

The Invasive *Buddleja davidii* (Butterfly Bush)

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Abstract *Buddleja davidii* Franchet (Synonym. *Buddleia davidii*; common name butterfly bush) is a perennial, semi-deciduous, multi-stemmed shrub that is resident in gardens and disturbed areas. Since its introduction to the United Kingdom from China in the late 1800s, *B. davidii* has become an important component in horticulture and human culture. Despite its popularity as a landscape plant, *B. davidii* is considered problematic because of its ability to naturalize outside of gardens and rapidly invade and dominate disturbed natural areas across a wide range of physical conditions. The primary goal of this paper is to synthesize what is known about *B. davidii* in order to understand the impacts caused by the continued presence of *B. davidii* in gardens and natural landscapes. We also address management of *B. davidii* and discuss the repercussions of management strategies and policies currently implemented to protect or remove *B. davidii* from natural ecosystems.

Zusammenfassung *Buddleja davidii* Franchet (Synonym *Buddleia davidii*, umgangssprachlich “Schmetterlingsflieder”) ist ein ausdauernder, halb-immergrüner, mehrstämmiger Busch welcher in Gärten und auf Umbruchflächen gedeiht. Seit seiner Einführung in die UK aus China im späten 19. Jahrhundert hat *B. davidii* in Pflanzenzucht und Kultivierung stark an Bedeutung gewonnen. Unabhängig von seiner Beliebtheit in der Landschaftsgestaltung stellt *B. davidii* wegen seiner Fähigkeit, sich über Gartengrenzen hinaus unter einer Vielzahl von Wachstumsbedingungen in gestörten Naturgebieten schnell auszubreiten und dort die einheimische Flora zu dominieren, ein grosses Problem dar. Das Ziel der vorliegenden Rezension ist es eine Synopsis zu erstellen, welche die Auswirkungen und Gefahren der konstanten Präsenz von *B. davidii* in Gärten und der Naturlandschaft verdeutlicht. Management Optionen und -Fehlschläge sowie aktuelle Regulationen zu dem Zwecke *B. davidii* aus natürlichen Ecosystemen zu entfernen oder sein Vordringen zu verhindern, werden ebenfalls diskutiert.

Keywords *Buddleja davidii* · Buddlejaceae · Butterfly Bush · Invasive Species

Introduction

Buddleja davidii Franchet is a perennial, semi-deciduous shrub or small multi-stemmed tree that readily establishes on disturbed sites in regions with temperate, subtropical, and tropical climates. Native to central and western China, *B. davidii* has been introduced as an ornamental to the Americas, Australia, Europe, and New Zealand because of its fragrant and colorful flowers (Synonym. *Buddleia davidii*, *Buddlea davidii*; *Buddleia variabilis* Hemsl., *Buddleia magnifica* Hort, *Buddleia nanoensis* Hort; Bailey & Bailey, 1976; Bricknell & Zuk, 1997; Family Buddlejaceae; Common names: butterfly bush, orange-eyed butterfly bush, summer lilac).

In the 100 years since *B. davidii*'s introduction, the tree has spread from gardens to disturbed and natural areas including floodplains, railroad and road edges, forest burns, and clear-cuts. Horticulturalists, landscapers, gardeners, butterfly enthusiasts, bird watchers, and the general public welcome and celebrate *B. davidii*'s colorful and fragrant place in urbanized landscapes (Coats, 1992; Dirr, 1997; Dole, 1997; Klingaman, 2002; Wilson et al., 2004a; Forrest, 2006; Stuart, 2006; KCGG, 2007; Savonen, 2009). However, many others consider *B. davidii* invasive and problematic. There is concern that it has potential negative and irreversible impacts on agricultural and wild lands it invades (Richardson et al., 1996; Reichard & Hamilton, 1997; Anisko & Im, 2001; Reinhardt et al., 2003; Wilson et al., 2004b; PIER, 2005; WSNWCB, 2006). The desire to protect the continued presence of *B. davidii* in gardens is matched by the concern by land managers to control *B. davidii*. It is clear that *B. davidii* is an important component of both horticulture and society (Stuart, 2006). Considering the level of interest in *B. davidii* by both the public and land managers, a thorough understanding of the ecological impacts of *B. davidii* naturalization over the long-term is required.

Despite research on the distribution, ecology, physiology, and management of *B. davidii* gaps exist in our knowledge about native and non-indigenous *B. davidii*. The primary goal of this paper is to synthesize what is known about *B. davidii* so that ecologists, horticulturalists, and others can fully appreciate the impacts of the continued presence of *B. davidii* in gardens and natural landscapes, and understand the repercussions of management efforts. This review of the literature concerning *B. davidii* is divided into seven sections: history, taxonomy, distribution, biology, ecology, human ecology, and management.

Literature Review

History of *B. davidii*

B. davidii was introduced to Europe in 1869 by French missionary, Father David from the Moupine Province, East Tibet, and, again, by Dr. Augustine Henry (Nelson, 1980) in 1887 from the I-ch'ang Province of China. The genus *Buddleja* was named by von Linné (1737) to honor the English amateur botanist, Reverend Adam Buddle (Chittenden, 1951; Buddle, 2008; Noltie, 2008). The species was named after Father David who collected and returned specimens of the Chinese flora and fauna to Adrien René Franchet at the Paris Musée National d'Histoire Naturelle (Bean, 1970).

David sent Franchet specimens of *B. davidii* in 1869 (Franchet, 1884, 1888). Specimens of the same species from I-ch'ang Province were collected by Henry and named by William Botting Hemsley in 1887 (Anon., 1925). Unaware of Franchet's description, Hemsley called the plant *B. variabilis* Hemsl. (Hemsley, 1889). The name was eventually reversed 25 years later, due to the discovery of Franchet's original description. However, *B. variabilis* is still listed as a synonym of *B. davidii*.

B. davidii seeds were first introduced to Europe from Russia by traders (Bean, 1970). These seeds were reported to produce, from a horticultural perspective, an inferior form (Bean, 1970; Coats, 1992). A second form was introduced to Louis DeVilmorin of France from Tatsienlu, China, in 1893 by Jean André Soulié (Herberman, 1919). This form produced what was considered a superior plant (i.e., erect habit, flowers in denser and longer panicles; Cox, 1986). Once grown, the plant resembled *B. davidii* var. *veitchiana* that was later introduced to the United Kingdom (UK) by Ernest Wilson (National Council for the Conservation of Plants and Gardens, 2007). DeVilmorin sent seed from the Tatsienlu specimens to the Kew Gardens in 1896 (Coats, 1992).

Further collections of *B. davidii* seeds were sent from Mt. O'mei Shan, China in 1896 by another French missionary (and botanist) Father Paul Guillaume Farges (ThePlantExplorers.com, 2007) and in the following year by Henry from I-ch'ang. Wilson collected *B. davidii* for its numerous and attractive seed capsules (not flowers) in the Hupeh and Szechwan regions of China during the years 1907–1910 from which the common garden-variety *B. davidii* descended (Rehder, 1927; Bean, 1970). However, some of the naturalized plants in the UK may have originated from the earlier seed collections or from hybrids with the original stocks (Miller, 1984).

Taxonomy of *B. davidii*

The Family Buddlejaceae

The classification of the genus *Buddleja* has been in flux for some time (Oxelman et al., 1999; Norman, 2000; Houghton et al., 2003). *Buddleja* was originally ascribed to the family Scrophulariaceae by de Jussieu (1789), Bartling (1830) and Lindley (1846), yet it was later reclassified in the Loganiaceae by Bentham (1857) and Bentham and Hooker (1876). Wagenitz (1959), Leenhouts (1963), Leeuwenberg (1979) and Leeuwenberg and Leenhouts (1980) continued to treat *Buddleja* and its allies as a tribe of Loganiaceae even though Wilhem (1910) gave Buddlejaceae family rank next to the Loganiaceae (Norman, 2000). Melchoir (1964) recognized the family Buddlejaceae which he placed in the Tubiflorae near the Scrophulariaceae. Cronquist (1981), Takhtajan (1980, 1986), Dahlgren (1983, 1989a, b), and Thorne (1992) concur with the placement yet when they elaborate the contents of the family, they do not completely agree (Norman, 2000; Houghton et al., 2003). Oxelman et al. (1999), Olmstead et al., (2001), Oxelman et al. (2005), and Tank et al. (2006) present strong evidence of the scrophulariaceous affinity of the Buddlejaceae based on molecular phylogenetic studies.

The confusion does have merit. Embryological studies support assignment to Scrophulariaceae (Norman, 2000). However, Scrophulariaceae does not have stipules as does the genus *Buddleja*. Furthermore, Houghton et al. (2003) excluded the genus *Buddleja* from the Loganiaceae based on chemosystematic aspects of

terpenoids (iridoids and aucubins) present in the plants and suggested that the genus should be included in a new taxon including the Scrophulariaceae and Lamiaceae. In spite of supporting and opposing evidence for place in various families the convention at present is to place the genus *Buddleja* and other related genera in the family Buddlejaceae based on morphology, embryology, and chemistry (Oxelman et al., 1999; Norman, 2000; Olmstead et al., 2001; Oxelman et al., 2005; Tank et al., 2006).

