FORUM

Some Perspectives on the Risks and Benefits of Biological Control of Invasive Alien Plants in the Management of Natural Ecosystems

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Abstract Globally, invasions by alien plants are rapidly increasing in extent and severity, leading to large-scale ecosystem degradation. Weed biological control offers opportunities to arrest or even reverse these trends and, although it is not always effective or appropriate as a management strategy, this practice has an excellent record of safety and many notable successes over two centuries. In recent years, growing concerns about the potential for unintended, non-target damage by biological control agents, and fears about other unpredictable effects on ecosystems, have created an increasingly demanding riskaverse regulatory environment. This development may be counter-productive because it tends to overemphasize potential problems and ignores or underestimates the benefits of weed biological control; it offers no viable alternatives; and it overlooks the inherent risks of a decision not to use biological control. The restoration of badly degraded ecosystems to a former pristine condition is not a realistic objective, but the protection of un-invaded or partial restoration of invaded ecosystems can be achieved safely, at low cost and sustainably through the informed and responsible application of biological control. This practice should therefore be given due consideration when

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V. C. Moran · J. H. Hoffmann Department of Biological Sciences, University of Cape Town, Rondebosch 7700, South Africa management of invasive alien plants is being planned. This discussion paper provides a perspective on the risks and benefits of classical weed biological control, and it is aimed at assisting environmental managers in their deliberations on whether or not to use this strategy in preference, or as a supplement to other alien invasive plant control practices.

Keywords Biodiversity · Environmental conservation · Weed biocontrol

Introduction

Invasive alien plant species ('weeds') are a large and growing threat to ecosystem integrity in many parts of the world (Mooney 2005). Ecosystem managers employ a range of methods in attempts to reduce or contain invasions by alien plants (van Wilgen and others 2011), and alien plant control is becoming an increasingly important component of environmental management across the world. The methods used include prevention (reducing the risk of introducing potentially invasive alien plants to new areas), eradication i.e. eliminating all individuals and their propagules from an area (Pleuss and others 2012), mechanical and chemical control (aimed at containing weed populations that cannot be eradicated, or reducing their density), and biological control.

The focus of this paper is on the practice of 'classical' weed biological control (WBC), which is an important approach for dealing with species that have already arrived and spread, where prevention and eradication are no longer options for their management, and where other forms of control may be ineffective, too expensive, or environmentally damaging. WBC involves the identification and collection of selected 'biocontrol agents' or 'natural

enemies', predominantly insect species and, less frequently, mites and pathogens, in the country of origin of the weed species, and the subsequent release of the agents in areas where the alien plants have become problematic. A key element in WBC is protracted testing, usually under quarantine conditions over several years, to ensure that the agents are sufficiently host-specific (i.e. they do not attack any species other than the target weed) before any releases are made on the target weed in its country of introduction (McEvoy and Coombs 2000; Sheppard and others 2003, 2005; Moran and others 2005; van Driesche and others 2010). WBC has been highly effective and enormously beneficial in controlling certain categories of problem plants in many parts of the world. The practice has been considered completely or substantially successful in suppressing target weeds in more than 50 % of the cases (Julien and Griffiths 1998; McFadyen 1998; Syrett and others 2000; Moran and others 2005; Klein 2011) and financial gains can be exceptionally favourable (Anon 2000; De Lange and van Wilgen 2010; Syrett and others 2000; van Wilgen and others 2004; Page and Lacey 2006). However, WBC is not a panacea. Its implementation may be inappropriate for some categories of weeds (e.g. grasses, because of their close relationship to important crop species, because they hybridize easily, and because they are attacked predominantly by polyphagous insects that are not suitable candidates for WBC). WBC may also in some cases contribute little to effective management or even fail completely in certain situations.

