalmente sicure". Anche nelle cultivar con organi maschili e femminili presumibilmente sterili, gli autori dei programmi d'ibridizzazione non garantiscono una sterilità a lungo termine. Infatti, il ripristino della fertilità potrebbe avvenire anche spontaneamente, come noto nelle piante coltivate. Benché non sia noto quante generazioni trascorrino fino ad un ripristino della fertilità, in termini di tempo possono essere anche meno di 20 anni, dato che le cultivar "sicure" sono apparse solamente nei primi anni del 2000.

Conclusione: Non abbiamo trovato alcuna prova documentata che la sterilità maschile e femminile sia mantenuta a lungo termine e che qualsiasi cultivar con produzione ridotta di semi o con assenza documentata di semi vitali sia sicura per l'ambiente e non contribuisca (in alcun modo) all'invasione di *B. davidii* o al suo comportamento invasivo. Pertanto, a fini di prevenzione, le cultivar con una produzione di semi ridotta o nulla dovrebbero sottostare alle stesse basi legali delle altre cultivar e dei taxa botanici di *B. davidii*. Per il loro commercio in Svizzera ciò significa che per queste piante attualmente vige l'obbligo di informazione e devono essere etichettate come neofite invasive.

INTRODUCTION

The prized ornamental butterfly shrub, *Buddleja davidii* Franch. (Scrophulariaceae, formerly Buddlejaceae), and its cultivated varieties have long been popular and appreciated garden and landscape plants with horticulturist and hobby gardeners. It is one of over 90 species in the genus *Buddleja* and, in addition to its seven subspecies, at least 90 varieties have been described (Stuart, 2006; Chau *et al*., 2017), and Wikipedia itself currently lists 270 taxa under the term "Category: Buddleja hybrids and cultivars" (Wikipedia, 2019a).
Native to central and southwestern China, in Switzerland and in many other countries worldwide, *B. davidii* is, however, considered a problematic alien plant, i.e. an invasive neophyte (Tallent-Halsell & Watt, 2009; see the Black List of Info Flora, 2014), having invaded much of the countries where it was introduced. They have spread from gardens into the wild, forming stable stands in a wide range of disturbed and natural areas including floodplains, railroad and road edges, forest burns and clear-cuts. Being a pioneer species, *B. davidii* is able to quickly colonize barren, nutrient-poor sites, such as gravel banks and open surfaces (Figure 1). It can quickly become dominant, forming pure stands and precluding establishment of native vegetation. Furthermore, because each *B. davidii* plant can produce up to 3 million seeds that are easily wind-dispersed over long distances (see review by Tallent-Halsell & Watt, 2009, and citations therein), seed dispersal is particularly efficient. *Buddleja davidii* is also of major concern in the light of global climate change, because analyses show that, under future climates, its potential distribution and climate suitability increases, most noticeably in North America and Europe (Kriticos *et al*., 2011).
Sale of *B. davidii* has been prohibited and discouraged in many places where it is recognized as a problematic invasive alien species, but elsewhere it is still sold as an attractive and lucrative landscape plant. To increase acceptance, elaborate breeding programs have tried to reduce fertility by developing sterile or almost sterile cultivars that have been sold on the market as "environmentally friendly", "environmentally safe", or even as "non-invasive". This triggered discussions among environmental authorities and horticulture representatives about how "friendly" and "safe" these cultivars really are and, therefore, the effective "environmental compatibility". The debate has probably been fueled by the fact that, in the United States, Oregon State prohibited *B. davidii* but allowed selling of cultivars in which the proportion of viable seeds could be documented to be less than 2% (Oregon Department of Agriculture, 2011). At submission of this paper, Oregon State Department of Agriculture was allowing the sale of 18 *Buddleja* cultivars, 14 of which were approved because they would meet the 2% criterion, whereas fertility had not been assessed in the remaining four (see Oregon State Department of Agriculture 2019).
In Switzerland, *Buddleja* 'Blue Chip' is a cultivar that raised concern on this topic among authorities a few years ago. In fact, while *B. davidii* and all its cultivars sold by garden centers and nurseries should be labelled as an invasive alien species to inform consumers on the invasiveness of the species and how to handle the plant (AGIN, 2015), sellers would argue that there is no need to label "environmentally safe" cultivars, given that they are not problematic. Article 3f of the Ordinance on the Handling of Organisms in the Environment (OEDA, 814.911) actually states that "alien organisms means organisms of a species, sub-species or lower taxonomic level that: […], 2. have not undergone selection for use in agriculture or horticultural production to such an extent that their viability in the wild is reduced". Hence "environmentally safe" cultivars could be considered as noninvasive. But, the Ordinance does not further explain the meaning of "viability in the wild is reduced". The problem remains thus unresolved.
A quick search in the literature found no immediate evidence demonstrating that such cultivars are not problematic in the wild, but also showed that information on this topic was poor. This prompted a first research and synthesis work that was presented in the form of a report to the Swiss authorities in 2018. Using this report as a basis to make the information publicly available, in the present paper we revisited the available literature on sterile *B. davidii* cultivars and cultivars with reduced fertility in order to provide an overview of the current state of knowledge, inquire and discuss the characteristics that make these cultivars supposedly "environmentally safe", and finally, draw our conclusions and outline recommendations to policy makers.