The Buddlejaceae consists of angiosperms that are trees, shrubs or lianas that are self-supporting or climbing. The eight genera in Buddlejaceae occur in warm, tropical, and subtropical climates (Norman, 2000): *Androya* (one species, Madagascar); *Buddleja*, (ca. 100 species and cultivars, native to the Americas, Africa and Asia); *Chilianthus* (three species, South Africa); *Emorya* (one species, Texas and Mexico); *Gomphostigma* (two species, South Africa); *Nuxia* (fifteen species, southern Arabia and tropical Africa); *Peltanthera* (one species, tropical America); and *Polypremum* (one species, warm regions in America). The African genera *Adenophusia* and *Nicodemia* were recently reclassified in *Buddleja* (Adkins, 2004). There are no native plants of the Buddlejaceae in Australia, New Zealand, or Europe (Stuart, 2006).

Chromosomal analyses indicate that the basic chromosome numbers of this family are seven and 19 (Moore, 1947; Norman, 2000). Ploidy levels recorded are two, four, six, 12, 16, and 38. About 48% of species in the genus *Buddleja* have been described based on differences in cytology. Polyploidy appears most frequently in Asian species (Moore, 1947, 1960). Chen et al. (Chen & Sun, 2006; Chen et al., 2007) found the basic chromosome number of 27 populations of 14 *Buddleja* species was $x=19$ with the presence of several ploidy levels. Specifically, the species *B. davidii* has a tetraploid number of $2n=76$ (Moore, 1960; Chen et al., 2007).

The Genus Buddleja

The genus *Buddleja* is a cosmopolitan genus of Buddlejaceae consisting of approximately 100 species in the tropical, subtropical, and temperate zones of the world (Marquand, 1930; Norman, 2000; Chen et al., 2007). Four *Buddleja* species have particularly wide distributions: *B. americana* (Central America south into northwestern regions of South America), *B. salvifolia* (Africa; Angola and Kenya to South Africa), *B. asiatica* (from eastern India into China), and *B. crispa* (Afghanistan to Kansu Province in China; Stuart, 2006). However, many species of *Buddleja* are localized and often found in isolated valleys or mountainsides (e.g., *B. utahensis* grows only in the Washington region of southwestern Utah).

The diversity centers of Old World *Buddleja* species are in South Africa and Madagascar (ca. 15%) and the Sino-Himalayan region of south-east Asia (ca. 21%; Leeuwenberg, 1979; Li & Leeuwenberg, 1996; Norman, 2000). The diversity centers in the New World are in southeastern Brazil, the Andes, Central America, and the southwestern USA which together account for approximately 63% of the species in the genus (Norman, 2000). Norman (2000) and Adkins (2004) accept the proposal put forth by Moore (1947) that the genus originated from Africa despite the fact that there is greater diversity of *Buddleja* species in Asia and the Americas. Moore (1947) hypothesized that because most of genetic diversity in the Buddlejaceae was found in South Africa, and that polyploidy was prevalent only in America and

Asia, that Africa was the most likely place for the origin of this family (Norman, 2000; Adkins & Werner, 2003; Adkins, 2004).

There is an on-going debate surrounding the spelling of the genus *Buddleja*. Dr. William Houston, a British naval surgeon and botanist who retrieved plants from Mexico and South America (Stearns, 1988), originally proposed naming specimens he collected in the West Indies (ca. 1730–1733) *Buddlea* to commemorate Rev. Buddle (Miller, 1835; Noltie, 2008). Houston's plant specimens were later officially named by von Linné *Buddleja americana* in his *Species Plantarum* (1753) and *Genera Plantarum* (1754). However, Hemsley (1889) and Robinson (1898) introduced another *Buddleja* species to English gardeners in different weekly horticultural journals as *Buddleia*. Bean (1970) spelled the genus *Buddleia* as well. Other versions, such as *Budlaea*, *Budlea*, and *Buddleya* have all been published (Coats, 1992).

Miller (1984) suggested that von Linné may have used the tailed “i” in his spelling of *Buddleja* (the i looks like a j), which was prevalent in the eighteenth century when an author wished to denote a consonant sound. However, Gillman (in Pellet, 2006) argued that...“Linné did not spell *Buddleja* correctly” and speculated that typesetters of the time used “j”s for “i”s, as well as using “v”s for “u”s and “f”s for “s”s in the main text, yet not in the indexes. In von Linné's work on plant systematics (1797) *Buddleja* with a “j” was written in the text, yet was listed in the index with an “i” thus suggesting that von Linné intended that it should have been spelled *Buddleia* with an “i”. Nevertheless, according to the International Rules of Nomenclature, Article 24 states that genera names can be taken from any source whatever and may even be composed in an absolutely arbitrary manner. Therefore, the spelling adopted by von Linné in 1753 and 1754 must be retained (Sprague, 1928) regardless of whether the name resulted from errors or misinterpretations. We follow Sprague's recommendation and spell *Buddleja* with a “j”.

B. davidii Franchet

Seven subspecies of *B. davidii* and 90 *B. davidii* cultivars have been described (Stuart, 2006). The subspecies, from various locations in China, were originally introduced at different times to the UK (Marquand, 1930) and generally vary in overall plant size, length of the inflorescence, size and color of the leaves and flowers. Some of these varieties are now considered heirloom plants that gain and fall in popularity over time (Findley et al., 1997; Stuart, 2006).

B. davidii breeding programs began as early as 1920, when W. van de Weyer developed interspecific hybrids resulting from crosses between *B. globosa* and *B. magnifica* (Moore, 1960; Wilson et al., 2004a). Since that time, cultivars have been bred for size, a variety of flower colors and environmental hardiness for the nursery trade. Several hybridization programs were initiated in the late 1990s under the direction of M. A. Dirr, J. T. Lindstrom, and D. J. Werner (Gaus & Adkins, 2002; Lindstrom et al., 2002; Adkins & Werner, 2003; Renfro & Lindstrom, 2003; Lindstrom et al., 2004). These plant hybridization programs have focused on the traits of flower color, inflorescence morphology, compact growth habit and gray pubescent foliage. 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 *B. davidii* ‘Lochinch’ (Wigtownshire, Scotland). *B. 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).

In addition to developing cultivars to exploit size (dwarfness; Podaras, 2005) and hardiness, and to enhance flower and leaf color (Lindstrom et al., 2004; Podaras, 2005), cultivars are sought to reduce inherent invasibility (CANR, 1996, 2007). Ruter, University of Georgia, (CANR, 2007) is experimenting with gamma irradiation techniques to induce sterility in *B. davidii* cultivars. Lindstrom (University of Arkansas) and Podaras (Cornell University) are working independently on developing *B. davidii* hybrids that are sterile (Podaras, 2005). Lindstrom et al. (2002, 2004) have sought to reduce potential invasiveness by producing hybrids that either alter plant morphology (specifically seed or fruit characteristics) or have an odd ploidy number. These researchers have used genetic engineering techniques to produce hybrids with dwarfed or nonfunctional reproductive organs or that produce heavier seeds that are not carried by the wind. In addition, intergeneric crosses have been accomplished between *B. davidii* and distantly related *Buddleja* cousins to produce pollen-sterile plants (Podaras, 2005). The offspring are not only sterile, but also more shade-tolerant than their parents and exhibit flowers that are more than twice the size of their female progenitor (i.e., *B. davidii* ‘White Profusion’).

B. davidii are shrubs or small multi-stemmed trees that have a great degree of morphological and physiological plasticity (Miller, 1984; Shi et al., 2006). *B. davidii* may be found as solitary individuals or in dense thickets. Some individuals have a spreading habit and are able to repeatedly grow from the base of the plant creating a total bole diameter of 40–50 cm and the entire plant may extend over an area of 2–3 m². Other individuals may have a single, slender, stem with a total cover of less than 1 m².

Descriptions of *B. davidii* may vary slightly depending on the environment. In general, stems are four-angled. Suborbicular to ovate stipules are present and range in size from 1–6 mm. The leaves are usually ovate (less commonly lanceolate) and shortly petiolate. The upper surfaces of the leaves are dark green and glabrous or free of hairs; below they are whitish to greyish tomentose (covered with many fine hairs) with stellate and glanduliferous hairs (Leeuwenberg, 1979; Webb et al., 1988; Zheng & Raven, 1996). Leaf edges are serrated. Leaves are wedge shaped, narrowing to a point and range in size from 5–20 cm long and 1–7 cm wide (Zheng & Raven, 1996). The glanduliferous hairs borne on the leaves and stems extrude crystals giving a characteristic sheen that enable identification of seedlings. See Fig. 1 for an illustration of some taxonomic features of *B. davidii*.

B. davidii is semi-deciduous: leaves are shed in the autumn and immediately replaced with a set of new, smaller leaves that persist until the following spring. The autumn leaves are covered with downy hairs. During the spring *B. davidii* produces a flush of leaves. Both spring shoots and leaves are pubescent, however the hairs disappear as the year progresses (Miller, 1984). *B. davidii* is unique because the main meristem grows underground and is not carried aurally as it is in many woody species. As a result, the plant has no main trunk. Instead, several stems originate from the belowground meristem.