Despite the levels of success achieved, low costs, a track record of safety, the advantages of sustainability, and the absence in many cases of viable alternatives to WBC, there are concerns about the risks associated with the practice, and these concerns often hamper the implementation of this form of environmental management. The primary aim of this discussion paper is to provide a perspective for environmental managers, who are not necessarily experts in the field of WBC, on the relative risks and benefits of the practice. It should enable them to make informed decisions in their particular circumstances, about the wisdom of implementing WBC, as an alternative or supplement to other invasive alien plant management strategies. Besides giving a brief historical account of the use of phytophagous insects in WBC, the basis of the paper is a consideration of the perceived risks of WBC since the 1980s, when doubts about the safety and wisdom of using WBC escalated because of perceptions that there may be unanticipated damage to non-target plants and disruption of food-webs and ecosystem functioning (Follett and Duan 2000; McEvoy and Coombs 2000; Louda and others 2003; Pearson and Callaway 2003). Counter-arguments are also presented emphasizing the consequences of unrealistically stringent regulatory frameworks that may inhibit WBC (e.g. Klein and others 2011) or, in the worst-case scenario, make WBC practically or economically impossible (Sheppard and others 2003).

The Practice of Weed Biological Control

The first documented case of WBC was inadvertent and fortuitous: a cochineal insect, Dactylopius ceylonicus (Green) (Hemiptera: Dactylopiidae) was introduced into India onto extensive infestations of the alien cactus Opuntia monacantha (Wildenow) Haworth (Cactaceae) in the late 18th century, in the hope of establishing a viable cochineal-dye i.e. carminic acid (Baranyovits 1978) production industry there (Tryon 1910; Green 1912; Lounsbury 1915; Rao and others 1971; Zimmermann and others 2009). The venture was not a success because D. ceylonicus was the wrong species of cochineal (it was mistakenly thought to be the high-yielding, carminic-acid-producer, Dactylopius coccus O. Costa). Substantial densities of D. ceylonicus kill their host plant and O. monacantha was virtually eliminated over large areas. This encouraged the redistribution of D. ceylonicus to other infestations of the weed in India, then into Ceylon (Sri Lanka), and between 1796 and 1809 spectacular control of the cactus was achieved. Much later, in 1903, D. ceylonicus was also opportunistically imported onto O. monacantha in Australia, a venture that failed. In 1913, D. ceylonicus was successfully released against O. monacantha in South Africa, prompting further releases in Australia in 1914 and leading to complete control of the target weed in both countries since then (Zimmermann and others 2009).

In 1902, the scientific basis for WBC was set during the program to combat the alien shrub Lantana camara L. (Verbenaceae) which had become highly problematic for both agriculture and nature conservation in Hawaii (Perkins and Swezey 1924). This case is often noted in passing in the literature but it deserves far wider acclaim as the pioneering work which laid down all the essential considerations for the implementation of WBC. In short, the then well-known naturalist, Albert Koebele (Abdoun 2012) was stationed for months in Mexico where he performed rearing and feeding tests on many lantana insects in their native habitat, routinely keeping meticulous notes on the climate and terrain at the collecting sites. His main concern was on the specificity of the agents and he went to considerable lengths to observe the realized host choices of the potential lantana WBC agents. He shipped (in increasingly efficient insect-proof receptacles), only those cultures of insects that he considered to be sufficiently host-specific. Robert Perkins, an influential and accomplished scientist in his own right (Liebherr and Polhemus 1997), who for years had been appalled at the number of potentially dangerous phytophagous insects that were routinely admitted into Hawaii through importations of commercially-exploitable plants, was fastidious in handling the shipments of lantana insects received from Koebele. Perkins must take credit for the establishment of the first WBC quarantine facility: "an excellent room was obtained ... and so fitted to be quite impervious to the most minute insects" (Perkins and Swezey 1924). Mostly using this facility, Perkins performed rearing and feeding tests "... with various food plants especially those which at the time were of primary value, e.g. sugar cane, banana, several of the chief forest trees, of which we had young plants, and others. Two or three Verbenaceous plants (other than Lantana), which are found in the islands were also used, although these are of no particular value or even useless weeds. A good deal of experimenting with such food plants was made with the latest and most successful sendings [sic] from Mexico, and one species [of a potential WBC insect] at least was lost in the process" (Perkins and Swezey 1924). This foundational methodology was followed and extended during the protracted WBC program against various cactus species which began in Australia in the 1920s (Dodd 1940; Mann 1969).

