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Lommen, S.T.E.; Beukeboom, L.W.

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INTRODUCTION

Special Issue: Biological Control of Weeds

Biological control of weeds – Context dependency matters

Suzanne T. E. Lommen^{1,2}  | **Leo W. Beukeboom³** 

¹Institute of Biology Leiden, Leiden University, PO Box 9505, 2300 RA Leiden, The Netherlands

²Koppert Biological Systems, Veilingweg 14, Postbus 155, 2650 AD Berkel en Rodenrijs, The Netherlands

³Groningen Institute for Evolutionary Life Sciences, University of Groningen, PO Box 11103, 9700 CC, Groningen, The Netherlands

Correspondence

Suzanne T.E. Lommen, Institute of Biology Leiden, Leiden University, PO Box 9505, 2300 RA Leiden, The Netherlands.
Email: s.t.e.lommen@biology.leidenuniv.nl

Abstract

Invasive alien plants (weeds) are a growing, worldwide problem. Importation ('classical') biological control, using exotic insects, may be a key component in controlling invasive plants. Two-thirds of plant species targeted worldwide by biocontrol programs experience some level of control, but the success rates are geographically variable and still hard to predict. Better understanding of the interactions of the species involved, and the effects of changing climate, may help to further improve both the efficacy and the predictability of this method. This requires pre-release studies, as well as post-release studies that quantify the impact at the population level to validate methodologies and assumptions of pre-release studies. The 12 original papers of this special issue include pre- and post-release studies on 13 insect species from five orders. The studies cover a wide range of methodologies and altogether they highlight that both target and non-target impact are highly context dependent. This dedicated issue includes directions for methodological improvements to better assess ecological host ranges of agents and to avoid rejection of safe agents.

KEYWORDS

alien plants, biocontrol agents, biodiversity, climate change, environmental safety, herbivore, host specificity, insect-plant interactions, integrated pest management, invasive, natural enemies, weeds

INTRODUCTION

Invasive alien plants are a major threat to biodiversity, and climate change is predicted to increase their incidence and impact (IPBES, 2019). Importation (or 'classical') biological control (hereafter 'weed biocontrol') entails the intentional release of specialist natural enemies from their native range into the introduced range of the invasive plant, to reduce the abundance of the invasive plant below an ecological or economic threshold and mitigate their negative impact (Müller-Schärer & Schaffner, 2008; Heimpel & Mills, 2017). A rigorous pre-release assessment in the native range or in quarantine conditions addresses the suitability of candidate agents and the environmental safety of the intended release. Biological control is a key component of many invasive alien plant control programs, sometimes as part of integrated management approaches (e.g., Hayes et al., 2013; Hill et al., 2020; Sun et al., 2022). Weed biocontrol has been practiced since 1795, with over 600 biocontrol agents being released against 250 species of target weeds in 150 countries (Winston et al., 2023). Insect herbivores are important agents for weed biocontrol and make up 69% of agents released (Brodeur et al., 2018). The insect order most used is Coleoptera (41% of agent species), followed

by Lepidoptera (27%), Diptera (12%), and Hemiptera (8%) (Schwarzländer et al., 2018).

Although the success of control is only rarely pre-defined, therefore hard to assess, and often poorly quantified after the release, weed biocontrol programs have resulted in some level of control for two-thirds of the invasive plants, and a quarter of the programs achieved heavy impact (i.e., need for other control methods greatly reduced or eliminated) (Hinz et al., 2020). These figures are raised to 85% of the target plants having experienced at least a slight impact and 36% heavy impact when selecting only the cases where at least one of the agents released got established, and only considering the highest impact level documented per target weed and country ($n=461$; Sun et al., 2022). Amongst the insect orders, estimates of weed biocontrol impact are highest for Coleoptera, Hemiptera, and Hymenoptera (Schwarzländer et al., 2018). Success rates show large geographic variation. Absence of impact has often been explained by failed establishment (e.g., by climate mismatch or lack of cold tolerance), whereas minimal impact is sometimes due to predation (Suckling, 2013). It thus remains a challenge to improve the frequency and magnitude of biocontrol impact.

Thanks to rigorous pre-release assessments of environmental safety, effects on non-target plants are rare in modern practices (Hinz et al., 2019). Concerns over undesirable impacts and the uncertainty of the realized ecological host range of candidate agents nevertheless remain. Overestimation of risk in pre-release studies may, on the flipside, result in erroneous rejections of safe candidates (Paynter et al., 2020; Müller-Schärer et al., 2023).

Biocontrol impact on target and non-target plants remains hard to predict, especially with changing climate. Understanding effects of the biotic and abiotic contexts in which biological control is applied may contribute to further increasing the success rate, safety, and predictability of weed biocontrol (Müller-Schärer & Schaffner, 2020). This requires both pre-release studies, and post-release studies in the field that may validate methodologies used and assumptions made based on pre-release studies. The practice of weed biocontrol finally provides great opportunities to validate ecological theory of insect-plant interactions in the real world (Müller-Schärer & Schaffner, 2020).

