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REVIEW

Traits of insect herbivores and target weeds associated with greater biological weed control establishment and impact

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Abstract Improving success rates of classical weed biocontrol programs is an ongoing effort that requires a variety of different approaches. Previous assessments indicated biocontrol agent taxonomy and feeding characteristics and weed life history traits are associated with better control outcomes. We examined weed biocontrol releases for correlations between biocontrol agent and target weed traits associated with different levels of reported establishment and 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 this global analysis. Published literature was used to augment the catalog with data for eight biocontrol agent traits and four target weed traits. Biocontrol agent establishment and impact data were analyzed against these traits using generalized linear mixed models and categorical models, respectively. Analyses for biocontrol agent establishment reveal the following agent traits were correlated with a greater probability of establishment: being an internal feeder, feeding on above-ground plant tissues, multivoltine agents and agents that feed during both their adult and immature life stages. Insect taxon did not affect establishment except for the order Lepidoptera, which had the lowest establishment probability. For weed traits, those occurring in aquatic or riparian habitats were associated with a higher probability of biocontrol agent establishment. Regarding agent impact, using the definition categories in the catalog, agents feeding externally and on vegetative plant tissues, multivoltine agents and those with both adult and immature plant-feeding life stages were strongly correlated with greater impact. Perennials, reproducing only vegetatively and invading aquatic or riparian habitats were

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associated with greater biocontrol impact. Our findings could facilitate both the prioritization of invasive plants targeted for biocontrol and the selection of suitable biocontrol agent candidates, which should further improve biocontrol project outcomes.

Keywords Classical weed biocontrol · Biocontrol agent · Life history traits · Invasive alien plants · Biocontrol success

Introduction

Globalization of trade and travel have increased the number of invasive non-native plants around the globe (van Kleunen et al. 2015). Consequently, the negative impacts of invasive non-native plants on the economy, biodiversity and ecosystem services have increased substantially (Simberloff et al. 2013; van Kleunen et al. 2015; Pyšek et al. 2020). Classical biocontrol is considered an economically sound and environmentally safe management strategy to control invasive non-native plants (McFadyen 1998; Fowler et al. 2000; Clewley et al. 2012; Schwarzländer et al. 2018).Typically, classical biocontrol of invasive non-native plants is referred to as biocontrol of weeds (also see Winston et al. 2014), this term will be used throughout this paper and will be referred to as BCW hereafter. Worldwide, BCW has been implemented in 90 countries, and by 2012, a total of 468 biocontrol agent species were intentionally released for the control of 175 target weeds (Winston et al. 2014; Schwarzländer et al. 2018). Successful control outcomes for BCW projects have been broadly documented (e.g., Julien 1982, 1987, 1992; Julien and Griffith 1998; Winston et al. 2014) and nearly two thirds of weeds targeted up to 2012 experienced medium, variable or heavy levels of damage using the definitions in Schwarzländer et al. (2018). However, only about a quarter of biocontrol releases led to heavy impact, defined as obviating the need for any other control measures (Schwarzländer et al. 2018). One factor hindering better outcomes of BCW projects is the difficulty of selecting the most effective biocontrol agent candidates a priori (Julien 1989). Similarly, it is challenging to prioritize target weeds based on their susceptibility to biocontrol (Canavan et al. 2021; Downey et al. 2021; Paterson et al. 2021; Panta 2022). A posteriori evaluation of successes and failures of BCW programs are still few (McEvoy and Coombs 1999; but see Paynter et al. 2012, 2019; Hoffman et al. 2019; Cullen et al. 2022) but could be used to identify agent or target weed traits associated with success as a guide to designing BCW programs (Panta 2022).

Previous efforts to analyze BCW projects for agent or target weed characteristics influencing program outcomes have yielded differing results. For example, Crawley (1989) and von Rütte (2013) found biocontrol agents within the order Coleoptera and especially in families Curculionidae and Chrysomelidae, were more successful than other biocontrol agents. Schwarzländer et al. (2018) reported a higher establishment rate for hemipteran biocontrol agents. Biocontrol agents feeding externally and on vegetative plant tissues were found to be more successful than others (von Rütte 2013). Higher success rates were also reported for agents with multiple generations per year (von Rütte 2013; Cullen et al. 2022). A recent catalog-based analysis of effectiveness of 288 biocontrol agents released in Australia (Cullen et al. 2022) reported that certain agent feeding guilds and target weed growth habits were associated with biocontrol success. Biocontrol agents that feed on roots or rootcrowns and sap feeders, controlled target weeds more effectively and herbaceous and perennial plants were more amenable to control (McClay 1989; Cullen et al. 2022). Paynter et al. (2012) found that BCW projects against plants reproducing asexually, including apomictic plants, and those invading aquatic ecosystems were more successful.

However, a systematic analysis of BCW results in combination with relevant weed and biocontrol agent trait information has been lacking (Panta 2022). We address that gap with this paper using data summarized in the 5th edition of 'Biological Control of Weeds: A World Catalogue of Agents and Their Target Weeds' (Winston et al. 2014), combined with biocontrol agent and target weed life history trait data to analyze which biocontrol agent or target weed traits lead to greater biocontrol agent establishment or increased control.

