RETROSPECTIVE ANALYSIS OF WORLDWIDE BIOCONTROL PROJECT SUCCESS AND STUDY OF SPECIALIZED SOIL TYPES EFFECTS ON BIOCONTROL AGENT HOST SPECIFICITY

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Abstract

Classical biological control of weeds is an important tool for weed management practiced around the world. However, it is not always successful. Examining historical records of biocontrol efforts would be an alternative approach to understand biocontrol agent and target weed traits correlations with success. The second chapter of this thesis is a review examining life history traits of biocontrol agent and target weed life history traits associated with biocontrol establishment and impact using the 5th edition of '*Biological Control of* Weeds: A World Catalogue of Agents and their Target Weeds' and other reports of biological control agents and target weed traits. This analysis showed that both biocontrol agent and target weed life history traits influenced the success of biological control programs, with the traits of agents more important than those of the weed. The analysis is intended to inform biological control practitioners of the importance agent and weed life history traits for establishment and successful control of weeds. Chapter 2 also revealed that biocontrol candidate agents are typically exposed to test plant species grown in nutrient-rich homogenous soil, but this could influence the susceptibility of herbivory that are adapted to special soil types, for example nutrient-poor metal-rich serpentine soil. Therefore, in the third chapter of this thesis, I tested these hypotheses in our system, the invasive weed, Lepidium draba L. (Brassicaeae), several nontarget species related to this weed and a biological control candidate, the stem and petiole gall-forming weevil *Ceutorhynchus cardariae* Korotyeav (Coleoptera: Curculionidae). Results showed that native serpentine soil influenced C. *cardariae* herbivory. Our data show that native species confamilial with the target restricted to specialized soil types may be at less risk of herbivore attack than predicted based on tests conducted in horticultural soil.

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Dedication

To my family!!

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CHAPTER 1 INTRODUCTION

Plant invasions

Globalization and increasing international trade accelerate the movement of nonindigenous plant species around the globe (van Kleunen et al. 2015). More than 13,000 plant species have become naturalized worldwide and North America has received the largest number of naturalized plant species with more than 5,000 species (van Kleunen et al. 2015). Only a small fraction of either purposefully or accidentally introduced plant species naturalize and become invasive (Jeschke and Pyšek 2018; Williamson and Fitter 1996). Invasive plant species are defined as exotic species whose introduction led to naturalization and rapid population increase which causes economic or environmental harm or harm to human health (Thomas and Reid 2007). Invasive plants can have far-ranging consequences for the economy, native biodiversity and ecosystem health and services (Pimentel 2009; Pyšek et al. 2012; Simberloff 2011). For example, plant invaders can have impacts on nutrient cycling and soil properties (Callaway et al. 2004; Liao et al. 2008; Weidenhamer and Callaway 2010), structural change in native habitats (Ehrenfeld 2010; Pyšek et al. 2012; Simberloff 2011), fire regime (e.g. fire frequency and intensity) (Brooks et al. 2004; Mack 2011; Pierson et al. 2011) and food webs (Ehrenfeld 2010; Lau 2013). The increasing accumulation of exotic plant species and their impacts increase the need for respective management efforts (Pimentel 2009; van Kleunen et al. 2015). Herbicide applications are by far the most common management strategy for invasive plants. In addition cultural and mechanical control strategies are useful for small isolated populations of invasive plants (DiTomaso et al. 2006; Kelton and Price 2009). However, these conventional control means require frequent applications over multiple years and often they are not feasible for remote locations and difficult terrain or large infestation because of associated costs (Culliney 2005; Fowler et al. 2000). The use of herbicides also causes collateral or nontarget effects on native and desirable vegetation (Matarczyk et al. 2002; Roshon et al. 1999) and can lead to increased environmental toxicity (Blossey et al. 2001). A potential alternative management strategy is classical biological control, which has been advocated as an economically and ecologically sound self-perpetuating method to mitigate invasive plants (McFadyen 1998; Schwarzländer et al. 2018).

Classical biological control of weeds and worldwide summary

Classical biological control of weeds (hereafter BCW) is defined as the practice of reuniting exotic weeds in the areas where they are invasive with host specific natural enemies from the weed's native range to reduce its vigor, reproductive ability and abundance (Thomas and Reid 2007). BCW can be a sustainable, long-term economical, self-perpetuating and effective method of control invasive plants (Fowler et al. 2000; McFadyen 1998). Worldwide deliberate release efforts for BCW are summarized in the *World Catalog of Agents and their Target Weeds* (Winston et al. 2014). The catalog compiled all deliberately released exotic, or native natural enemies to control exotic weeds and lists biocontrol agents that now occur in regions or countries in which they were not intentionally introduced. Biological control of weeds has been practiced in 150 countries and a total of 601 biological control agents were released against 261 weeds (Winston et al. 2022). In total, 511 exotic biocontrol organisms, including 13 mites, two nematodes, 37 fungi and 459 insect species, were deliberately introduced and released against 210 weed species in 55 plant families worldwide until 2021 (Winston et al. 2022).

The World Catalog data have been summarized with regard to establishment and categorized impact of biological control releases by Schwarzländer et al. (2018). The authors reported that 70.9% of agents established and that 65.7% of targeted weeds experienced some level of control. However, establishment rates of released agents and their impact on target weeds varied among different countries and ranges in which an agent was released. Recently, biocontrol practitioners have emphasized the selection of suitable target weed species and focused on effective biocontrol agents that are more likely to establish and inflict damage to the target weed to maximize project success rates (e. g. McClay 1989a; Sheppard 2003; Sheppard 2006). An assessment of past biocontrol project outcomes with regard to characteristics and traits of biocontrol agents could further improve biological weed control outcomes.

The second chapter of this thesis includes a retrospective analysis of life history traits of biocontrol agents and target weeds, as they relate to biocontrol project outcomes, specifically the establishment of biocontrol agents and impact (damage level) on the target weed. The data basis for this analysis is the data reported in the 5th edition of "*Biological*

Control of Weeds: A World Catalogue of Agents and their Target Weeds" (Winston et al. (2014).

Host specificity testing

Pre-release host specificity testing is being conducted to define the experimental host range, the level of preference for feeding, oviposition, or development of biocontrol candidate species on nontarget plants. The resulting data set is collectively used to predict the likelihood of post-release nontarget attack (Day and Urban 2003; Heard 2002; Marohasy 1998; van Klinken 1999). Various factors such as host-plant interactions, plant demography and abiotic factors (e. g. Briese 2000a; Davis et al. 2006; Impson et al. 2004; Zalucki and Van Klinken 2006), have been considered to reliably assess and predict the environmental safety of biological control candidates post-release, while other environmental factors such as soil chemical properties and soil nutrient condition have received little attention (e. g. Milbrath et al. 2018).

In the third chapter of this thesis, I report a study on the effect of specialized soil types on the performance of a biocontrol candidate on native nontarget plant species confamilial to the target weed that are adapted to specialized soils. The invasive Eurasian perennial herbaceous hoary cress, *Lepidium draba* L. (Brassicaceae), four confamilial nontarget plant species and the Eurasian stem and petiole gall-forming weevil, *Ceutorhynchus cardariae* Korotyeav (Coleoptera: Curculionidae) were used as a model system to study the effects of metalliferous soils on biocontrol candidate performance.

Study system

<u>Lepidium draba</u>

Hoary cress, *Lepidium draba* L. (Brassicaceae), is a Eurasian herbaceous, perennial clonal mustard (Francis and Warwick 2008; Mulligan and Findlay 1974). *Lepidium draba* root system supports numerous aerial shoots, which can grow up to 90 cm tall (Francis and Warwick 2008; Mulligan and Findlay 1974; Mulligan and Frankton 1962). Leaves are sparse to densely pubescent and are irregularly toothed to entire and narrowed towards petiole.

Stems are mostly erect, and branches at the top of the plant give rise to flowering stalks (Francis and Warwick 2008; Mulligan and Frankton 1962). The flower consists of 2-4 cm long four white petals and is in a compact corymb arrangement with very small or no leaves (Francis and Warwick 2008; Mulligan and Frankton 1962). *Lepidium draba* fruits are glabrous silicles and generally have two seeds per pod (Francis and Warwick 2008; Mulligan and Frankton 1962). *Lepidium draba* fruits are glabrous silicles and generally have two seeds per pod (Francis and Warwick 2008; Mulligan and Frankton 1962). *Lepidium draba* is a self-incompatible flowering plant favoring obligate-outcrossing (Francis and Warwick 2008; Mulligan and Frankton 1962) and can produce large quantities of seeds. For example, a flowering stem of hoary cress can produce up to 850 seed pods (Corns and Frankton 1952; Francis and Warwick 2008) and as many as 17,000 viable seeds per square foot in a single year (McInnis et al. 2003). Although a single plant can produce large quantities of seeds, invasion with vegetative reproduction is the major contributor to patch-size expansion (Gaskin 2006). A study by Kirk et al. (1943) reported that, in the absence of competition, a single plant can produce as much as 400 ramets and spread at a rapid rate covering about a 4 m diameter and have radial growth up to 76 cm annually (Selleck 1965).

Lepidium draba was inadvertently introduced to North America in the late 19th century (Francis and Warwick 2008; Mulligan and Findlay 1974) through seed contaminants and ship-ballast (Bellue 1946; Groh 1940). Since its introduction, *L. draba* has been spreading throughout the country. It is particularly problematic in the western United States, but has also sporadically been reported in the eastern United States (Gaskin et al. 2005a). It is a declared noxious weed in 15 U.S. states (USDA-NRCS 2021a).

Lepidium draba can invade different microsites with soil types ranging from light and coarse sandy to heavy clayey soils and is neutral to alkaline pH levels (Scurfield 1962). Commonly invaded habitats include cropland, pasture and rangelands, roadsides and other disturbed areas. *Lepidium draba* is particularly problematic in irrigated or semi-irrigated crops and pastures (Francis and Warwick 2008; McInnis et al. 2003; Scurfield 1962). *Lepidium draba* invasions have caused economic impacts (McInnis et al. 2003), can serve as alternative host plants to crop pests (Cripps et al. 2006; Mason et al. 2004), impede riparian functions like sediment trapping, bank stabilization, and filtration (Francis and Warwick 2008), displace or decrease native flora genetic diversity and abundance (Mealor et al. 2004),

or can inhibit germination and seedling growth of neighboring plant species through root exudates (allelopathy effects) (Caesar 2003; Egli and Olckers 2017). In addition, the plant is toxic to grazing animals as its tissue sulfur concentrations (0.7 to 2.7%) are far above tolerance limits of livestock ($\leq 0.4\%$) (McInnis et al. 2003).

Different management options have been used to control *L. draba*. These include tilling (McInnis et al. 2003; Mulligan and Findlay 1974), repeated grazing using small sheep or goats (Francis and Warwick 2008 and reftherein), hand pulling (Francis and Warwick 2008; Graves-Medley and Mangold 2018), and application of herbicides (Francis and Warwick 2008; Graves-Medley and Mangold 2018). These management practices all control *L. draba* in smaller infestations; however, all these methods are not particularly feasible for large or remote infestations and all of them need to be repeated over multiple years (Ani et al. 2018; Francis and Warwick 2008).

Ceutorhynchus cardariae Korotyaev (Coleoptera, Curculionidae)

Ceutorhynchus cardariae Korotyaev is a Eurasian leaf, petiole, or stem gall-forming weevil (Hinz and Diaconu 2015; Korotyaev 1992). Lepidium draba is the only host plant reported in its native range and a field-host range study only found the congener L. campestre (L.) W. T. Aiton (Brassicaceae) to also support adult development (Hinz and Diaconu 2015). The weevil is primarily univoltine with a possible second generation (Hinz and Diaconu 2015). Overwintering adult females start to lay eggs in early spring. Lifetime fecundity is on average 125 eggs (Hinz and Diaconu 2015). Female oviposition (sometimes even oviposition attempts) causes the formation of plant galls and the three larval stages feed on parenchymatic tissues within those galls prior to pupating in the soil (Hinz and Diaconu 2015). In the native range, C. cardariae development from egg to adult takes about 12 weeks and adults of the F1 generation start to emerge from May onward. Immediately, following emergence weevils begin to feed on L. draba foliage and continue to do so for 2-3 weeks before weevils aestivate during the summer, which coincides with L. draba senescence (Hinz and Diaconu 2015). Weevils recommence feeding in late August through late fall when they enter hibernation. Gall formation by C. cardariae can severely stunt or prematurely kill shoots at higher weevil herbivory intensity, reduce plant vigor and decrease the competitive ability of L. draba (Hinz and Diaconu 2015). In addition, C. cardariae has a long oviposition

period and attacks both phenological stages of *L. draba*, rosette and bolting plants, (Hinz et al. 2006; Hinz and Diaconu 2015), making it difficult for *L. draba* to escape weevil attack.

