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Evaluation and economics: synthesis of session 7

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Introduction

People have increasingly come to recognize the economic and biological implications of biological invasions that result from the introduction of species where they do not occur naturally. Growing numbers of plant invaders are bringing a new sense of mission to scientists working in biological weed control. Evidence of a growing problem comes from an analysis by Peter Rice, of the University of Montana, of plant invasions for the five northwestern states of the United States of America. Prior to the turn of the century, the rate of new introductions was between 90 and 120 species per decade. New introductions declined to as low as 30 species per decade during the Great Depression and World War II. With the resumption of increasing global commerce and travel, the rate of new introductions began to increase and is again approaching 100 species per decade. Growing awareness of plant invasions has stimulated growth in biological control activity, evidenced by the rising numbers of target weeds and control organisms in the region's biological control portfolio. The number of control-organism species is increasing faster than the number of target-organism species, so there appears to be an increase in the number of control-organisms per target-organism.

While increasing concern about biological invasions has brought greater opportunities for biological control, it has also brought greater scrutiny from scientists, conservationists, and regulators. Scientists question the simplifying assumptions made in biological control about the causes and cures of non-indigenous species (NIS) problems (e.g. 'absence of natural enemies is the cause, addition of natural enemies is the cure'). Many years of experience in biological control has translated into a better understanding of biological invasions, their causes, and the appropriate prophylactic measures. Yet claims of increased efficiency appear to be contradicted by the observed increase in the mean number of control-organism species introduced per target-weed species. We should ask whether appropriate effort is being made to improve existing protocols for selecting targets (McClay 1989) and selecting control organisms (Goeden 1983; Harris 1973). Conservationists' concern about the potential harm caused by NIS makes them wary of introducing one NIS for control of another NIS and flatly opposed to using NIS to control native target species (Howarth 1991; Miller and Aplet 1993). Generic arguments for and against the safety of introducing NIS are misleading. Risk assessments should be based on the attributes of the organisms and the recipient environments. Regulators struggle to revise laws and regulations regarding NIS to exclude harmful NIS and facilitate introduction of beneficial NIS. However, they receive conflicting messages from constituencies involved in, or affected by, the movement of organisms around the world, making it difficult to decide what level of pre-release scrutiny of biological control introductions (and post-release follow up) is warranted. Biological control practitioners feel growing pressure from science and society to improve the prediction of safety and effectiveness of control-organism introductions.

The Symposium session on 'evaluation and economics' represented an opportunity to compare case-histories and discuss development and testing of theory for understanding, predicting, and managing plant invasions. Evaluation studies presented at the meeting emphasized retrospective analyses of case-histories, which can be valuable for: (i) showing whether current control organisms are adequate, or whether new control organisms are needed; (ii) creating a more reliable basis for extrapolation to new areas; and (iii) elaborating and testing principles and predictions about host-specificity and effectiveness. The framework for prospective analysis needs more attention. Before introducing a control organism, the costs and benefits must be weighed in economic and environmental terms. The need for a predictive theory of weed biological control can be simply stated: if we can predict the costs but not the benefits of a proposed action, how can we effectively weigh benefits and costs?

Economic evaluation

The Symposium featured only one report on the economics of biological weed control. Coombs *et al.* (this Volume) reported on an economic evaluation of ragwort, *Senecio jacobaea*, biological control in Oregon, USA, based on collaboration among biological control practitioners, ecologists, and economists. Successful control of one weed is often used to justify attempts to control another. In this case, the benefits of controlling one weed species were sufficient to offset the costs of managing all 58 control-organisms and 26 target-organisms currently in Oregon's biological weed control portfolio.

The discussion following session 7 focused on the problems with economic analysis. A widely-shared sentiment was that assigning costs is relatively easy because they are concentrated and easy to measure, but the benefits are diffuse and difficult to quantify. Care should be taken not to underestimate costs or to exaggerate benefits. Costs include the costs of successful as well as failed or incomplete projects. Replacement of one weed by another unrelated-weed can set in motion a 'biological control treadmill' and create a continuing cost of control with little to show for the investment. Even when benefits appear to exceed costs, a decision may not be easy (U.S. Congress Office of Technology Assessment 1993): (i) the magnitude of the costs may be so high as to make the action unacceptable or unfeasible; (ii) the people who reap the benefits may not be the ones who bear the costs, raising questions of fairness; and (iii) excessive uncertainty or questionable valuation techniques may undercut the analysis. The future of biological control, to a large degree, rests on how effectively we deal with the issues of containing environmental and economic costs, of identifying and resolving conflicting interests and of improving techniques for prediction and evaluation of outcomes.

Environmental evaluation

Tactics for managing risks related to non-indigenous plant species include 'prevention' and 'mitigation'. The first line of defence is to 'predict' which species have the potential to become pests and 'prevent' them from reaching their pest potential, for example by barring their entry into a country or preventing movement within the country. When prevention fails, attention shifts to 'early detection and rapid eradication' of newly-arriving pests, primarily through application of conventional pesticides. The last line of defence involves 'mitigation', through 'control' of widely established pests, and 're-vegetation', using competitive, desirable plants. Control is primarily by application of biologically-based technologies (BBTs) such as biological control and microbial pesticides.

