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Relative performance on test and target plants in laboratory tests predicts the risk of non-target attack in the field for arthropod weed biocontrol agents

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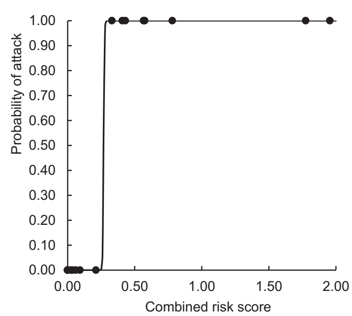
HIGHLIGHTS

- We investigated field host use of arthropod weed biocontrol agents in New Zealand.
- We calculated relative performance on test and target plants in specificity tests.
- Host use correlated to relative performance in starvation and oviposition tests.
- We calculated a combined risk score for starvation and oviposition tests.
- Combined risk score threshold predicted field host use.

GRAPHICAL ABSTRACT



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ABSTRACT

We tested the hypothesis that quantifying the relative performance of candidate weed biocontrol agents on test and target plants during laboratory host-range testing can predict the probability of test plants being attacked in the field. For arthropod weed biocontrol agents established in New Zealand between 1929 and 2010, the probability of host use was positively correlated with relative performance for both no-choice starvation tests and no-choice oviposition tests. Moreover, multiplying together the relative performance scores for no-choice starvation and oviposition tests to create a combined risk score for no-choice tests resulted in a clear-cut threshold indicating that for scores between 0.21 and 0.33 the probability of host use (including minor spillover attack) occurring rose from close to zero to a virtual certainty. Choice oviposition test data showed a similar pattern to no-choice data, except there were two cases where host use occurred in the field on plant species that had very low relative performance scores in the choice tests. Both of these cases were associated with asynchrony between seed-feeding biocontrol agent activity and the reproductive phenology of the target plant, indicating that choice tests may be inappropriate for certain guilds of biocontrol agent that attack ephemeral plant structures.

We conclude that quantitative laboratory testing data can help predict risk of non-target attack. The ability to refer to threshold relative performance scores when deciding whether an agent is safe to release has the potential to ensure fewer environmentally safe candidate biocontrol agents are erroneously rejected, thereby enhancing efficiency in the selection and approval of new agents.

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1. Introduction

Host-specificity testing is used to discard potential weed biological control agents that are likely to cause significant undesirable non-target damage to either native or valued exotic plants. For arthropod agents, the simplest tests to interpret are 'no-choice' starvation tests where, most commonly, the immature stages of candidate agents are confined on a particular test plant and either feed and develop, or starve and die. Results are extremely robust and can be used to reliably define the 'fundamental' host range of a particular species, (i.e., all the plant species an agent can survive (complete development) on; Van Klinken and Heard, 2000; henceforth 'fundamental hosts').

Reliance on no-choice starvation tests, however, carries a risk of needlessly rejecting specific agents because, given no choice, candidate biocontrol agents are often inclined to feed on species that they would not attack under natural field conditions (e.g., Fowler et al., 2012; Groenteman et al., 2011; Marohasy, 1998). In other words, the 'realised' or 'field' host range of a biocontrol agent is commonly a subset of the fundamental host range (Van Klinken and Heard, 2000). Oviposition tests are often used as an aid to predicting an agent's field host range because it is assumed that the risk to a non-target plant that lies within the fundamental host range (i.e., it supports development in tests in confinement) should be low if females will not lay eggs on the plant. No-choice oviposition tests are also prone to 'false positives' because pre-alighting cues may be bypassed when arthropods are tested in a restrictive environment, such as a cage, or because females may eventually 'dump' eggs in the absence of their normal host (Marohasy, 1998).

Choice tests (where the candidate agent is presented with a choice between the target weed and one or more potential non-target plant species) were developed to provide test conditions that were considered more realistic (and therefore, less likely to give a misleading result) than no-choice tests (Marohasy, 1998). These tests also have potential pitfalls, for example false negatives might occur if the agent is unresponsive to lower-ranked plant species in the presence of the target plant (i.e., "associational resistance" *sensu* Tahvanainen and Root, 1972), while false positives might result from associational susceptibility (*sensu* Brown and Ewel, 1987) if an insect's acceptance of a non-target species temporarily increases as a result of being stimulated by the chemistry of nearby target plants (Marohasy, 1998). Choice-minus-target tests (i.e., where multiple non-target species are presented without the target; Sheppard et al., 2005) have been developed to overcome some of these potential problems, but still require careful interpretation because of the potential for arthropod behavior to be affected by the restrictive caged environment (Sheppard et al., 2005).