Ceutorhynchus cardariae host-specificity testing

The experimental host range of C. cardariae has been studied at CABI Switzerland since 2003. No-choice-, choice-, and field cage tests have been used to define the experimental host range of C. cardariae. Pre-release oviposition, feeding and development tests were conducted with 157 plant species(Weyl et al. 2019a, Unpublished). A total of 112 plant species (~72%) were native to North America (hereafter NA) including 11 federally listed threatened or endangered (hereafter T&E) plant species in the USA (Weyl et al. 2019a, Unpublished). Under no-choice conditions, 45 NA plant species supported gall development to some degree. Ceutorhynchus cardariae adults emerged from 26 NA plant species, including the confamilial *Caulanthus anceps* E. B Payson, C. flavescens (Hook.) E. B. Payson, C. inflatus S.Watson and T&E Streptanthus glandulosus subsp. albidus Al-Shehbaz, M. S. Mayer & D.W. Taylor (Weyl et al. 2019a, Unpublished). Fourteen NA plant species supported larval development of C. cardariae and only seven NA plant species supported adult development of the weevil under choice conditions. In open field tests with eight NA plant species that were grown more than two meters distant to L. draba, no nontarget attack was found (Weyl et al. 2019a, Unpublished). Host-specificity data indicate that C. cardariae has a broader physiological host range, i.e., plant species that support development of the weevil under no-choice conditions (Schaffner 2001), covering species within all three tribes of the Brassicaceae family (Schwarzländer et al. 2019, Unpublished). However, during open-field tests, C. cardariae demonstrated a much narrower ecological host range, i.e., plant species the weevil chooses to attack (Schwarzländer et al. 2019, Unpublished). Generally, C. cardariae growth and reproduction was impaired on almost all nontarget plant species when compared to L. draba (Schwarzländer et al. 2019, Unpublished).

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CHAPTER 2: A REVIEW OF BIOLOGICAL CONTROL AGENT AND TARGET WEED TRAITS ASSOCIATED WITH ESTABLISHMENT AND IMPACT

Abstract

Classical biological control is a sustainable and ecologically sound strategy for the management of alien invasive plants. Improving success rates of weed biocontrol programs is an ongoing effort requiring a variety of different approaches. Previous assessments of life history traits of released biocontrol agents and respective target weeds with regard to agent establishment and impact indicated that certain attributes of agents and target weeds such as agent feeding niche, guild and weed life cycle and methods of reproduction are associated with better control outcomes. Here we examined the past biocontrol projects for correlations between target biocontrol agent and target weed traits that are associated with different levels of achieved control. Data collated in the 5th edition of 'Biological Control of Weeds: A World Catalogue of Agents and their Target Weeds' were used as the basis for a global analysis. Seven biological control agent traits and four target weed traits, respectively were added to the data set for each biocontrol agent or target weed based on published literature. Analyses of agent establishment showed that biocontrol agent traits were correlated with successful establishment: Biological control agents feeding internally on aboveground plant parts, multivoltine agents, and agent with both, adult and immature feeding life stages had a higher probability of establishment. For weeds, those occurring in aquatic or riparian habitats were associated with higher biocontrol agent establishment rates. Biocontrol agent traits feeding habit, feeding place, feeding parts, feeding niche, feeding guild, voltinism and damaging stages and target weed traits life cycle, propagation modes and ecosystem with the exception of plant growth habit, were strongly correlated with agent impact. Agents included exophytic feeders, feeding on vegetative plant parts, multivoltine agents and biocontrol agents with adult and immature feeding life stages. Perennial weeds, weeds reproducing vegetatively and weeds from aquatic or riparian habitats were associated with greater biocontrol success. This analysis may facilitate biological weed control target prioritization or biological control candidate selection, which in turn could help improving biocontrol project successes. Further investigations to strengthen the predictability of agent control success such as analyzing biocontrol agent and target weed traits in combinations, or inclusion of climatic variability traits would be useful.

Introduction

Globalization of trade and travel have increased the number of invasive plant species around the globe (van Kleunen et al. 2015). As a consequence, impacts caused by invasive plants on the economy, biodiversity and ecosystem services have increased substantially (Pyšek et al. 2020; Simberloff et al. 2013; van Kleunen et al. 2015). Classical biological control of weeds (hereafter BCW) is considered an economically sound and environmentally safe management strategy to control invasive plants (Clewley et al. 2012; Fowler et al. 2000; McFadyen 1998; Schwarzländer et al. 2018). Worldwide, BCW has been implemented in 150 countries and until 2012, a total of 468 biocontrol agent species have been intentionally released for the control of 175 invasive plant species (Winston et al. 2014). Successful control outcomes for BCW projects are well documented (e.g. Julien 1989; Winston et al. 2014) and nearly two third of weed targeted up to 2012 received some level of control (Schwarzländer et al. 2018). However, the level of success is only categorized broadly and for many weed biocontrol projects evaluations of outcomes lack peer reviewed studies (see Winston et al. 2014). One factor influencing the outcome of BCW projects is the difficulty in selecting the most effective biocontrol agents that impose the most damage to a target weed a *priori* (Julien 1989). Similarly, prioritization of target weeds based on their susceptibility to BCW could facilitate more successful project outcomes (but see Canavan et al. 2021; Downey et al. 2021; Paterson et al. 2021). A posteriori evaluations of successes and failures of BCW programs still receive relatively little attention (McEvoy and Coombs 1999), despite the fact that broad analyses may reveal agent or target weed patterns that could be used to improve future BCW project success rates. The data compiled in the 5 editions of 'Biological Control of Weeds: A World Catalogue of Agents and their Target Weeds' (Julien 1982; Julien 1987; Julien 1992; Julien and Griffiths 1998; Winston et al. 2014) provide an ideal opportunity to identify factors associated with biocontrol project outcomes since the data represents an near-complete lists of BCW activities but only few analysis have been conducted: Biocontrol agents within the order Coleoptera especially in the Curculionidae and Chrysomelidae families were more successful than other biocontrol agents (Crawley 1989; von Rütte 2013). Schwarzländer et al. (2018), summarized catalog data and reported a higher establishment rate also for hemipteran biocontrol agents. von Rütte (2013) analyzed 123 weed species and 318 biocontrol agents compiled in the 4th edition of '*Biological Control of*

Weeds: A *World Catalogue of Agents and their Target Weeds* ' (Julien and Griffiths 1998) reported that mainly biocontrol agent life history traits were correlated with the success. Biocontrol agents feeding externally and on vegetative plant tissues were more successful than others. Higher success rates were also reported for agents with multiple generations per year (Cullen et al. 2022; von Rütte 2013). A recent catalog-based analysis of effectiveness of 288 biocontrol agents released in Australia (Cullen et al. 2022) reported that agent feeding guild and target weed growth habits were correlated with the biocontrol success. Biocontrol agents that feed on root/crown and sap feeders control target were effective and herbaceous perennial plants were more amenable to control (Cullen et al. 2022). Paynter et al., (2012) found in a study not based on the catalog data that BCW projects against plants reproducing only vegetatively, including apomictic plants and those in aquatic ecosystems were more successful. Other reviews found that biocontrol was more successful for perennials weeds (McClay, 1989) or that herbaceous weeds could be more successfully managed using BCW than shrubs or trees (Straw and Sheppard 1992).

In this study, we used biocontrol projects from the 5th edition of '*Biological Control of Weeds: A World Catalogue of Agents and their Target Weeds*' (Winston et al. 2014) and added data for seven biocontrol agent traits and four target weed life history traits, respectively (see Appendix C and D for agent and weed traits, respectively for references). Our aim was to analyze whether biocontrol agent or targeted weed life history traits are associated with higher biocontrol agent establishment rates or impact. Our hypotheses were that weed biocontrol success depends upon 1) tissue type attacks, 2) whether agent attack in external or internal, 3) voltinism of agent, 4) terrestrial or aquatic weeds, 5) methods of weed reproduction (details in materials and methods section).

Materials and Methods

<u>Data Source</u>

This analysis used an updated version of the 5th edition of '*Biological Control of Weeds: A World Catalogue of Agents and Their Target Weeds*' (Winston et al. 2014; Winston et al. 2022) (hereafter, the catalog). The catalog compiles all deliberate weed

biocontrol releases worldwide with detailed information on release year(s) country of origin of the biocontrol agent(s), etc. As such, it provides a complete list of targeted weed species and biocontrol agent species released. While updating the catalog is an ongoing effort (Winston et al. 2022), we used for the purpose of this analysis all agent species released from pre 1900 until 2012 i.e., data included in the printed version of the 5th edition of the catalog (Winston et al. 2014). The catalog is formatted by agent releases rather than biocontrol agent species released. Often, the same biocontrol agent species was released in different countries or more than once in the same country (Winston et al. 2014). The curators of the catalog treated releases as individual cases when one of the following criteria applied: 1) the same agent was released in a different country, 2) the same agent was released in the same country but from a different source, 3) the same agent was released within the same country and from the same source but for a different weed, or 4) the same agent was released in the same country, but at least five years apart (Winston et al. 2014). For this analysis, we only considered biocontrol agents from the weed's native range that were intentionally introduced and we included only insects and mites as agents. In total we considered 1,498 releases of 436 biocontrol agent species (426 insects and 10 mites) against 171 target weeds in 48 plant families (Winston et al 2014).

Biological control agent and weed life history trait data

Updated establishment and impact data of each releases/ projects listed in the 5th edition of catalog information were directly imported from the catalog (Winston et al. 2014). We added information on different life history traits for each biocontrol agent and target weed species by searching species names in Google, Google Scholar or the CABI Invasive Species Compendium (CABI 2022). We used published literature, unpublished technical reports and in a few cases extension publications as references for each trait value of each biocontrol agent or weed. If information for a biocontrol agent or a weed differed between their respective native and introduced range(s), only information for the introduced range was considered (Reference lists for biocontrol agent and target weed life history trait information are provided as Appendix C and Appendix D, respectively). The biocontrol agent traits used for the analysis were: 1) Biocontrol agent feeding habit, because earlier studies indicated higher success rates for exophytic feeders (von Rütte 2013); 2) agent

feeding guild and 3) feeding niche, because there are assumptions that control success is associated with biocontrol agent feeding on plant vascular systems or mechanical support systems (Goeden 1983; Harris 1973); 4) plant part attacked and 5) plant tissues attacked by biocontrol agents. Based on the reviews that agents attacking vegetative tissues (Harris 1973) and belowground feeders (Blossey and Hunt-Joshi 2003) are associated with greater success; 6) voltinism because there are several studies that indicate that control success is more likely for multivoltine biocontrol agents (Goeden 1983; Harris 1973; Zalucki and Van Klinken 2006); and 7) the number damaging life stages (see Table 1 for details).

For target weeds, the following life history traits were used: 1) life cycle, since it has been proposed that perennial weed species have a better control potential than annual or biennial plants (McClay 1989b; Straw and Sheppard 1992); 2) invaded ecosystem, because studies reported that aquatic weeds have greater control potential than terrestrial plants (Paynter et al. 2012); 3) mode of propagation, because greater biocontrol program success has been linked to plants that only reproduce vegetatively (Burdon and Marshall 1981; Paynter et al. 2012), though Chaboudez and Sheppard (1995) argued that biocontrol success was independent of species reproductive mode; and 4) plant growth habit, because it has been proposed that herbaceous plants are easier to control than shrubs or trees (Straw and Sheppard 1992) (see Table 2.1 for details on traits and their levels; Appendix A and Appendix B for agent and weed traits levels definitions)).

Biocontrol project outcome data

The catalog reports agent establishment and categorically the level of damage inflicted (impact) on target weed for each release recorded (Table 1 in Winston et al. 2014)(Appendix A). For the catalog, curators classified level of control on the target weed based on distribution and abundance of the agent, extent and degree of target weed suppression, and the need of supplementary management practices (Schwarzländer et al. 2018; Winston et al. 2014). For this analysis, we used the impact categories as stated in the catalog (Winston et al. 2014). Establishment of biocontrol agents and impact on the target weed were classified for each release by the catalog curators based on reviews of published literature, if available, or unpublished technical documents and personal communications with subject experts. For this analysis, we included all BWC releases made pre 1900 through 2012, but we updated information on establishment and impact for all releases from the current catalog (Winston et al. 2022).