Observations and simulations reported by Isaacson *et al.* (this Volume) indicated that biological control, appropriately timed and placed, can slow the advance of an incipient invader. There are statistical difficulties in mapping invasions and estimating invasion-rates (population growth and spread) for an invader that advances in 'leaps and bounds'. This challenges our ability to predict whether an incipient invader is likely to become a problem, whether biological control is likely to be effective in turning back an incipient invader, or whether control actions (once taken) are having the desired effect. While it is true that 'an ounce of prevention is worth a pound of cure', such foresight requires confident prediction of pest-potential to divert attention and resources from actual, current pest problems in order to avert potential, future weed problems. The theoretical literature on biological invasions has examined the single-species case in detail, but a more refined theory and better data are needed before we can have a reliable predictive theory of invasions that incorporates species interactions.

Progress toward improving biological control success can be made by improving the establishment rate of biological control organisms. Ecological theory, used to address the causes and cures of rarity in conservation biology, is now being applied to improve establishment of biological weed control organisms. Establishment of biological control organisms is typically from small populations, and small populations face a number of genetic and demographic hazards. Independent investigations reported in session 4 by Memmott *et al.* (this Volume) and Grevstad (this Volume) used a combination of deductive and inductive approaches to devise optimal release strategies to guide manipulation of the size and spacing of releases.

Control-organism behaviour and population dynamics

Weed biological control is following the lead of insect biological control by expanding research on population dynamics of interacting species. There are some fundamental questions. What are the patterns in the dynamics of interacting populations? How are they regulated? How do they respond to perturbations in organism density? Recent discussion of 'non-equilibrium' and 'equilibrium' approaches has not changed the type of questions that must be asked about species persistence, rather it has expanded the kind of answers that are possible (Murdoch 1994).

Gassmann (this Volume) concluded from a literature survey that weed-control researchers have been slower than insect-control researchers to investigate links between the demography and behaviour of the control-organism and the dynamics of interacting populations. An insect's reproductive success is predominantly determined by the quality of the host it chooses. If host quality varies, then so will the insect's reproductive potential and, with it, its density and, in some cases, sex ratio. The behavioural approach to evaluation of natural enemies helps us understand the value of hosts from the insect's perspective and thereby predict the intensity and efficiency of host-exploitation.

As if heeding Gassmann's call, a number of delegates at the Symposium reported on behaviour and demography of control-organisms. Center and Jubinsky (this Volume) called attention to the disruptive influence of weed control practices (including herbicide application) that caused local extinction of water hyacinth, *Eichhornia crassipes*, and its control-organism, the weevil *Neochetina eichhorniae*. Weed control breaks down when the weed re-invades more rapidly than the control-organism. Augmenting insect populations is a possible way around the problem, but augmentation is costly and subject to an ecological law of diminishing returns due to the insect's behavioural response. The growth and spread of experimental weed-populations did not decline with increase in weevil density from 1000 to 4000 weevils due to density-dependent beetle emigration. McEvoy and Fitzpatrick (this Volume) have shown that strong and stable suppression of ragwort, *Senecio jacobaea*, by the ragwort flea beetle, *Longitarsus jacobaeae*, does not arise as a result of spatial heterogeneity and insect searching behaviour within fields, where plant-insect interactions spiral down to local extinction. An alternative possibility is that regulation occurs on more global scales through spatial heterogeneity and migratory movement between fields in a landscape. However, controlled and replicated experiments are impossible to perform in such large-scale systems, leaving ample scope for differing interpretations. Reznik (this Volume) reported that suppression of ragweed, *Ambrosia artemisiifolia*, by *Zygogramma suturalis* has been more pronounced in perennial- than in annual-crop systems. *Zygogramma suturalis* lacks the life-history attributes (high dispersal and searching ability) needed to temper fluctuations in the resource base caused by annual cultivation and harvest. Morris (this Volume) added another successful case history to the annals of biological control, reporting that populations of *Acacia saligna* trees declined by 80-94%, six or seven years after the rust fungus, *Uromycladium tepperianum*, was established. Fire stimulates weed resurgence due to germination of seeds stored in soil, but the fungus survives most fires and readily reinfects and restrains the growing weed-populations.

These case histories exhibit a number of common features. The outcome of biological control reflects a balance in the forces of disturbance, colonization (re-invasion), and local organism interactions (McEvoy, *et al.* 1993). Alternative biological control strategies are needed to yield persistent suppression of average weed-density in a setting where local extinction and recolonization play an organizing role. Two such strategies are 'search and destroy' and 'sit and wait' (Murdoch *et al.* 1985). The 'search and destroy' strategy assumes that the control-organism is monophagous on the target weed, or nearly so, and highly capable of finding and destroying it. This strategy is exemplified by *L. jacaobaeae* introduced to control ragwort, *S. jacobaea*. The 'sit and wait' control strategy requires the more-or-less continuous presence of the control-organism in local areas subject to pest infestation, combined with adequate attack on the weed when it re-invades or begins to increase. This strategy appears to be exemplified by the rust fungus, *U. tepperianum*, introduced to control *A. saligna*.

