# Ruling out a host-range expansion as the cause of the unpredicted non-target attack on tagasaste (*Chamaecytisus proliferus*) by *Bruchidius villosus*

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*Summary*

Scotch broom (*Cytisus scoparius*) is a woody shrub of European origin that is an invasive weed in New Zealand. *Bruchidius villosus* was released in New Zealand in 1986 as a biological control agent of Scotch broom, after tests indicated that it was specific to this species. However, in 1999, *B. villosus* was discovered developing in the seeds of an unpredicted host, tagasaste or tree lucerne (*Chamaecytisus proliferus*). Although the original choice tests carried out in quarantine failed to predict acceptance of *C. proliferus* by ovipositing females, the current population in New Zealand clearly finds this species an acceptable host. An investigation of the original host-testing procedures revealed a number of possible limitations in the tests conducted in the 1980s. Concerns that a host-range expansion might have occurred in a weed biological control agent led to this study in which beetles from the original population (Silwood Park, United Kingdom) were reimported and the original handling and host choice tests were replicated. Despite showing a strong preference for Scotch broom, the beetles tested in this study accepted *C. proliferus* for oviposition. These results allow us to rule out the possibility that a host-range expansion has occurred.

***Keywords***: *Bruchidius villosus*, *Chamaecytisus proliferus*, *Cytisus scoparius*, host-range expansion, host-specificity testing.

## Introduction

Scotch broom, *Cytisus scoparius* (L.), Link is a woody shrub of European origin that is an invasive weed in many countries, including New Zealand, Australia and North America. The broom seed beetle *Bruchidius villosus* (F.) (previously referred to as *B. ater* (Marsham)) was identified as a potential biological control agent for New Zealand's Scotch broom weed problem because it was thought to attack only *Cytisus* species. Host-specificity testing began in the Inted Kingdom (UK) in 1985 and consisted of no-choice oviposition tests with adults being confined to either whole potted plants or to single branches of larger plants inside cotton mesh sleeve cages (Syrett & O'Donnell 1987). All hosts were required to be bearing young green pods (the stage of pod on which the broom seed beetle oviposits) at the time of testing. Thirteen species of non-target plants were tested, also seven species of potted non-target plants were tested together with *C. scoparius* in a choice test within a field cage in the UK (Syrett & O'Donnell 1987). In all these assays, eggs were only laid on *Cytisus* species (*C. scoparius* and *C. praecox* cv. Allgold). The insect was released as a biological control agent in New Zealand in 1986.

In 1985, *B. villosus* was imported into quarantine in New Zealand as newly emerged beetles from the UK *C. scoparius* pods. Normally in the UK, such beetles would overwinter for about six months, feeding on flowers in the following spring, pbefore becoming

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reproductively mature. However, because New Zealand is in the Southern Hemisphere, the beetles were fed on arrival with bee pollen, honey water and/or fresh flowers for approximately eight weeks (without overwintering), bringing them into reproductive maturity for the oviposition tests. The results of the choice tests with nine species of pod-bearing plants (six New Zealand natives and three exotics), indicated that *B. villosus* would be host-specific to *C. scoparius* in New Zealand (Syrett & O'Donnell 1987). One of the exotic species was tagasaste, *Chamaecytisus proliferus* (L. f.) Link (known as *C. palmensis* (Christ) Bisby & K. Nicholls in New Zealand).

In spring 1994, adults of *B. villosus* reared from *C. scoparius* from New Zealand were imported into quarantine in Australia. The results of choice tests on 18 native Australian species and 10 exotic species supported the New Zealand results, also indicating that *B. villosus* was host-specific to *Cytisus* species (A. Sheppard, unpublished data).

In 1999, however, *B. villosus* was found emerging from *C. proliferus* seeds in New Zealand, and further studies showed that this plant was a suitable and commonly utilized alternative host (Syrett 1999). At the time *C. proliferus* had only been tested in choice tests with *C. scoparius* as a control, in quarantine in both New Zealand and Australia. It was not included in the UK no-choice and choice tests because it does not produce pods in the colder climate of the UK. *C. proliferus* is native to the Canary Islands, which have a significantly warmer climate than the UK, and is grown abundantly in New Zealand where it has naturalized extensively. It is regarded as weedy in some places in New Zealand (Williams & Timmins 1990), but also has benefits including use as fodder in high country farms when there is drought (Douglas *et al.* 1996), as a pollen source for beekeepers (Dann & Trimmer 1986), and as a supplementary food source for the threatened native pigeon in New Zealand (McEwan 1978).