Establishment of released agents was reported in the catalog under three categories: 1) established, 2) not established, or 3) unknown (Winston et al. 2014; Winston et al. 2022). For this analysis, releases whose establishment was stated as unknown (n=41, 2.5% of all releases), were excluded leaving 1,457 releases for analysis. We then excluded releases that did not result in establishment (n=501) for analysis of biocontrol agent's impacts. Levels of damage inflicted or impacts on target weed were grouped into one of seven categories for those agents that established: too early post release, unknown, none, slight, medium, variable, and heavy. In addition, six releases were categorized as too early post- release for impact estimation and the impact of 69 releases was determined unknown. These releases were excluded from the analysis. The data set analyzed for biocontrol agent's impact on target weed comprised 881 releases. Of the 881 releases, 199 (22.59%) had heavy impact, 127 (14.42%) had medium impact and 182 (20.66%) had variable impact, 306 releases (34.73%) had slight impact, and 67 (7.60%) had no impact on the target weed. We consolidated these five impact categories into three levels because there were insufficient observations for some impact categories regarding certain traits (mode of propagation, plant life cycle, agent feeding place), complicating analyses of data. The three levels are heavy, medium/variable and slight/none (Table 2). Of the 881 releases used for the analysis, 199 (22.59%) had heavy impact, 309 (35.07%) had medium/variable impact and 373 (42.34%) releases had slight or no impact.

Statistical analysis

Information on biocontrol agent released and target weed was summarized by agent order and weed family respectively. Biocontrol agent establishment data (binary yes/no) were analyzed using generalized linear mixed models (SAS Proc GLIMMIX), assuming a binomial distribution with a logit link function. Life history traits for biocontrol agents or weed species were treated as fixed effects while country of a biocontrol project or agent release were considered as random effects. Separate models were fit to individual life history predictor variables to test hypotheses that agent and target weed life history traits could potentially influence the establishment of released biocontrol agents. Pairwise comparisons were used to assess differences in probabilities of establishment. Odds were calculated as the ratio of proportion of successful establishment to proportion of failure.

Given establishment, a categorical model (SAS Proc CATMOD) was used to fit the tabulated impact outcome of each release assuming a multinomial distribution with a generalized logit link. Impact outcome levels were designated as heavy, medium/variable and slight/none. Similar to the establishment analysis, separate models were estimated for agent and weed life-history traits.

All statistical analysis were performed using the statistical software package SAS version 9.4 (SAS Institute, Cary, NC). Detectable effects for all models were determined for test results of p<0.05.

Results

Summary of biocontrol agents and target weeds

Through 2012, a total of 426 insect and ten mite species were deliberately released in countries outside their native range to control weeds in 1,498 releases (Fig. 2.1). All biocontrol agents belonged to seven insect orders. Of the 426 insects and mites, 193 species (44.27%) are Coleoptera (Fig. 2.1). Insects from four orders (Coleoptera, Lepidoptera, Diptera and Hemiptera) accounted for 94.0% of biocontrol agent species released and 95.1% of all releases (Fig. 2.1). The water hyacinth weevil, *Neochetina eichhorniae* Warner (Coleoptera: Curculionidae) was the most often released biocontrol agent species with 45 releases. Of the 426 insect and mite species, 156 or 37% belonged to two beetle families the Curculionidae and Chrysomelidae.

A total of 175 invasive plant species within 48 families were or are biological control targets. The largest number of biological control agents was released for the control of *Lantana camera* L. *sensu latu* (Verbenaceae) with 41 (9.4%) of all agents species released. Most of the 175 targeted plants were Asteraceae (44 species or 25.1%) (Fig. 2.2). More than half of the targeted plant species (approximately 53%) were Asteraceae, Cactaceae or Fabaceae (Fig. 2.2).

Biocontrol agent establishment with regard to agent traits

Five of seven biocontrol agent life history traits analyzed were strongly associated with greater biocontrol agent establishment. These were: feeding habit, feeding place, voltinism, damaging life stage(s) and feeding guild (Table 2.3). The results indicated a higher proportion of establishment for biocontrol agents that feed internally and on aboveground plant parts (Table 2.4; Fig 2.3). Similarly, biocontrol agents that were multivoltine and agents with both adult and immature life stages damaging the target weed had higher proportions of establishment (Table 2.4; Fig 2.3). Establishment rates for borers feeding externally did not differ from establishment rates compared to internal feeders (Table 2.4; Fig 2.3). There was no difference in establishment rates between agents feeding on plant reproductive or vegetative plant tissues (Table 2.4; Fig 2.3).

Biocontrol agent establishment with regard to weed traits

For plant life history traits, invaded ecosystem was strongly associated with increased establishment rates of biocontrol agent (Table 2.5). The odds plots indicate a higher likelihood for target weeds in aquatic or riparian ecosystem than for weeds in terrestrial ecosystems (Table 2.6; Fig. 2.4). In contrast, agent establishment was similar regardless of weed reproductive mode, plant life cycle, or growth habit (Table 2.6; Fig. 2.4).

Biocontrol agent impact with regard to agent traits

All biocontrol agent life history traits tested were associated with biocontrol agent impact (Table 2.7). Biocontrol agents that feed externally on target weeds were most frequently associated with heavy impact and the proportion of releases of external feeders inflicting heavy impact was 34% higher than that of internal feeders (Table 2.7; Fig. 2.5A). For guild, feeding by sucking insects was more frequently associated with heavy impact. Similarly, boring and chewing insects were associated with heavy impact (Table 2.7; Fig. 2.5B).

Biocontrol agents feeding on vegetative plant tissues caused more frequently heavy impacts than those feeding on reproductive plant parts (Table 2.7; Fig. 2.5C). Inflorescence feeding was least often associated with heavy impact whereas root and stem feeding caused most heavy impact (Table 2.7; Fig. 2.5D). Overall, the proportion releases of vegetative

tissue-feeding biocontrol agents causing heavy impact was 247% higher than that of reproductive tissue-feeding agents (Table 2.7; Fig. 2.5C & D).

Releases of biocontrol agents attacking belowground plant tissues were 57% more frequently associated with heavy impact than releases of biocontrol agent feeding on aboveground plant tissues (Table 2.7; Fig. 2.5E). Insect biocontrol agents with adult and immature life stages feeding on weeds caused heavy impacts most frequently (Fig. 2.5F). Similarly, multivoltine biocontrol agents had more frequently heavy impacts on their respective target weeds, followed by univoltine agents and bivoltine biocontrol agents (Table 2.7; Fig. 2.5G).

Biocontrol agent impact with regard to weed traits

Biocontrol agent impact indicated a strong association with the following weed life history traits: 1) ecosystem, 2) plant life cycle and 3) propagation mode but there was no association between biocontrol impact and weed growth habit (Table 2.8). Biocontrol agents released against target weeds in aquatic or riparian ecosystems were more frequently having heavy impact on their respective target weeds and the proportion of releases against aquatic/riparian weeds causing heavy impacts was 67% higher compared to proportion of biocontrol releases against weeds in terrestrial ecosystems (Table 2.8; Fig. 2.6A, C).

Biocontrol projects against perennial weeds more frequently resulted in heavy impacts and the proportion of releases against perennial weeds inflicting heavy impact was 86% and 193% higher, than those for biennial and annual weeds, respectively (Table 2.8; Fig. 2.5B). Biological control projects for strictly vegetatively reproducing target weeds had more frequently heavy impacts whereas projects against weeds reproducing solely by seed resulted least often in heavy impact outcomes (Table 2.8; Fig. 2.6C).

Discussion

Retrospective analysis of past biocontrol projects shows that the traits of the biological control agent and the target weed life history, influenced the probability of establishment and the level of impact of biocontrol releases on target weeds, similar to previous findings (e. g. Cullen et al. 2022; von Rütte 2013). For the probability of establishment of a biocontrol agent release, agent life history traits may be more important than weed traits. This could be that host specific agent was released from the weed's native range in a enemy free environments and are not resource limited in the invaded region. (e. g. Kéry et al. 2001; Root 1973; Sholes 2008; Stephens and Myers 2012). However, all biocontrol agent and target weed life history traits with the exception of weed growth habit were correlated with biological control release impact.

Biological control agent establishment

Overall, biocontrol agents that feed internally had a higher establishment rate than external feeders such as chewers. Predation and parasitism are two major biotic factors limiting agent establishment and success of biocontrol (Harms et al. 2020) and endophagous insect herbivores may be less likely to suffer from predation and parasitism (Cornell and Hawkins 1995; Paynter et al. 2018). Paynter et al. (2018) reported reduced predation on internally feeding weed biocontrol agents in New Zealand compared to external feeders. Survival of two leaf feeders, the broom leaf beetle (*Gonioctena olivacea* Forster) and the Honshu White admiral butterfly (*Limenitis glorifica* Fruhstorfer), biocontrol agents of Scotch broom (*Cytisus scoparius* (L.) Link) and Japanese honeysuckle (*Lonicera japonica* Thunb.) respectively, increased during predator exclusion experiments (Paynter et al. 2019). In addition, internal feeders may be less affected by abiotic environmental factors e.g. precipitation (e. g. Downey et al. 2021). Although sucking insects are external feeders, their establishment rate was similar to that of borers. This might be due to the ability of sucking insects to avoid predation by dropping off from plants when threatened (Dhileepan et al. 2006).

Our results support the assumptions that multivoltine species are more likely to have a higher establishment rate (Goeden 1983; Harris 1973). Similar results were reported for arthropod biocontrol agents (Zalucki and Van Klinken 2006). And biocontrol agents with both, adult and immature life stages feeding on the respective target weed had a higher probability of establishment. A similar result was reported by Forno & Julien (2000) in an analysis of aquatic WBC programs worldwide. The analysis indicated a higher likelihood of establishment for biocontrol agents on weeds of aquatic/riparian ecosystem (Forno & Julien 2000).

Biological control agent impact

Overall, externally feeding biocontrol agents, once established were more effective weed biocontrol agents in our analysis compared to internal feeders, supporting previous findings (von Rütte 2013) but contrary to assumption that internal feeders are more likely to inflict effective control (Crawley 1989). It has been speculated that external feeders may facilitate secondary infections and cause additional damage to weeds, as has been observed in cacti (Moran and Zimmermann 1984), or in corn (Kurtz et al. 2010) or that greater damage may be the result of the higher fecundity of exophytic feeders, which could compensate for predation (Cornell and Hawkins 1995). Our analysis showed that exophytic feeders (139.77 \pm 1.03, mean eggs/generation \pm SE) had a higher fecundity (approximately two-fold of that of endophytic feeders (204.38 \pm 1.04, mean eggs/generation \pm SE) (t₇₈₇= -6.51, P< 0.0001). Among external feeders, biocontrol agents in the sucking guild seem to be promising for successfully controlling weeds. Sucking insects have the capability to inflict damage to host plants through direct feeding damage and indirectly through the direct or indirect transmission of plant pathogens and viruses (Dhileepan et al. 2006; von Rütte 2013). In addition, sucking insect attributes such as short life cycles, high intrinsic rate of increase (Dhileepan et al. 2006) and good dispersal ability (Williams et al. 2008) may further contribute to their better probability of effectiveness.

With regard to plant tissues attacked, our analysis implies that biocontrol agent feeding on plant vegetative tissues may be more effective in inflicting heavy damage to the target weed than feeding on reproductive structures, supporting Harris (1973) assumption that agent feeding on vegetative tissue control target weeds effectively by direct feeding damage and increasing plants vulnerability to secondary infections (e. g. Caesar 2003). It has long been argued that agents feeding on or destroying vascular or mechanical support tissues are more likely to control target weeds (Goeden 1983; Harris 1973), however there are few studies testing that hypothesis directly (Goeden and Ricker 1979). Insect feeding on plant reproductive structures and inflorescence are less likely to inflict heavy damage. Potential explanations for the ineffectiveness of reproductive tissue feeders range from the unavailability of reproductive structures during the breeding period of the biocontrol agent (Impson et al. 2021), the lack of seed-limited population biology of weeds (Impson and Hoffmann 2019; Kéry et al. 2001), to long-lived and large seed banks like that for Australian *Acacia* species, or *Onopordium* thistles (Briese 2000b; Impson et al. 2004). However, other authors have stressed the importance of the supplementary role of inflorescence feeders in reducing seed banks, seedling recruitment, and spread of weeds (Impson et al. 2021; Impson and Hoffmann 2019; Milbrath et al. 2018).

Biocontrol agents that feed on belowground plant tissues are more likely to be effective in controlling target weeds, as proposed by Blossey & Hunt-Joshi (2003). Root herbivory helps suppressing weeds by disrupting crucial functions of plants such as resource uptake, reserve storage and it exposes the plant to other biotic and abiotic stresses (Blossey and Hunt-Joshi 2003; Caesar 2003). Other studies found that root herbivores have a lower risk of predation compared to aboveground herbivores and that the spatial niche potentially could protect root herbivores better from adverse environmental conditions aboveground (Egli and Olckers 2017; Feeny 1976; Simelane 2010).