MATERIAL AND METHODS

The first literature search was done in fall 2017 and early 2018, and a second round was done in early 2019 for the present paper. The search was done in Google and Google Scholar to access scientific information that should be publicly available, preferably peer-reviewed publications, in English, German, French, and Italian. The search focused first on *Buddleja* 'Blue Chip', other *Buddleja* Chip-hybrids and similar cultivars, and then expanded to other known or investigated invasive alien species with so-called "environmentally safe" cultivars. The recently updated listing of the Oregon State Department of Agriculture on the dedicated webpage "Butterfly Bush Approved Cultivars" (2019) proved helpful in guiding our search. In addition to the cultivar names just mentioned, the starting key words used were "*Buddleja davidii*" or "invasive alien" alone and in different combinations with "sterile cultivars", "reduced fertility", or "environmentally safe". We refined key words depending on the results of the first round of findings, and also searched for relevant literature cited in other publications.

RESULTS AND DISCUSSION

Most of the *Buddleja* cultivars considered sterile or with reduced fertility that emerged in our survey are stabile hybrids from complex breeding programs involving

Figure 1: *Buddleja davidii* in Switzerland. A-B, individuals colonizing river banks nearby Brusio (Canton Graubünden): A, individuals bearing inflorescences of different colors; B, close-up of A to highlight white and pink inflorescences. C, individual on a forest margin, nearby a managed grassland area in Rovio (Cantone Ticino). D-E, inflorescences at different flowering stages: D, in full flowering; E, partially fruiting. Photo courtesy by Andrea De Micheli (A, B) and Sofia Mangili (C-E).

B. davidii and a number of other species and varieties. This seems to be the case in general for breeding of *Buddleja* cultivars, which probably explains why they are sold using the contracted name as by convention (Brickell, 2016), consisting of only the genus and the cultivar name, for example: *Buddleja* 'White Profusion'. This designation does not indicate that the problematic *B. davidii* is involved in the breeding program, hampering control, prevention and management efforts. Where the species escaped from gardens and naturalized, most plants found in the wild appear more or less as direct descendants of the wild form with flower colors ranging from light pink to dark purple, but there are also some with white flowers. The latter derive most likely from white-flowered cultivars, commonly sold along with other *Buddleja* cultivars (Ream, 2006; see Fig. 1A-B), rather than from white forms that can appear sometimes in the native range and variation of the straight species. In the following, we review the cultivar of interest to this study, and then discuss how "environmentally safe" they are.

Cultivar overview. The information on sterility or reduced fertility in *Buddleja* cultivars is sparse, as shown in the literature cited in the present study. We found detailed information on breeding programs of sterile cultivars or cultivars with reduced fertility, but no publications with values that quantify "reduced fertility". Efforts to breed sterile cultivars have been done in the United Kingdom and especially in the United States. In the United Kingdom, the cultivar 'Lonchich' is reported by Tallent-Halsell & Watt (2009) as follows: "The development of sterile plants and novel B. davidii hybrids has been created with the use of less common species. The cross between *B. davidii* and *B. fallowiana* is named *Buddleja davidii* 'Lochinch' (Wigtownshire, Scotland). *Buddleja davidii* 'Lochinch' was thought to be sterile and therefore an ideal alternative to *B. davidii*. However, field observations reveal that the hybrid

reproduces abundantly by seeds and shows invasive characteristics (EPPO, 2005)". It is possible that this cultivar reverted to fertility.