THIS ISSUE

This issue comprises 12 papers with original research on weed biocontrol by insects, covering pre- and post-release studies (Figure 1). Four focus on the interaction between the biocontrol agent and the target, and two on the interaction with non-target plants. Two papers report on population-level impact of biocontrol agents post release, and four address how climatic changes may affect the impact of biocontrol agents already used. The studies include a total of 13 insect species, eight of which are coleopterans (four chrysomelids, three curculionids, and one buprestid), reflecting the dominance of this insect order in use and impact in weed biocontrol, and two species are hemipterans, another order with high impact (Schwarzländer

et al., 2018). The three remaining are a lepidopteran, a dipteran, and an orthopteran species. Ten target weeds are studied, including eight terrestrial, one aquatic, and one amphibious species.

Interaction between agent and target: matching genotypes and phenotypes

In the early stage of a weed biocontrol program, after the exploration of the native range for natural enemies, candidate biocontrol agents are prioritized and their suitability is assessed. Impact studies on the target species are a key element in this. Four studies in this issue focus on the biotic interaction between the agent and the target species. Impact may mainly depend on the genotype of the agent (i.e., some agents being more effective against most target genotypes), on that of the target (i.e., some host plant genotypes more susceptible to most agent genotypes), or on the specific interaction between both (i.e., host plant genotypes require different agent genotypes), as conceptualized by Sun et al. (2020a).

In this issue, Sanderson et al. (2023) conclude from feeding and life-history studies in the field and laboratory that a prioritized leaf beetle from Australia showed promise for the control of invasive acacias in Florida, USA. They demonstrated that a beetle population collected from a region with plants with a similar genotype as those of the invasive plant population, performed better on the target than an allopatric population. Biocontrol impact may also depend on phenotype (e.g., life stages or forms) used, both of the agent and the target. Rahman et al. (2023) show in a glasshouse experiment that impact of a jewel beetle differs between two life forms of a climbing vine, with one life form experiencing larger short-term per capita impact but the other one prone to higher impact at larger time scales. Jones et al. (2023a) found in a laboratory study that all life stages of a psyllid,

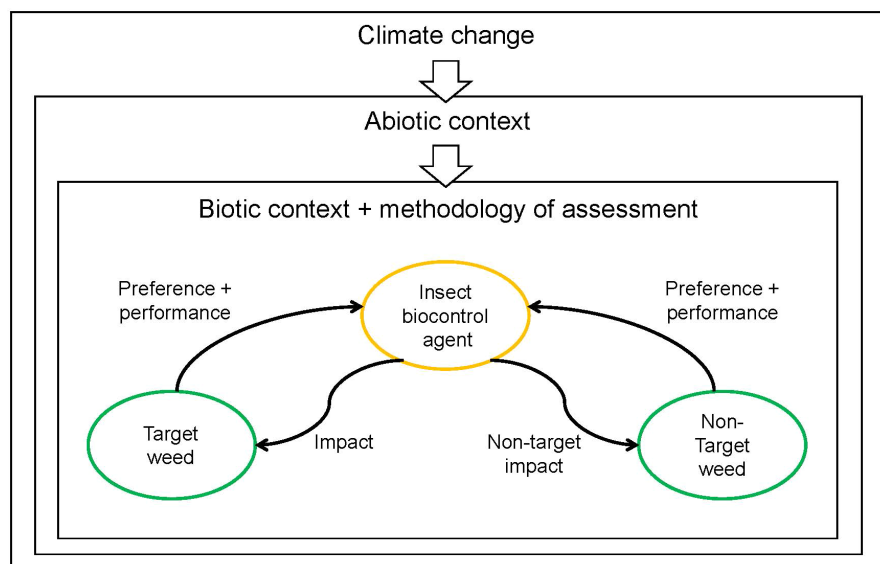


FIGURE 1 Context dependency matters in insect biocontrol of weeds: interactions and contexts addressed in this journal issue dedicated to the biological control of weeds.

a biocontrol agent of knotweed, feed on the leaves. However, leaf rolling, which reduces the capacity to photosynthesize and causes leaf damage, was only inflicted by a specific combination of life stages of the agent (juveniles) and age of the leaves (young leaves). Hernández-López et al. (2023) investigated the use of host plants by an oligophagous gall-inducing fly. The species is used for the control of an invasive herb of ambiguous taxonomy that includes many ornamental varieties and has become naturalized worldwide. The success of control is geographically variable. Field surveys in the native range revealed that the incidence, density, gall size, and impact were higher on another closely related native host species than on the species targeted worldwide for biocontrol.

Together these papers highlight the importance of an informed choice of populations of biocontrol agents, and underline that target impact depends on the genotype, phenotype, and co-occurring related species of the target host population.

Non-target effects: being too strict may exclude potentially safe and effective agents

Another key element in pre-release studies of the suitability of candidates is the risk assessment for non-target host plants. These typically rely on no-choice and choice feeding, oviposition, and development rates of individual agents in the laboratory, and the resulting predictions for attacks on non-target plant species are >99% accurate (Hinz et al., 2020). However, two papers in this issue warn that these traditional studies may exclude potentially safe agents that can to some extent feed, oviposit, or develop on non-targets in such conservative setups, but that are not expected to attack them in the field (see also Paynter et al., 2020; Fung et al., 2021). Therefore, they suggest additional methods to better assess risks to non-targets in the field for pre-release environmental safety assessments.