Fig. 1 Illustration of *Buddleja davidii* Franchet *a* flowering branch, *b* flower, *c* pistil, *d* open corolla, *e* fruit and *f* seed (Illustrator: P. Grossman)



Fig. 2 The native range (provinces) of *Buddleja davidii* in China are shown in gray

Distribution

Native Distribution

B. davidii is native to central and southwestern China at elevations up to 3,500 m (Fig. 2). The native range of *B. davidii* are the Chinese provinces; Gansu, Guangdong, Gaungxi, Guizhou, Hubei, Hunan, Jiangsu, Jiangxi, Shaanxi, Sichuan, Xizang, Yunnan, and Zhejiang where it can be found as thickets on mountainous slopes (Starr et al., 2003; Stuart, 2006). Wilson (1913) describes stands of *B. davidii* in bottomlands and abandoned cultivated areas in the northwestern Szechuan Province as “...thousands of bushes, each one with masses of violet-purple flowers, delighting the eye on all sides.”

Introduced Range

The Industrial Revolution in Europe led to the rise of the middle class, which led to an increase in the number of personal gardens enclosed in and around European towns (Miller, 1984). In particular, the practice of including exotic species in gardens became popular during the Victorian Age (Thacker, 1979). No emphasis was placed on preventing the spread of these introduced species. Only a few species introduced from the Far East at that time were able to survive outside of gardens and arboreta. One of these species was *B. davidii*.

Several species of *Buddleja* including *B. davidii* were introduced to Europe in the late 1800s and became popular additions to English gardens by the end of the nineteenth century (Robinson, 1898; Webb, 1985). Prior to 1935, there were few reported instances of *B. davidii* naturalizing outside of gardens in the UK (Miller, 1984). It is probable that *B. davidii* had escaped earlier than 1935 from gardens because the species seeded freely

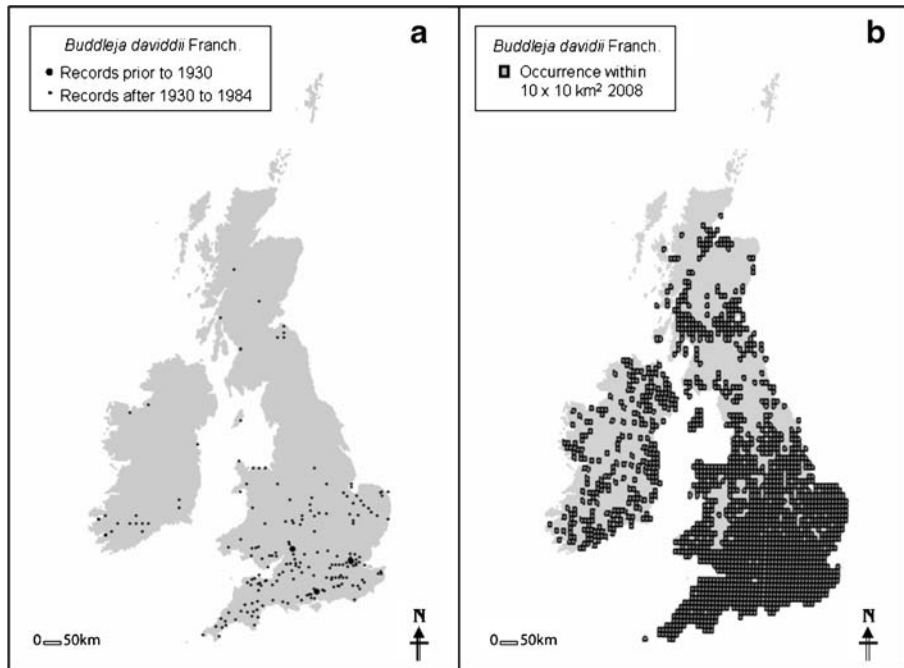


Fig. 3 Distribution of *Buddleja davidii* in the UK in **a** 1984 and **b** 2008. The larger dots on (a) denote locations where *Buddleja davidii* was recorded as naturalized prior to 1930. The smaller dots on (a) are locations of *Buddleja davidii* between 1930 and 1984. Both of the dots on the left describe locations on a 10 km² grid according to the Institute of Terrestrial Ecology at Monks Wood, UK (Miller 1984). Squares in (b) are based upon the data of the National Biodiversity Network (2007; i.e., Botanical Society of the British Isles, Bristol Regional Environmental Records Centre, Environment and Heritage Service, Greenspace Information for Greater London, Lothian Wildlife Information Centre and Staffordshire Ecological Record, NBN Gateway)

in gardens and therefore, had the potential for dispersal and establishment outside of the garden (Thurston, 1930). Observations obtained from the Biological Records Centre at the Institute of Terrestrial Ecology, show that *B. davidii* first became naturalized on a significant scale in the 1930s in limestone quarries, on old walls and on areas of exposed chalk in Great Britain (Fig. 3a; Owen & Whiteway, 1980).

Naturalized *B. davidii* populations expanded, especially in urban areas, after the destruction of European cities during World War II. Bombed sites and building rubble were suitable colonization habitat, and therefore dense *B. davidii* thickets established on these sites (Owen & Whiteway, 1980; Miller, 1984; Coats, 1992). In the 1950s and 1960s in the UK, *B. davidii* became a popular garden shrub, which further contributed to its escape from cultivation and naturalization in the wild (Owen & Whiteway, 1980; Miller, 1984). Local floras provided a description of *B. davidii* distribution post 1945 (Miller, 1984): *B. davidii* appeared to have spread originally along rail tracks where seeds were either carried on the locomotives or blown and drawn along in the slipstream of trains (Miller, 1984). Furthermore, the rock and gravel that lined the railroad were ideal *B. davidii* habitat. Abandoned railway lines where weeds are not controlled expedite the spread of *B. davidii* when they grow into productive thickets in the railway corridors (Blacker, 2000).

B. davidii is currently well established in the UK, primarily in disturbed areas (Anisko & Im, 2001; Stokes et al., 2004; Doughty, 2007). A comparison of distribution in 1984 and 2008 (National Biodiversity Network, 2007) indicates that the distribution of *B. davidii* in the UK has increased by 83% (Fig. 3a, b). *B. davidii* is one of the most common and widely distributed naturalized non-indigenous plant species in the UK flora (Webb, 1985; Thompson et al., 2005): “It is...likely that *Buddleia* occurs as a garden plant or as an escape in almost every town in the British Isles” (Owen & Whiteway, 1980). The National Biodiversity Vascular Plant Database (Botanical Society of British Isles, 2007) lists over 6,000 incidences of *B. davidii* in UK (Fig. 3b).

B. davidii distribution in Europe has been noted as extending from the Mediterranean in the south to Bergen, Norway in the north, and from Spain in the west through to Bulgaria in the east (Sheppard et al., 2006, D. Kriticos unpub. data). In France, *B. davidii* is present in the Paris basin, Pyrenees Mountains, Gironde Estuary, Brittany and the Alpes-Maritimes (ISSG, 2008) and is the most frequently encountered species in wastelands in Brussels, Belgium (Godefroid et al., 2007). *B. davidii* has also been recorded as growing in Germany, Denmark, Italy, Czech Republic, Austria and Switzerland (D. Kriticos unpub. data).

B. davidii is found naturalized in South Africa, Zambia and Zimbabwe (Aluka, 2008) and was introduced to several Asian countries, such as South Korea, where the species is not native (Stuart, 2006). Soon after being introduced to Europe (ca. 1900), *B. davidii* was brought to North America. The species probably escaped cultivation along the eastern coastline and now occurs almost along the entire coastline, and as far inland as Tennessee (Fig. 4). On the west coast, the species occurs from California to British Columbia, Canada (Reichard, 1996; NatureServe, 2007). In South and Central America the species is found in Peru, Ecuador, Bolivia, Columbia, Panama and Mexico (D. Kriticos, unpub. data).

Within Australasia, the species has been recorded as occurring in all Australian states apart from Western Australia and the Northern Territory (D. Kriticos, unpub. data). After naturalizing during 1946 (Healy, 1946) in New Zealand the species has spread widely throughout New Zealand, with the most invasive populations occurring in the North Island (Esler, 1988; Webb et al., 1988; Gibb, 1994).

Influence of Climate on Distribution

As climate is the primary determinant of plant distribution (Andrewartha & Birch, 1984; Woodward, 1987), an examination of the climatic thresholds that regulate occurrence of *B. davidii* provides an insight into the factors governing the current and potential distribution of the species. The current distribution of *B. davidii* indicates the core distribution to be in warmer humid regions that include temperate, subtropical, and Mediterranean climates. The species does extend into cooler continental climates, but the distribution in these areas is somewhat limited. The following description of climatic constraints draws on the findings of Kriticos et al. (2007) who fitted a process based distribution model to observed records in both the introduced and native range of the species. This model was used to both infer the climatic constraints limiting distribution and develop a worldwide potential distribution for *B. davidii*.