Today, WBC practice includes several distinct activities: selection of suitable agents in the country of origin of the target weed; risk assessment that is largely involving host-specificity tests to assess whether the agent would attack other plant species apart from the target weed; decisions as to whether or not the agent is safe for release and whether or not it has the potential to impact on the target weed; determinations of whether or not the agent has become established on the target host in the country of introduction and, where necessary, re-distribution of the agent to hasten its spread; and post-release evaluation to assess the impact of the agent(s) on the density and distribution of the target weed populations.

Host-specificity testing of the agents, usually under strict quarantine conditions in the country of introduction (but sometimes in the laboratory and in the field in the country of origin of the weed), is the pivotal activity in the practice of WBC. Data from South Africa indicate that these tests can be protracted (from 1 to 9 years, averaging 3.9 years of specificity-testing per agent) depending on the complexity of the tests and the perceived risks (Moran and others 2005). Typically the potential agents are subjected to experiments to determine whether they can feed on, or lay eggs on, and/or develop on plants species other than their native host. The test plants are usually selected according to the 'centrifugal method' of Wapshere (1974), in which the species of plants taxonomically most closely related to the target weed are given priority, but test plants also include a wide range of beneficial and crop plants, and, more recently, native plants that may potentially be at risk. The methods, experimental designs and analyses of these specificity tests have become increasingly sophisticated and exacting and there is a copious literature on the subject (e.g. Huffaker 1974; Blossey and others 1994; McEvoy 1996; Marohasy 1998; van Klinken 2000; Spafford and Briese 2003; Sheppard and others 2005; Fowler and others 2012).

Specificity testing in WBC is designed to accumulate all reasonable evidence needed to determine whether the agent is host-specific and thus safe for release in the field. Hostspecificity (monophagy) provides assurances (but not an absolute guarantee—see later) that the agent cannot and will not attack plants other than the target species, and if populations of the host should become extinct locally, that the agent populations will not survive. The decision on whether or not to release a WBC agent is usually taken at a political level, e.g. following a process of consultation with possibly-affected stakeholders who consider the outcomes of the risk assessment and the potential for success, prior to issuing or refusing a release permit.

The 1902 Hawaiian lantana project serves to emphasize that, right from the outset in WBC, the host-specificity (monophagy) of the intended agents has been the fundamental issue. However, in certain special circumstances in WBC it has been expedient and deemed to be safe to introduce agents that feed and develop on several species of plants that are closely related to the target weed (i.e. oligophagous agents). For example, the oligophagous cactus moth *Cactoblastis cactorum* (Berg) (Pyralidae) has been introduced to many countries outside of its indigenous range in the Americas because native cacti do not occur in those countries, and because the ability of the agent to attack more than one pest cactus weed has been a distinct advantage, not a problem.

In contrast to WBC, host-specificity has not been the primary issue underlying the practice of biological control against insect pests, at least until relatively recently. Indeed the practice of biological control of insect pests has sometimes favoured agents that are not host-specific because they may be easier to culture (often on "unnatural" i.e. novel hosts that are easier to maintain in culture than the natural hosts), because they have a better chance of establishment over wider areas and more variable climates, and, with a ready supply of alternative (native) hosts in the field, they have the potential of building up to larger and more stable populations and thus becoming more effective in suppressing the target pests (Huffaker 1959,1964; DeBach and Bartlett 1964; DeBach and Schlinger 1964; Doutt 1964; Finney and Fisher 1964). Traditherefore, insect biological control tionally, has predominantly relied on generalist-polyphagous (i.e. nonhost-specific) predators (e.g. ladybird beetles in the family Coccinellidae) and generalist parasitoids (usually parasitic wasp species in the order Hymenoptera). While these agents attack the target insects pests, they often also attack native insect species, usually in closely related taxa to those of the target pest (for recent perspectives on the biological control of insect pests, see e.g. Ehler 2000; Lynch and others 2001; Obrycki and others 2000; Hoddle 2004; van Driesche and others 2010; van Driesche 2012).