Biocontrol agents with adult and immature life stages feeding on a weed are more likely to inflict effective control, in line with Forno & Julien (2000) who stated that effective control is more likely with biocontrol agent with both adult and immatures damaging the target weeds. For example, *Agasicles hygrophila* Selman & Vogt adult and immatures feeding on aquatic weed, *Alternenthera philoxeroides* caused heavy damages, while *Macrorrhina endonephele* (Hampson) immatures caused either medium or variable damages (Winston et al. 2014). Adult and immature life stage feeding simply lengthen the duration of time the plant is exposed to herbivory (Forno and Julien 2000). In addition, when the adults and immature stages feed on different plant tissues this could additionally harm the plants (e. g. *Octotoma scabeipennis* Guérin-Méneville, (Coleoptera: Chrysomelidae) adults chew leaves and larvae mine the leaves, Johns et al. 2003, . Our data also suggest that multivoltine biocontrol agents would be more likely to provide effective control of weeds, following speculations that Harris (1973) made.

Our study supports reports made elsewhere (e. g. Paynter et al. 2012) that weeds in aquatic or riparian habitats experience more damage or are more successfully controlled by

biocontrol agents than weeds occurring in other ecosystems. Paynter et al, (2012) similarly found that higher control success of aquatic or wetland weeds compared to terrestrial weeds. Majority of releases of control agent against aquatic weed were only on few weed species such as *Salvina molessta* D. S. Mitch, *Pontederia crassipes* Mart. These weeds, which are invasive in many countries have received a greater number of releases compared to weeds that were limited to a few countries and since a number of these were successful, it may bias comparisons of successful between aquatic and terrestrial weeds. For example, *P. crassipes* received almost half of all releases for weeds in aquatic ecosystems (118 of 243 releases) (Winston et al. 2014). Other factors that might have contributed to the success of biocontrol in aquatic ecosystems may include wind and waves, which may in larger water bodies fragment the biocontrol agent-stressed waterweed stands (Cilliers et al. 2003).

Our data suggest that weeds that are reproducing only vegetatively may be more suitable targets for BCW. This may be due to lower genetic diversity or plasticity of vegetatively reproducing weeds in comparison to sexually reproducing plants (Burdon and Marshall 1981). However, in a different study weed biocontrol success was found to be independent of reproductive mode (Chaboudez and Sheppard 1995; Li and Ye 2006). Detail studies on modes of reproduction and genetic plasticity of weeds in their invaded ranges (in comparison to their native ranges), are increasingly conducted (Gaskin et al. 2011; Gaskin et al. 2005b), and should probably be part of any BCW program in order to relate biocontrol success or failure to this weed reproductive trait. McClay (1989b) assumed in a study on agriculturally important weeds in Canada that biennial and perennial weeds are better control targets. This may be that perennial plants are more apparent in spatiotemporal scale (Feeny 1976; Martini et al. 2021; Sholes 2008). Our data support the notion that perennial weeds are more suitable targets than annual weeds.

With greater demands on return on investments and in order to improve outcomes of weed biocontrol programs, the results of this analysis may aid biocontrol practitioners in efforts to prioritize biological control projects based on target weed traits and available agent candidate species if known. The data presented are only based on association of increased probabilities and as such are not strongly indicative by any means. Practitioners will need to give preference first to factors such as agent host specificity, climate matching and economic and public health aspects of invasive weeds when selecting BCW projects before considering biological traits of candidate agents or potential target weeds.

Predicting agent establishment rates and successful BCW outcomes may be enhanced by analyzing agent and weed traits in combination. For example, the benefit of foliage feeding insects have been documented for annual weeds (Day and Urban 2003; Harris 1973; Harris 1991). We were not able to predict that associations based on our analysis because life history traits were only analyzed individually. We anticipate with biocontrol researchers continuing to update the online version of the catalog and an increasing number of quantitative BCW outcome analyses, larger and more comprehensive analyses will be possible. The biocontrol agent and weed trait data collected for this analysis along with its references will be shared with the curators of the catalog as a step to facilitate future analysis.

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Life history trait	Levels	References
Biocontrol agent		
Feeding habit	Internal, external	Crawley 1989, von Rutte 2013
Feeding place	Aboveground, belowground	Blossey & Hunt-Joshi 2003
Feeding part	Vegetative, reproductive	Harris 1973
Feeding niche	Root, stem, foliage, inflorescence	Harris 1973; Goeden 1983
Feeding guild	Chewing, borer, sucking, galling	Harris 1973; Goeden 1983
Damaging life stage	Adult & immature, immature	Forno & Julien 2000
Voltinism	Univoltine, bivoltine, multivoltine	Harris 1973; Goeden 1983; Kimberling 2004
Target weed		
Growth habit	Herbs, shrubs, shrubs/tree	Straw & Sheppard 1992
Life cycle	Annual, biennial, perennial	McClay 1989
Invaded ecosystem	Terrestrial, aquatic/riparian	McClay 1989; Straw & Sheppard 1992
Mode of reproduction	Seeds, vegetative, seeds & vegetative	Chaboudez & Sheppard, 1995; Burdon & Marshall 1981

Table 2.1 Biocontrol agent and target weed life history traits and their levels selected for the study of correlation with the agent establishment and impacts on the target weeds

Table 2.2 Biocontrol agent's impact categories and their definitions adopted from Winston et al, (2014) and Schwarzlaender et al, (2018)

Category	Definition
Heavy	If a biocontrol agent inflicts sufficient damage on target weed and
	no other management measures needed or minimal management
	measures, if needed are grouped under heavy impact category
Medium	If a biocontrol agent caused some damage to target weed and other
	management options are needed to supplement biocontrol are
	assigned a medium impact category
Variable	Impacts were assigned variable impact if an agent release caused
	heavy damage in some sites or countries/regions and low or
	medium impact in other sites or countries/regions
Slight	If a biocontrol agent inflicted limited damage or unlikely to have
	significant impact on weed population
None	No apparent impact on the target weed

were fitted to each	agent trait			
Agent trait	Level	df	F-	P-value
			value	
Feeding habits	Internal, external	1, 1370	7.22	0.0073
Feeding place	Aboveground, belowground	1, 1370	4.73	0.0297
Feeding part	Reproductive, vegetative	1, 1370	0.15	0.6976
Feeding niche	Foliage, inflorescence, root, stem	3, 1368	1.61	0.1848
Feeding guild	Borer, Chewing, Galling, Sucking	3, 1368	9.11	< 0.0001
Damaging stage	Adult & immature, immature only	1, 1370	18.9	< 0.0001
Voltinism	Univoltine, bivoltine, multivoltine	2, 1367	14.8	< 0.0001

Table 2.3 Results for logistic regression ANOVAs testing the influence of biocontrol agent life history traits on agent establishment (established, or not established). Separate models were fitted to each agent trait

Table 2.4 Predicted probabilities of successful establishment (\pm SE) for biocontrol agent life history traits from logistic regression analysis. Values are taken from logistic regressions fitted to each trait individually. Pairwise least square mean comparisons were performed for significance within each trait groups at *P* ≤0.05 and traits denoted by different letter within each trait category differ significantly

Agent trait	Levels	Probability of establishment
Feeding habit	Internal	$0.694 \pm 0.025a$
	External	$0.624\pm0.029b$
Feeding place	Aboveground	$0.674\pm0.024a$
	Belowground	$0.583\pm0.047b$
Feeding part	Reproductive	0.683 ± 0.038
	Vegetative	0.670 ± 0.027
Feeding niche	Foliage	$0.677 \pm 0.026a$
	Inflorescence	$0.670\pm0.037ab$
	Root	$0.582\pm0.048ab$
	Stem	$0.667\pm0.034b$
Feeding guild	Borer	$0.700 \pm 0.026a$
	Chewing	$0.557\pm0.035b$
	Galling	$0.625\pm0.047ab$
	Sucking	$0.734 \pm 0.035 ac$
Damaging life stage	Adult & immature	$0.717 \pm 0.025a$
	Immature	$0.060\pm0.030b$
Voltinism	Univoltine	$0.592 \pm 0.035a$
	Bivoltine	$0.605 \pm 0.032a$
	Multivoltine	$0.754 \pm 0.026b$

fitted individually during logistic regression				
Plant trait	Levels	df	<i>F</i> - value	<i>P</i> -value
Growth habits	Herb, shrub, shrub/tree	2, 1369	2.02	0.1324
Life cycle	Annual, biennial, perennial	2, 1369	2.17	0.1148
Ecosystem	Aquatic/riparian, terrestrial	1, 1370	24.09	< 0.0001
Propagation	Seed, vegetative, seed &	2, 1369	0.22	0.8065
	vegetative			

Table 2.5 Results for logistic regression ANOVAs of agent establishment (established, or not established) evaluating influence of invasive plant life history trait categories. Each trait was fitted individually during logistic regression

Table 2.6 Predicted probabilities of successful establishment (\pm SE) for each weed life history traits from logistic regression. Values are taken from logistic regressions fitted to each trait individually Pairwise least square mean comparisons were performed for significance within each trait groups at *P* ≤0.05 and traits denoted by different letter within each trait category differ significantly

Weed traits	Levels	Probability of establishment
Growth habit	Herb	0.6770 ± 0.027
	Shrub	0.6468 ± 0.029
	Shrub/tree	0.7545 ± 0.051
Life cycle	Annual	0.5736 ± 0.053
	Biennial	0.6459 ± 0.051
	Perennial	0.6723 ± 0.023
Propagation	Seed	0.6749 ± 0.030
	Vegetative	0.6801 ± 0.050
	Vegetative & seed	0.6593 ± 0.026
Ecosystem	Aquatic/riparian	$0.8027 \pm 0.029a$
	Terrestrial	$0.6141\pm0.028b$

Table 2.7 Results for categorical generalized model ANOVAs of biocontrol agent impact (heavy, medium, variable, slight, none) evaluating the influence of biocontrol agent life history traits

mstory traits				
Agent traits	Levels	df	χ2	P-value
Feeding habit	Internal, External	2	6.59	0.0371
Feeding place	Aboveground, Belowground	2	9.78	0.0075
Feeding part	Reproductive, Vegetative	2	42.32	< 0.0001
Feeding niche	Foliage, Inflorescence, Root, Stem	6	56.39	< 0.0001
Feeding guild	Borer, Chewing, Galling, Sucking	6	26.29	0.0002
Damaging stage	Adult & immature, Immature only	2	97.37	< 0.0001
Voltinism	Univoltine, Bivoltine, Multivoltine	4	22.81	0.0001

Table 2.8 Results of categorical generalized logit model ANOVA evaluating the influence of weed life history traits for impact (heavy, medium, variable, slight, none). Significance of each weed trait was determined at $P \le 0.05$

Propagation Seed, vegetative, seed & vegetative 4	Weed traits	evels	df	χ2	P-value
Propagation Seed, vegetative, seed & vegetative 4	Growth habits	Ierb, shrub, shrub/small tree	4	1.68	0.7947
	Life cycle	Annual, biennial, perennial	4	17.59	0.0015
	Propagation	eed, vegetative, seed & vegetative	4	25.13	< 0.0001
Ecosystem Aquatic/riparian, terrestrial 2	Ecosystem	Aquatic/riparian, terrestrial	2	32.09	< 0.0001

Fig. 2.1 Intentional classical biological control agent species and total releases made by insect orders and mites. Black bars represent the biocontrol agent species and white bars represent the proportion of releases for respective agent orders

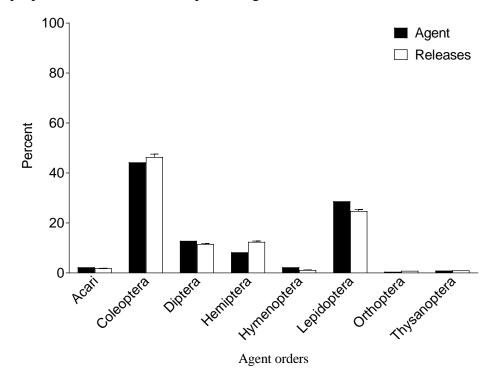


Fig. 2.2 Number of invasive plant species targeted for classical biological control by plant family (plant families with less than 2 target weed species not shown)