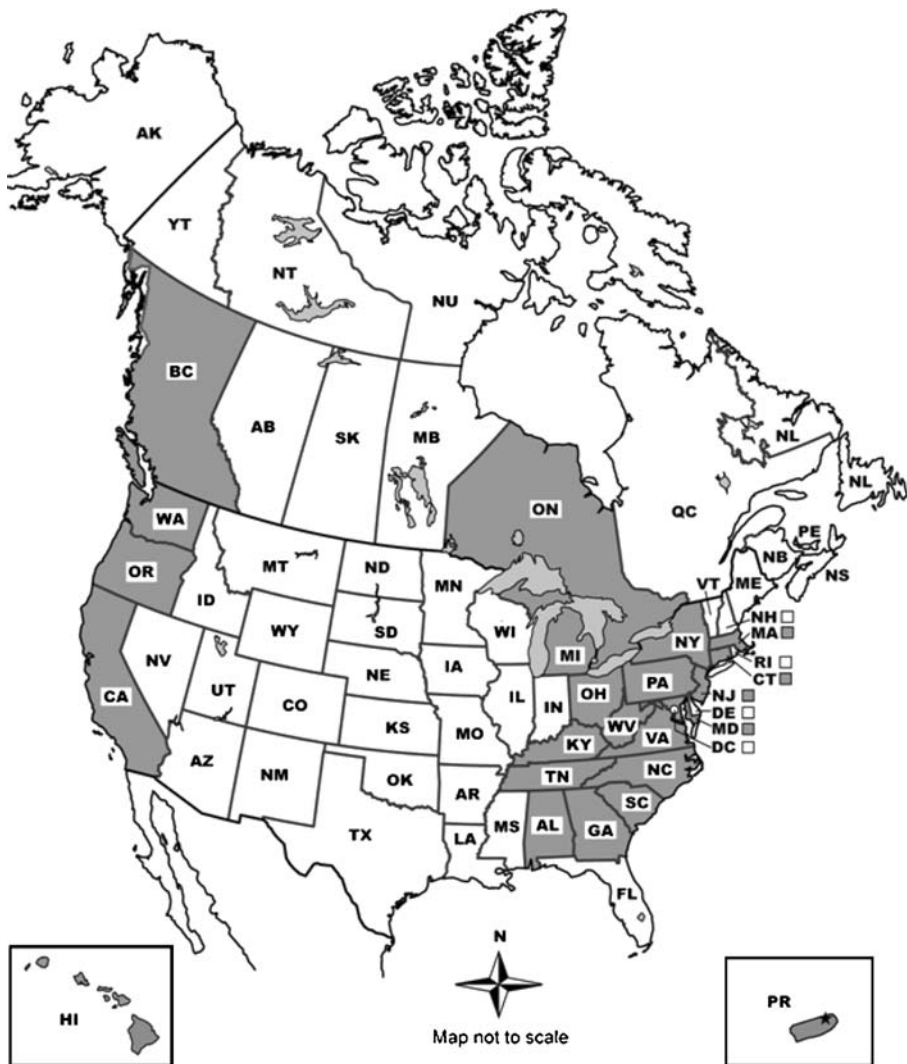


Fig. 4 Distribution of naturalized *Buddleja davidii* in the states, territories, and provinces of the United States and Canada. The shaded states, territories, and provinces in the United States and Canada are locations where *Buddleja davidii* has been recorded as naturalized by NatureServe (2007) and other sources; Alabama (Clark, 1971), California (Roja, 1998; CALFLORA 2007), Connecticut, Georgia, Hawaii (Shannon & Wagner 1996; Wagner et al., 1999; Starr et al., 2003), Kentucky (Gunn, 1959), Maryland, Massachusetts, Michigan, New Jersey, New York (Stalter & Lamont 2002), North Carolina (Mellicamp et al., 1987), Ohio, Oregon (Ream, 2006); Pennsylvania, Puerto Rico (Starr et al. 2003) South Carolina (Mellicamp et al., 1987), Tennessee (Watch List A, 2007), Virginia, Washington (DeFerrari & Naiman 1994; Leach 2007), West Virginia (PLANTS, 2007), and British Columbia and Ontario, Canada (Craig & McCoy, 2005)

B. davidii can tolerate severe cold (-28.8°C ; Stuart, 2006), is considered a USDA zone 5 plant (Podaras, 2005), and is found in regions as cold as Switzerland, northern Scotland, southern Norway, and southwestern British Columbia (Haber, 1996a). Kriticos et al. (2007) found stress from cold combined with insufficient

thermal accumulation excluded the species from eastern and northern China within the native range and prevented the spread of the species into most of Canada, the Russian Federation, Scandinavia, and northern inland USA. Cold hardiness has been found to vary among cultivars, with cold hardy cultivars originating from northwestern China (Podaras, 2005). In colder climates, cultivars bred for milder climates, will shed all leaves and stems, back to ground level, and produce new shoots in the spring (Fell, 1990; Coats, 1992).

The distribution model developed by Kriticos et al. (2007) found that heat stress excluded the distribution of the species from most low lying areas within the tropics. This stress limits the native distribution from extending southwards into low lying areas in Southeast Asia (Laos, Vietnam, Myanmar, Thailand). Other subtropical regions within the introduced range, such as the southern and central USA, also show distinct boundaries that in all likelihood result from heat stress. Heat stress accounts for the absence of the species in low lying northern regions in South America, most African regions north of the equator (with the exception of Ethiopia, and the coastal fringe of the Mediterranean Sea), interior Australia and coastal regions in Australia north of Brisbane.

Dry stress appears to exclude *B. davidii* from the dry Steppe and Desert climatic regions throughout the world (Kriticos et al., 2007). These climatic zones predominantly occur in northern and southwestern Africa, the Middle East, central Asia, central Australia, and the southwestern USA. Given that *B. davidii* occurs in naturalized communities in some of the worlds wettest climates (e.g. in locations on the west coast of New Zealand with a mean annual rainfall of 5,311 mm year⁻¹) the plant does not appear to be very susceptible to wet stress.

Potential Distribution

The process based distribution model developed by Kriticos et al. (2007) projected potential for further expansion. Areas most at risk included Eastern Europe, South Africa, Western Australia, and a broad coastal strip of land within South America from Rio de Janeiro in the north to central Argentina in the south.

Biology

Flowering, Fruiting, and Seed Production

B. davidii cultivars have flower colors ranging from white to yellow and red, but it is the common lilac and purple varieties that occur in the wild (Stuart, 2006). Each *B. davidii* flower is made up of four petals that are fused for three-quarters of their length into a corolla tube. Individual plants, as well as flowers, show a wide range of morphological plasticity: some plants bear mostly four-petalled flowers, but also are expressed as variants possessing five to nine petals in one flower. These variants usually occur in the middle of the inflorescence (Fig. 1a, Miller, 1984). The flowers are zygomorphic, possessing four stamens with filaments fused to the corolla wall and anthers situated about two-thirds along the length of the tube. The corolla tube is 5–8 mm long, opening at the top to form separate petals. Generally, this part of the flower is colored a variant of purple, while the interior of the flower is orange with a

series of yellow nectar guides leading to the interior of the tube (Fig. 1d). This intense orange-yellow spot at the base of the inner surface of the corolla tube of each *B. davidii* flower can be attributed to a diterpene (non-cyclic crocetin-gentiobiose ester). This diester has the same chemical composition as a yellow colorant in foods (Aoki et al., 2001; Houghton et al., 2003). Fine hairs line the length of the tube and are most dense at the top. The superior ovary is bilocular with a stigma and style that extend along one third of the tube and ends well short of the anthers. There is a small ring of sepals around the base of the corolla tube. The corolla tube elongates until it is three to four times the length of the sepals, before the petals finally open. Flowers have minute pedicels, if any (Leeuwenberg, 1979).

B. davidii inflorescences are indeterminate corymbose-panicles that can extend up to 30 cm in length (Findley et al., 1997). Some inflorescences may be densely massed, others may be sparsely assembled around the stem (Miller, 1984). Each stem normally bears one large terminal inflorescence and two smaller lateral panicles arising directly behind it (Miller, 1984).

Flowering is asynchronous (Miller, 1984), and normally occurs when the plant reaches 2 years of age (Watt et al., 2007), although anecdotal information indicates that it may occasionally occur in the first year (Owen & Whiteway, 1980; M. Watson, pers. comm.). Each panicle consists of individual flowers that mature acropetally from the base to the top of the inflorescence (Findley et al., 1997). *B. davidii*, classed as a summer-flowering species (Moore, 1960), grows rapidly, and flowers freely for several weeks on new growth from mid-summer until frost. Flowering is initiated in response to the long days of summer (>12 h of day; Moore, 1960). The flowering period has been found to extend from late spring to the mid-autumn in the northern hemisphere (Zheng & Raven, 1996) and from early summer to late summer, and occasionally as late as mid-autumn, in the southern hemisphere (Webb et al., 1988). Individual flowers last for 1–3 days and a panicle may persist for >2 weeks (Findley et al., 1997). Wide variation in the time of first flowering has been noted both between years, individuals, and locations in the UK (Miller, 1984; Fitter & Fitter, 2002). Findley et al. (1997) found that exposing *B. davidii* cultivars to elevated, twice-ambient ozone concentrations delayed first flowering date by 4 days.