Most efforts to breed sterile cultivars have been done in the United States, where business with these plants is probably worth the expensive breeding programs to fulfill strict requirements, such as those of Oregon State. Most of these cultivars have been patented in the meantime. Interest in sterile cultivars appears to have started in the early 2000's, but all of the 14 *Buddleja* cultivars studied in Wilson *et al.* (2004) produced seeds, the germination of 13 of them could be tested under greenhouse conditions and resulted positive. Just two years later, in 2006, Dr. Jon T. Lindstrom of the University of Arkansas (United States), produced and released the cultivar *Buddleja* 'Asian Moon' (Wikipedia, 2019b), as supposedly a totally sterile cultivar producing vestigial fruits devoid of seeds or with non-viable reduced seeds (Renfro *et al.,* 2007). No evidence has been provided that this cultivar remains sterile in time, but Oregon State allows its sale (Oregon Department of Agriculture, 2018). The plant is very vigorous, as it has been conceived for growing easily in hot, dry and sunny locations. According to the Gardening Help Site of the Missouri Botanical Garden (2017) it does poorly in wet conditions.

One other known line of such cultivars has been resulting from a formal breeding program in North Carolina, established by Dennis J. Werner and Layne K. Snelling at the North Carolina State University, in Raleigh (Werner & Snelling, 2009a, 2011). They started with the 'Blue Chip', a complex hybrid containing three species (*B. davidii*, *B. globosa*, *B. lindleyana*) and one botanical variety of *Buddleja* (*B. davidii* var. *manhoensis*) (Werner & Snelling, 2009a). Along with 'Blue Chip', the authors also presented 'Miss Ruby' and reported both cultivars as having a reduced seed production (Werner & Snelling, 2009b), thus not being totally sterile, as also mentioned in release notices by the North Carolina Agricultural Research Service (2007, 2013). Continuing on the work started on 'Blue Chip', patents have been issued for a number of cultivars (for example, in order of appearance: 'Ice Chip', 'Lilac Chip', 'Blue Chip Jr.', 'Pink Micro Chip', and 'Miss Violet'; Werner & Snelling, 2013a, b; Werner 2016a; Werner, 2016b; Werner, 2017, respectively). One of the goals of the breeding program was to develop plants with reduced male and female fertility, because explicitly considered an asset in landscape plantings. Indeed, Oregon State allows their sale (Oregon Department of Agriculture, 2018). The program included test plantings and performance evaluation over four or five years at a research station and a greenhouse. Flowers of the cultivars have been documented as showing a reduced male and female fertility, in which stamens can be malformed and lacking pollen and the pistil only rarely develops into a capsule (e.g. 'Miss Violet'; Werner, 2017) or sets no seeds at all (e.g. 'Blue Chip Jr.' and 'Pink Micro Chip'; Werner, 2016a, b). Such characteristics are reported to be maintained through the replicated field trials during the test period; they were observed in clones, because all trials were done by propagating plants asexually via stem cuttings. No quantitative data are made available. Even in those cultivars that did not set any seed in trials (e.g. 'Blue Chip Jr.' and 'Pink Micro Chip'), the author remains cautious about the apparent sterility by stating that, in fact, he "does not preclude the possibility that seed set may be observed on rare occasions" (Werner, 2016b), recognizing that there is no guarantee that these cultivars remain sterile in the long term.

The meaning of "environmentally safe". In all cases, reduced fertility or sterility are used to mean "reduced or no fruit and/or seed production", and "environmentally safe" thus only refers to the dispersal of the plant by seed, i.e. its ability to disperse and set seedlings. Furthermore, no values are provided in any of the publications on cultivars with reduced seed production. In their review, Knight *et al.* (2011) conclude 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 (though they looked at other species than *B. davidii*). This is in part due to the fact that the contribution of a cultivar to the invasion is not necessarily only measurable in the number of dispersed seeds.