Materials and methods

Data sources

The base source for this analysis was the updated version of the 5th edition of 'Biological Control of Weeds: A World Catalogue of Agents and Their Target Weeds' (Winston et al. 2014, 2021) (hereafter, the catalog). The catalog compiles all deliberate weed biocontrol releases worldwide with detailed information on targeted weed species, biocontrol agent species released, release year, biocontrol agent source and country of origin (see Winston et al. 2014, or online catalog and Winston et al. (2021) for more information). For this paper we used data included in the printed version of the 5th edition of the catalog (Winston et al. 2014), which included all species and releases made worldwide through 2012. However, for each release included in the printed version, we included updated data for agent establishment and impact published online until December 2021 (Winston et al. 2021). Biocontrol agent species are sometimes released in multiple countries or against more than one weed species, and the catalog is organized by agent release events rather than biocontrol agent species (Winston et al. 2014). To qualify as a unique release event, one of the following criteria were 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 but for a different weed, or (4) the same agent was released in the same country and from the same source, but at least five years apart, unless the earliest release failed to establish (Winston et al. 2014). For this analysis, we only considered classical biocontrol agents from the weed's native range that were intentionally introduced, and we included only insects and mites. In total, the analysis included 1498 releases of 436 biocontrol agent species (426 insects and ten mites) against 171 target weeds in 48 plant families (Supplementary Fig. S1) (Winston et al. 2014).

Biocontrol agent and weed life history trait data

We added information on life history traits for each biocontrol agent and target weed species by searching respective names in Google™, Google Scholar™ and the CABI Invasive Species Compendium (CABI 2021). Biocontrol agent life history traits included in the analysis were: (1) biocontrol agent feeding habit, (2) feeding place, (3) feeding part, (4) feeding niche, (5) feeding guild, (6) voltinism, (7) whether only immatures or both adults and immature stages feed on the target weed, and (8) biocontrol agent taxonomy (see Table 1 for agent life history traits and levels and Supplementary Table S1 for agent life history traits level definitions). For the target weeds, life history traits included were: (1) invaded ecosystem, (2) life cycle, (3) mode of propagation, and (4) plant growth habit (see Table 1 for traits and trait levels, see Supplementary Table S2 for target weed trait level definitions; Panta 2022).

We used published literature, technical reports and in a few case publications from the USA Extension Service System or equivalent agencies elsewhere as references for each trait value and cataloged the references accordingly (see Supplementary Table S3 and Supplementary Table S4 for biocontrol agent and weed life history traits references, respectively). If information for a biocontrol agent or a weed differed between their native and introduced ranges, only information for the introduced range was considered.

Biocontrol release outcome data

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 reports and personal communications with subject experts. For this analysis, we included all BCW releases included by Winston et al. (2014) plus updated establishment and impact data for each release imported from the catalog database in December 2021 (Winston et al. 2021).

Establishment of released agents was reported in the catalog under three categories: (1) established, (2) not established, or (3) unknown (Winston et al. 2014, 2021). For this analysis, releases with unknown establishment ($n = 41$, 2.5% of all releases) were excluded, leaving 1457 releases for analyses (Fig. 1).

In the catalog, impact is defined as the level of control of the target weed based on distribution and abundance of the agent, extent and degree of target weed suppression, and the need for supplementary management practices (Schwarzländer et al. 2018; Winston et al. 2014). For this analysis, we used the

Table 1 Biocontrol agent and target weed life history traits and their levels selected for the study of correlation with agent establishment and impacts on target weeds. The life history traits and their levels, for biocontrol agent and target weed are defined in the Supplementary Table S1 and Supplementary Table S2, respectively

Life history trait	Levels	References
Biocontrol agent		
Feeding habit	Internal, external	Crawley (1989), von Rütte (2013)
Feeding place	Abov-eground, below-ground	Blossey and Hunt-Joshi (2003)
Feeding part	Vegetative, reproductive	Harris (1973), von Rütte (2013)
Feeding niche	Root, stem, foliage, inflorescence	Harris (1973), Goeden (1983)
Feeding guild	Chewing, borer, sucking, galling	Harris (1973), Goeden (1983), Cullen et al. (2022)
Voltinism	Univoltine, bivoltine, multivoltine	Harris (1973), Goeden (1983), von Rütte (2013), Cullen et al. (2022)
Damaging life stage	Adult and immature, immature	Forno and Julien (2000)
Taxa	Acari, Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera	Crawley (1989), Clewley et al. (2012), von Rütte (2013), Schwarzländer et al. (2018)
Target weed		
Invaded ecosystem	Terrestrial, aquatic/riparian	McClay (1989), Straw and Sheppard (1995), Paynter et al. (2012)
Life cycle	Annual, biennial, perennial	McClay (1989), Paynter et al. (2012), Cullen et al. (2022)
Mode of reproduction	Seeds, vegetative, seeds and vegetative	Burdon and Marshall (1981), Chaboudez and Sheppard (1995), Paynter et al. (2012)
Growth habit	Herbs, shrubs, shrubs/tree	Straw and Sheppard (1995), Cullen et al. (2022)