The seed capsules (Fig. 1e) are brown, narrowly ellipsoid to narrowly ovoid, 5–9×1.5–2 mm, acute at the apex, narrowed towards the base, mostly 3–4 times as long as the calyx, and are often smooth, or have stellate hairs (Zheng & Raven, 1996; Wilson et al., 2004b). The capsule has an impressed line along the line of dehiscence (Leeuwenberg, 1979). The flowers are borne upright, which apparently favors pollinating insects and enables ready dissemination of seeds from the capsule (Miller, 1984).

Seeds are medium brown, thread-like, and long-winged, and are borne in a cylindrical two-valved capsule. The fine seeds range in size from 3–4×0.5 mm with the center slightly thickened (Fig. 1f; Norman, 2000). The seed body is no more than 0.5 mm in length and <0.06 mg in weight (Cornelissen et al., 1996). Seeds are also minutely reticulate, with long wings (axial placentas) at each end. Seeds are arranged tightly packed, with their long sides aligned with the axis of the capsule (Miller, 1984).

B. davidii does not self-pollinate and therefore depends on insect pollinators (Miller, 1984; Norman, 2000). The absence of self-pollination has been linked to the heavy allocation of resources to insect attractants in other species, which is consistent

with the presence of conspicuous flowers, pungent scent and abundant nectar in *B. davidii* (Miller, 1984; Houghton et al., 2003). A single mature *B. davidii* individual can produce millions of seeds; however, estimates of the number of seeds produced vary (100,000 to 3,000,000) among *B. davidii* cultivars (Miller, 1984; Brown, 1990; Wilson et al., 2004b; Thomas et al., 2008c). Seed formation and ripening typically occurs within 3 weeks after flowering (maturing in the autumn; Miller, 1984; Stuart, 2006).

Dispersal

Naturalized *B. davidii* plants in the UK retain seeds on the plant throughout winter, and then release the seeds in early spring into summer (Miller, 1984). During arid periods, the sides of the seed capsules dry and curl outward (Miller, 1984). The distal ends of the capsule open outwardly, which exposes them to the air and enables seeds to disperse if there is sufficient air movement to shake them free of the capsule (Miller, 1984; Stuart, 2006). With an increase in humidity, the capsule closes (in less than 5 min) and dispersal ceases until the humidity declines again. *B. davidii* in Oregon does not release its seeds until mid to late winter (Ream, 2006) while in New Zealand dispersal can start as early as late autumn through to early winter (D. Peltzer and M. Thomas, pers. comm., N. Tallent-Halsell, unpubl.).

Seed dispersal may take place over an extended period of time depending on the conditions (Miller, 1984; Wilson et al., 2004b). Seeds dispersed prematurely were confirmed to be less viable than those retained in the capsule (Miller, 1984). Once released, the majority (95%) of seeds from an individual *B. davidii* plant were dispersed 10 m or greater beyond the parent (Miller, 1984). The maximum dispersal distance for *B. davidii* seeds has not been determined.

B. davidii seeds are also reported to be water-dispersed, especially along sea coasts, floodplains, and riparian corridors (Miller, 1984; Webb et al., 1988; Brown, 1990). Seeds can be washed downstream during flood events, where they can establish in new habitats (ISSG, 2008). Automobiles have been found to physically disperse *B. davidii* seeds (von der Lippe & Kowarik, 2007), while the low pressure drag created by trains most likely has spread *B. davidii* seeds throughout railway networks in Europe and North America (Blacker, 2000). Germinants have been observed in the mud stuck to machinery (N. Tallent-Halsell, unpubl.).

Plants readily reproduce asexually from stem and root fragments (Miller, 1984; Smale, 1990). *B. davidii* individuals that have been disturbed by flooding and mechanical means have been observed regenerating from buried stems, stumps, and roots soon after the disruption (N. Tallent-Halsell, unpubl.). *B. davidii* debris, left after removal attempts, can regenerate, flower, and spread, if left in on site on floodplains (H. Turnbull, pers. comm.).

Soil Seed Bank

B. davidii is relatively short-lived in the seedbank. Seed viability in the laboratory was found to remain high up to 2.5 years, but declined rapidly between 2.5 and 3.5 years, after which time no seed was found to be viable (Miller, 1984). Under field conditions viability is likely to be considerably less. Several environmental factors such as soil type and moisture, seed depth, seed predation and microbial and

fungus activity contribute to reduced viability and removal of *B. davidii* from the seed bank (Miller, 1984). In a survey of gardens in the UK, Thompson et al. (2005) found *B. davidii* seeds were the most abundant non-indigenous seeds in the seed bank. *B. davidii* seeds have also been found in woodland seedbanks in the UK (Warr et al., 1994).

Germination

Within 24 h after the *B. davidii* seed is hydrated, the seed releases a yellow pigment (the composition and function of which is unknown; Miller, 1984). The membranous outer seed coat, which has two wings for dispersal, swells during imbibition to form a sheath in which the embryo expands and the radicle elongates. The radicle ruptures the seed coat at a point about half-way along the length of a wing (Miller, 1984). Immediately before the seed ruptures, a circular ring of fine hairs, originating from the junction between the hypocotyl and the epicotyl, extends through the seed coat. The hairs apparently function as initial absorptive organs: the hairs absorb water that may support the rapid expansion and proliferation of cells in the subsequent stages of development. Once the radicle has emerged, the gap in the seed coat is widened by the growth of the hypocotyl until the cotyledons are drawn out behind it. Although the seedling is completely free of the seed coat at this stage, it can remain attached to the cotyledons for several days (Miller, 1984). Germinants produce roots that may extend more than 10 cm, branch multiple times yet remain near the surface, within the first 3 weeks before shoot development begins (i.e., before the extension of the cotyledons; Miller, 1984).

Both seedbed water potential and temperature are the critical determinants of germination rate and the total germination percentage. Recent research has shown that under constant conditions *B. davidii* will not germinate below a base temperature of 6°C and a base water potential of −1.8 MPa. Numerous studies have demonstrated the optimum constant temperature for germination to be 25°C (Jay, 2006; Watt et al., unpubl.), while the ceiling temperature above which germination ceases is predicted to be ~35°C (Jay, 2006). The hydrothermal time germination model has been successfully used to model *B. davidii* seed germination across a wide range of constant water potentials over both sub- and supra-optimal temperatures (Watt et al. unpubl.).

B. davidii seeds do not demonstrate innate dormancy (Miller, 1984) but are very sensitive to burial depth. Previous research shows that at burial depths of 1.0 and 1.5 cm there is respectively <10% and <1% emergence (Miller, 1984). *B. davidii* seeds were not found to be capable of germinating under anaerobic conditions (Miller, 1984). Although very low (1.05%) oxygen tensions prevent germination, at oxygen tensions exceeding 5% germination is unaffected (Miller, 1984). Soil pH has been found to have a negligible effect on germination (Miller, 1984), and intraspecific allelopathy has no direct effect on *B. davidii* germination.

Growth and Metabolism

Seedling shoots are obtusely angled, floccose (appear cottony) and tomentose (having very fine hairs on the surface) when young (Zheng & Raven, 1996). Germinants up to 4 weeks old are sensitive to drought (Miller, 1984), and require



Fig. 5 *Buddleja davidii* seedlings in floodplain gravel soil (Kowhai River, South Island, New Zealand)

full sun (Feng et al., 2007). After 4 weeks, seedlings become drought-tolerant (Feng et al., 2007). Crystals have been noted to form on the leaves. These crystals may aid drought resistance and salinity tolerance (Miller, 1984).

Seedlings can grow on nitrogen (N) poor substrates (Feng et al., 2007). Initial seedling survival may be enhanced by microsites of gravel and stone shelters found on floodplains (Miller, 1984). Stony soils are well aerated and provide numerous microsites in which atmospheric humidity can increase, preventing desiccation of the seed and seedlings (Fig. 5). However, there is no evidence that *B. davidii* dominates New Zealand floodplains by establishing in different microsite types than native species (Walker et al., 2006).

B. davidii is fast-growing and has been reported to be able to increase between 0.5 and 2 m in height annually (Owen & Whiteway, 1980; Watt et al., 2007). Seedling stem diameter can increase annually by as much as 5.6 cm year⁻¹ (Watt et al., 2007). *B. davidii* seedling mean relative growth rate (RGR mean±SE 0.200±0.0048 g day⁻¹, *n*=36) was the second fastest reported by Cornelissen et al. (1996) in a comparison of the seedling growth of 80 woody species from the UK and North Spain. As an example of this rapid growth a flush of *B. davidii* plants established on a building rubbish heap, grew to an average height of 2 m and flowered in one season. Within the next 3 to 4 years, the thicket formed with an average height of more than 4 m (Owen & Whiteway, 1980). *B. davidii* roots grow rapidly and develop extensive networks of fine roots. Main root development extends down 4 m or more in the soil (Miller, 1984) and roots are capable of surviving damage sustained during flooding and mechanical removal.