Open field tests, which are performed in the native range of the candidate agent, are considered the most natural and, therefore, the most reliable form of host-range testing. However, they cannot always be performed because, for example, it may not be possible to obtain permits to import and grow test plant species that are not already present in the native range of the target weed. Interpretation of field tests can still be problematic because, as noted above, the presence of the normal host plant may make females unresponsive to lower-ranked potential hosts (Marohasy, 1998). Moreover, if choice-minus-target field tests are performed it may be difficult to determine whether the test plants were exposed to sufficient numbers of the candidate agent to make the test valid.

Another methodology for investigating whether a fundamental host plant is likely to be a field host has been to compare the relative performance (e.g., percentage survival) of a candidate agent on test plant species and the target weed. Relative performance data has been reported for many years, for example, Newton (1933) reported the percentage survival of adult *Longitarsus jacobaeae* Waterhouse beetles that were fed exclusively on the normal host plant (*Jacobaea vulgaris* Gaertn.) compared to beetles that were fed on other related plant species. It is commonly implied that relative performance should be positively correlated with the risk that a plant will be a suitable field host (e.g., Frick, 1969). Wan and Harris (1997) further developed this methodology based on the premise that host suitability is influenced by multiple factors, such as acceptance for oviposition and suitability for larval development, and that the overall risk of non-target attack is a product of these factors. For example, they stated that if larval survival on a test plant is 1% of that on the host plant and the survivors lay only 1% of the normal number of eggs, then the relative performance on the test plant is $0.01 \times 0.01 = 0.0001$, "so the deterrent against utilization is 100 times greater than indicated by larval survival alone". Olckers and Borea (2009) used a similar approach to predict the realized host range of the tingid bug *Gargaphia decoris* Drake, where they multiplied scores together to create multifactorial "feeding risk" and "reproductive risk" scores.

Although it has been assumed that quantifying agent relative performance on test and target plants should help inform risk assessment, to our knowledge, there has been no attempt to validate this hypothesis despite the obvious potential relevance to risk assessment. For example, this approach could be a useful tool for regulatory authorities if there is a threshold score below which non-target attack is extremely unlikely. In this manuscript, we test the hypothesis that quantifying the relative performance of candidate agents on test versus target plants can predict whether a non-target plant will be attacked in the field.

2. Materials and methods

We restricted our analysis to arthropod agents released in New Zealand, where extensive systematic surveys for non-target attack have been conducted (Barton, 2004; Fowler et al., 2000; Paynter et al., 2008a,b, 2004; Withers et al., 2008), countering potential criticism that the detected cases of non-target attack must be a fraction of those that have occurred (e.g., Simberloff and Stiling, 1996). Moreover, it can sometimes be difficult to differentiate between spillover non-target attack and full utilization of non-target hosts (*sensu* Sheppard et al., 2005) and extensive follow-up work has also been conducted in New Zealand to investigate the nature of non-target attack. For example, the old man's beard leaf-miner *Phytomyza vitalbae* Kaltenbach was found attacking native New Zealand *Clematis foetida* Raoul growing in the absence of the target host *Clematis vitalba* L. Subsequent work showed that the ovaries of newly emerged female *P. vitalbae* flies did not mature unless they had first fed on *C. vitalba*, so although the pattern of attack indicated full utilization of *C. foetida*, the attack must have been spillover from distant *C. vitalba* infestations (Paynter et al., 2008b).

2.1. Literature review and surveys

Published data on host-range testing conducted on all arthropod weed biocontrol agents that were confirmed to have established in New Zealand (by October 2013) were searched for using Google scholar and Web of Knowledge (all databases) using the biocontrol agent name (or synonyms) and "specificity" or "testing" as search terms. Unpublished reports that documented the host-range testing of biocontrol agents released in New Zealand were also obtained. The publications and reports were used to generate a database of plant species that were shown to be within the fundamental host-ranges of the tested agents (i.e., they supported development through to adult during starvation tests) or that were considered highly likely to be within the fundamental host-range