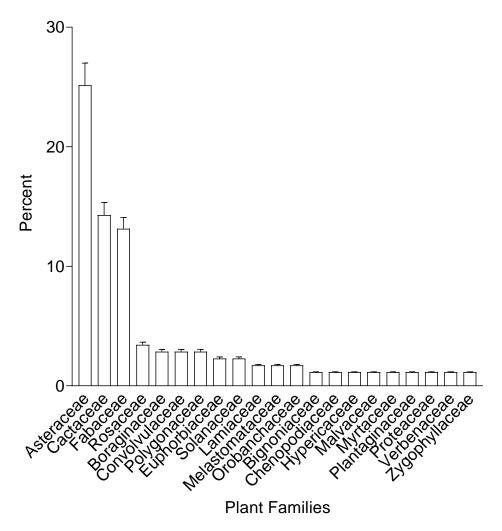


Fig. 2.3 Forest plots showing the odds of establishment of a species with regard to different biocontrol agent life history traits. Odds for each trait (proportion of success/proportion of failure) were calculated using predicted probabilities of successful establishment from logistic regression analysis (see Table 4 for values). The dotted vertical line represents equal probabilities of success and failure (odds = 1) as reference. Black circles are the mean odds for each trait and the horizontal lines indicate the confidence interval

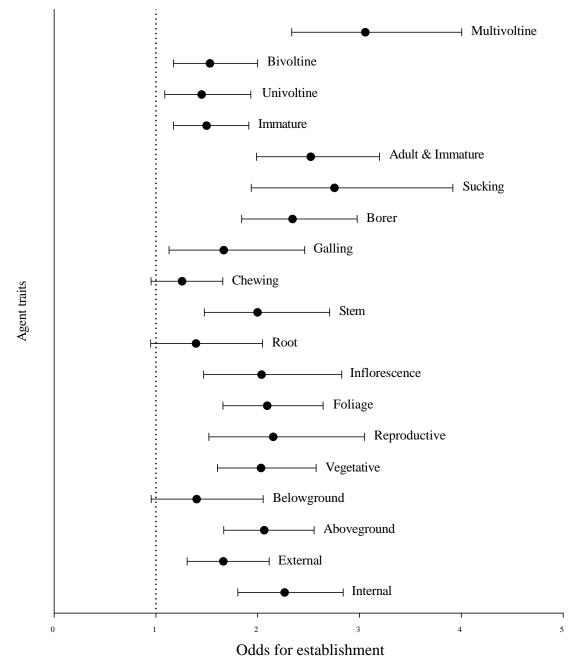


Fig. 2.4 Forest plots showing the odds of establishment for different target weed life history traits with 95% confidence interval. Odds for each trait (proportion of success/failure) were calculated using predicted probabilities of successful establishment from logistic regression analyses. The dotted vertical lines represent equal probabilities of success and failure (odds = 1). Black circles represent the mean odds for each trait and horizontal lines indicate the confidence interval

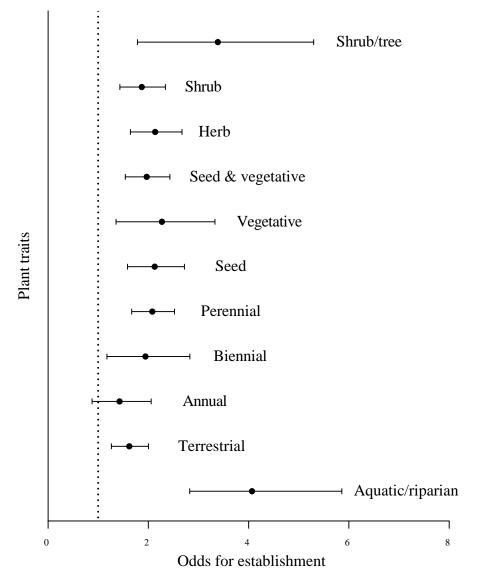


Fig. 2.5 Proportion of biocontrol agent releases associated with different biocontrol agent impact categories on target weed with regard agent life history traits. Proportions are based on total number of releases qualifying for that trait. The sum of proportions across the three impact categories therefore is 1. Error bars are Standard Errors

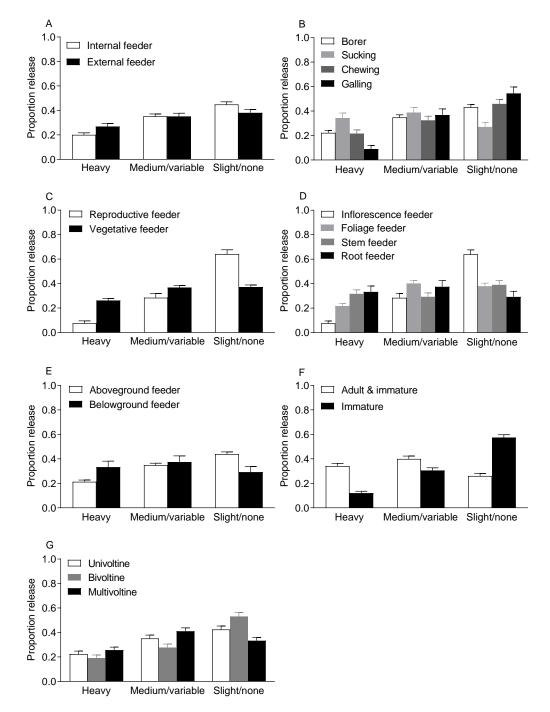
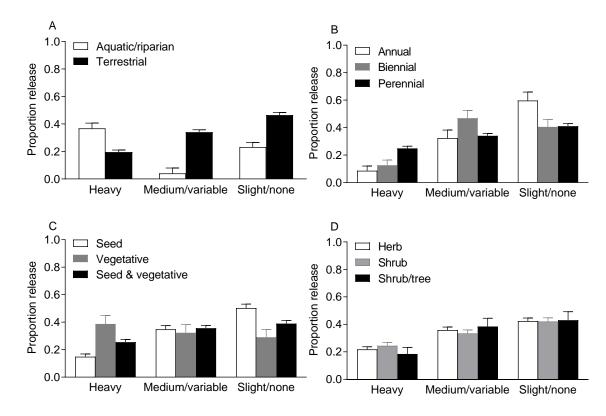


Fig. 2.6 Proportion of categorical biocontrol agent impact on target weed regard to target weed life history traits. Proportions are based on total number of releases qualifying for that trait. The sum of proportions across the three impact categories therefore is 1. Error bars are Standard Errors



Life history traits	Levels	Definition
Feeding habits	Internal External	If agent's immature feeds on the target plant internally, regardless of the oviposition sites, are described as an internal feeder and the immatures feed on the plant externally, are external feeder
Feeding places	Aboveground Belowground	If immature feeds on aboveground plant parts are described as an aboveground feeder and agents feeding on plants belowground structures including roots and modified stem, for example rhizome, bulbs, tubers etc., are belowground feeders. Additionally, an agent that mines/bores through aboveground tissue and spent the majority of its life feeding on belowground parts is also grouped as a belowground feeder
Feeding parts	Vegetative Reproductive	An immature that feeds on vegetative plant parts, either above or belowground, is described as a vegetative. An immature feeding on plant reproductive parts (e. g. seed, flower, etc.) is assigned to the reproductive category
Feeding niches	Foliage, Stem, Root Inflorescence	Four categories were selected based on the agent primarily feeding plant parts and cause the most damage. If immatures feed on a leaf (e. g. leaf, petiole, vegetative buds, etc.), are called foliage feeder. Immatures feeding on stem (e. g. stem, branch, shoot, stem collar, or meristematic tip, etc.), are classified as a stem feeder. Similarly, immature that feds on roots including the rhizome, is root feeder. Immatures that feed on a plant's reproductive parts are grouped into inflorescence feeders
Feeding guilds	Borer, Chewing, Galling Sucking	An immature that bores into the plant parts and feeds internally, including miners, are grouped as borer. Immature that chews on the plant parts/ tissues externally are assigned to chewing group. If immatures cause galls on target weeds and feed inside the gall are grouped to galling category. Similarly, immature feeding by sucking plant sap is described as a sucking
Damaging stages	Immature & Adult/immat ure	If biocontrol agent's both adult and immature stages, inflict sufficient damages to target weed, they are categorized under adult/immature. If only immature caused significant damage to target wed, then they are grouped under immature

Appendix A Biocontrol agent life history trait categories and levels used for this analysis Life history Levels Definition

Life cycle	Univoltine,	Agents with one generation, sometimes partial second
	Bivoltine &	generations per year, or agents requiring more than a
	Multivoltine	year to complete a generation are assigned to
		univoltine group. Similarly, agents with two
		generations per year are classified as a bivoltine.
		Agents with more than two generations per year are
		grouped under the multivoltine category

The classification of each trait and its definition are based exclusively on immature's feeding, except damaging stage where adult damage was also considered

Traits	Levels	Definition
Growth	Herb	Vascular plants that lack significant woody tissues above
habit	Shrub	or at the ground- herbs
	Shrub/ tree	Perennial, multi-segmented woody plants and typically
		have several stems arising from or near the ground- shrub
		Perennial woody plants with a single stem (trunk) and
		usually grow tall (>5 meters)- tree
Life cycle	Annual	A plant that completes its life cycle (from seed
		germination to seed production and then die off) in a
	Biennial	single year is grouped as an annual
		A plant that usually completes its rosette stage in the first
	Perennial	year and reproduces in its second year and dies off
		grouped as a biennial
		A plant that requires more than two years to complete its
		lifecycle is grouped as a perennial. Additionally, plant
		that resembles annual or biennial in aboveground growth
		but remains alive underground and regrowth following
		season is also classify as perennial. For example, rush
		skeleton weed
Ecosystem	Terrestrial	Plants that grow and spend its entire lifecycle on the land
5	Aquatic/riparian	mass is grouped as a terrestrial, and plants on water
	1	bodies and water-land interface are grouped under
		aquatic/riparian. Plant such as <i>Alternanthera</i> is classified
		as an aquatic/riparian species
Propagation	Seed	Plant reproducing using seeds, both sexually and
10		apomictic seeds are ground under seeds,
	Vegetative	Plant reproducing exclusively by using vegetative
	2	propagules (stem and stem modification, root and root
	Seeds and	modification etc.) are vegetative, and
	vegetative	Plant reproducing using both seeds and vegetative
	5	propagules are seeds and vegetative group.

Appendix B Target weed life history and ecological traits selected for this study, their levels and definitions

Definition of growth habits are adopted from USDA-NRCS with some modifications

Reference

USDA-NRCS, 2021. https://plants.usda.gov/growth_habits_def.html.

Appendix C List of references used to collect information on life history traits of biological control agent

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CHAPTER 3: SPECIALIZED SOIL TYPES AFFECT HOST ACCEPTABILITY AND PERFORMANCE OF WEED BIOCONTROL CANDIDATES: IMPLICATIONS FOR HOST SPECIFICITY ASSESSMENTS

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Abstract

The Eurasian gall-forming weevil *Ceutorhynchus cardariae* Korotyeav (Coleoptera: Curculionidae) is a biological control candidate for the invasive Eurasian Lepidium draba L. (Brassicaceae) in the western USA. Among 157 nontarget plant species that have been tested, some North American Caulanthus and Streptanthus species, confamilial with Lepidium, were found to be at potential risk of attack by C. cardariae. Many Caulanthus and Streptanthus species grow on serpentine soils, which are characterized by low nutrient content and high concentrations of various combinations of heavy metals. Some of these species accumulate heavy metals, which have been shown to act as deterrents against insect herbivory. Standard pre-release host specificity tests with C. cardariae used plants propagated on horticultural soils, which could have inflated performance by C. cardariae on Caulanthus and Streptanthus species. To examine this possibility, we assessed the performance of C. cardariae on three Caulanthus species, the federally listed threatened and endangered Streptanthus glandulosus ssp. albidus, and Lepidium draba, on plants propagated in horticultural soil or in native serpentine soil. Our study showed that native serpentine soil influenced C. cardariae attack. All plant species, including L. draba, received less feeding damage and gall formation when grown in serpentine soil. In addition, feeding by C. cardariae was much less and fewer galls were formed on the confamilial species than on L. *draba*, regardless of soil type. Our data show that native confamilial species restricted to specialized soil types may be at less risk of herbivore attack than predicted based on tests conducted in horticultural soil.

Keywords: Biocontrol, serpentine soil, host specificity, *Lepidium draba*, *Ceutorhynchus cardariae*

Introduction

Classical biological control of weeds requires extensive pre-release host specificity testing to ensure that biological control candidates are unlikely to harm nontarget plant species post-release (Hinz et al. 2019). Reliable pre-release assessment of biological control candidates remains a fundamental task in weed biological control (Schaffner et al. 2018). Typically, candidate species are exposed to nontarget plant species grown in nutrient-rich homogenous potting soils, but this could influence the susceptibility of nontarget species to herbivory that are adapted to special soil types (Meindl et al. 2013; Weyl et al. 2019b). For example, plant species adapted to nutrient-poor serpentine soils experienced lower herbivory when grown on these soils than when grown on more fertile soils (Meindl et al. 2013). If biocontrol candidates perform better on nontarget species grown in standardized soil than they do on the same species grown in their native soils, this could overestimate the likelihood of impacts on these nontarget species.