B. davidii accumulates soil phosphorus (P) (Bellingham et al., 2005; Dickie et al., 2007). Although Harley and Harley (1987) reported *B. davidii* as non-mycorrhizal, Camargo-Ricalde et al. (2003) found *Buddleja* spp. (species unidentified) in Mexico

as possessing arbuscular mycorrhizal (AM) fungal structures. Dickie et al. (2007) confirmed the presence of AM in *B. davidii* growing in New Zealand, the UK and North America.

The life span of *B. davidii* is variable. Individual plants may not live for more than 20 years. Plants older than 20 years were found to die from stem rot (Smale, 1990; Binggeli, 1998). However, based on aerial photographs and ring counts *B. davidii* > 30 years old were found at the Kowhai River, South Island, New Zealand (Bellingham et al., 2005).

Ecology

Habitat

Around the world, native and non-indigenous *B. davidii* is an opportunist that readily establishes in natural and disturbed areas and is able to tolerate a wide range of physical conditions (Fig. 6; Wilson, 1913; Williams, 1979; Miller, 1984; Smale, 1990; Reinhardt et al., 2003; Bellingham et al., 2005; Godefroid et al., 2007). In both its native and introduced range, *B. davidii* establishes naturally or on anthropogenically disturbed sites such as quarries, urban waste grounds, abandoned cultivated areas, clearcut forests, along transport corridors (Godefroid et al., 2007) and on walls and rock faces (Wilson, 1913; Rishbeth, 1949; Segal, 1969; Owen & Whiteway, 1980; Miller, 1984). The ability of *B. davidii* to withstand the extreme environment of the disturbed landscape may enable it to fill vacant niches (Rohde, 2005; Woodley, 2006). Segal (1969) found *B. davidii* to be a late colonizer in a survey of vegetation established on European walls.



Fig. 6 *Buddleja davidii* (shrub on the right) on Conway River floodplain, South Island, New Zealand

B. davidii thrives on a wide range of soil types. The species is able to establish on piles of calcium based building debris and masonry walls (Owen & Whiteway, 1980; Miller, 1984; Godefroid et al., 2007). Surveys of *B. davidii* thickets in disturbed areas of southern England (Miller, 1984) and Belgium (Godefroid et al., 2007) found that soils on which these thickets established were high in sand, nutrient poor, and high in calcareous substrates (including concrete and building debris). Yet *B. davidii* does not appear to be an obligate calcicole: It is able to flourish in calcium-deficient soils as well (Humphries & Guarino, 1987). Miller (1984) and Godefroid et al. (2007) have found that *B. davidii* was capable of colonizing areas with a high pH. Dolomitic lime additions increased *B. davidii* growth by increasing the uptake of calcium and magnesium (Gillman et al., 1998).

Biotic Interactions

Self thinning of *B. davidii* is quite marked during the years immediately following stand establishment. In a New Zealand stand of *B. davidii* located in Urewera National Park, Smale (1990) measured stand densities for *B. davidii* across a range of age classes. Intense self thinning was found to occur over the first few years with stand densities declining from several million plants per hectare in a 1 year old population, to an average of about 13,000 plants ha⁻¹ in 3 to 5 year old stands. Self thinning was found to be complete by the time stands reach about 10 years of age, at which time density averaged 2,500 plants ha⁻¹ (Smale, 1990).

B. davidii seems to have both an inhibitory and facilitative influence on co-occurring native plants. Field surveys and experiments have demonstrated that *B. davidii* is shade-intolerant. The absence of *B. davidii* seedlings beneath dense *B. davidii* thickets (Miller, 1984; Bellingham et al., 2005) is apparently due to competition for light, not self-allopathy (Miller, 1984). Only 5% of seeds of naturalized *B. davidii* plant studied in the UK fell within 10 m of the parent plant while ca. 95% were dispersed >10 m (Miller, 1984). The dispersal of the majority of seed well beyond the parent plant may be advantageous to early colonizing species as it reduces the likelihood of out-crossing between siblings and self (Miller, 1984).

Succession

Although *B. davidii* colonizes disturbed sites, whether it alters successional trajectories over the long term is yet undetermined (Tallent-Halsell, 2008). To address the impact that *B. davidii* may have on successional trajectories in disturbed habitats Miller (1984) surveyed the dispersal pattern and densities of *B. davidii* in three different stages of the plant's life cycle as it established in an abandoned gravel pit in Slindon, West Sussex, UK. Her analysis did not reveal a high level of intraspecific competition nor predictable development sequences of vegetation associated with the presence of *B. davidii*. Conversely, studies by Williams (1979) and Smale (1990) in Urewera National Park, North Island, New Zealand revealed that *B. davidii* quickly displaced primary native colonizers, both herbaceous, and woody species such as *Kunzea ericodes* on New Zealand floodplains. This accelerated the reforestation process back to native forest in streambeds (Smale, 1990).

Morphological and Physiological Traits

There are a number of characteristics that allow *B. davidii* to dominate when introduced into disturbed environments. One key factor is the high propagule pressure exhibited by the species that allow the dispersal of a large amount of seed that germinates within a relatively short time, under adequate seedbed moisture and temperature (Walker et al. 2006; Watt et al., unpubl.). The resulting seedlings can establish and grow relatively quickly and the species exhibits rapid growth during both the juvenile and adult stages as long as light availability remains optimal (Smith & Knapp, 2001; Daehler, 2003). Other competitive advantages include a relatively short time to flowering and low susceptibility to herbivory and disease (Gillman, 1998).

B. davidii plants have been reported to retain most seed on the plant over winter (Miller, 1984; Ream, 2006), and only release seed under dry conditions. Given that *B. davidii* has no primary dormancy mechanism, retention of the seed on the plant until spring is a useful strategy for reducing the chance of seed encountering unfavorable conditions for germination and seedling growth. Release of seed during dry periods, when they are capable of becoming airborne, may be an adaptation to increase the distance to which seed can be dispersed (Miller, 1984).

Nitrogen and water are important resources that often limit plant growth. Invasive species, especially in dry and infertile environments, can increase invasiveness by increasing N- and water-utilization efficiencies (Feng et al., 2007). Several ecophysiological characteristics have been identified that facilitate *B. davidii* invasiveness in infertile environments. *B. davidii* leaves are high in N and P concentrations relative to other woody species (Cornelissen et al., 1996; Bellingham et al., 2005; Feng et al., 2007; Thomas, 2007). A characteristic common to many woody colonizers, including *B. davidii*, is the ability to assimilate nitrate (i.e., process through which inorganic N is converted to ammonia and then to organic N) in their leaves rather than in roots or stems (Al Gharbi & Hipkin, 1984). In addition to high leaf N, *B. davidii* has been found to allocate more leaf N to photosynthesis, and consequently has a higher photosynthetic capacity, than a number of other woody species (i.e., *Berberis vulgaris* L., *Cornus sanguinea*, *Sambucus nigra*, *Crataegus monogyna* Jacq. and *Betula pendula* Roth; Feng et al., 2007).

The high specific leaf area of *B. davidii* may also confer competitiveness. In a comparison of eighty woody species from the UK and North Spain *B. davidii* seedling specific leaf area (SLA) was found to be the second highest SLA (SLA mean \pm SE 52.44 \pm 1.77 mm² mg⁻¹, $n=36$; Cornelissen et al., 1996) which increased more rapidly than most species as the plants matured (Feng et al., 2007; Thomas, 2007). High values for SLA allow greater light interception per unit leaf area, which in turn is likely to be associated with higher growth rates, as light interception is the main determinant of potential growth (Monteith, 1977). Previous research has shown specific leaf area to be significantly higher in invasive species than native species (Daehler, 2003).

Herbivory

B. davidii appears to be resistant to attack by most herbivorous insects in the western world. This resistance has been noted in the literature and has been attributed to the production of defense compounds that are not common (Gillman, 1998). *B. davidii*

leaves are palatable to cattle and goats, but apparently not to deer (Gillman, 1998). In addition, leaves appear to be palatable to slugs, snails and other polyphagous insects such as the aphids (*Myzus persicae*), the red spider mites (*Tetranychus urticae*), the glass house whiteflies (*Trialeurodes vaporariorum*) and certain oligophagous insect species (Miller, 1984). A few specialized insects have been found feeding on *B. davidii*, including the weevils *Gymnaetron tetrum*, *Cleopus japonicus*, and *Mecynolobus erro*, a dipteran leaf miner (*Amaroumyza verbasci*) and a leaf bug (*Campylomma verbasci*).

B. davidii has evolved strategies to survive defoliation. In comparison to undefoliated plants, Watt et al. (2007) found high defoliation induced increased light use efficiency, biomass allocation to leaves, specific leaf area, and reduced rates of leaf loss. Partially defoliated *B. davidii* plants have also been found to have greater leaf size and retain leaves for longer periods, than undefoliated plants (Thomas et al. 2008b). However, defoliation does appear to reduce seed number and mass per plant (Thomas et al. 2008c).