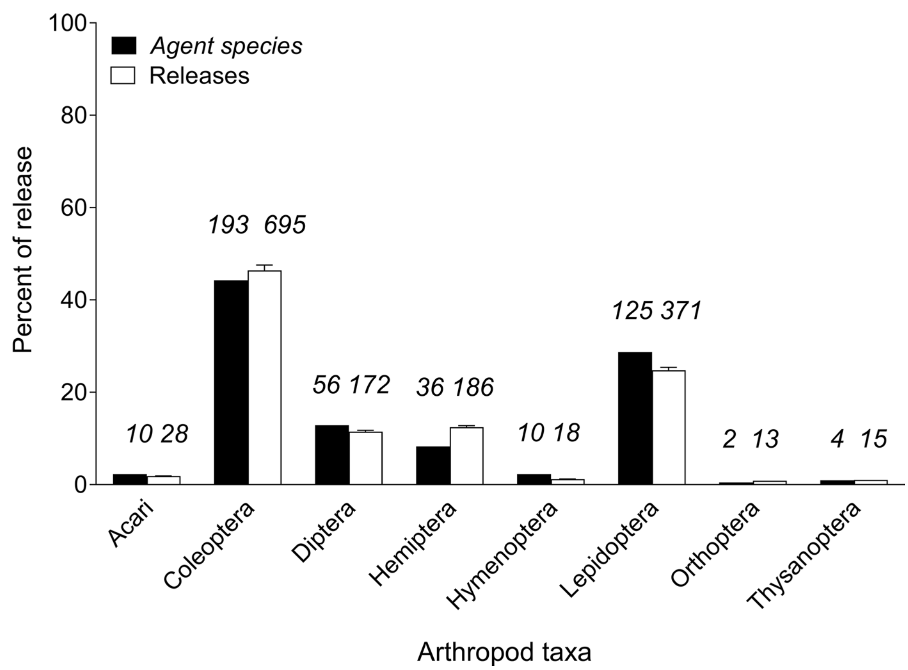


Fig. 1 Intentional releases of classical biocontrol agents by species and by total number of releases according to insect orders and Acari (mites). Black bars represent the biocontrol agent species and white bars represent the proportion of releases for respective agent orders (+SE). Numbers on top of each bar represent the total number of biocontrol agent species and total number of releases made, respectively. The total number of control agents include only insects and mites and total number of releases include both established and not established releases but not releases with unknown establishment. The numbers on top of bars represent replications

five impact categories as stated in the catalog: none, slight, medium, variable and heavy control (Winston et al. 2014) (see Supplementary Table S5 for definitions).

For analysis of biocontrol agent impact, we excluded releases that did not result in establishment (n = 501), those categorized as too early post-release for impact estimation (n = 6) and releases for which impact was recorded as unknown (n = 69). The final dataset analyzed for biocontrol impact on a target weed comprised 881 releases. Of these, 199 (22.59%) led to heavy impact, 127 (14.42%) resulted in medium impact, 182 (20.66%) in variable impact, 306 releases (34.73%) caused slight impact, and 67 (7.60%) had no impact on the target weed. We further consolidated the five impact categories into three levels because of insufficient observation numbers for some impact categories pertaining to certain traits (target weed mode of propagation, life cycle, and agent feeding place). The three consolidated levels were: (1) heavy with 199 (22.59%) releases, (2) medium and variable with 309 (35.07%) releases, and (3) slight or no impact with 373 (42.34%) releases.

Biocontrol agents in the Acari were excluded from impact analyses due to insufficient observation numbers. Of 28 releases of ten biocontrol agent species in the Acari, 13 (45%) caused medium/variable impact and 15 (55%) of the releases caused slight or no impact on the target weed. Biocontrol agents in two insect orders, Orthoptera and Thysanoptera, were excluded from analyses examining the association of biocontrol agent taxa and establishment and impact because too few species were released (two Orthoptera and four Thysanoptera species with 13 and 15 releases, respectively).

Statistical analysis

Binary biocontrol agent establishment data were analyzed using generalized linear mixed models (SAS Proc GLIMMIX), assuming a binomial distribution with a logit link function. Biocontrol agent taxonomy and life history traits for biocontrol agents or target weed species were treated as fixed effects while country of a biocontrol agent release was considered a random effect. Separate models were fitted to individual life history predictor variables to test hypotheses whether agent and target weed life history traits could 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.

If a release resulted in 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 biocontrol agent and target weed life history traits. All statistical analyses were performed using the statistical software package SAS version 9 (SAS Institute, Cary, NC, USA). Detectable effects for all models were determined for test results of $P < 0.05$.

Results

Biocontrol agent traits and establishment

Six of eight 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), feeding guild, and biocontrol agent taxa (Table 2). The results indicated a higher proportion of establishment for biocontrol agents that feed internally and or on aboveground plant tissue (Table 2; Fig. 2a, b). Similarly, multivoltine biocontrol agents and agents inflicting damage as adults and immatures had higher proportions of establishment (Table 2; Fig. 2c, d). Results showed high establishment rates for all biocontrol agent taxa except Lepidoptera (Table 2; Fig. 2e). There was no difference in establishment rates between agents feeding on plant reproductive or vegetative tissues (Table 2; Fig. 2f, g).

Biocontrol agent traits and impact

All biocontrol agent life history traits tested were associated with biocontrol agent impact (Table 2). The proportion of releases of external feeders inflicting heavy impact was 34.00 ± 1.59% (±SE) higher than that of internal feeders (Table 2; Fig. 3a). Among guilds, feeding by sucking insects was most frequently associated with heavy impact.

Table 2 Results of significance tests from logistic regression and categorical generalized models testing the influence of biocontrol agent life history traits on agent establishment (established or not established) and agent impact (heavy, medium/variable and slight/none), respectively. Separate models were fitted for each trait. The significance of each weed trait was determined at $P \leq 0.05$

Agent life history traits	Traits levels	Agent establishment			Agent impact		
		df	*F*-value	*P*-value	*df*	$\chi2$	*P*-value
Feeding habit	Internal, external	1, 1370	7.22	0.0073	2	6.59	0.0371
Feeding place	Above-ground, below-ground	1, 1370	4.73	0.0297	2	9.78	0.0075
Voltinism	Univoltine, bivoltine, multivoltine	2, 1367	14.8	<0.0001	4	22.81	0.0001
Damaging stage	Adult and immature, immature only	1, 1370	18.9	<0.0001	2	97.37	<0.0001
Taxa (agent orders)	Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Thysanoptera	5, 1339	6.83	<0.0001	10	77.19	<0.0001
Feeding part	Reproductive, vegetative	1, 1370	0.15	0.6976	2	42.32	<0.0001
Feeding niche	Foliage, inflorescence, root, stem	3, 1368	1.61	0.1848	6	56.39	<0.0001
Feeding guild	Borer, chewing, galling, sucking	3, 1368	9.11	<0.0001	6	26.29	0.0002

Boring and chewing insects were more frequently associated with heavy impact compared to galling insects (Table 2; Fig. 3b). Biocontrol agents feeding on vegetative plant tissues caused heavy impacts more frequently than those feeding on reproductive plant parts (Table 2; Fig. 3c). Inflorescence feeding was least often associated with heavy impacts whereas root and stem feeding caused most heavy impacts (Table 2; Fig. 3d). Overall, the proportion of releases of vegetative tissue-feeding biocontrol agents causing heavy impacts was 247.00 ± 6.42% higher than that of reproductive tissue-feeding agents (Table 2; Fig. 3c, d).

