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Editorial overview: Biological control of plant invaders: a continued stimulus and yet untapped potential to link and advance applied and basic research Heinz Müller-Schärer and Urs Schaffner



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In the era of global change, biological homogenization and resulting novel species interactions have become a focal interest in ecology and evolution. Prominent, in this context, is the consideration of the negative impacts of invasive alien species on nature and human well-being and of biological control programs against these invaders.

Biological control of weeds and invasive plants is the use of natural enemies, mainly arthropods (insects and mites) and plant pathogens (fungi, bacteria, viruses, and nematodes) to bring about suppression of the density or spread of noxious plants. Different approaches towards this goal can be distinguished based on target habitat, origin of the control agent, and the amount of initial inoculum used [1]. In this series of reviews, we focus on the inoculative or classical approach, also termed biological control by importation [2], which is the establishment of self-sustaining specialized, co-evolved phytophagous insects from the weed's native range to control plants that have been introduced into areas outside their native range and that have become invasive. Classical biological control (CBC) of weeds, mainly oriented towards controlling plant invaders in non-crop habitats, has a history dating back over 150 years [3].

This series of reviews aims to provide an overview of the present status of CBC of weeds and potential future directions, especially identifying opportunities for reciprocal benefits with ecological and evolutionary theory. Biological control directly addresses one driver of global change, the spread of invasive species, sustainably and at low cost. While CBC thus is in large part an applied science, it involves targeted manipulations of species interactions and thus offers great opportunities for testing hypotheses of basic ecology and evolution [4]. For many years the fields of CBC and fundamental research on insect-plant relations have developed in conjunction. For example, a CBC project was one of the first studies to use choice experiments to assess host plant preference of an insect herbivore [5], predating the first seminal papers in basic insect/plant ecology (e.g., Singer [6]; Wiklund [7]). When Harris and Zwölfer [8] and Wapshere [9] proposed the centrifugal phylogenetic method for selecting test plant species in CBC projects, they largely structured their arguments on Ehrlich and Raven's [10] analysis of the coevolution between butterflies and their host plants and on an emerging research field at the time, chemotaxonomy (e.g., Hegnauer [11]). Moreover, early key papers assessing the composition of insect communities were based on collaborations between basic and CBC ecologists (e.g., Lawton and Schröder [12]). involved in a number of research projects in Europe, North America, Asia and Africa. Currently he leads a multi-partner project on assessing the environmental and socioeconomic effects of invasive trees in Eastern Africa and implementing management strategies that mitigate their negative impacts. These close partnerships contributed to the development of guidelines for pre-release assessment of non-target risks in weed CBC from the late 1960s onwards, long before non-target risk assessments were implemented in CBC of arthropod pests.

In our series of reviews, Hinz et al. provide an overview of today's evidence of the efficacy and safety in weed CBC. Mainly based on Schwarzländer et al. [3] and Hinz et al. [13], they conclude that of the 313 established biological control agent species recorded until 2012 and for which impact could be assessed, a majority (55%) caused medium to high levels of damage and with almost a quarter of all releases causing heavy impact (i.e., when other control methods were greatly reduced or no longer necessary), resulting in two thirds of all targeted weed species experiencing some level of control. Furthermore, they report that incidences and severity of non-target attack are decreasing over time. Pre-release testing predictions for non-target attack are more than 99% accurate, an impressive accuracy in ecological forecasting. Thus, it is time to move away from the cane toad story, which is often cited as an example of a CBC program going havoc, although it is not even a CBC project as the target pests were native species (the grey-backed cane beetle Dermolepida albohirtum and French's beetle Lepidiota frenchi). New approaches for further improving predictiveness of non-target effects and species interactions related to the deliberate introduction of CBC agents are summarized by Paynter et al. For example, the relative performance of CBC candidates on test and target plants in laboratory tests can help to determine the probability of test plants being attacked in the field [14]. Also, CBC candidates are predictably susceptible to attack by parasitoids that attack ecological analogues (taxonomically related arthropods with similar feeding niche) native to the target region, thus potentially increasing the risk of indirect non-target impacts in food webs [15].

Despite its long history and continued success, CBC of weeds is still considered by some to be unnecessarily risky and marginally effective (e. g., Havens et al. [16]). Both direct and non-target effects associated with introductions of organisms into new habitats pose some non-zero environmental risk, including potential evolutionary changes post-release. Müller-Schärer et al. discuss novel approaches to predict potential postrelease evolutionary changes in host specificity and under novel environmental settings and argue that incorporation of carefully designed studies pre-release may help in estimating the likelihood of rapid post-release evolution. Benefiting from basic research (e.g., Futuyma et al. [17], the proposed studies of experimental evolution using field populations provide new insights into the basic aspects of (rapid) evolution and thus revive the cross-stimulation of basic and CBC research. In another novel approach to complement quarantine-based host-specificity tests and also gain insights on potential interactions of biological control agents, Ollivier et al. advocate network ecology ('food-cycles' that describe flows of matter and energy within a community) as a promising approach to decipher tri-trophic interactions in both the native and the introduced ranges and thus to enhance the development of safe biological control strategies. They show how network analyses, supplemented by advanced molecular methods, may help to select CBC candidates that are specific to the target plant based on natural interactions and that possess few natural enemies or natural enemies that belong to taxonomic groups not encountered in the range of introduction.