Despite the relatively strong compensatory response to defoliation that *B. davidii* exhibits, repeated herbivory over several growing seasons is likely to negatively impact growth. *B. davidii* has been found to remobilize N for new spring growth from older leaves with little contribution of N from woody tissue, even when they are substantially defoliated (Thomas et al. 2008a). This has important implications for biocontrol of *B. davidii*. New growth early in the season depends largely on stored N, but the amount of N that can be released is determined by the pool size of the storage tissues (Millard & Proe, 1993; Grelet et al., 2003). Thus, in species, such as *B. davidii*, that store N primarily in leaves, ongoing defoliation will greatly diminish their storage capacity and thus weaken the foundation for future spring growth. At the same time this defoliation will compromise the plant's assimilatory capacity and ability to engage compensatory growth following herbivore attack. This detrimental impact on growth will be particularly pronounced on N deficient sites, as defoliated plants rely more on soil uptake than undefoliated plants to supplement the remobilization from leaves (Thomas et al., 2008a).

B. davidii demonstrates little susceptibility to disease: however, some cultivars carry cucumber mosaic virus, alfalfa mosaic or tomato ringspot virus. These viruses could negatively affect the horticultural industry (Eric & Grbelja, 1985; Perkins, 1991; Hughes & Scott, 2003). Viral infections such as these reduce plant vigor and adaptability and provide a source for cross-contamination of landscape plants or crops. When viruses are eliminated during tissue culture plant health can be improved (Duron & Morand, 1978; Perkins & Hicks, 1989). Cultivars of the genus *Buddleja* in Europe suffer from apical dieback, a disorder that reduces plant quality. Micropropagation techniques are currently being developed that eliminate endogenous bacteria and produce healthy stock plants (Phelan et al., 2005).

Human Ecology of *B. davidii*

Medicinal Uses

Widespread sources indicate that certain species of *Buddleja* have been used for centuries as folk medicine for a variety of ills such as cancer, snakebite, infections, hemorrhage, cardiac disease, kidney disorders, sedative effects, digestive disorders, arthritis, rheumatism, and skin and respiratory conditions (Norman, 2000; Fan et al.,

2008). Nevertheless, various *Buddleja* species have played a relatively minor role in traditional medicine (Houghton 1984; Houghton et al. 2003; Fan et al., 2008). Several types of chemical compounds have been isolated from plants, including flavonoids (i.e., secondary metabolites that produce pigments and are associated with protection from microbes and insects) and other shikimate-derived compounds (i.e., the common aromatic biosynthetic pathway; Houghton et al., 2003; Sprenger, 2007). Leaves of certain species of *Buddleja* have been used for centuries in China for fishing because they are known to kill fish. Three glycosides, catalpol, methylcatalpol and aucubin, were found initially by Duff et al. (1965). Additionally, five novel toxic sesquiterpenes (buddledin A, B, C, D and E) that are piscicidal (i.e., toxic to fish) have been isolated from the root bark (Yoshida et al., 1976). These sesquiterpenes may also have deterrent effects on potential herbivores. Further work on toxic compounds found in *B. davidii* has been expanded on by Houghton et al. (2003; i.e., buddledin A 28 fungicidal properties) and Fan et al. (2008; i.e., linarin has acetylcholinesterase-inhibitory activity).

Horticulture and Butterfly Enthusiasts

B. davidii is a widely cultivated and popular garden plant of economic value to the horticultural industry (Turnbull, 2004; Wilson et al., 2004a). Certain *B. davidii* cultivars were worth over \$200,000/year to Georgia, USA, plant growers (Dirr, 1997). To growers outside of Georgia, plants were worth over \$1,000,000 annually (CANR, 1996). Oregon exports approximately 66% of its *B. davidii* nursery crops to other states and Canadian provinces outside of the Pacific Northwest (Ream, 2006).

In addition to the aesthetic and fragrant appearance of *B. davidii*, the flowering shrub has been closely linked with butterflies, moths, and hummingbirds. Butterflies (Order Lepidoptera) observed visiting *B. davidii* include the Peacock butterfly (*Inachis io*), the Marbled white butterfly (*Melanargia galathea*), the Eastern comma butterfly (*Polygonia comma*), the Monarch butterfly (*Danaus plexippus*) and several Swallowtail butterflies, including the Common, Eastern tiger and Spicebush butterflies (*Papilio machaon*, *P. glaucus*, *P. troilus*), Sachem (*Atalopedes campestris*), Silver-spotted skipper (*Epargyreus clarus*) and Painted lady (*Vanessa cardui*; Giuliano et al., 2004; Stuart, 2006). Also, many other types of wildlife are attracted to the clear, sugary nectar of *B. davidii* flowers. Moths (including the hummingbird hawk-moth, *Macroglossum stellatum*), broad-bordered bee hawk-moth (*Hemaris fuciformis*), wasps, hornets, lacewings and beetles have all been noted as visitors to *B. davidii* flowers (Stuart, 2006). In the New World, Hummingbirds (Trochilidae) have been observed to visit gardens with *B. davidii* (Pickens, 1931; Stuart, 2006).

Bruner (2005) found that *B. davidii* were visited by native butterflies more than five other *Buddleja* species. Giuliano et al. (2004) studied plant preference by Lepidopteran species, and found that Lepidopteran in urban parks in New York City used (i.e., as a food source and resting area) *B. davidii* more than other plants in the same vicinity.

Policy

Human activity is an increasingly important mechanism of plant dispersal (Hodkinson & Thompson, 1997). Gardening is a worldwide recreational pastime

that has contributed to the spread of many plants species around the globe (Thacker, 1979; Hodkinson & Thompson, 1997; Reichard & Hamilton, 1997; Reichard & White, 2001). In particular, the horticultural trade has been recognized as one of the main pathways for plant invasions (Dehnen-Schmutz et al., 2007).

Naturalized *B. davidii* is considered by some problematic because it may potentially out-compete native, agricultural, and forestry taxa. It competes strongly with plantation pine species for light, and thus, has a substantial detrimental impact on growth of plantation species in a number of countries, including New Zealand (Richardson et al., 1996), where it is considered to be the fifth most problematic exotic weed (Watt et al., 2008). *B. davidii* colonizes abandoned areas and is considered an urban invasive (Reinhardt et al., 2003). Transportation routes have been negatively affected by naturalized *B. davidii* in Europe (Reinhardt et al., 2003; Blacker, 2000). *B. davidii* was listed as noxious in 1973, 1993 and 2000 by the New Zealand Ministry of Agriculture and Forestry and cannot be propagated, released, displayed or sold under the Biosecurity Act Sections 52 and 53 (NZ MAF, 2009). In the Blue Mountains of Australia, the species has been listed as a bush invader (Weeds of Blue Mountain Bushland, 2007). However, *B. davidii* has not yet recognized as a weed of national significance in other areas of Australia even though congeners *B. asiatica* and *B. dysophylla* have (Weeds Australia, 2007).

In the USA *B. davidii* is currently listed as a “B” designated noxious weed by the Oregon Department of Agriculture. It appears on the “most invasive” species list of the Pacific Northwest Exotic Pest Plant Council and the native Plant Societies of Oregon and Washington (Savonen, 2009). The Oregon State University Extension Service Master Gardener Program no longer recommends *B. davidii* for butterfly gardens because of its invasiveness (Savonen, 2009). The species is on the invasive species prohibited plant list in Eugene, Oregon and is listed as a Class B noxious weed by the Washington State Noxious Weed Control Board (USDA, 2009; WSNWCB, 2007). The California Invasive Pest Plant Council (Cal-IPC) has evaluated *B. davidii* but it has yet to be listed (CALFLORA, 2009). The species is a category 3 watch species in the New York metropolitan region (Brooklyn Botanic Garden, 2007). The US EPA Green Landscaping:Greenacres and US Fish and Wildlife Service BayScapes programs specifically identified *B. davidii* as an ornamental that should no longer be used for landscaping (USFWS, 2007; Welker & Green, 2007).

Leach (2007) and Ream (2006) reported that *B. davidii* has invaded riparian areas in Oregon and Washington, and has replaced riparian native *Salix* spp. and *Populus* spp. *B. davidii* encroachment along riparian corridors may affect salmon spawning habitat (H. Turnbull, pers. comm.). Although gardens have been identified as the primary source of invasive *B. davidii* seedlings in Oregon (67%), production nurseries contributed seedlings as well (Ream, 2006). Furthermore, plants sold by the nurseries probably increase the amount of seeds that can disperse to wild lands in Oregon. Efforts to curtail the spread of *B. davidii* in Oregon prove ineffective because only *B. davidii* was elevated to the noxious weed quarantine list in 2004. None of the cultivars were included on the list. All *B. davidii* sold in Oregon are of named cultivated varieties, such as “Black Knight” and “White Profusion,” and thus, are exempt from regulation (Ream, 2006). The cultivars are fertile members of the species and are capable of setting seed. Seed dispersal from cultivars is evident as

white flowers have appeared on wild plants in places that once only had the common lilac and purple varieties (Stuart, 2006).

In Canada, *B. davidii* has invaded Garry Oak ecosystems (Craig & McCoy, 2005) and has been included as an “alien” species on Canadian plant lists (Haber, 1995, 1996b, c; Lomer et al., 2002). However, it has not been legally designated as a noxious species. Since the time the species was introduced to Germany in 1900, *B. davidii* has become one of the most common opportunistic plants (Kreh, 1952; Bönsel et al., 2000; Reinhardt et al., 2003). *B. davidii* is considered one of the top 20 weeds in Western Europe (Sheppard et al., 2006).