Subedi et al. (2023) focus on behavioural barriers for agents in finding non-target species in the field. They present behavioural studies elucidating which multimodal cues are used by a weevil in host finding. The results suggest that risks for non-targets in the field are reduced compared to conclusions reached following the standard interpretation of traditional choice studies. Franceschini et al. (2023) assessed the ecological host range of an oligophagous biocontrol agent released against water hyacinth post-release by laboratory no-choice trials with various life stages and gut analysis of field-collected specimens. They found the realized host range to be narrower than the fundamental host range determined by traditional pre-release studies, justifying the release of this oligophagous agent. They call to reconsider potential agents that were rejected due to lack of host specificity based on limited laboratory

pre-release studies, expanding the options for weed biocontrol programs.

Post-release monitoring: still greatly understudied

Success of biocontrol programs is often not well predefined or documented. Post-release monitoring should therefore be quantitative, targeted, and long-term (Hinz et al., 2020), and target impacts should be assessed at the population level (Hoffmann et al., 2019). The next two contributions to this special issue report on post-release impact. Faltlhauser et al. (2023) report an exceptionally long-term post-release study of >50 years of the biological control of water hyacinth in South America by a weevil. The results suggest complete control has been achieved. This adds to the iconic status of biological control of water hyacinth, which has been extremely successful in some parts of the world (although success is also for this system geographically variable). As reintroduction or resurgence of the weed is a risk, the authors emphasize that public awareness of the weed problem and the success of biological control are essential for successful management programmes. The second monitoring study in this journal issue reports on the impact of an adventive weevil, that has been accidentally introduced – i.e., not deliberately released as part of a biocontrol program – into the USA where it is spreading. It is a seed predator of an invasive herb. Pitcairn & Popescu (2023) show that population-level seed production in field populations of this weed is negatively correlated with the intensity of weevil attack, and the weevil populations are expected to increase further.

Climate adaptation

The suitability of a biocontrol agent for its new environment in its target region, and the interaction with the target species is also affected by local abiotic conditions, and these may be altered positively or negatively by climate change (Hogg & Moran, 2020; Sun et al., 2020b; Mulaudzi et al., 2022). The last four papers in this special issue address how altered abiotic conditions may affect biocontrol agents, studying species that have already been released in biocontrol programs. Jones et al. (2023b) used pupal cold storage experiments to assess the effects of entering diapause early by a lepidopteran biocontrol agent observed in its introduced range where summer days are shorter than in its native range. They found no effects of cold storage on some key life-history traits and indicate their data may aid mass rearing programs in synchronising adult emergence for releases. Paper et al. (2023) conclude that elevated carbon dioxide has mixed effects on two biocontrol agents that are already used in South Africa for the control of water hyacinth, and that represent different

feeding guilds. Based on a laboratory study fed into a structural equation model they hypothesize that phloem-feeders will have higher probability of biocontrol success than leaf-feeding agents under elevated CO₂ levels.

Sosa et al. (2023), using spatial ecological niche models, project the future distribution of the aquatic alligator weed in the Americas to expand, whereas the distributions of three flea beetles currently used for biological control remain unchanged. They point out the necessity of finding alternative agents for the expanding invasive populations of this weed. Knight et al. (2023) elaborate on this problem in the USA, where alligator weed is expanding into more temperate climates and put forward that agent populations that are cold tolerant may provide a solution. To that end they study intraspecific variation in cold tolerance of one of the flea beetle species. Interestingly, they include not only populations from the native range as is traditionally done to find populations to match climates, but also consider introduced populations that have already established in the USA to acknowledge that these may have adapted already to more temperate conditions. Together these studies indicate that other species or populations of agents may be needed when climate changes or when target weeds expand.

CONCLUDING REMARKS

This journal issue highlights that impact of weed biocontrol agents on target and non-target species is highly context dependent (Figure 1). This calls for careful consideration of conditions chosen for pre-release studies to inform selection of agent species and populations used, as well as target populations and regions. Several papers demonstrate how post-release studies can contribute to understanding the effects of the field context, and feed back to improve pre-release studies. Specifically, additional methods are suggested for pre-release safety studies to improve accuracy of prediction of risks for non-targets in the field, and to avoid rejection of potentially safe candidate agents. Taken together, the studies presented in this special issue of *Entomologia Experimentalis et Applicata* show that weed biocontrol research may provide basic and applied knowledge on the biology of the insect agents used and their interactions with invasive plants. They further improve our insights in the biological control of weeds.

AUTHOR CONTRIBUTIONS

Leo W. Beukeboom: Conceptualization (equal); validation (equal); writing – review and editing (lead). **Suzanne Lommen:** Conceptualization (equal); formal analysis (lead); validation (equal); writing – original draft (lead).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

ORCID

Suzanne T. E. Lommen  <https://orcid.org/0000-0003-2457-9849>

Leo W. Beukeboom  <https://orcid.org/0000-0001-9838-9314>

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