Although it has now been shown that choice tests including the target species are not the most robust method for observing acceptance of lower ranked alternative host plants (Marohasy 1998, Edwards 1999, Hill 1999, Heard 2000, Purcell *et al.* 2000, Barton Browne & Withers 2002), we are nevertheless surprised that the original choice tests in New Zealand did not reveal the relative acceptability of *C. proliferus*. It seemed plausible that a host-range expansion (Dennill *et al.* 1993), otherwise referred to as a host shift (Howarth 1991), had occurred in the population of established beetles in New Zealand some time in the 14 years since its introduction (Syrett 1999). Many purported host-range expansions, defined by Marohasy 1996 as "feeding by biological control agents on plant species other than those on which they were known to feed prior to their release", have been reported in weed biological control. Marohasy (1996) argued that these were caused by other phenomena, such as preadaptation (established behavioural concepts), threshold change as a result of host deprivation, or effects of experience (learning). This study investigates the possibility that a host-range expansion may have occurred in *B. villosus*. Oviposition acceptance behaviour of the current New Zealand population of *B. villosus* was compared with beetles collected from Silwood Park, the same field site where the original beetles had been collected for shipment to New Zealand in the 1980s. Our hypothesis was that, if British beetles still refused to accept *C. proliferus* for oviposition, while their New Zealand progeny now accepted it, then a host-range expansion would indeed be the most likely explanation.

## Materials and methods

In June 2002, adult *B. villosus* were beaten from *C. scoparius* at Silwood Park, UK. These beetles were placed into 1 m diameter by 2 m long, 1 mm mesh sleeve cages on branches of *C. scoparius* bearing young pods. In July, infested pods were picked from the sleeves and held in a glasshouse in mesh bags until emergence. The emerged adult beetles were reimported into quarantine in New Zealand in August 2002. Repeating the same procedure as carried out in 1985, 150 adults were maintained in Perspex cages with ample bee pollen and honey water, followed by *C. scoparius* flowers, under a 22:16°C (day:night) temperature regime with a day length of 14:10 L:D. Relative humidity was approximately 70%.

Host-specificity tests undertaken in the original study in 1985 were replicated as far as possible in 2002 using UK beetles, and in 2001 using New Zealand beetles (field collected from *C. scoparius*). The procedures recorded in the original quarantine laboratory books were followed as closely as possible, however minor differences were required with regard to timing and experimental design.

Perspex boxes (220 × 130 × 100 mm), with flexible push-on lids and four, 25-mm diameter gauze-covered holes for ventilation, were used as test cages. Moistened blotting paper was placed at the bottom of the cage, and several pieces of tissue paper were included to absorb excreta. *Cytisus scoparius* twigs, approximately 200 mm long, bearing young green pods, were placed in vials of water in each test cage. A disc of plastizote, 6 mm thick, with the twigs pushed through its centre, acted as a stopper for the vial, which was supported at an angle to ensure the shoot remained in the water. Twigs of each test plant were selected such that they had approximately equal amounts of pod material and pods judged to be at an equivalent developmental stage to the *C. scoparius* pods. Test material of the different plant species, prepared in the same way as the *C. scoparius*, was placed in each cage with an equivalent amount of *C. scoparius*, to constitute paired choice tests comprising *C. scoparius* and a test plant (Syrett & O'Donnell 1987).

Test-plant material was collected from at least three different plants for each species. Beetles were held in each test cage for 6 days during the tests. Beetles were fed pollen and provided with cotton dental rolls soaked in a honey–water solution. After the beetles were removed, all plant material and cages were carefully examined for eggs. The numbers of eggs found on the pods of *C. scoparius* and each of the test species were recorded. Each phase of the experiment was conducted when each of the test-plant species had pods available at the appropriate stage of development (Table 1). Not all plant species were tested at the same time, therefore. Every attempt was made to ensure laboratory conditions, cage type used, number and sex ratio of beetles, bee pollen source, twig size, approximate number of pods presented, the presentation of pod material, duration of assays, and approximate timing of presentation of various host plants, were the same as in the 1985 experiments (Table 1).

In the original choice tests conducted in 1985, one or two replicates were used for each test plant species, whereas 4 replicates for each test plant were used in 2001 and 10 in 2002. Each replicate contained five male and five female beetles.

