The disintegration of the Scrophulariaceae and the biological control of *Buddleja davidii*

M.K. Kay,1 B. Gresham,1 R.L. Hill2 and X. Zhang3

Summary

The woody shrub buddleia, *Buddleja davidii* Franchet, is an escalating weed problem for a number of resource managers in temperate regions. The plant’s taxonomic isolation within the Buddlejaceae was seen as beneficial for its biological control in both Europe and New Zealand. However, the recent revision of the Scrophulariaceae has returned *Buddleja* L. to the Scrophulariaceae *sensu stricto*. Although this proved of little consequence to the New Zealand situation, it may well compromise European biocontrol considerations. Host-specificity tests concluded that the biocontrol agent, *Cleopus japonicus* Wingelmüller (Coleoptera, Curculionidae), was safe to release in New Zealand. This leaf-feeding weevil proved capable of utilising a few non-target plants within the same clade as *Buddleja* but exhibited increased mortality and development times. The recent release of the weevil in New Zealand offers an opportunity to safely assess the risk of this agent to European species belonging to the Scrophulariaceae.

Keywords: *Cleopus*, *Buddleja*, taxonomic revision, phylogeny.

Introduction

There are approximately 90 species of *Buddleja* L. indigenous to the Americas, Asia and Africa (Leeuwemberg, 1979), and a number have become naturalized outside their native ranges (Holm et al., 1979). *Buddleia*, *Buddleja davidii* Franchet, in particular, is an escalating problem for resource managers in temperate regions and has been identified as a target for classical biological control in New Zealand (Kay and Smale, 1990) and Europe (Sheppard et al., 2006).

*Buddleia* is a large woody shrub of Asian origin that was introduced to the rest of the world as an ornamental species in the 1890s. It was considered naturalized in the UK in the 1930s and in New Zealand in the 1940s (Esler, 1988). It has many of the features that characterize successful weed species, and it is ranked in the top ten invasive plants of Britain (Crawley, 1987). It matures quickly, is capable of flowering in its first year of life and produces an extraordinary number of small seeds that are efficiently dispersed by wind. However, there is no significant soil seed bank. The seed germinates almost immediately, and the density and rapid early growth of *buddleia* seedlings suppresses other pioneer species (Smale, 1990).

As a naturalized species, *buddleia* is a shade-intolerant colonizer of urban wastelands, riparian margins and other disturbed sites, where it may displace indigenous species, alter nutrient dynamics and impede access (Smale, 1990; Bellingham et al., 2005). In New Zealand, on sites prepared for exotic forest plantations, the rapid growth of *buddleia* causes the suppression and a quantifiable loss of growth in newly planted *Pinus radiata* Don. (Richardson et al., 1996). The inefficiencies of conventional controls prompted the investigation of classical biological control (Kay and Smale, 1990).

The taxonomic isolation of a target weed from indigenous and other valued non-target plant species reduces the risk posed by introduced biological control agents. However, taxonomy is far from an exact science, and the taxonomy of the paraphyletic *Buddleja* has had a chequered history. *Buddleja* has variously been placed within the families, Scrophulariaceae, Loganiaceae, the conveniently promoted Buddlejaceae and, most recently, returned to the Scrophulariaceae, which has been a recognized repository for undefined Lamiales (Tank et al., 2006). The on-going reconstructing of the Scrophulariaceae combines morphological,
embryological, molecular and chemical parameters, as well as the host preferences of specialist invertebrates (Stevens, 2001).

Fortunately, there are few close relatives of buddleia within the New Zealand indigenous Scrophulariaceae s.s., although the indigenous shrub, Myoporum laetum G. Forst., Myoporaceae, has now been relegated to the tribe Myoporeae, within the same clade as Buddlejeae (Tank et al., 2006). Most other New Zealand genera previously placed in the Scrophulariaceae, including the manifold Hebe Comm. ex Juss., are now better defined in other clades within the Scrophulariaceae sensu lato.

During a survey of insects and pathogens associated with B. davidii in China, Cleopus japonicus Wingel-müller (Coleoptera, Curculionidae) appeared to be a potential biological control agent because of its apparent host specificity and ubiquity. The adults and larvae feed externally on leaves. Eggs are oviposited singly within excavated leaf cavities, and the emergent slug-like larvae remain attached to the plant by secreting a coating of viscous fluid.

The host-specificity studies reported in this paper evaluated whether C. japonicus is a safe biological control agent for buddleia in New Zealand.