Considering the differing philosophical and methodological approaches adopted by WBC practitioners and those involved in biological control against insect pests, and considering the complexities of comparing organisms over different trophic levels, it is not justified to draw conclusions about the safety of WBC from analyses of data sets which include a relatively small sub-set of entries on WBC among numerous examples from insect biological control (Moran and others 2005). This is a common practice that has often led to misleading but pervasive statements about the implementation, efficacy (e.g. Hokkanen and Pimentel 1984; and see Goeden and Kok 1986) and, particularly, the safety of WBC (e.g. Stiling and Simberloff 2000). This becomes extremely misleading when the term 'biological control' is equated with the use of generalist vertebrate predators or herbivores that have historically been used in misguided attempts to control pests or undesirable vegetation, mostly with highly detrimental outcomes (Santha and others 1991; Lever 2001; Peacock and Abbott 2010).

The fact of the matter is that, over the last hundred years, in more than 1050 deliberate releases, at least 365 species of invertebrates and fungi have been deployed for WBC in at least 75 countries, with an excellent record of safety-an assertion which is discussed more fully in the following section (Julien and Griffiths 1998; McFadyen 1998; McEvoy and Coombs 2000; Moran and others 2005; Klein 2011; Barton 2012) and success (Holloway 1964; Andres and others 1976; McFadyen 1998; Syrett and others 2000; Sheppard and others 2003; Zwölfer and Zimmermann 2004; Moran and others 2005; Sheppard and others 2005; Klein 2011). For example, in South Africa, 106 WBC-agent species have been released on 48 invasive alien plant species. Of these targeted alien plant species, 21 % have been completely controlled, most for several decades (i.e. no other control measures are needed), and 38 % are under substantial control (i.e. other methods are needed but less effort is required-meaning, e.g. less frequent herbicide applications or less herbicide) (Klein 2011). Similar interventions elsewhere have brought significant economic benefits, although these have seldom been accurately quantified. The cost of developing WBC solutions (roughly US\$1.2 million per genus of weed species in South Africa, De Lange and van Wilgen 2010) is modest when compared to the value of ecosystem benefits being protected, indicating very attractive returns on investment, with estimated benefit:cost ratios of between 50:1 and >3,000:1 (de Lange and van Wilgen 2010; van Wilgen and others 2004). In Australia, Page and Lacey (2006), analyzed nearly 40 individual WBC cases and summarised the returns on investment as follows: "The aggregate results of the individual CBA [cost: benefit analysis] programs indicate an overall benefit: cost ratio (BCR) of 23.1. This implies that for every [Australian] dollar invested in the weed biocontrol effort a benefit of \$23.10 is generated. Based on this ratio and where an annual investment in weed biocontrol of approximately \$4.3 million is continued into the future, it is expected that weed biocontrol projects may provide, on average, an annual net benefit of \$95.3 million of which \$71.8 million is expected to flow to the agricultural sector. Initial costs of biocontrol programs have increased and are likely to continue to increase, due to expanded regulatory requirements over time. However, the overall benefits are so large that even were program costs to double the overall BCR would still be 11.6, i.e. a return of \$11.60 for each \$1 invested."