## Results

In 1985 female *B. villosus* laid a mean of between 4.2 and 18.4 eggs each on *C. scoparius* and 0 eggs on the test plants (Table 2). In 2002 tests, *B. villosus* laid a mean of between 3.0 and 12.3 eggs each on *C. scoparius*, and 0.7 eggs on the test plant *C. proliferus*. The range of eggs laid on *C. proliferus* in 2002 was between 0 and 2.6 eggs per female and only 4 out of 10 replicates had eggs laid on them at all. In the 2001 tests using beetles field caught from *C. scoparius* in New Zealand, female beetles laid a mean of between 18.1 and 25.5 eggs on *C. scoparius* and a mean of 1.0 egg each on the test plant *C. proliferus.* The range on *C. proliferus* was between 0.2 and 2.6 eggs per female and in each of the 4 replicates at least 1 egg had been laid.

In the four replicates of the 2001 tests with New Zealand field-collected beetles, a total of 20 eggs was laid on *C. proliferus* by a maximum of 12 females. In

**Table 1.** Timing of two-choice tests with material presented to *Bruchidius villosus* from various origins. The tests included the target weed *Cytisus scoparius* and the following plant species: *Carmichaelia australis* G. Simpson, *Carmichaelia petriei* T. Kirk, *Carmichaelia stevensonii* (Cheeseman) Heenan, *Carmichaelia williamsii* T. Kirk, *Chamaecytisus proliferus*, *Clianthus puniceus* (G. Don.) Sol., *Cytisus multiflorus* (L'Her) Sweet., *Genista monspessulana* (L.) L.A.S. Johnson, *Laburnum anagyroides* Medikus., *Sophora microphylla* Aiton, and *Sophora prostrata* J. Buchanan.

| *Weeks* | 1985 UK import (1 or 2 reps) | 2001 NZ origin (4 reps) | 2002 UK import (10 reps) |
|---|---|---|---|
| 1–5. (2nd week Sept – 3rd week Oct) | *C. scoparius* flowers and bee pollen | | *C. scoparius* + *C. proliferus* flowers and bee pollen |
| 6. (4th week Oct) | *C. scoparius* flowers, green pods and bee pollen | Beetles collected continuously off *C. scoparius* | C. scoparius vs *C. proliferus* No eggs laid |
| 7. (1st week Nov) | *C. scoparius* flowers, green pods and bee pollen First eggs laid | *C. scoparius* vs *C. proliferus* First eggs laid | C. scoparius vs *C. proliferus* No eggs laid |
| 8. (2nd week Nov) | *C. scoparius* vs *C. proliferus* | *C. scoparius* vs *S. microphylla* | *C. scoparius* vs *C. proliferus* First eggs laid |
| 9. (3rd week Nov) | *C. scoparius* vs *S. microphylla* | *C. scoparius* vs *S. prostrata* | *C. scoparius* vs *S. microphylla* |
| 10. (4th week Nov) | – | *C. scoparius* vs *C. multiflorus* | *C. scoparius* vs *C. australis* |
| 11. (1st week Dec) | *C. scoparius* vs *C. australis* | *C. scoparius* vs *G. monspessulana* | *C. scoparius* vs *C. petriei* |
| 12. (2nd week Dec) | *C. scoparius* vs *C. petriei*, *C. williamsii, G. monspessulana*, *C. puniceus* & *C. multiflorus* | *C. scoparius* vs *L. anagyroides* | *C. scoparius* vs *C. williamsii* |
| 13. (3rd week Dec) | Repeated *C. scoparius* vs *C. multiflorus* | | *C. scoparius* vs *C. puniceus* |
| 14. (4th week Dec) | – | | *C. scoparius* vs *C. multiflorus* |
| 15. (1st week Jan) | – | | *C. scoparius* vs *G. monspessulana* |
| 16. (2nd week Jan) | – | | *C. scoparius* vs *C. stevensonii* |
| 17. (3rd week Jan) | *C. scoparius* vs *C. stevensonii* | | C. *scoparius* vs *L. anagyroides* |

Note: in Syrett and O'Donnell (1987), *C. proliferus* was referred to as *C. palmensis* (Christ) Bisby & Nicholls, *C. australis* as *C. ovata* G.Simpson, and *C. stevensonii* as *Chordospartium stevensonii.*

the 10 replicates in 2002 with UK imported beetles, a total of 33 eggs was laid by a maximum of 19 females in only 4 of the replicates. There was no significant difference in the overall mean number of eggs laid per female per replicate on *C. scoparius* between the sequential choice tests conducted in 1985 and 2002 with beetles imported from the UK (*t*-test, $P = 0.5$, df = 12). The overall mean number of eggs per female per replicate was 9.1 and 7.9, for beetles in 1985 and 2002, respectively (excluding *Laburnum anagyroides* which was an extra plant in the 2002 sequence). The overall mean number of eggs laid per female per replicate in the 2001 tests on New Zealand field-collected beetles was 22.3, which is more than double the mean in the other tests.