Methods and materials
Preliminary trials conducted in China tested species from 16 plant families. C. japonicus was then imported into quarantine in New Zealand. The 76 plant taxa tested in New Zealand were selected following the internationally accepted 'centrifugal phylogenetic system' of Wapshere (1974). The relative susceptibility of 14 Buddleja taxa was tested. Thirty-five New Zealand indigenous plant species were tested, including Genistoma rupestre J.R. Forst.& G. Forst., the only endemic representative of the Loganiaceae, and 21 species from the Scrophulariaceae s.l. Given the uncertain nature of Buddleja taxonomy, it was considered prudent to give extensive coverage of New Zealand scrophularia species, particularly the many species of Hebe. A further 11 species of Scrophulariaceae s.l. that are exotic to New Zealand were tested, along with 16 exotic species from other families that commonly grow in association with buddleia in New Zealand. The New Zealand trials were conducted in a quarantine insectary maintained at 20°C ± 2 and 70% ± 10 RH, 14-h photoperiod.

Tests were run with naïve and pre-fed adults, in both choice and no-choice trials. The degree of feeding, oviposition and mortality was scored against that of insects placed on concurrent buddleia controls. No-choice larval trials utilized both pre-fed and naïve first instar larvae. To obtain naïve larvae, eggs of known age were monitored closely for larval eclosion. Emerging larvae were transferred to the test plant material before feeding.

Results
A full account of trial results is available on the Environmental Risk Management Authority website (www. ermanz.org). Adult C. japonicus did not oviposit, or feed, on any of the 35 species belonging to 24 plant families outside of the Scrophulariaceae in either of the preliminary trials in China or the trials conducted in New Zealand. However, the weevil did lay a very small number of eggs on a few of the 21 New Zealand indigenous species within the family Scrophulariaceae s.l. These eggs were laid externally, rather than in purposefully excavated sites, and failed to produce larvae. Larvae transferred to these plants also developed poorly. Within the genus Buddleja, C. japonicus could complete development on all, except Buddleja salviifolia (L.) Lam and Buddleja auriculata Bentham. but performed best and had a significant preference for B. davidii (Table 1).

Newly emerged larvae transferred to the foliage of 17 New Zealand indigenous Hebe species died quickly without completing development. One anomaly occurred when one larva of one replicate completed development to adult on the foliage of an ornamental specimen of Hebe speciosa (A.Cunn.) Ckn. & Allan. One larva also completed development on each of the indigenous Limosella lineata Glück, [Limosellae

<table>
<thead>
<tr>
<th>Buddleja species</th>
<th>Section</th>
<th>Origin</th>
<th>Rank</th>
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<tbody>
<tr>
<td>B. davidii Franch. var. lochinch</td>
<td>Neemda</td>
<td>SE Asia</td>
<td>1</td>
</tr>
<tr>
<td>B. davidii Franch. var. weyriana</td>
<td></td>
<td></td>
<td>2</td>
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<tr>
<td>B. madagascariensis Lam.</td>
<td>Nicodemia</td>
<td>Madagascar</td>
<td>3</td>
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<tr>
<td>B. japonica Hemsl. Maxim.</td>
<td>Neemda</td>
<td>SE Asia</td>
<td>5</td>
</tr>
<tr>
<td>B. alterniflora</td>
<td>Neemda</td>
<td>SE Asia</td>
<td>6</td>
</tr>
<tr>
<td>B. globosa Hope B. lindleyana</td>
<td>Neemda</td>
<td>SE Asia</td>
<td>7</td>
</tr>
<tr>
<td>Fortune</td>
<td>Neemda</td>
<td>N America</td>
<td>9</td>
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<tr>
<td>B. asiatica Lour.</td>
<td>Neemda</td>
<td>SE Asia</td>
<td>10</td>
</tr>
<tr>
<td>B. colvillei Hook. f. et Thoms</td>
<td>Neemda</td>
<td>India</td>
<td>10</td>
</tr>
<tr>
<td>B. dysophylla (Benth.) Radlk.</td>
<td>Chilianthus</td>
<td>S Africa</td>
<td>12</td>
</tr>
<tr>
<td>B. auriculata Bentham.</td>
<td>Neemda</td>
<td>S Africa</td>
<td>13</td>
</tr>
<tr>
<td>B. salviifolia (L.) Lam.</td>
<td>Neemda</td>
<td>S Africa</td>
<td>14</td>
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(Scroph I) and *Glossostigma elatinoides* Benth. ex Hook. f. [Phrymaceae (Scroph IV)], but adult weevils did not oviposit on these species.

Most exotic scrophularia appeared to be immune to attack by the weevils, but larval and adult feeding and oviposition occurred on the weedy European species *Verbascum thapsus* L., *Verbascum virgatum* Stokes and *Scrophularia auriculata* L. (Scroph II) and that they fed indifferently upon *Scrophularia* and *Verbascum*.