On the other hand, efforts by the Keep Croyley Green group (KCGG) in the UK have resulted in the Development Control Committee of Hertfordshire registering a *B. davidii* field as a “Village Green” and thus guaranteeing its protection from destruction in perpetuity (KCGG, 2007). A quarry that was later used as an asbestos waste dumping area after mining was abandoned, now has naturalized thickets of *B. davidii* that are valued for beauty and wildlife (i.e., butterflies, birds, grass snakes, foxes, bats and badgers) attraction (Doughty, 2007; KCGG, 2007; Theivam & Allen, 2007). According to the Countryside and Rights of Way Act of 2000 (MOJ, 2008), any plant, shrub or tree, of whatever origin, is assigned as a natural feature of the protected landscape. Therefore, the act protects native and non-indigenous species from destruction. The consequence of protecting an invasive non-indigenous plant species in this case can be debated. However, efforts to control *B. davidii*, should it prove to be invasive and problematic, would be hampered by legal protection.

Management

Land managers are tasked with the conservation and preservation of wild lands. This often involves rehabilitating areas that are infested with invasive non-indigenous plant species. Several methods are available (Reichard, 1996; Reinhardt et al., 2003; Ream, 2006). Mechanical, physical, or combined mechanical and physical methods have had mixed results in controlling *B. davidii*. Dead-heading (removing seed capsules before they ripen) is recommended to reduce the spread of seeds (Turnbull, 2004; Ream, 2006; Savonen, 2009). Yet many gardeners are reluctant to deadhead because it reduces the quality of the shrub in subsequent years. Deadheading also increases the plant’s susceptibility to disease (Warr et al., 2002).

Physical removal on a small spatial scale may help in the early stages of invasion. Young shrubs can be dug up, although this method is not recommended for mature plants in well established populations. Cut plants should be treated with glyphosate herbicides (Kaufman & Kaufman, 2007). Small-scale eradication efforts may be successful; however, the removal efforts can be so damaging that they change the habitat so it is no longer suitable for desired species and again susceptible to reinvasion (Zavaleta et al., 2001; Myers & Bazeley, 2003). *B. davidii* removal sites should be replanted with native species and monitored for regrowth of *B. davidii*.

Glyphosate herbicides without surfactants were effective against small shrubs in Oregon (Ream, 2006). Large shrubs that have heavy pubescence were somewhat less vulnerable to foliar application. Treatment with triclopyr or imazapyr did not appear to be effective, and there was concern about the negative consequences to native plants and invertebrates potentially impacted by spraying these herbicides (Ream,

2006). Directed and precise application, such as painting cut stumps, was effective, but more labor intensive and costly than spraying. Additionally, Ream (2006) noted that some seeds appeared to have matured on the herbicide treated plants. Zazirska and Altland (2006) prefer cutting and painting over the direct spraying method. The nature of cutting and painting removes all flowers and seeds; therefore, if cut stems are removed from site, seed maturation and dispersal are not of concern. Care must be taken in removing *B. davidii* debris because stem and root fragments readily regenerate. Debris piles that are not burned, composted, or otherwise treated in such a way to kill all seeds and stems and root fragments can become a concentrated source of plants in the next season.

In New Zealand *B. davidii* is typically controlled in recently clearcut stands using herbicides that are usually aerially applied immediately before and then again after planting of plantation conifers. This method has been used with some success to control *B. davidii* for up to a year after planting, and typical herbicides used include glyphosate and metsulfuron (prior to planting) and terbuthylazine and hexazinone (M. Watson unpubl.). Another method that is relatively widely used is the aerial sowing of cover grasses such as *Holcus lanatus* (Yorkshire fog) in the autumn prior to planting. Oversowing using these grasses has been found to effectively suppress the growth of young *B. davidii* seedlings. In 2006, New Zealand introduced the weevil *Cleopus japonicus* as a potential biocontrol agent for *B. davidii* (Kay & Smale, 1990). Laboratory testing of *Cleopus japonicus* indicated that grazing by *C. japonicus* had a substantial negative effect on *B. davidii* growth (Brockhoff et al., 1999). Although it is too early to judge the field effectiveness of this agent an initial evaluation indicated that *C. japonicus* defoliated approximately 60% of foliage on plants within the immediate release area (M. Watson unpubl.).

Sterile cultivars are being developed to allow the continued presence of *B. davidii* in gardens, and curtail invasiveness (Pellett, 2006). The *B. davidii* breeding program at the University of Arkansas has been successful in developing a sterile *B. davidii* hybrid to replace the invasive varieties (Lindstrom et al., 2002). Sterile strains may extend *B. davidii* flowering time as resources may be no longer shunted to fruit and seed production. This could, in turn increase the tree's attractiveness to butterflies. Bruner (2005) speculates that *B. davidii*'s attractiveness to butterflies could be enhanced further if sterility could be achieved without disrupting normal nectar production.

Conclusion

Prolific seed production, a short juvenile period, aggressive growth, and a wide range of tolerances to various environmental conditions are several of a suite of traits shared by plant species bred for horticulture. Invasive plant species share these same qualities (Reichard 1996; Rejmánek & Richardson 1996; Wilson et al. 2004b). These same characters allow *B. davidii* to readily colonize disturbed sites. Extremely low temperatures (<28.8°C), drought (most likely for seedlings only) and low-light levels (shade) are factors known to limit *B. davidii*'s distribution worldwide. The absence of the species from low lying areas in the tropics also suggests that *B. davidii* suffers from heat stress at high temperatures, which prevents colonization of tropical regions.

Consequently, the species is found primarily in regions with Mediterranean, temperate, subtropical and continental climates. Within these regions *B. davidii* colonizes frequently disturbed open, lightly-vegetated areas and anthropogenically manipulated landscapes, such as abandoned urban areas, agricultural fields, gardens, road and railroad edges, forest clearcuts and natural floodplains. Analyses from a process-based distribution model suggest that the species may extend its range. Areas most at risk include European countries, south of Scandinavia, in which it does not yet occur, South Africa, Western Australia, and southeastern South America.

B. davidii is difficult to remove or manage once it has established in a disturbed area. Manual removal is laborious and costly. Herbicides are effective in small areas in the short term, but must be applied manually and repeatedly. Biocontrol methods currently being used in New Zealand may prove effective. However, the deliberate introduction of another non-indigenous species (i.e., the biocontrol agent itself) to an ecosystem is sometimes considered too risky to be considered (Sheppard et al., 2006).

In the absence of disturbance, natural plant succession may lead to the elimination of *B. davidii*. However, *B. davidii*, by nature, establishes on frequently disturbed sites which provide source for satellite populations that can repopulate new and post-disturbance landscapes. As it is well known that species invasion via multiple loci is the most effective means of establishing non-indigenous species in a new environment (Mack et al., 2000), the continued presence of non-sterile *B. davidii* cultivars in urban, residential, and wild areas guarantees continued reintroduction into native areas (regardless of native control efforts).

Despite the potential for *B. davidii* to usurp native species, gardeners and horticulturalists continue to enjoy this beautiful and fragrant shrub. Furthermore the continued sale of the plant economically benefits the horticulture and nursery trades. This leads to the conundrum of whether to implement policies to limit the spread of *B. davidii* and curtail current distribution, to continue to promote its presence, or to develop means that best satisfy both desires.

What are not often acknowledged in the ecological study of biological invasions are the anthropogenic cultural and emotional dimensions that drive land management strategies (Kendle & Rose, 2000). When a species is pleasing to the public, regardless of its origins, the public becomes the champion who advocates for the species protection and propagation. *B. davidii*'s post-World War II establishment onto urban debris in Europe may have added an explosion of color and thus, transformed ravaged landscapes. Perhaps the passion expressed by Europeans for *B. davidii* is inadvertently linked to their appreciation for the beauty that followed such a dark and violent period in history. Even if methods were found for the efficient removal of *B. davidii*, it seems unlikely that the European public would condone such actions. As with the case of the now protected *B. davidii* field in Croxley Green, removing this non-indigenous plant species in the Croxley Green is no longer an option (even if removal were feasible). Ecologists must continue to examine the impacts *B. davidii* has on natural ecosystems in order to promote informed, rather than emotional, decisions.

In summary, ornamental plant species are often at the top of invasive species lists (Reichard & Campbell, 1996; Leland, 2005; Dehnen-Schmutz et al., 2007). Many "charismatic" plant species (i.e., popular garden shrubs and trees) have naturalized their way into the public's emotional landscape (Culley & Hardiman, 2007). It is

unlikely that management strategies that include eradication of these “charismatic species” will be successful either logistically or culturally. The repercussions of *B. davidii* naturalization are unknown. Therefore, further ecological research is needed to determine the long-term impacts to native ecosystems and landscapes inhabited by *B. davidii* and to predict the ecological consequences of the subsequent continued reintroduction of *B. davidii*. We also must consider the relationship that humans have with *B. davidii* as well.

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