## Discussion

For an expansion in fundamental host range to occur in phytophagous insects, so that an insect can move from one host plant to another, a "host race" must first develop. To be classified as a host race (defined in Marohasy 1996) populations must first fulfil the following criteria: (1) be non-interbreeding and sympatric; (2) differ in biological characteristics, but not (or only marginally) in morphology; and finally (3) be prevented from interbreeding as a result either of preference for different host-plant species, or as a consequence of physiological adaptation to different host-plant species.

So which of the above criteria have either been fulfilled or have the potential to be fulfilled in New Zealand with *B. villosus*? Firstly, it seems that *B. villosus* adults emerging from both *C. scoparius* and *C. proliferus* are interbreeding. Beetles emerging from each species of pods at similar times have been observed mating (M. Haines, personal observation). Furthermore, both plant species frequently grow in the same area, and within the same habitats in New Zealand (no geographical isolation). *Bruchidius villosus* shows high mobility, and therefore it appears the insects continue to interbreed after emerging from different host pods. Seasonal asynchrony is, however, a possible mechanism that could also lead to sympatric speciation. Certainly *C. proliferus* flowers earlier than *C. scoparius* in spring and is the first available pollen source to *B. villosus* when it emerges from its overwintering period (Fowler *et al.* 2000). However, *C. proliferus* flowers for a longer period and simultaneously with *C. scoparius* over summer, suggesting seasonal asynchrony in New Zealand may be insufficient to lead to sympatric speciation or to prevent interbreeding.

Secondly, the possibility that *B. villosus* has begun to develop different biological characteristics on the two host plants has also started to be investigated. Field observations and initial data gathering in 1999 (M. Haines, unpublished results) and in 2000 (Wittenberg & Thomann 2001) have suggested there is phenotypic plasticity in body size and colour of *B. villosus* depending on the host-plant seed in which they have developed. Adults emerging from seeds of *C. proliferus* are generally larger and sometimes browner in colour than those emerging from the usual host *C. scoparius,* which are smaller and blacker in colour. Whether this phenotypic plasticity is suggestive of different performance or suitability of genotypes according to host plant has yet to be ascertained, but the development of different biological characteristics cannot be ruled out. Laboratory studies will be used to investigate whether or not lines of *B. villosus* reared from different host-plant pods retain oviposition preferences for the species of pod in which they spent their larval development.

Thirdly, we need to establish that *B. villosus* is in the process of being prevented from interbreeding as a result of a preference developing for the new host-plant species. *Cytisus scoparius* remains the preferred host over *C. proliferus* in all choice tests to date (M. Haines, unpublished results), suggesting that no preference has yet developed for *C. proliferus.* The 2001 test results confirm this (Table 2), as beetles randomly collected from the field laid on average 25 times as many eggs on *C. scoparius* as on *C. proliferus.*

So it appears that the criteria that would indicate that a host race has developed, or is in the early stages of developing in *B. villosus,* are not met. The fact that reimported UK beetles accepted *C. proliferus* suggests that a host-range expansion has not occurred in New Zealand, but that for some reason the 1985 tests failed to elicit oviposition on *C. proliferus.*

There are at least two possible explanations for the discrepancy in laboratory testing results between 1985 (no eggs were laid on *C. proliferus*) and 2002 (some eggs were laid on *C. proliferus*). There were differences in the number of *B. villosus* tested (smaller sample sizes in 1985), and beetles may have been treated subtly differently between tests despite best attempts to replicate conditions (Table 1). For example, the 1985 beetles were held for two weeks before testing with very small pods and flowers of *C. scoparius*, which may have caused an unusual degree of excitation towards *C. scoparius* in 1985. In 2002, beetles were held before testing with pods of both *C. scoparius* and *C. proliferus* at the same time, to check for onset of oviposition. In both cases, all beetles imported from the UK had never experienced *C. proliferus* pods before being imported into New Zealand quarantine. All testing was conducted sequentially, but in both 1985 and 2002, the same groups of beetles were reused for each test plant, whereas in 2001, independent groups of beetles were used for each test plant in the sequence.