Releases of biocontrol agents attacking below-ground plant tissues were 57.00 ± 1.67% more frequently associated with heavy impacts than releases of biocontrol agents feeding on above-ground plant tissues (Table 2; Fig. 3e). Insect biocontrol agents with adult and immature life stages feeding on the target weed caused heavy impacts most frequently (Table 2; Fig. 3f). Similarly, multivoltine biocontrol agents more frequently had heavy impacts on their target weeds, followed by univoltine agents and then bivoltine biocontrol agents (Table 2; Fig. 3g). In respect to agent taxon, hemipterans were most frequently associated with heavy impacts to their target weed while dipteran biocontrol agents were most frequently associated with slight or no impacts (Table 2; Fig. 3h).

Target weed traits and biocontrol agent establishment

For plant life history traits, odds plots indicated a higher likelihood of agent establishment on target weeds in aquatic or riparian ecosystems compared to terrestrial ecosystem (Table 3; Fig. 4a). In contrast, agent establishment was similar regardless of weed life cycle, reproductive mode, or growth habit (Table 3; Fig. 4b, c and d, respectively).

Target weed traits and biocontrol agent impact

Biocontrol agent impact was strongly associated with the following target weed life history traits: (1) ecosystem, (2) life cycle, and (3) propagation mode. There was no association between biocontrol impact and growth habit (Table 3). Biocontrol agents released against target weeds in aquatic or riparian ecosystems most frequently had heavy impacts on their target weeds, proportionally 67.00 ± 1.58% higher compared to releases against terrestrial weeds (Table 3; Fig. 5a). Biocontrol releases against perennial target weeds more frequently resulted in heavy impacts—proportionally 86.00 ± 1.17% and 193.00 ± 4.51% higher than for biennial and annual, respectively (Table 3; Fig. 5b). Biocontrol releases made on strictly vegetatively reproducing target weeds more frequently had heavy impacts whereas releases against weeds reproducing solely by seed, including both sexually produced and apomictic seeds, most often resulted in slight or no impacts (Table 3; Fig. 5c).

Discussion

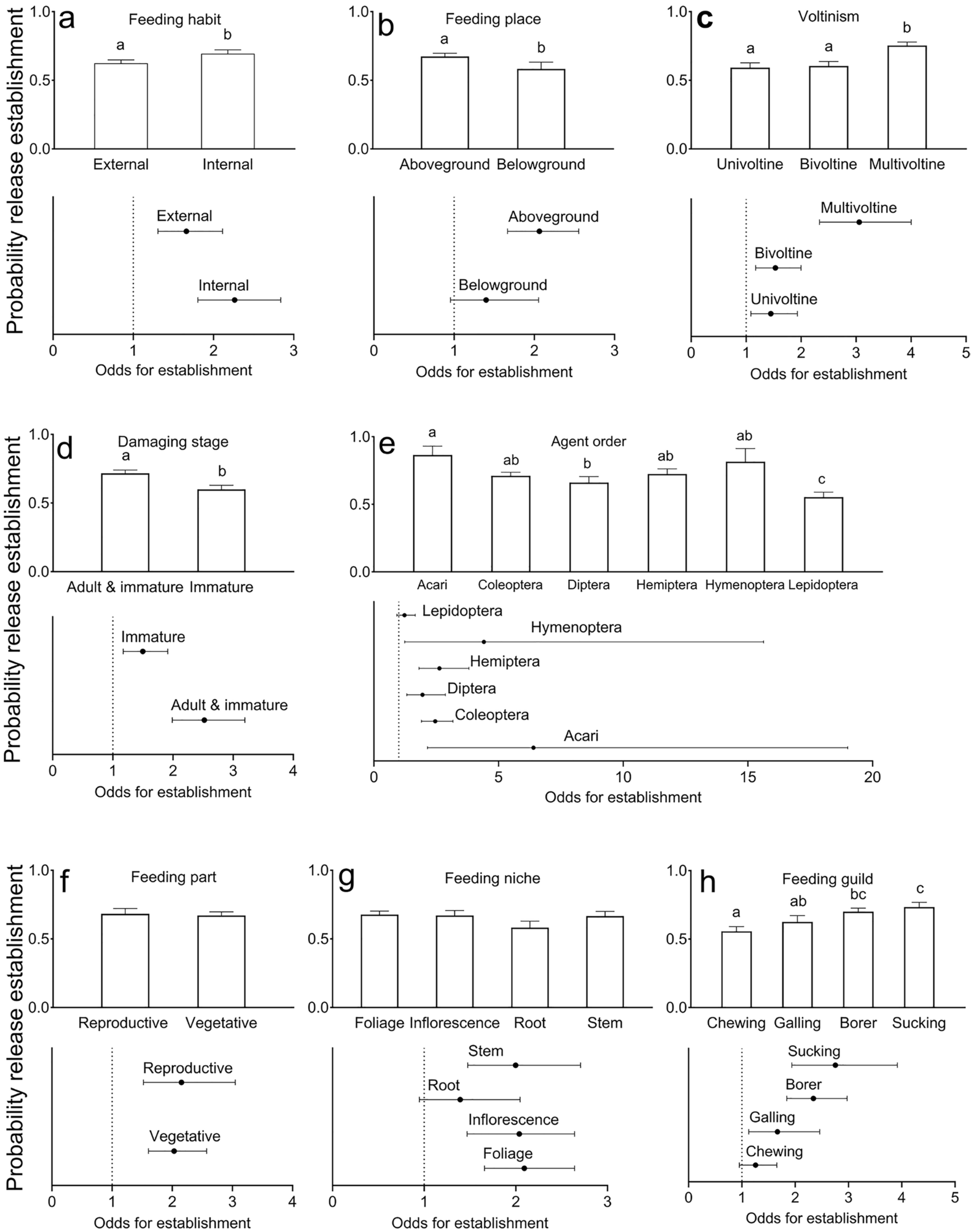
Results of our retrospective analysis of past biocontrol releases supports the findings of other similar studies (von Rütte 2013; Cullen et al. 2022) in showing that certain traits associated with biocontrol agents and target weeds influence the probability of agent establishment and/or the level of impact inflicted on the target.