Changed Perceptions Since the 1980s

Two events, in particular, have undermined confidence in the practice of WBC. Firstly, Bennett and Habeck (1995) reported the presence, from at least 1989, of the renowned WBC agent, the oligophagous cactus moth, C. cactcorum, on native Cactaceae in Florida. This incursion, possibly via the nursery trade from the Caribbean Islands (Pemberton 1995), poses a considerable threat to the rich indigenous cactus flora of North, Central and South America (Simberloff and Stiling 1996; Zimmermann and others 2001). As at 2011, and in spite of vigorous and expensive attempts at containment, the cactus moth has extended its range on native Opuntia species across much of Florida, and along the coast northwards to South Carolina and eastwards to Louisiana (Rose and others 2011). Alarmingly, in 2006, the cactus moth was discovered on Isla Mujeres, a small island off the northeast coast of the Yucatan peninsula, in Mexico (Zimmermann and Pérez-Sandi 2006). Immediate and concerted action, involving extirpation of cacti on the Island, trapping and sterile-male techniques, successfully eradicated these populations of C. cactorum (Hight SD personal communication 2013; Zimmermann HG personal communication 2013).

Secondly, much has been reported (Louda and others 1997; Louda 1998; Gassmann and Louda 2001; Louda and Stiling 2003) on the consequences of the release in the 1960s of the oligophagous weevil *Rhinocyllus conicus* (Frölich) (Curculionidae) in the United States. Besides destroying the seed heads of its target hosts (invasive European species of *Carduus* thistles), *R. conicus* damages several species of native thistles in the genus *Cirsium*

(Louda 2000). The weevil is now widely established in the United States and recent studies have shown that populations of some native thistles are being negatively impacted (e.g. Platte thistle, see Rose and others 2005).

In retrospect, it is clear that the decision to introduce the oligophagous C. cactorum in an attempt to control problematic native Cactaceae in the Caribbean, so close to the American mainland, was unwise (Pemberton 1995; Simberloff and Stiling 1996; Zimmermann and others 2001, 2009). Similarly, it could be argued that the decision to release R. conicus was imprudent because it was known from pre-release screening tests in the 1960s (Zwölfer and Harris 1984) that it was also an oligophagous species and could develop on native thistles (see Louda 2000). Although these two oligophagous agents are central to arguments against the implementation of WBC, the decisions that were taken to use them seemed to be entirely rational and potentially beneficial, at the time. In coming to these decisions, the scientists involved, backed up by all the relevant regulatory authorities, exercised due diligence (Zwölfer and Harris 1984; Pemberton 1995, 2000). However, over the last 40 years societal norms have changed and more value is placed on the conservation of native plant species, and these programs are consequently and understandably now subjected to criticism.

There are some other records of WBC agents attacking non-target host plants both anticipated and unexpected (e.g. Pemberton 2000; Dhileepan and others 2006; Sheppard and others 2006; Post and others 2010) but these have been mostly either temporary or localised, and inconsequential. Bearing in mind that these few instances have arisen from over 1000 releases of nearly 400 species of WBC agents over the last two centuries (Julien and Griffiths 1998; Klein 2011) the 'built in' risk of unanticipated host-selection behaviour is very low and certainly seems to justify an endeavor that holds the promise of such substantial gains.

While anomalous cases such as the two described above merit full attention, they have mostly been attributable to incomplete investigations, misjudgments or inappropriate decisions being made, rather than to fundamental deficiencies in the processes that are required for WBC (e.g. Sheppard and others 2003). Neither individually nor collectively do any of these cases invalidate the principles or the practices of WBC. They do however re-emphasize the need for thorough screening to ensure host-specificity and the importance of releasing WBC agents only when the level of risk is agreed to be acceptably low by all of the main stakeholders, and when there is every prospect that they will significantly impede the target weed if they are released (Sheppard and others 2003; Coombs and others 2004). Other authors have followed these concerns about 'non-target effects' with various well-founded warnings that the introduction of WBC agents would undoubtedly have consequences for native food webs (e.g. Memmott 2000; Strong and Pemberton 2001; Wajnberg and others 2001) and for 'ecosystem functioning' (e.g. Pearson and Callaway 2003).