Soil physical and chemical properties vary across the landscapes and this variation can mediate insect-plant interactions through changes in plant tissue chemistry and morphology (Meindl et al. 2013). For example, plant species occurring on metal-rich (metalliferous) soils can have altered plant tissue chemistry or morphology, which in turn affect their interactions with herbivores (Boyd and Moar 1999; Meindl et al. 2013). Plant species adapted to metalliferous soil can accumulate several times higher concentrations of heavy metals (e.g., Ni, Co, Cr) than is normal for most plants (Reeves and Baker 2000; van der Ent et al. 2013), which may function as defense against herbivores (Boyd and Moar 1999; Martens and Boyd 1994) and pathogens (Boyd and Martens 1994). Plant species with elevated heavy metal concentrations defend against herbivores through two main mechanisms. Firstly, metal toxicity can cause lethal effects or sublethal effects such as reduced fecundity and/or decreased herbivore growth (Boyd and Martens 1994; Boyd and Moar 1999). Secondly, deterrence, in which herbivores avoid or consume less plant tissue from plants with elevated metal concentrations (Behmer et al. 2005; Kazemi-Dinan et al. 2015). Therefore, conducting host specificity tests with test plant species grown in their native soil, for example, metalliferous soil, could improve nontarget attack predictions. We hypothesized that attack by a candidate biocontrol agent is reduced on both target and

nontarget species grown in metalliferous soil compared to plants grown in standard horticultural soil. Further, we hypothesized that relative attack among target and nontarget species grown in native metalliferous soils differs from relative attack when they are tested in horticultural soils. We tested these hypotheses in our system: the invasive weed, *Lepidium draba* L. (Brassicaceae), several nontarget species related to this weed, and a biological control candidate, the stem and petiole gall-forming weevil *Ceutorhynchus cardariae* Korotyeav (Coleoptera: Curculionidae).

Lepidium draba is a perennial clonal herb of Eurasian origin (Francis and Warwick 2008). Since its introduction to the USA in the late 19th century (Francis and Warwick 2008), *L. draba* has been spreading throughout the country and it is a declared noxious weed in 15 US states, particularly in the western USA (Gaskin et al. 2005a; USDA-NRCS 2021b). Field and laboratory studies suggest that *C. cardariae* is host specific to *L. draba* and that it has the potential to kill shoots prematurely and reduce the vigor of *L. draba* (Hinz and Diaconu 2015). Under no-choice testing conditions, host specificity tests conducted with 157 nontarget plant species predicted limited potential risk of spillover nontarget attack on confamilial native North American plant species in the genera *Caulanthus* and *Streptanthus* (*C. cardariae* petition, unpublished data, M. Schwarzländer et al.). As is typical, all these tests were conducted with plants grown in horticultural soil. However, many *Caulanthus* and *Streptanthus* and *Streptanthus* species occur in or are endemic to serpentine soils, thus the risk that *C. cardariae* could attack these species under natural conditions may have been inaccurately assessed.

Over 90% of known metal hyperaccumulator plant species (species that can accumulate unusually high concentrations of metal in van der Ent et al. 2013) grow in serpentine soils (Pollard et al. 2014). Serpentine soils are formed by weathering of ultramafic rocks (an igneous rock with very low silica and rich in magnesium and iron containing minerals; Downes 2021), and are uncommon but occur in patches throughout North America (Whittaker 1954). The soils create a stressful environment for most plant species due to low concentrations of mineral nutrients (e. g. Ca, N, or P etc.), low Ca: Mg ratios and high concentrations of some heavy metals including Ni, Cr and Cd (Whittaker 1954). However, these soils host high levels of plant endemism where they occur (Anacker 2011). For

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example, California's serpentine soils harbor approximately 13% of the state's endemic flora. *Streptanthus* (Brassicaceae) is the most diverse genus within this flora with 18 serpentine endemic species, more than 7% of the serpentine-endemic species in California (Safford et al. 2005). *Caulanthus* species are also commonly reported occurring in serpentine soil in North America with at least one serpentine-endemic species in California (Al-Shehbaz 2012; Baldwin et al. 2012).

In a previous study, several species within *Caulanthus* and *Streptanthus* grown in horticultural soil were attacked by *C. cardariae* (Weyl et al. 2019b). Here, we compare attack by the same weevil on some of these species growing in native serpentine soil compared to horticultural soil to determine if nontarget risk assessments can be improved using plants grown in native soils.

Materials and Methods

Insect, plants and soil

Ceutorhynchus cardariae, which were originally collected at a field site in Romania (Hinz and Diaconu 2015), were reared at the CABI Switzerland Centre in Delémont, Switzerland and adults (n=300 and n=228) were sent to the University of Idaho Quarantine Facility, Moscow, Idaho, USA on November 21, 2017 and January 8, 2019, respectively. Weevils of the same sex were separated into groups of ten and placed in transparent plastic cylinders (11 cm diameter, 15 cm height, Semadeni AG, Ostermundigen, Switzerland), covered with a mesh lid. Excised *L. draba* leaves, on moist foam blocks (FloraCraft®, Ludington, Michigan, USA) in vacuum-sealed plastic (FoodSaver®, Atlanta, Georgia, USA) were provided as food to weevils in each container and leaves were changed every 2-3 days. *Ceutorhynchus cardariae* adults received on 21 November 2017 were kept inside an environmental chamber (Percival Scientific Incubator, Model C-30, Percival Scientific, Inc., Perry, Iowa, USA) at 12: 12 (L:D) at 5 °C to meet the overwintering requirements of the weevils until January 2018. All *C. cardariae* adults, including overwintered weevils received in 2019, were kept under ambient conditions from January 2019 in the quarantine laboratory with an average temperature 20.2 ± 0.5 °C and relative humidity 31.2 ± 1.3 % until experimentation.

Four annual herbaceous native North American plant species were selected for our study based on results of previous host specificity tests (*C. cardariae* petition, unpublished data, M. Schwarzländer et al.): A serpentine endemic and federally listed threatened and endangered species *Streptanthus glandulosus* subsp. *albidus* (Greene) Al-Shehbaz, M. S. Mayer & D.W. Taylor (Safford et al. 2005), *Caulanthus flavescens* (Hook.) E. B. Payson (*=Streptanthus flavescens* Hook) often occurring on serpentine soil (Baldwin et al. 2012), *Caulanthus anceps* E. B. Payson (*=Streptanthus anceps* (Payson) Hoover) rarely occurring on serpentine soil (Al-Shehbaz 2012) and *Caulanthus inflatus* (*=Streptanthus inflatus* (S. Watson) Greene) not recorded on serpentine soil. Seeds of *C. anceps*, *C. flavescens* and *C. inflatus* were obtained from the Rancho Santa Ana Botanical Garden, Claremont, California, USA and seeds of *S. glandulosus* ssp. *albidus* were provided by CABI Switzerland, which had previously obtained these as part of a previous study.

Serpentine soil was collected in Siskiyou County, California, USA (41.302630°N, 122.755312° W) from a site that could be accessed and for which no additional permits were required (Jodi Aceves, personal communication). Soil was collected on 28 March 2018 and immediately transported to the University of Idaho in sealed 19 l food-grade plastic buckets (20 buckets; API Kirk Containers, Commerce, California, USA). The soil was air dried in the laboratory and stored in the same plastic buckets until experimentation. Standardized horticultural soil (potting soil hereafter) was prepared by mixing 18 kg of Sunshine Professional Growing Mix #4 (SunGro® Horticulture Canada Ltd., Vancouver, Canada) with 2.5g trace elements (FRIT Industries, Inc., Ozark, Alabama, USA), 1.25g chelated iron (Grow More Inc., Gardena, California, USA), 48g triple super phosphate (Bonide Products, Inc., Oriskany, New York, USA), 185g Osmocote fertilizer (The Scotts Company LLC., Marysville, Ohio, USA) and 125g Dolomite lime (Grow More Inc., Gardena, California, USA).

Plants were propagated either through root cuttings (*L. draba*) or seeds (all other species) between 2 and 17 February 2019. *Lepidium draba* was propagated from one local clade (Clade-G) (Puliafico 2008) maintained at the University of Idaho *L. draba* genotype

garden since 2007. The root cuttings were directly planted into black plastic pots (13 cm diameter, 13 cm height, McConkey, Sumner, Washington, USA) using potting soil or serpentine soil. Seeds of test species were soaked in tap water for an hour and the seed coat was carefully removed using forceps under a stereo microscope. Peeled seeds were germinated on filter paper moistened with distilled water in Petri dishes (11 cm diameter) for 48 hours. Seedlings were then transferred to seedling trays. After one week in the seedling tray, bare root seedlings were carefully transplanted into the same black plastic pots as *L. draba* above, filled with either potting soil or serpentine soil. All plants were maintained in an environmentally controlled greenhouse at ambient temperatures (14.2-21.1 °C) and 16:8 (L:D) at the University of Idaho's Parker Research Farm, Moscow, Idaho, USA. All species were propagated successfully, except for *S. glandulosus* subsp. *albidus*, of which only three individuals could be grown.

Experimental setup

Ceutorhynchus cardariae males and females were kept together in plastic cylinders in a 2F:1M ratio two weeks prior to the setup of the experiment in order to facilitate mating. *Lepidium draba* leaves provided as food were dissected on a regular basis to monitor oviposition by females in all cylinders. A total of 163 potted plants were transferred to the University of Idaho quarantine facility to conduct no-choice feeding and development tests: 20 replicates of potting soil and serpentine soil for each of the three *Caulanthus* species and *L. draba*, and the three replicates of *S. glandulosus* subsp. *albidus* grown in serpentine soil. Each potted plant was individually caged with organdy (30 cm diameter, 60 cm height, Seattle Fabrics, Inc., Seattle, Washington, USA). Plants were arranged in randomized blocks (n=4) using four metal racks (12 cm by 45 cm by 183 cm) with 2 shelves each (for a total 8 shelves) (Trinity International Industries, Dallas, Texas, USA). Each shelf (approximately 80 cm height) was supplied with two full spectrum compound LED lights (Roleadro 300W LED Grow Light, Grow-light.org, San Francisco, California, USA) set to 14:10 (L: D). Racks were arranged next to each other in the quarantine facility.

Experiments were conducted between 10 March and 16 July 2019 at ambient temperatures (20.2 ± 0.5 °C). Experiments were conducted in four temporal cohorts (10, 13, 15 and 18 March 2019) and these cohorts represented the four blocks. Each cohort included 5 replicates of potting and serpentine soil grown plants of three test species and *L. draba* and one replicate of *S. glandulosus* subsp. *albidus* grown in serpentine soil for the first three cohorts (41 plants total).

No-choice developmental tests were conducted using methods similar to those described in Weyl et al. (2019b). Two mated females and one male of C. cardariae were placed onto individually caged test and L. draba plants. Ceutorhynchus cardariae adults were allowed to feed and oviposit on plants for 72 hours. They were then retrieved and placed back in plastic cylinders with cut L. draba foliage for two to three days to ensure females were still laying eggs before they were placed randomly on experimental plants of the next cohort. Following weevil retrieval, organdy cages were removed from experimental plants. Cages were replaced eight weeks later to capture emerging weevils after pupation. Experimental plants were checked for gall development two weeks following retrieval of weevils and adult emergence was recorded between eight and 18 weeks after parental weevils were retrieved. All newly emerged adults were immediately removed from plants. Since adult emergence was much less than expected from the number of galls on experimental plants, all plants with galls were dissected 18 weeks after the experimental setup. During dissection, both dead and living larvae were removed from the galls and counted. Larvae that were alive during dissection were treated as successful development for all subsequent analysis. At the end of the experiment, all aboveground plant biomass was harvested and dried in an oven (Model 637, Fisher Scientific, Waltham, Massachusetts, USA) at 65° C for 48 hours and weighted.

The growth of nontarget and *L. draba* plants was assessed by counting the total number of leaves and the length of the longest leaf (cm) of each plant at the experiment setup (10, 13, 15 and 18 March 2019), when plants were approximately one month old. *Ceutorhynchus cardariae* feeding was assessed by counting the number of leaves of each plant with and without feeding marks and expressed as the proportion of leaves fed upon. We also estimated the total leaf area consumed for each plant by counting the typical feeding punctures left by the weevil. Both variables, proportion of leaves with feeding and leaf area consumed, were recorded on the day of weevil retrieval (14, 17, 19 and 22 March 2019). For area consumed, the diameters of ten random feeding punctures were averaged for each

individual plant with feeding punctures. This value was then used as a standard size multiplier to calculate the area consumed (mm²) based on total feeding punctures of that plant.