Westwood (1849 in Scott 1937) remarked that *Cionus scrophulariae* L.;

“...long ago discovered the Natural System, and proved by the fact of their sometimes indiscriminately feeding on mulleins [*Verbascum*] and figworts [*Scrophularia*] that these plants were in truth closely allied in Nature.”

Scott (1937) records the same weevil feeding on the introduced Cape figwort *Phygelius capensis* Benth. (Scroph I) and notes the observations, by others, of *Cionus* and *Cleopus* occasionally feeding on introduced *Buddleja* in the UK. In the UK, the only specialist Lepidopteran to occasionally feed on *buddleia* is the mullein moth, *Cucullia verbasci* L., which normally has the same host range as the figwort weevils (Owen and Whiteway, 1980). The flea beetles, *Longitarsus* spp. Latreille, also only have the hosts *Scrophularia* and *Verbascum*, and in summary of these observations, Allen (1960) stated: “Yet none of these insects, apparently, is known ever to attack *Lanaria* or *Antirrhinum* [both of Antirrhineae, Scroph II] in a state of nature, and I am aware of no instance of a *Linaria* feeder (of which there are many) having *Scrophularia* as a host.”

Elements of the distinctive iridoid and terpenoid phytochemistry of *Buddleja* have been shown to be

**Discussion**

*Cleopus* Dejean, belonging to a tribe (Cionini) of host-specific ‘figwort’ weevils and the European representatives (*Cionus* Clairville and *Cleopus* species), feed on *Scrophularia*, *Verbascum* and occasionally on adventive *Buddleja* (Walker, 1914, Hoffman, 1958; Cunningham, 1974, 1975; Williams, 1974; Read, 1976, 1978; Bullock, 1987; Smith, 1992). Conversely, the Asian species, *C. japonicus* has only been recorded from *B. davidii* (Zhang et al., 1993), and this study found that it could only complete its life cycle on a few *Buddleja* taxa, but could feed on *Scrophularia* and *Verbascum*. The host associations of these species appear to support the recent revision of the Scrophulariaceae (Fig. 1).

Other invertebrates are also known to feed exclusively on these plant species, which have been recognized as a distinct clade, Scrophulariaceae s.s. ['Scroph I' of Olmstead and Reeves (1995) and Olmstead et al., (2001)] within the Scrophulariaceae s.l. Allen (1960) noted that weevils of the Gymnetrini distinguished between the Plantaginaceae (Scroph II) and the Scroph I clade and that they fed indifferently upon *Scrophularia* and *Verbascum*.

Elements of the distinctive iridoid and terpenoid phytochemistry of *Buddleja* have been shown to be

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**Figure 1.** Summary of the phylogenetic relationships among the tribes and the unresolved genus, *Phygelius*, of the Scrophulariaceae *sensu stricto* (after Tank et al., 2006). Low (*single asterisk*) to high level (*triple asterisk*) of feeding by *Cleopus japonicus*.  

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biologically active (Yoshida et al., 1976; Houghton et al., 2003) and may well influence the invertebrate feeding guild associated with this and closely related genera. Iridoids are known to be feeding stimulants for specialist Lepidoptera (Bowers, 1988) and deterrents for generalists (Stephenson, 1982).

The study reported in this paper not only confirms the restricted host preference of the Cionini and demonstrates the low risk of C. japonicus to the New Zealand flora but also supports the current position of Buddleja within the new taxonomy. Bearing in mind that laboratory studies are thought to overestimate the host range of potential biological control agents (Hill, 1999), the host range of C. japonicus in the field may be more limited. However, these results cannot preclude the possibility that, if released, C. japonicus could produce self-sustaining populations on Verbascum, Scrophularia and Buddleja species. Four other species of Buddleja [B. salvifolia L., Buddleja madagascariensis Lam., Buddleja globosa Hope and B. dysophylla (Benth.) Radlk.] have already partially naturalized in New Zealand. The early flowering B. salvifolia is valued as a spring nectar source for bees (Kay and Smale, 1990). However, C. japonicus adults fed poorly, larvae failed to feed and no eggs were laid on B. salvifolia. It is unlikely that this species would be colonized by C. japonicus. In contrast, B. madagascariensis is one of a number of Buddleja species to be considered strongly invasive on the west coast of USA and Hawaii (Randall and Marinelli, 1996). It ranked highly as a host of C. japonicus and could be expected to be at least as host-specific as C. globosa.

C. japonicus exhibits considerable radiation, resulting in 400–500 species of Scrophularia and Verbascum. A number of these are rare or endangered (Wigginton, 1999), and rigorous testing would be advisable.


References