Scientists involved in WBC research must assume at least partial responsibility for some of the negative perceptions about the practice of WBC. For several decades WBC practitioners failed to recognize that their records of agent establishment, fluctuations in population numbers of the agents, and measures of damage to the target weed did not provide any direct evidence of overall success in WBC. Such evidence can only be measured by reductions in the distribution, densities and rates of spread of targeted weed species (e.g. Huffaker and Kennett 1959; Crawley 1989; McEvoy and others 1991; Coombs and others 1996; Moran and Hoffmann 2012). Consequently, although there are notable exceptions, the science of WBC has relatively few convincing long-term data sets that unequivocally demonstrate the effects of biological control on weed populations. Until fairly recently (e.g. McConnachie and others 2003; van Wilgen and others 2004; Page and Lacey 2006; De Lange and van Wilgen 2010), WBC practitioners have failed to translate their achievements into economic measures which are more readily understood by decisionmakers. WBC practitioners have often tended to act defensively to criticisms about non-target effects and changes to food webs and ecosystems, and have been reactive rather than proactive in guiding the structuring of tightened regulations and more stringent safety tests.

WBC practitioners have been further criticized for not systematically investigating possible non-target effects, or food web changes, post hoc, in spite of the obvious practical and economic constraints they would have faced in order to do this. Fowler and others (2012) comment as follows: "More case studies of indirect non-target impacts of introduced insects and pathogens as weed biocontrol agents are probably needed before valuable generalizations emerge. Whether microbial or insect-focused, we urge that future case studies take a holistic approach to risk assessment, considering spatial and temporal scales as well as the straightforward magnitude of negative (or positive) effects. Overall of course, risk assessment needs to consider the impact of the status quo with the invasive weed. What is needed is a more holistic view-more of an environmental balance sheet." It seems unlikely, however, that, in spite of the considerable merits of these sorts of studies, in principle, that funding will be readily forthcoming to support them. This is mainly due to competition for resources that are needed to deal with the immediate and urgent problems of ongoing invasions of alien plants in conservation areas. Perhaps a pragmatic and constructive approach to this philosophical impasse would be to do whatever is necessary to explore the reasons for any negative consequences of WBC if and when they are discovered, to learn from these unusual cases, and to devise expedients to prevent reoccurrences (as is presently the case with studies on *C. cactorum* and *R. conicus*). Certainly, a greater degree of engagement with stakeholders, the general public, regulators, politicians and especially those involved in management and conservation efforts would have lessened the degree of apprehension that now detracts from the science of WBC (Simberloff 2012; Warner 2012).

Assessing the Risks

Because of the uncertainties about the prudence of releasing WBC agents, McEvoy and Coombs (2000) advocated guidelines that adhere to the "precautionary principle" (O'Riordan and Cameron 1994; Lonsdale and others 2001) as follows:

- "First, potential harm to non-target organisms can arise from the release of biological control organisms;
- Second, actual harm to non-target organisms of sufficient magnitude and severity has occurred to warrant new principles for conducting biological control introductions;
- Third, the burden of proof for showing [that] those new control organisms are necessary, safe, and effective rests with those proposing the activity; [and]
- Fourth, the process of applying the precautionary principle must be open, informed and democratic and must include potentially affected parties. It must also involve an examination of the full range of alternatives, including no action."

The phrase "including no action" is of particular significance and is not new. Both Miller (1936) and Wilson (1949) addressed this issue. Huffaker (1964) noted that while "there is the possibility of an insect's adopting new hosts", it would be "folly" to allow this relatively small possibility to retard or delay the practice of WBC. He concluded: "Miller stated that if we are to deny the utilization of specialized [i.e. monophagous] phytophagous insects for weed control because of this comparatively rare element of danger, and after all possible precautions have been taken, then we must be prepared to have our crops [and natural ecosystems] overrun...".