Agent traits

For biocontrol agent establishment, life history traits of the agent may be more important than traits of the respective target weed. Because biocontrol agents are introduced and released in a more enemy-free environment with unlimited host resources, it has been argued that weed traits are less important factors affecting the probability of agent establishment (Root 1973; Kéry et al. 2001; Sholes 2008; Stephens and Myers 2012). Although we did not explicitly test the importance of agent traits vs. plant traits, our results anecdotally support this argument in that six of eight biocontrol agent life history traits included in this analysis were strongly associated with establishment, while this was true for only one of four target weed traits analyzed. In contrast to biocontrol agent establishment, all biocontrol agent traits and all but one target weed life history trait (growth habit) in this analysis were correlated with biocontrol agent impact.

We found higher establishment rates for internally (boring and galling insects) vs. externally feeding biocontrol agents which could be due to reduced predation and parasitism in the introduced range, as has been stated by others previously (Cornell and Hawkins 1995; Paynter et al. 2019; Harms et al. 2020). For example, survival of two external feeders, broom leaf beetle (*Gonioctena olivacea* Forster) and 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). Likewise, the establishment failure of the foliage-feeding *Calophasia lunula* (Hufnagel) on *Linaria* spp. in Kamloops, British Columbia, Canada was related to the nearly 90% parasitism of its pupae (McClay and Hughes 1995). However, our results indicate externally feeding biocontrol agents, once established, are more frequently effective biocontrol agents. This supports some earlier findings (von Rütte 2013) but contradicts others that concluded internal feeders are more likely to inflict effective control (Crawley 1989). It has been speculated that external feeders may facilitate secondary infections, such as those by pathogens that cause additional damage to plant tissues, as has been observed in cacti (Moran and Zimmermann 1984) and water hyacinth (*Pontederia crassipes* Mart.) (Venter et al. 2013), or that higher impacts may be the result of the higher fecundity rates of external feeders, which could compensate for greater predation (Cornell and Hawkins 1995).

Overall, our results suggest that sucking biocontrol agents (Hemiptera) have the most promise for successful control due to their establishment rates being comparable to that of internal feeders and their higher association with inflicting heavy damage to their target weed. For example, 68.4% of *Dactylopius opuntiae* (Cockerell) releases (n = 19) inflicted heavy impacts to most of the invasive *Opuntia* species targeted, and 84.6% (n = 13) of *Heteropsylla spinulosa* Muddim, Hodkinson & Hollis releases inflicted heavy impacts to *Mimosa diplotricha* C. Wright ex Sauvalle (Winston et al. 2021). Sucking insect attributes, such as short life cycles, high intrinsic rates of increase (Dhileepan et al. 2006) and good dispersal abilities (Williams et al. 2008), may further contribute to their higher probability of inflicting heavier impacts on their target weeds. Although some studies have suggested biocontrol agents that feed by boring are successful due to the structural injury they cause to weed tissue (Goeden 1983), or to lower predation rates (McFadyen and Jacob 2004). Our results suggest most boring biocontrol agents were largely associated with only limited impacts. An interesting example in this context is the recent report on the long-term evaluation of biocontrol of the invasive cactus *Opuntia stricta* (Haw.) Haw. in South Africa, which was thought to be successfully controlled by the cladode feeding pyralid *Cactoblastis cactorum* (Berg), for decades, but for which it has now been shown that control is actually caused by the sap-sucking cochineal, *Dactylopius opuntiae* (Cockerell) (Hoffman et al. 2020). The more frequent association of sucking insects with heavy damage may be driven by the relatively low number of released species in this feeding guild and that most were released against weeds


Probability release establishment
a
Feeding habit
External
Internal
Odds for establishment
b
Feeding place
Aboveground
Belowground
Odds for establishment
c
Voltinism
Univoltine
Bivoltine
Multivoltine
Odds for establishment
d
Damaging stage
Adult & immature
Immature
Odds for establishment
e
Agent order
Acari
Coleoptera
Diptera
Hemiptera
Hymenoptera
Lepidoptera
Odds for establishment
f
Feeding part
Reproductive
Vegetative
Odds for establishment
g
Feeding niche
Foliage
Inflorescence
Root
Stem
Odds for establishment
h
Feeding guild
Chewing
Galling
Borer
Sucking
Odds for establishment

◂**Fig. 2** The probability of releases establishing with regard to different biocontrol agent life history traits. Bars (+SE) with different letters were significantly different at $P<0.05$. Significant pairwise comparisons were shown with lettering on top of the bar whenever a significant difference was present. Odds for each trait (proportion of success/proportion of failure) were calculated using predicted probabilities of successful establishment from logistic regression analysis. 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 95% confidence interval

in the family Cactaceae. Nevertheless, it demonstrates the potential of sucking insects to be successful biocontrol agents.