Having ruled out a host-range expansion, why did the original choice tests not indicate some acceptability of *C. proliferus* pods? The hierarchy-threshold model of host selection (Courtney *et al.* 1989) hypothesizes that insects rank hosts in a hierarchical fashion and that selection of diet by individual insects is determined by

**Table 2.** Mean number of eggs laid per *Bruchidius villosus* female per replicate in paired cut-shoot choice tests run sequentially over time. The tests included the host plant *Cytisus scoparius* and the following test-plant species: *Carmichaelia australis* G.Simpson, *Carmichaelia petriei* T. Kirk, *Carmichaelia stevensonii* (Cheeseman) Heenan, *Carmichaelia williamsii* T. Kirk, *Chamaecytisus proliferus*, *Clianthus puniceus* (G. Don.) Sol., *Cytisus multiflorus* (L'Her) Sweet., *Genista monspessulana* (L.) L.A.S. Johnson, *Laburnum anagyroides* Medikus., *Sophora microphylla* Aiton, and *Sophora prostrata* J. Buchanan.

| Plant material | 1985 UK import | | 2001 New Zealand field | | 2002 UK import | |
|---|---|---|---|---|---|---|
| | test plant | *C. scoparius* | test plant | *C. scoparius* | test plant | *C. scoparius* |
| *Chamaecytisus proliferus* | 0 | 18.4 | 1 | 25.5 | 0.7 | 12.3 |
| *Sophora microphylla* | 0 | 6.2 | 0 | 19.3 | 0 | 4.8 |
| *Carmichaelia australis* | 0 | 12.2 | – | – | 0 | 7.4 |
| *Carmichaelia petriei* | 0 | 7 | – | – | 0 | 9.2 |
| *Carmichaelia williamsii* | 0 | 4.2 | – | – | 0 | 8.5 |
| *Genista monspessulana* | 0 | 10 | 0 | 18.1 | 0 | 9.5 |
| *Clianthus puniceus* | 0 | 7.6 | – | – | 0 | 4.3 |
| *Cytisus multiflorus* | 0 | 12.2 | 0 | 21.7 | 0 | 9.0 |
| *Carmichaelia stevensonii* | 0 | 4.2 | – | – | 0 | 5.3 |
| *Sophora prostrata* | – | – | 0 | 25.2 | – | – |
| *Laburnum anagyroides* | – | – | 0 | 24.8 | 0 | 3.0 |

the host's "acceptability". One prediction of the model is that female oviposition behaviour is influenced by female egg load, such that when egg load is high, so is the tendency for a wider range of hosts to become acceptable (Courtney *et al.* 1989). The overall mean number of eggs laid per female was significantly higher in the New Zealand field-collected beetles tested in 2001 (more than twice that of both 1985 and 2002 UK imported beetles), suggesting these beetles had a higher egg-load than their imported counterparts. So could egg-load explain why the original host tests were not indicative of field host range? The number of eggs laid per female in the 2002 imported beetles was almost three-fold less than that of the 2001 New Zealand field-collected population. Yet, the lower-ranking host *C. proliferus* was still accepted for oviposition at an equivalent rate despite the reduced egg-laying. In both experiments, the minimum number of eggs laid per female on *C. proliferus* was 1.7, and more eggs were laid on *C. proliferus* by beetles with a comparatively low egg-load in an equal number of replicates. So, it appears unlikely that egg-load is responsible for the discrepancy in test results.

We conclude that a host-range expansion has not occurred, but that the 1985 host testing failed to detect the non-target impact of *B. villosus* on *C. proliferus.* From the 2001 and 2002 test results indicating that *B. villosus* laid 18–26 times as many eggs on *C. scoparius* as on *C. proliferus* (Table 2), we might have predicted that its non-target impact in the field would be minor, but the level of seed attack by the beetle in New Zealand is in fact substantial (M. Haines, unpublished data). The implication for biological control releases is that we cannot assume non-target impacts will be insignificant on the grounds that results of choice tests indicate a strong preference for the target plant. On a more positive note, despite the non-target attack on the exotic plant *C. proliferus*, *B. villosus* remains a useful agent against *C. scoparius* in New Zealand as all the test results consistently predict that no native Fabaceae are under any risk of attack (M. Haines, unpublished data).

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