The actual plant reproduction is not explicitly considered in any of the "environmentally safe" cultivars; in other words, it is not primarily a matter of sterility or reduced fertility of male and female organs. In almost all cultivars, their stamens can still release viable pollen that can reach the stigmas of normally fertile *B. davidii* wild taxa, and their stigmas can receive pollen from these wild individuals. *Buddleja davidii* is known to strongly rely on cross-pollination for successful reproduction (Ebeling *et al*., 2012). Because gene transfer is possible in this way, genetic recombination could ultimately lead to fertility restoration in seedlings from "environmentally safe" cultivars. That supposedly sterile *Buddleja* cultivars can revert to fertile plants in time is mentioned in several blogs by people in the US active in the green sector, and has been reported in Europe by EPPO (2005). However, it is not clear where blogs authors obtained the information and how fast fertility reversion can occur (in terms of number of generations). Nevertheless, spontaneous reversion to fertility is long known and well understood in crop plants, like maize (*Zea mais*) and beans (*Phaseolous vulgaris*) (MacKenzie *et al*., 1988; Janska *et al.,* 1998; Guo & Liu, 2014).

Finally, genetic recombination could also pass on characteristics for which the "environmentally safe" cultivar was selected in the first place to *Buddleja* plants in the wild. In other words, they can still interbreed with normal fertile cultivars or wild individuals and could ultimately even contribute to originate more resilient lineages of invasive *B. davidii*, able to colonize new habitats thanks to an expanded niche. In their study, Ebeling *et al.* (2008, p. 231) conclude that "traits that might be related to invasion success have been found by several authors in some of 70 existing cultivars of *B. davidii* (Anisko & Im, 2001; Wilson *et al*., 2004). It is likely that cultivars rather than native genotypes are the source of the *B. davidii* invasion, thus selection by breeders may be one reason for the differences in plant

traits among native and invasive populations revealed in our study". For instance, experiments on the quantity of seeds produced and germination capacity (Drin, 2006) showed that common *Buddleja* cultivars from classical breeding had an equal or superior potential for spread compared to the naturalized forms. This increased potential for spread could be explained (at least in part) by the fact that horticultural selections have been made to obtain a large size of inflorescences, precocity and long-lasting period of flowering, vigorous growth, and resistance to pest, disease and harsh climate (Drin, 2006).

CONCLUSIONS

This study provides an overview on the debated subject of sterile *B. davidii* cultivars or with reduced fertility that are sold as "environmentally safe". Although we are aware that it is not an exhaustive review, at least five main points emerge from our synthesis on *B. davidii* "safe" cultivars: 1) Reduced fertility is still fertility; 2) Cultivated reduced-fertile or sterile cultivars can cross with the invasive individuals found nearby in the wild; 3) Gene transfer from reduced-fertile or no-seed cultivars can modify wild individuals and, conversely, 4) gen transfer from fertile wild individuals can modify reduced-fertile or no-seed cultivars; 5) Sterile plants can revert to fertile plants in time (by gene transfer or spontaneously). Although it is unclear how many generations are needed for fertility to be restored, it surely can take less than 20 years, because "safe" cultivars did not exist before.

We found no documented evidence that male and female sterility is maintained in the long term and that any cultivar with reduced seed production or even documented absence of viable seeds is environmentally safe and does not contribute (in any way) to the invasion of *B. davidii* or to its invasive behavior. Sterile plants can revert spontaneously to fertile plants, and in general these cultivars can still transfer genes through their pollen to other normally fertile cultivars, sharing characteristics they were selected for, such as being more resistant to extreme environmental conditions. For prevention purposes, there is no reason to discriminate between cultivars with reduced or no seed production and normally fertile cultivars and wild taxa of *B. davidii*, but should all be subjected to the same legal bases.

In Switzerland, all marketed cultivars of *B. davidii* and hybrids involving *B. davidii* should thus be labelled as invasive neophytes to inform consumers on the invasiveness of the species and how to handle the plant. Sellers have to make sure themselves which cultivars have to be labelled, by clarifying whether *B. davidii* (or any of its varieties) is present as a crossing parent. For this purpose, breeding information must be requested and consulted, and if *B. davidii* is involved in the breeding program, sellers must assume an invasive potential and label the plants accordingly.

ACKNOWLEDGMENTS

We thank Claudia Ruprecht for assistance in the previous report to authorities, Sofia Mangili for sharing the photographs illustrated in Figure 1C-E, and David George, Guido Maspoli and Marco Moretti for valuable comments on this manuscript.

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