Soil and plant elemental analysis

Four serpentine soil samples, 4-6 cores per sample using Tube Auger (2.54 cm diameter, Oakfield Apparatus, Oakfield, Wisconsin, USA) were taken at the time of collection on 28 March 2018 and stored in airtight zip-lock bags and airdried at the University of Idaho for 72 hours. Air dried serpentine soil samples were sent to the Research Analytical Laboratory, University of Minnesota, St Paul, Minnesota, USA for analysis of nutrient and heavy metal concentrations. For potting soil, four homogenous samples were taken, air dried for 72 hours and analyzed for nutrient and heavy metal concentrations at the University of Idaho's Analytical Science Laboratory, Moscow, Idaho, USA following a similar standardized laboratory procedure (Warner et al. 2018). Soil (1 g dry weight) was digested in trace metal grade nitric acid and 30% hydrogen peroxide. The digestate was then refluxed with concentrations, using inductively coupled plasma optical emission spectrometer (ICP-OES). Analyses included total elemental concentrations for Ca, K, P, Mg, Al, Cd, Co, Cr, Cu, Fe, Mn, Mo, Ni, and Zn (Appendix F).

Four leaves were collected from four to six plants of each species (except *S*. *glandulosus* subsp. *albidus*, due to the small plant numbers) from each soil type, one day prior to the start of the experiment. Plants were approximately one month old and plant leaves were sampled randomly within the plants. Leaves were pooled by plant species for each soil type due to the limited amount of foliage produced on plants grown in serpentine soil. Leaves were cleaned to remove surface soil contamination and oven-dried at 65° C for 48 hours. Leaves were analyzed at the University of Idaho's Analytical Soil Laboratory for elemental concentrations following standardized laboratory procedures (Anderson et al. 2010). Plant leaves were digested with concentrated trace metal grade nitric acid. After appropriate digestion and dilution, the solution was analyzed either with the Inductively Coupled Plasma Optical Emission Spectrometer (ICP-OES), or Inductively Coupled Plasma

Mass Spectrometer (ICP-MS). The analysis included Ca, P, K, Mg, S, Al, Cd, Cr, Co, Cu, Fe, Mn, Mo, Ni, and Zn (Appendix G).

<u>Statistical analysis</u>

A generalized linear mixed model was used to fit the randomized complete block design with experiment setup date as a random blocking effect and soil type, plant species and their interaction as fixed treatment effects. A zero-inflated negative binomial distribution model was used to analyze the number of galls developed. The proportion of leaves with feeding assumed a binomial distribution, while total leaves and number of galls assumed a negative binomial distribution. Leaf area consumed and aboveground dry weight assumed a normal distribution, while leaf length assumed a lognormal distribution (Stroup 2015). Logit link function was used for proportion of leaves with feeding, log link for total leaves and number of galls and identity link function for leaf length, aboveground dry biomass and leaf area consumed. Means comparisons were carried out with single degree-of-freedom contrasts. *Streptanthus glandulosus* subsp. *albidus* was not included in the analysis as only three plants grown on serpentine soil were available to weevils. Concentrations of soil elements were analyzed with generalized linear mixed model procedures with soil types as fixed effect, samples as random effects and assumed a normal distribution and used identity link function All analyses were conducted using SAS version 9.4 (SAS Institute 2015).

Results

<u>Elemental analysis</u>

Essential nutrients (P, K and Ca) concentrations were 15- to 25-fold higher for potting soil in comparison to serpentine soil (Appendix F). Serpentine soil contained higher concentrations of magnesium and some other metals (Co, Cr, Cu, Fe, Mn and Ni) (Appendix F), with greatest differences for Ni and Cr (380 and 111-fold, respectively), while the concentration of Zn was approximately double in potting soil (Appendix F). The Ca:Mg ratio was 400-fold higher in potting soil than that on serpentine soil (Appendix F). In addition, plant tissue elemental analysis showed that all plant species grown in serpentine soil had elevated metal concentrations in their tissue, particularly Cr, Ni and Fe compared to average tissue element concentrations of most plants (Appendix G).

<u>Plant growth</u>

After approximately one month of growth on both potting and serpentine soil, both soil type and plant species affected the number of leaves produced (Table 3.1; Fig. 3.1a). Across species, plants grown on serpentine soil produced $30.6 \pm 5.4\%$ (mean \pm SE) fewer leaves compared to species grown in potting soil. There was no significant interaction between soil type and plant species for the number of leaves per plant (Table 3.1; Fig. 3.1a).

Length of leaves was also influenced by soil type and plant species (Table 3.1; Fig. 3.1b). The maximum length of leaves of plants grown in serpentine soil was $66.6 \pm 5.9\%$ (mean \pm SE) shorter than the leaf length of plants grown in potting soil. There was a significant soil type by plant species interaction, indicating that soil type affected the leaf length differently in plant species. The leaf length reduction of plants grown in serpentine soil was greater for *C. anceps* than *C. flavescens* and *L. draba* and least in *C. inflatus* (Table 3.1; Fig. 3.1b).

Aboveground dry biomass of plant species measured at the end of the experiment differed between soil types and with plant species (Table 3.1; Fig. 3.1c). Aboveground biomass of plants grown in serpentine soil was $93.9 \pm 1.6\%$ (mean \pm SE) less than those grown in potting soil. There was a significant soil type by plant species interaction reflecting a greater biomass reduction for *C. anceps* than *C. flavescens, C. inflatus* or *L. draba* (Table 3.1; Fig. 3.1c).

Ceutorhynchus cardariae herbivory

Over the 72-hour feeding period, the proportion of leaves with feeding marks from *C*. *cardariae* differed between soil type and among plant species (Table 3.2; Fig. 3.2a). The proportion of leaves with feeding marks across plant species was $21.9 \pm 6.1\%$ (mean \pm SE) higher for plants grown in serpentine soil than those grown in potting soil. There was no interaction between soil type and plant species, indicating that feeding on all plant species was similarly affected by the soil type (Table 3.2; Fig. 3.2a).

The leaf area consumed by *C. cardariae* differed between soil types but not among plant species (Table 3.2; Fig. 3.2b). The weevils consumed $21.4 \pm 3.9\%$ (mean \pm SE) less leaf area of plants grown in serpentine soil than of those plants grown in potting soil. There was no soil type by plant species interaction (Table 3.2; Fig. 3.2b).

In previous no-choice host range tests, *C. cardariae* produced galls on all plant species tested and larvae were able to successfully develop through to adults (Appendix E). The number of galls produced per plant was influenced by soil type and plant species (Table 3.3; Fig. 3.3). Plants grown in serpentine soil produced $82.5 \pm 3.6\%$ (mean \pm SE) fewer galls per plant than plants grown in potting soil. Although the soil type by plant species interaction was not significant (Table 3.3; Fig. 3.3) the relative reduction in number of galls on serpentine soils was greater for *L. draba* and possibly for *C. anceps* than the other two species (Table 3.3; Fig. 3.3). One of the three *S. glandulosus* subsp. *albidus* plants grown in serpentine soil supported the development of a single *C. cardariae* gall without any adult emergence (Appendix H) but as stated above plants of this species were excluded from analyses.

Few adult *C. cardariae* emerged from galls in our experiment (total n=13 weevils) (Appendix H). Weevils emerged from galls produced on *L. draba* (84% of all weevils, n=11), *C. anceps* (7%, n=1) and *C. flavescens* (7%, n=1; Appendix H) and exclusively emerged from galls of plants grown in potting soil (Appendix H).

Discussion

The severity of attack by the biological control candidate *C. cardariae* on selected confamilial nontarget plant species grown in field-collected serpentine soil was lower compared to attack in plants grown in nutrient-rich potting soil, confirming the first hypothesis motivating this study. Our study also showed that plant species affected the number of galls produced on the different soil type, as the number of galls produced decreased more severely for *L. draba* in serpentine soil relative to potting soil than it did for the nontarget species in serpentine soil, confirming our second hypothesis for this herbivory variable. These findings highlight the need to understand the key ecological filters affecting

attack by a potential biological control agent on nontarget species. Including host range tests under appropriate soil types, so as not to incorrectly estimate the risk of attack under natural conditions, may be especially important for those nontarget plant species that are restricted to specialized soil types, such as serpentine soil.

Soil elemental analysis in the current study showed that the serpentine soil used contained lower amounts of some mineral nutrients (P, K, Ca), reduced Ca: Mg ratio and higher concentrations of heavy metals compared to potting soil (Appendix F), supporting the notion that serpentine soils are edaphically stressful environments for plants (Kruckeberg 1985). In the current study this resulted in consistently smaller plants of all species grown in serpentine soils compared to plants grown in nutrient-rich potting soil, similar to the results reported by O'Dell et al. (2006). The reduced size of plant grown in serpentine soil reflects nutrient deprivation, but could also be linked to the metabolic cost of higher concentration of magnesium and heavy metals in the serpentine soil (Brady et al. 2005; Maestri et al. 2010).

The elemental analysis confirmed what is indicated by plant growth, that the plants accumulated higher concentrations of heavy metals in the serpentine soil (Appendix G). This is consistent with other studies reporting higher heavy metal concentrations in serpentine soil leading to elevated levels of heavy metals in tissues of plant species, especially in the Brassicaceae (Jhee et al. 2005; Kazemi-Dinan et al. 2015). Plant species adapted to metalrich or serpentine soil, may be defended against plant herbivory by the elevated concentrations of heavy metals in their tissues (Behmer et al. 2005; Boyd and Martens 1994). Plant species with elevated metal concentrations defend against herbivores either using metal concentrations alone (Boyd and Martens 1994) or through additive effect between different metals, or metals and organic acids (Jhee et al. 2006a). In the present study, C. cardariae attacked all plant species and preferred L. draba 2:1 over the other plant species tested with regards to the proportion of leaves attacked, regardless of soil type, but consistantly fed less on those growing in serpentine soil while attacking more leaves per plant on all of them. This pattern suggests the plants in serpentine soil were less palatable or less preferred for feeding. Herbivores have been shown to preferrentially feed on low-metal concentration plants when compared to high-metal concentration plants (Behmer et al. 2005).

The number of galls on all plant species grown in serpentine soil was lower than on potting soil, with *C. cardariae* clearly prefering *L. draba* over nontargets in potting soil but that preference was less distinct when plants were grown in serpentine soil, however a smilar pattern is evident. Gall initiation is a function of *C. cardariae* oviposition or attempted oviposition (i.e. a gall may form without egg deposition) (Hinz and Diaconu 2015) and consequently, the lower gall numbers on serpentine soil-grown plants may indicate avoidance behavior by *C. cardariae* females. Mogren and Trumble (2010) reported that female insectss may avoid toxic substrates for ovipositon to protect their progeny from possible exposure to toxic metal-rich plant tissue. Diamondback moth females, *Plutella xylostella* L. (Lepidoptera: Plutellidae), laid more eggs on low-Ni compared to high-Ni concentration leaves of *Streptanthus polygaloides* Gray (Brassicaceae) (Jhee et al. 2006b), and female *Drosophila melanogaster* Meigen (Diptera: Drosophilidae) avoided high-metal concentrations substrate for oviposition (Bahadorani and Hilliker 2009).

Nontarget plant species grown in native metal-rich soil can cause delayed development and increased mortality of immature stages of insects, with toxicity increasing with exposure duration (Trumble and Jensen 2004). Ceutorhynchus cardariae development, from eggs to adult takes about 12 weeks in its native range (Hinz and Diaconu 2015). In our study, first adults emerged from L. draba grown in potting soil after about 10 weeks, while there was no adult development recorded from nontarget plant species grown in serpetine soil after 18 weeks, including L. draba grown in serpentine soil. This is longer that previously reported for C. cardariae (Hinz and Diaconu 2015) in which plant species supported weevil development in host specificity tests, with a mean of 11 adults per plant for L. draba and between 0.1-4.6 adults per plant for test plant species in question (Apendix E). A plausible explaination is that the elevated metal levels in the gall tissues due to serpentine soils affected C. cardariae development and caused high larval mortality. An herbivore not typically associated with host plants growing in serpentine soils such as C. cardariae may be especially vulnerable to heavy metal defensive function compared to herbivores co-evolved with serpentine endemics. For example, the development of *Chrysolina pardalina* (Fabricius) (Coleoptera: Chrysomilidae) is unhindered on the serpentine-endemic Berkheya coddll Roessl. (Asteraceae), and similarly Melanotrichus boydi Schwartz and Wall (Hemiptera: Miridae) on *Streptanthus polygaloides*, because they are adapted to tolerate higher

concentrations of heavy metals (Przybylowicz and Mesjasz-Przybylowicz 2001; Wall and Boyd 2006).