Another area where coupled CBC and basic research may add joint value is in the understanding of the impact of climate change on species interactions and ecological interaction networks. Considering the deliberate releases of CBC agents as opportunities to experimentally assess both direct and indirect species interactions under different climatic conditions, CBC introductions can be used to test hypotheses based on pre-release studies or on basic ecological or evolutionary theories. Sun *et al.* synthesize recent studies describing the potential ecological and evolutionary outcomes for biological control agents/candidates for plant invaders under climate change and discuss a suite of promising approaches towards predicting biological control efficacy under climate change. These include species distribution models (SDMs), genomic-enabled SDMs, population dynamic models, and experimental evolutionary studies.

Despite general agreement among both CBC experts and the more basic scientific community about the usefulness and importance of well-designed post-release studies, the assessment of CBC outcomes is still largely neglected and underfunded. Schaffner et al. review some of the advances in the past years and conclude that more efforts should be made to better understand the demography of biological control agents released into a novel environment, their impact on the target weed and the consequences at the community and ecosystem level. They propose that welldesigned post-release studies offer unique but largely untapped opportunities to test predictions based on pre-release studies and to inform management on when and how CBC should be integrated with other management options. As a consequence, economic assessments of CBC are also lacking. van Wilgen *et al.* review the few studies, mainly from Australia and South Africa, on returns on investment from biological control of alien plants that invade natural ecosystems. They conclude that successful CBC delivers attractive returns on investment (from 8:1 to over 3000:1), which increase over time as the value of avoided impacts accumulates. In a recent study, Schaffner et al. [18] assessed the effects of the allergenic common ragweed Ambrosia artemisiifolia on public health in Europe and quantified the potential impact of the accidentally introduced leaf beetle Ophraella communa on the number of patients and healthcare costs. They found that 13.5 million persons suffered from Ambrosia-induced allergies in Europe, causing costs of Euro 7.4 billion annually, and that biological control will reduce the number of patients by 2.3 million and the health costs by Euro 1.1 billion per year. This analysis clearly indicates that the currently discussed economic costs of invasive alien plants highly underestimate the real costs and thus also the benefits from biological control.

Another untapped feature of CBC is its application as low-cost management approach on low-yield land or in regions with limited resources to fight early stages of biological invasions. As shown by Paini *et al.* [19], the number of introductions of new species tends to be higher in countries with a high trade volume, but the low-income countries in for example, Sub-Saharan Africa, Asia or the Pacific that are disproportionately vulnerable to invasions, and less equipped to deal with them. Day *et al.* summarize weed CBC activities in low and middle-income countries and show to what extent this approach has contributed to sustainable management of some key invaders in terrestrial and aquatic systems. Despite this, and in sharp contrast to arthropod biological control, weed biological control in the developing world remains understudied and underexploited. One of the main lessons learned from the 'Working for Water' program in South Africa is that sustainable management of invasive plants is only achievable if CBC is part of an integrated management approach [20].

Still in its infancies are the application, and/or combination of, new gene technologies presently under consideration in weed management for biological control of weeds. Kumaran et al. review methodological and technological difficulties when applying gene silencing and/or gene drive technologies and discuss strategies and resources accessible to accelerate the development of such tools for weed management. For example, although it might be theoretically possible to integrate RNAi with bioherbicides and gene drive with CBC, outcomes need to be carefully evaluated, as gene drive alleles or silenced genes may indirectly affect the life history traits of biological control agents by rendering the plant nutritionally unsuitable. Furthermore, concerns of intellectual property, environmental equity, and social acceptance are additional hurdles when combining gene technologies with CBC.

We view this special issue on 'a close-up on weed biological control with arthropods' as an up-to-date inventory of research in the various fields of CBC. The collection of nine reviews document the recent scientific achievements, discuss ongoing work and define areas of research most timely needed and rewarding. With the broad availability of *-omics* tools and the increased incorporation of evolutionary processes to study interactions between the plant invaders and the biological control agents, especially when scaling up to predict their future species distributions, tight links between practitioners and academia will become ever more important in the future. Still many opportunities remain to be tapped to make CBC of plant invaders even more efficient, predictable, sustainable and safe.

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