Obviously all the parties involved in the debates about the safety and efficacy of WBC share a desire for the same outcome—a reduction in the negative impacts of invasive alien plant species on natural ecosystems. However, we are of the opinion that the emphasis on risk that now permeates WBC has become counter-productive because it leads to exaggeration of the potential problems which hampers the implementation of solutions (Finkel 2011); it offers no alternatives if the risks of WBC should be considered too high; it does not formally consider the consequences of no action (i.e. the environmental outcomes that would follow conscious decisions not to use WBC and to suffer the resultant impacts); and because it has led to arguably unrealistically stringent safety and approval requirements to regulate the release of new agents, which have substantially delayed, or even halted, the process (e.g. Klein and others 2011).

As with virtually any other human endeavor, WBC is not risk-free (Pemberton 2000), and this is the basis for concerns that introduced agents will: (1) attack non-target plants; (2) disrupt food webs by serving as hosts for native parasitoids and as a food source for predators; (3) hybridize with related species; (4) experience physiological or evolutionary changes, possibly driven by climate change, which will fundamentally alter the behavior of the agents (Simberloff 2012); and (5) spread beyond the intended limits of their range in the country of introduction (e.g. Simberloff and Stiling 1996; Zimmermann and others 2001; Pratt and Center 2012). While the host-specificity and efficacy of potential WBC agents can be determined with reasonable certainty a priori (McEvoy 1996), the other concerns cannot be addressed with any degree of confidence (Fowler and others 2012). The problem therefore remains that a decision has to be made in every case about whether the chances of success are worth the risks, without absolute certainty of what might happen if a release goes ahead. The risks need to be weighed against potential benefits as best they can within a realistic framework, given that each case will involve a unique set of circumstances. The challenge is to make these assessments objective.

Three papers in particular sum up the risks and benefits of the practice of biological control of invasive alien plants (WBC): McEvoy and Coombs (2000) suggested guidelines for deciding whether or not it is safe to release a potential WBC agent (see above) and Sheppard and others (2003) and Sheppard and others (2005) provided global views of risk-benefit-cost analyses of WBC, in which various expedients to improve the predictability and safety of this practice were discussed. Sheppard and others (2003) concluded that the requirements for testing procedures are becoming, in an increasingly risk-averse world, more complex, expensive and stringent, and that these requirements are precipitating "a high risk of grinding [weed] biological control releases to a halt in a world where the 'precautionary approach' ['guilty until proven innocent', in the words of McEvoy and Coombs (2000)] has been adopted...". Sheppard and others (2003) referred to a "crisis in the making", a view that was brought into sharp focus at a recent meeting entitled "The 2010 Biological Control for Nature Conference" (van Driesche 2012). We believe that further procrastinations or, at worst, the complete cessation of WBC would allow invasive alien plants to proliferate and that this would inevitably lead to substantial and irreversible damage to, and transformation of, the remnants of our natural ecosystems.

Default risk-aversion is a behavioral trait that arises from the failure to recognize that in environmental management, and in many other spheres, to do nothing is also a conscious decision that carries risk. Maguire and Albright (2005) point out that the cumulative and unwitting use of "mental shortcuts" can lead to management decisions that are excessively risk-averse, to the point of jeopardizing stated management goals. This applies to the risks associated with the release of a WBC agent, in which the outcomes of an assumed "risky" release are compared to those of the supposedly "safer" option of no release. There are several aspects of risk-averse behavior (Maguire and Albright 2005) that could apply here:

- *Certainty bias*: describing one of the options in such a way that it appears safer than other options, e.g. by describing the risks associated with the release of a WBC agent, instead of simultaneously considering the risks of not releasing it. This biases the choice in favor of the (false) safe option;
- Status quo bias: when the outcomes of a decision are uncertain, it seems safer to maintain the status quo – i.e. in the case of WBC, not to release rather than to release an agent; and
- *Discounting*: the consequences of a WBC agent having adverse effects could be immediately detrimental. A decision not to release could also have consequences (once the weed has spread) but these may be felt much later, making them seem preferable, even though they may be of a far greater magnitude.