Regarding plant tissue attacked, our findings indicate biocontrol agents feeding on vegetative parts, including those below-ground (root feeders), cause heavy impacts to target weeds more frequently than those feeding on reproductive tissue. This supports the assumptions of others that agents feeding on vegetative tissues (Harris 1973) and below-ground tissues (Blossey and Hunt-Joshi 2003) would control target weeds effectively. Similar to sucking agents, those feeding on vegetative tissues control target weeds through direct damage of plant tissues and by facilitating the plant's vulnerability to diseases (e.g. Caesar 2003). Direct damage caused by root feeders in particular can disrupt functional processes such as resource uptake and reserve energy storage (Blossey and Hunt-Joshi 2003; Caesar 2003; Zvereva and Kozlov 2012). It has long been argued that agents feeding on and damaging vascular or mechanical support tissues are more likely to control target weeds (Harris 1973; Goeden 1983), but there are few BCW studies testing this hypothesis directly (Goeden and Ricker 1979). Our results suggest biocontrol agents feeding on plant reproductive structures and inflorescences 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), to many target weeds not being seed-limited (Kéry et al. 2001; Impson and Hoffmann 2019), or being very long-lived and/or with very large seed banks such as Australian *Acacia* species or *Onopordum* thistles (Briese 2000; Impson et al. 2004). Nonetheless, numerous authors have stressed the importance of the supplementary role of inflorescence feeders in reducing seed banks, seedling recruitment, and the spread and dispersal of the target (Milbrath et al. 2018; Impson and Hoffmann 2019; Impson et al. 2021).

Biocontrol agents that damage the target weed during both the adult and immature stages had a greater establishment probability and caused heavier impacts than agents in which only the immatures cause damage, supporting the argument that more herbivory is more damaging to the weed (Forno and Julien 2000). For example, *Longitarsus echii* (Koch) adults and larvae feeding on *Echium plantagineum* L. caused variable impact while *Opsilia coerulescens* (Scopoli), which feeds on the same weed but only as larvae, caused no damage (Winston et al. 2014). Adult and immature life stage feeding lengthen the duration of herbivory the target is exposed to, thus increasing the damage inflicted (Forno and Julien 2000). If adults and immature stages feed on different plant tissues, this could lead to synergistic effects that further impair the plant. For example, *Mecinus janthiniformis* Toševski & Caldara has successfully controlled its target weed *Linaria dalmatica* (L.) Mill. throughout much of North America (Winston et al. 2021); adults feed externally on foliage in spring while larvae feed internally within stems throughout spring and summer.

Our findings indicate multivoltine biocontrol agents had higher establishment rates than univoltine and bivoltine biocontrol agents. This may, in part, be the result of multivoltine agents creating a greater propagule pressure since they have more than two generations per year (e.g., Berggren 2001). Multivoltine biocontrol agents were also more frequently associated with heavy impacts to target weeds, supporting the assumption that multiple generations would increase the duration and level of herbivory damage to weeds (Harris 1973).

Target weed traits

Our analyses support the contention that weeds in aquatic or riparian habitats experience more damage or are more successfully controlled by biocontrol agents than terrestrial weeds (Paynter et al. 2012). However, apparent successful control of aquatic weeds may also be a result of biased data. Worldwide, the 1255 releases through 2012 were made against 159 terrestrial weed species, while only 243 releases were made against ten aquatic/riparian weed species