Target-organism demography and population dynamics

Recent theoretical investigations on the demography and dynamics of populations in uncertain environments may help us target, more effectively, a weed's vulnerabilities. They bring together investigations of the evolution of life-histories and population dynamics (Caswell 1989; Tuljapurkar 1989, 1990). There are a variety of homeostatic mechanisms by which steady weed-populations can be maintained in the face of temporal fluctuations in seed-yield, including dispersal, dormancy, perenniality and iteroparity. These mechanisms have the potential to reduce the effects of natural enemies and soften the effects of a fluctuating resource base. According to the storage-effect hypothesis (Chesson 1983; Warner and Chesson 1985) environmental conditions affecting natural populations are to some degree unpredictable over time and strong recruitment in good years can be stored in an invulnerable stage (e.g. perennial rosette, iteroparous adult or dormant seed) that is capable of contributing to reproduction when favourable conditions prevail.

My co-workers and I have shown how disturbance, plant competition and herbivory by biological control insects manifest their influence on the life-cycle and population dynamics of ragwort, *S. jacobaea* (McEvoy and Rudd 1993; McEvoy *et al.* 1993). There have been recent attempts to investigate the steadying influence of the soil seed-bank using matrix population models and life-table response experiments (Caswell 1989). Paynter *et al.* (this Volume) predicted the consequences of reduction in seed yield for growth and spread of Scotch broom, *Cytisus scoparius*, populations. It is possible that very high levels of seed destruction reduce spread by the short-range mechanism of ballistic dispersal, but the effects on long-range transport by animals are unknown and hard to measure. Norambuena and Piper (this Volume) measured how seed-feeding by the weevil, *Apion ulicis*, affects the growth and spread of gorse, *Ulex europaeus*, populations (and the persistence of soil seed-banks) in areas with, and without, competition. The study encompasses longer periods of observation than is typical for field experiments, including more organizational complexity (following fates of parents and offspring, actively-growing and dormant stages), longer temporal scales (three years of continuous observation reported so far), and more explicit spatial scales (counting seedlings at 1, 2, 3, 4 m from the parent). This study is bound to stimulate better measurements of the effects of disturbance and organism interactions on weed population-growth and spread. Root (this Volume) measured the consequences of fluctuations in herbivore pressure for plant performance in native populations of goldenrod, *Solidago altissima/canadensis*, a long-lived perennial. Storage in perennial rootstocks can dampen the effects of shoot-feeders, but the vulnerability of below-ground reserves to root-feeders has not been directly assessed. Comparative studies of the native- and introduced-weed populations in relation to competitors and natural enemies can only help identify a weed's vulnerabilities and guide the selection of effective controls.

In summary, the effects of seed-reducing agents appear to be ripe for re-analysis. The early faith that seed-reducing agents must have some effect on plant population dynamics has given way to scepticism, which is based on increasing evidence that seed-reducing agents often have no measurable effect on plant abundance from year to year. The scepticism has been strengthened by the increasing number of seed-sowing experiments (Crawley 1989) in which sowing large numbers of seeds failed to increase the number of established plants. However, local seed-sowing experiments may underestimate the opportunities available to organisms with complex life-cycles living in a spatially and, or, temporally variable environment, and may therefore underestimate the true expectation of reproductive success. The ephemeral nature of successional habitats requires that inhabitants forsake the 'here and now' for opportunities 'elsewhere' or 'later' (Southwood 1977). Under the storage-effect hypothesis, infrequent recruitment events can have large consequences. The challenge is to obtain a representative sample of the area over which the organism can move (e.g. as dispersing seed), or the time-period over which it can survive (e.g. as perennial rosette, iteroparous adult or dormant seed) when not reproducing. Environmental states which occur with low probability in space and time (so low that we may often fail to detect them in samples) can lead to such high growth-rates that they can have important consequences (they dominate expectation values). As a result, local seed-sowing experiments can seriously underestimate the true expectation because they tend to be dominated by the most probable environmental states (but least consequential in terms of reproductive success).

One of the main problems in obtaining and interpreting population data is that of scale, i.e. what is the correct spatio-temporal scale to view the subject population? Our basic concept of population usually presumes a space-time horizon large and long enough to encompass the normal behaviour and dynamic repertoire of the species in question. Biological control researchers and practitioners are coming to grips with the problem by looking across scales and applying methods for linking processes on different scales. The problem of pattern and scale is arguably the central problem of ecology (Levin 1992) and cross-scale studies are critical to complement more traditional studies carried out on narrow, single scales of space, time and organizational complexity. By addressing this challenge, we can enhance our understanding of biological control systems and develop the theoretical basis necessary to manage them.

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