In summary, *C. cardariae* prefers its host *L. draba* for feeding and oviposition over all nontarget plant species tested, regardless of soil type. Fewer galls developed on test species than on *L. draba*, whether grown in potting soil or in serpentine soil. In addition, all plant species growin in serpentine soil supported fewer galls compared to plants grown in potting soil. Additionally, it appears that the three *Caulanthus* species used in our study can accumulate elevated concentrations of heavy metals when grown in serpentine soil (Appendix G) without autotoxicity symptoms such as leaf chlorosis and necrosis (S. Panta personal observation). Therefore, we can expect lower risk of attack from *C. cardariae* on *Caulanthus* species or populations that occur on serpentine soils.

Host specificity tests conducted previously cannot rule out the possibility of nontarget attack but these tests were all conducted on plants grown in nutritionally balanced potting soil. The current study suggests that native soil types such as serpentine soil, influence *C. cardariae* attack calling prior results into question. All plant species, including *L. draba* grown in serpentine soil received less leaf damage and supported fewer galls compared to plants grown in standardized potting soil. We suggest that host range tests conducted using potting soil may need to be carefully interpreted since severity and risk of nontarget attack by biocontrol agents may be mediated by soil types to which nontarget plant species are adapted or restricted. We contend that soil type can act as an ecological filter, in addition to other biotic and abiotic factors, in further restricting the ecological host range of *C. cardariae*, especially for about one third of *Streptanthus* species (total 35 species) and one fifth of *Caulanthus* species (total 17 species) that are endemic to or tolerant of serpentine soil in North America.

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Table 3.1 Result of generalized linear mixed model ANOVA of plant performance traits: Total leaves, longest leaf length andaboveground dry biomass for target weed and the nontarget plant species grown in both, potting and serpentine soil

Effects	Plant performance traits										
	Total leaves			Leaf length			Aboveground dry biomass				
	<i>df</i> (num., den)	F	<i>P</i> -value	<i>df</i> (num., den)	F	<i>P</i> -value	<i>df</i> (num., den)	F	<i>P</i> -value		
Soil type	1, 21	43.47	< 0.0001	1, 149	923.08	< 0.0001	1, 149	797.97	< 0.0001		
Plant species	3, 21	10.43	0.0002	3, 149	47.49	<0.0001	3, 149	30.45	< 0.0001		
Soil type \times	3, 21	0.63	0.6067	3, 149	28.59	< 0.0001	3, 149	33.47	< 0.0001		
Plant species											

Significance of effects at P ≤ 0.05

Table 3.2 Generalized linear mixed model ANOVA on *Ceutorhynchus cardariae* herbivory and development (proportion leaves with feeding and leaf area consumed) for target weed and the nontarget plant species grown in both, potting and serpentine soil

Effects	Ceutorhynchus cardariae feeding and development									
	Proportion 1	eaves fed		Leaf area consumed						
	<i>df</i> (num., den)	F	<i>P</i> -value	<i>df</i> (num., den)	F	<i>P</i> -value				
Soil type	1, 21	4.69	0.0420	1, 149	30.81	< 0.0001				
Plant species	3, 21	14.07	< 0.0001	3, 149	1.43	0.2370				
Soil type ×Plant species	3, 21	1.88	0.0645	3, 149	1.80	0.1499				
Significance of eff	Tects at $P \leq 0.0$)5								

Table 3.3 Zero-inflated negative binomial model on number of *Ceutorhynchus cardariae* galls developed for target weed and the nontarget plant species grown in both, potting and serpentine soil

Effects	No. of galls developed						
	df	χ^2	<i>P</i> -value				
Soil type	1	49.74	< 0.0001				
Plant species	3	30.16	< 0.0001				
Soil type \times	3	5.07	0.1665				
Plant species							

Significance of effects at $P \leq 0.05$

Fig. 3.1 Plant parameters for *Lepidium draba* and *Caulanthus anceps, C. flavescens, and C. inflatus* grown in potting soil and serpentine soil; a) number of leaves per plant; b) longest leaf length per plant; and c) aboveground dry biomass per plant. For the latter two traits, interaction plots were used to illustrate the significant interaction between soil type and plant species (P < 0.05, pairwise mean comparison). Bars are means (SE)

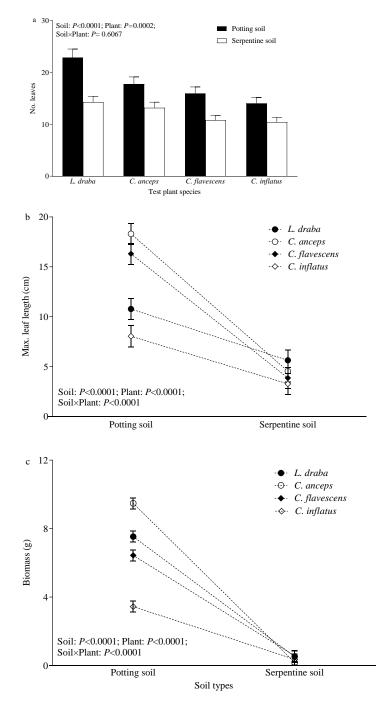


Fig. 3.2 *Ceutorhynchus cardariae* herbivory on *Lepidium draba, Caulanthus anceps, C. flavescens, and C. inflatus* plants grown in potting soil or serpentine soil; a) proportion leaves per plant with feeding marks; and b) leaf area consumed per plant. Bars are means (SE)

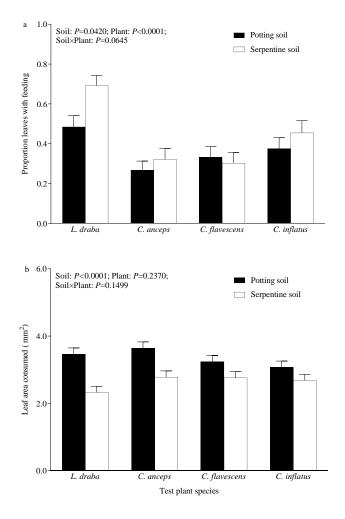
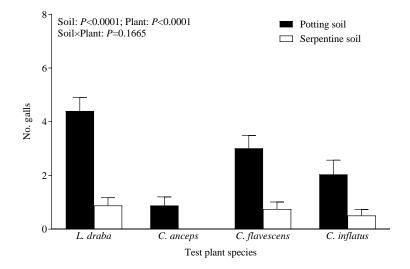


Fig. 3.3 Number of *Ceutorhynchus cardariae* galls developed on *Lepidium draba*, *Caulanthus anceps*, *C. flavescens*, *and C. inflatus* grown in potting and serpentine soil. Bars are means (SE)



Appendices

Appendix E No-choice gall development and adult emergence tests with *Ceutorhynchus cardariae* conducted at CABI, Switzerland between 2003 and 2019 (Source: *C. cardariae* petition, unpublished, M. Schwarzländer et al.). No. of galls and adults are mean \pm SE

Plant species	No of plants exposed	No of plants with galls	Mean galls per plant	Mean adults per plant
Lepidium draba	128	113	7.1 ± 0.7	11.0 ± 1.5
Caulanthus anceps	46	41	4.6 ± 0.5	2.1 ± 0.5
Caulanthus flavescens	41	39	6.1 ± 0.5	4.6 ± 1.1
Caulanthus inflatus	80	41	1.6 ± 0.3	1.0 ± 0.3
Streptanthus glandulosus subsp. albidus	7	6	2.7 ± 0.9	0.1 ± 0.1

Appendix F Elemental analysis of field-collected serpentine soil and laboratory prepared standard potting soil. For elemental analysis, n=4 per soil type. Element concentrations are mean \pm SE. Means for an element with differing superscript indicate a significant difference at *P*<0.05

Elements	Soil	
$(\mu g g^{-1})$	Potting soil	Serpentine soil
Phosphorous (P)	$2,\!100.00\pm129.10^{\rm a}$	129.53 ± 105.95^{b}
Potassium (K)	$2{,}525.00 \pm 197.38^{a}$	$104.65 \pm 51.66^{\rm b}$
Magnesium (Mg)	$4{,}675.00\pm286.87^{\text{ a}}$	$132,539.66 \pm 16246.61$ ^b
Calcium (Ca)	$19,250.00 \pm 853.91^{a}$	1,281.85 ±753.42 ^b
Cobalt (Co)	$5.28\pm0.28^{\text{ a}}$	158.39 ± 22.62^{b}
Chromium (Cr)	12.30 ± 1.95 ^a	$1,\!369.46\pm268.15^{b}$
Copper (Cu)	19.25 ± 0.63 ^a	$39.31 \pm 3.86^{\ b}$
Iron (Fe)	$8,775.00\pm658.76^{a}$	$81,\!791.00\pm9874.77^{b}$
Manganese (Mn)	$240.00 \pm 7.07^{\ a}$	$1,566.16 \pm 250.31$ ^b
Nickel (Ni)	$7.90\pm0.70^{\text{ a}}$	$2,\!970.50\pm607.13^{b}$
Zinc (Zn)	57.75 ± 3.35 ^a	$31.78 \pm 1.92^{\ b}$
Ca: Mg ratio	$4.13\pm0.09^{\text{ a}}$	0.01 ± 0.01 ^b

Elements	Plant Species								Concentrations	
$\mu g g^{-1}$	Lepidium draba		Caulant	Caulanthus		Caulanthus		hus	range*	
			anceps		flavescens		inflatus			
	PS	SS	PS	SS	PS	SS	PS	SS	-	
Calcium (Ca)	23000	6600	25000	7200	36000	9800	46000	15000	1000-50000	
Potassium (K)	81000	14000	47000	27000	81000	26000	82000	34000	5000-34000	
Magnesium (Mg)	4600	9700	4700	16000	4900	13000	6200	19000	1000-9000	
Phosphorous (P)	9100	2500	13000	6700	10000	5900	11000	8300	120-30000	
Aluminum (Al)	<20	1300	<20	810	23	240	<20	250	90-530	
Chromium (Cr)	<2.0	36.0	<2.0	34.0	<2.0	12.0	<2.0	8.8	0.2-1.5	
Copper (Cu)	6.0	5.2	5.7	7.2	8.7	5.7	5.3	7.2	2-20	
Iron (Fe)	73	1500	61	1800	70	740	86	710	5-200	
Manganese (Mn)	130	41	46	48	98	42	54	73	1-700	
Nickel (Ni)	<2.0	36.0	<2.0	74.0	2.3	37.0	<2.0	34.0	0.4-10#	
Zinc (Zn)	270	31	140	73	170	63	240	140	15-150	
Ca: Mg ratio	5.00	0.68	5.32	0.45	7.35	0.75	7.42	0.79	1-6	

Appendix G Total elemental analysis of plant tissue grown on serpentine and standard potting mix soil. Plant tissue metal concentrations are µg per g dry mass of plants

For elemental analysis, n=1 leaves sample/plant species/soil type. Values present with '<' indicates the concentration of the corresponding element at or below detection limits. Ca: Mg ratio calculated by dividing total calcium concentrations by total magnesium concentrations. *Average concentrations ranges are the typical worldwide element concentrations from all plants reported in the literature (See Dunn 2007; Strawn et al. 2019 and refstherein). [#]Upper limit for nickel concentrations value was reported by Reeves et al., (1981). PS = potting soil mixture and SS =serpentine soil (see materials and methods for details) Reference

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Appendix H The plant species exposed at the rosette stage to *C. cardariae* and the summary of no-choice feeding and development tests conducted at the University of Idaho quarantine facility. Adult emergence includes emerged adult plus live larvae during dissection, while empty galls are where no larvae were found during dissection. PS = potting soil mixture and SS = serpentine soil (see materials and methods for details)

Plant species	Soil type	No. valid replicates	No. plant with galls	No. Galls	No. adult emerged	No. dead larvae in gall	No. empty galls
Lepidium draba	PS	20	19	86	11	30	33
	SS	20	8	13	0	2	10
Caulanthus anceps	PS	20	5	12	1	8	2
	SS	20	0	0	0	0	0
Caulanthus flavescens	PS	20	11	47	1	13	11
	SS	20	8	11	0	4	3
Caulanthus inflatus	PS	20	7	26	0	10	2
	SS	20	4	7	0	4	3
Streptanthus glandulosus subsp. albidus	SS	3	1	1	0	0	1