The assessment of the potential risk of a WBC agent attacking a non-target species (i.e. specificity-testing) is a sine qua non in the responsible application of WBC. The risks of secondary impacts of WBC agents on ecosystem processes are not easily addressed in current risk assessments and it would be extremely difficult, if not impossible, to ever do so reliably. Such levels of uncertainty emphasize the estimated risks of WBC, and favor decisions not to use WBC. However, it would be equally difficult to predict the negative impacts of the invasive weed species on ecosystems in the absence of WBC, something that is currently seldom considered. In considering management options, the potential undesirable side-effects of the release of a WBC agent need to be weighed against the depredation that is inflicted on ecosystems by invasive alien plants, especially those that are prominent enough to have attracted attention for biological control in the first instance.

When dealing with the biological control of invasive alien plant species that also have commercial or economic value, or deliver some kind of benefit, consideration needs to be given, in the first instance, to the use of guilds of agents that damage the reproductive parts of the plants (such as the seeds) but do not decrease vegetative growth and the value of the plants themselves (e.g. Impson and others 2011). However, when economic assessments of the costs and benefits associated with the economically-beneficial target species indicate that the costs of invasions exceed the benefits that the species delivers (De Wit and others 2001; Hoffmann and others 2011; van Wilgen and others 2011; Wise and others 2012), the use of more destructive WBC agents would be justified.

While WBC carries some environmental risks and implementation costs, it should arguably also be a requirement to consider the risks and costs associated with alternative forms of control (e.g. herbicides, physical removal, and the use of fire). Herbicidal control may be effective in the short-term, with highly visible results, but WBC is substantially cheaper (van Wyk and van Wilgen 2002), permanent, and less environmentally damaging. The fact that degradation of ecosystems can be diminished (because WBC reduces the need for alternative methods of control) emphasizes that these benefits should be considered in risk assessments.

The question of sustainability is also relevant and important. Except in cases where special circumstances allow for eradication (e.g. where the novel distribution of a potential weed is well known and very localized, and where seed dispersal is limited and there is no soil-stored seed bank), it is virtually impossible to eradicate an established invasive alien plant species (Moore and others 2011). Experience thus shows that control programs will inevitably fail in the long term if the alternatives to WBC (mechanical or chemical control) are not sustained in perpetuity. Firstly, it is an unrealistic expectation that any mechanical or chemical control program can be sustained indefinitely. Secondly, even unrealistically generous allocations of funding towards mechanical or herbicidal control are likely to be insufficient to nullify the continued spread and problems associated with invasive plant species. For example, van Wilgen and others (2012) found that, in South Africa, despite substantial spending and effort for over 20 years, mechanical control operations at a national level only reached a relatively small portion of the estimated invaded area, and invasions continued to increase. Similarly, McConnachie and others (2012) estimated that it would take several decades, or perhaps centuries, to clear invasive alien trees from a watershed that had been targeted as a priority area for conventional chemical and mechanical control, even if an assumption was made that the weeds would not spread further. Both studies concluded that WBC offered the only realistic and sustainable solution to an otherwise intractable problem.

Conclusions

Ecosystems everywhere are subject to disturbance, fragmentation, and invasion by alien species that are driving them outside of their historical ranges of variability (Seastedt and others 2008) and thus they become 'novel ecosystems' as described by Hobbs and others (2006). The restoration of novel ecosystems to their original state is practically and almost always unachievable (Seastedt and others 2008). Where conventional mechanical and chemical control or other non-biological methods for dealing with invasive alien plants prove to be ineffective, WBC becomes the only viable, sustainable solution. In areas that are already severely and irreversibly degraded (or will become so in the absence of WBC), it would be incorrect, or misleading, or arguably unethical to insist that WBC agents should not be used because they have the potential to effect some changes to existing ecosystem processes, their composition and structure. The imperative is to find solutions appropriate to novel ecosystems where a return to pristine conditions is not an option. WBC should routinely be considered for environmental management because it can safely reduce the impacts of already-established and abundant invasive alien plants, and perhaps more importantly, it can protect relatively unaltered ecosystems by preventing or retarding the spread of damaging invasive alien plants to such areas.

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