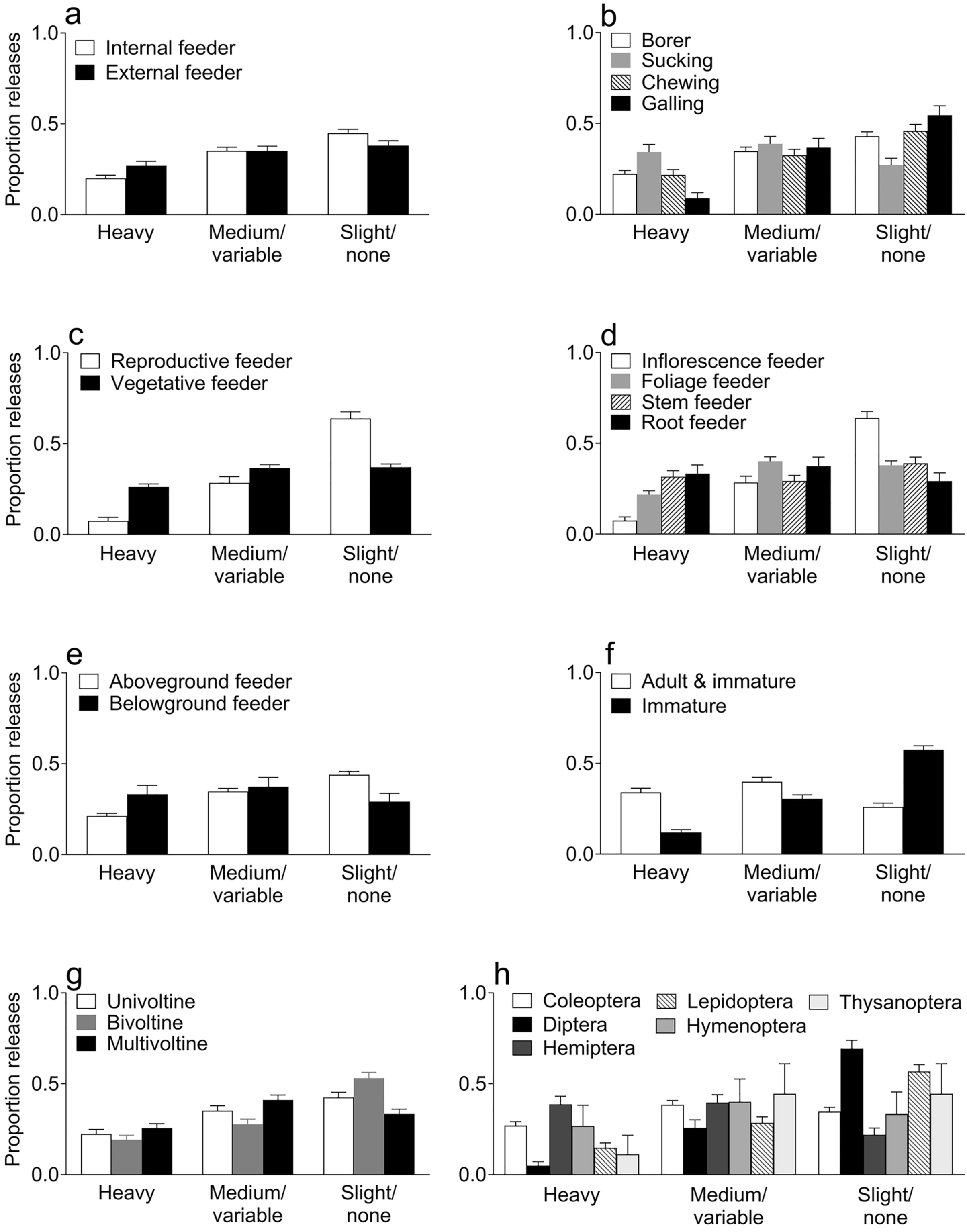


Fig. 3 Proportion of biocontrol agent releases (+SE) associated with different impact categories on target weeds with regard to agent life history traits. Proportions are based on total number of releases qualifying for that trait. The sum of proportions across the three impact categories therefore is 1

Table 3 Results of significant tests from logistic regression and categorical generalized model testing the influence of target weed life history traits on agent establishment (established or not established) and agent impact (heavy, medium/variable, slight/none), respectively. Separate models were fitted for each trait. Significance of each weed trait was determined at $P \leq 0.05$

Weed life history traits	Trait levels	Agent establishment			Agent impact		
		df	*F*-value	*P*-value	*df*	$\chi 2$	*P*-value
Ecosystem	Aquatic/riparian, terrestrial	1, 1370	24.09	<0.0001	4	25.13	<0.0001
Life cycle	Annual, biennial, perennial	2, 1369	2.17	0.1148	4	17.59	0.0015
Propagation	Seed, vegetative, seed and vegetative	2, 1369	0.22	0.8065	4	32.09	<0.0001
Growth habits	Herb, shrub, shrub/tree	2, 1369	2.02	0.1324	4	1.68	0.7947

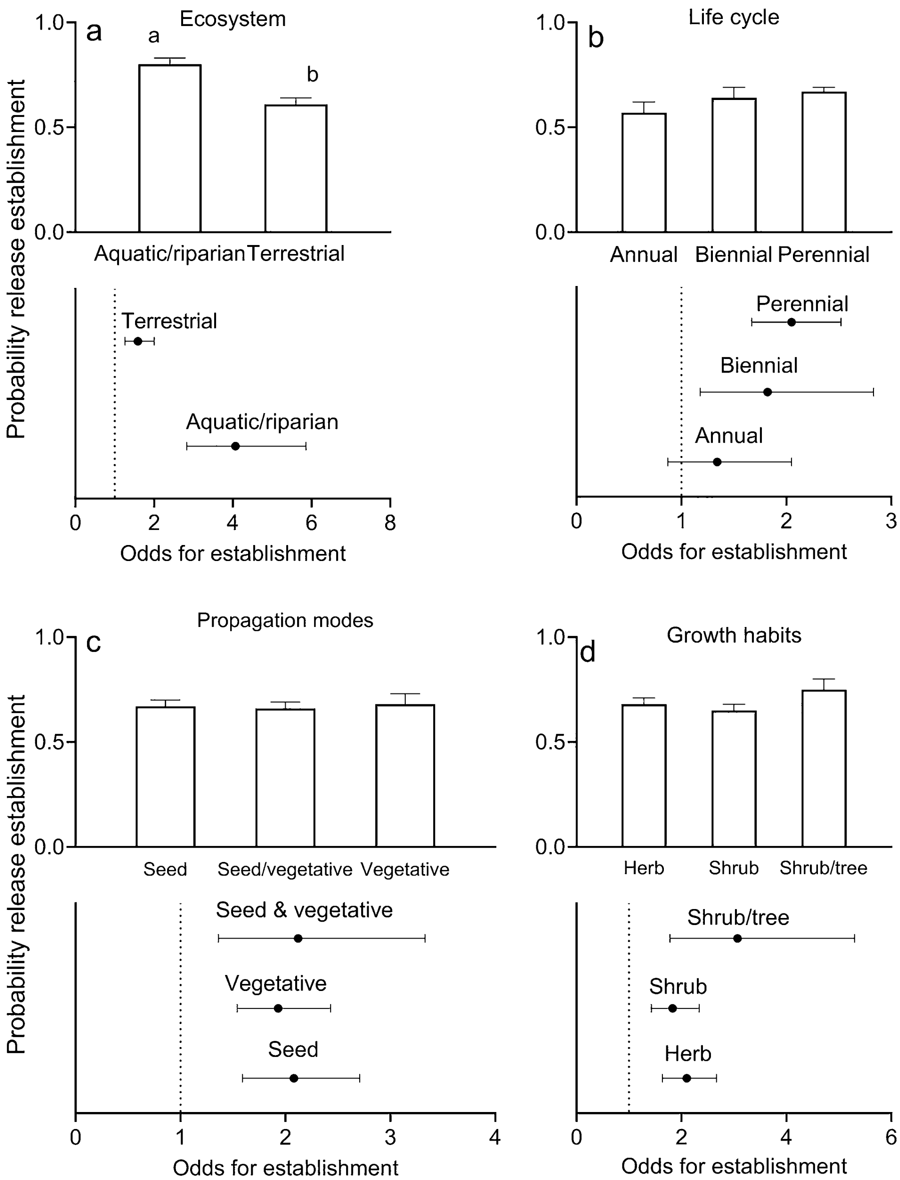
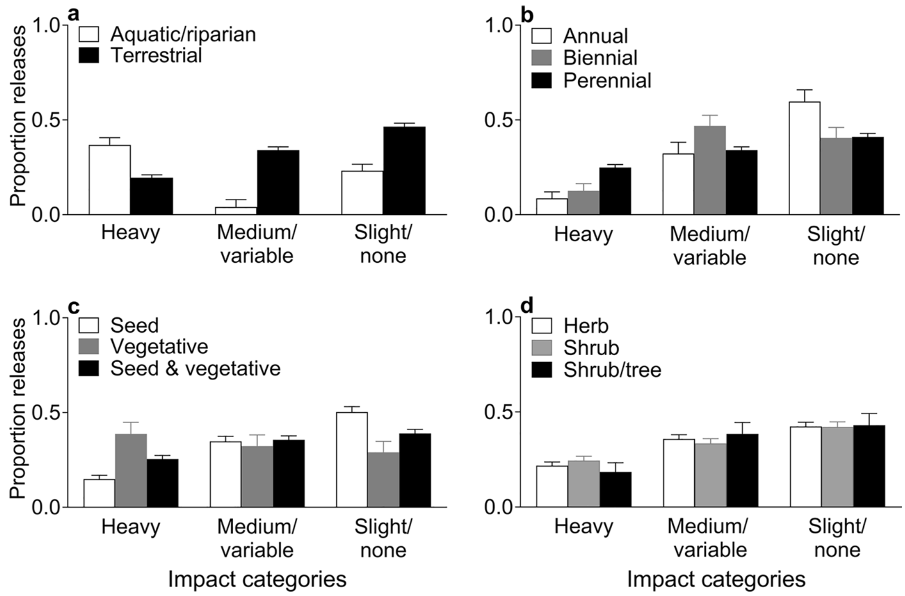


Fig. 4 The probability of releases establishing with regard to different target weed life history traits. Bars (+SE) with different letter differ significantly at $P < 0.05$. Significant pairwise comparisons were shown with lettering on top of the bar whenever a significant difference was present. Odds 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 95% confidence interval

Fig. 5 Proportion of biocontrol agent releases (+SE) associated with different impact categories on target weeds with 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



(Winston et al. 2014). A few aquatic weeds are invasive in many countries and have therefore received a disproportionate number of successful releases, potentially biasing the conclusions about aquatic weeds in general. For example, *P. crassipes* received almost half of all releases for weeds in aquatic ecosystems (118 of 243 releases), and of those that established approximately 60% had medium/variable or heavy impact (see Paynter et al. 2012; Winston et al. 2014).

Our analyses suggest that target weeds which reproduce solely 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, other studies on BCW programs found control success to be independent of reproductive mode (Chaboudez and Sheppard 1995). Detailed studies on modes of reproduction and/or genetic plasticity of targets in their invaded ranges (preferably in comparison to their native ranges) are increasing (Gaskin et al. 2005, 2011, 2023; Gaskin 2024 in press), and should ideally be part of any BCW program in order to more empirically relate biocontrol success or failure to this target weed trait.

Finally, we found that perennial targets are more frequently controlled compared to annual and biennial targets. A study on agriculturally important weeds in Canada concluded that biennial and perennial weeds should be better biocontrol targets compared to annual species (McClay 1989). This may be explained by perennial plants being more apparent in the landscape, both temporally and spatially (Feeny 1976; Sholes 2008; Martini et al. 2021), or it could be due to biocontrol agents failing to impact seed production of annual plants sufficiently within a single growing season to reduce the target populations (McClay 1989).

Significance for biocontrol and outlook

The results of our analyses may aid efforts to prioritize future biocontrol target weeds or biocontrol agent candidates based on some of the traits described herein. The data presented in this analysis are based only on associations of increased probabilities. As such, they are indicative of correlation but not causation. In addition to the traits of candidate agents and potential target weeds reported here, biocontrol researchers exploring new weed biocontrol systems must also continue taking other factors into consideration, such as agent host range, climate matching, invasiveness of the targeted plant in the native range, and the socio-economic feasibility of initiating a new biocontrol program against a specific target weed (Paynter et al. 2012; Panta et al. 2021; Paterson et al. 2021).

Predicting agent establishment rates and successful BCW outcomes may be enhanced by analyzing agent and weed traits in combination. For example, the benefits of foliage-feeding herbivores have been documented for annual weeds, in particular (Harris 1973, 1991; Day and Urban 2004). Also, the dispersal ability of biocontrol agents and dispersal mode of target weeds have been identified as important traits for control success (Isaacson et al. 1996; Paynter and Bellgard 2011), though we were unable to include the traits in this study. We did attempt to include trait combinations but low case numbers for combinations did not allow robust statistical inferences. We anticipate that with the continuing updating and expansion of the catalog (Winston et al. 2021), and with increasing numbers of quantitative studies of BCW program outcomes, more comprehensive and precise analyses will be feasible. For instance, recent efforts were made to develop more refined impact measures at the population level of target weeds (Hoffmann et al. 2019; Moran et al. 2021). To support these future analyses, biocontrol agent and weed trait data collected for this analysis, along with all supporting references, will be incorporated into the catalog as a step toward facilitating more expansive future analyses.

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Declarations

Conflict of interest We, authors do not have any conflicts of interest to disclose.

Ethical approval There were no human or animals (vertebrate) participants in this study.

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