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Classical biological control of weeds with insects: a case for emphasizing agent demography

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Abstract. In order to improve the success rate of classical biological control of weeds and the selection of potential agents, much recent research has focused on the biology and ecology of the weed species and the effects of insects on the population dynamics of the target weed. It is axiomatic in weed biocontrol that insect herbivores have the potential to become abundant and devastating when freed from natural enemies and when ecoclimatically pre-adapted to the environment into which they are introduced. This paper is based on the hypothesis that: (i) with the exception of many seed-feeders, there is a level of herbivory above which most plant populations are not able to compensate; and (ii) the prerequisite for success is that the herbivore reaches high densities. Comparative studies of the reproductive biology and other fitness traits of agent species or biotypes have been largely neglected, although a number of life tables suggest that variation in fecundity is the most important factor regulating the population dynamics of insects. A few cases (e.g. *Salvinia molesta*) are now documented which indicate that levels of plant nitrogen content may be critical in weed biocontrol success in that they increase insect fecundity. However, very few studies of natural populations have addressed the demographic consequences for herbivores of host-plant genotype variations. Moreover, the way host-plant attributes influence insect performance is generally neglected. The study of insect attributes and fitness traits, the impact of plant resources on insect performance, and the construction of comparative life-tables, are the first steps towards an improvement of the success rate of biological weed control.

Introduction

After about a hundred years of weed biological control, the determination of the potential effectiveness of agents remains a complex problem which is far from being resolved. Criteria for prioritizing the selection of insect biological control agents against weeds were first developed by Harris (1973) and revised by Goeden (1983). These approaches emphasized both the importance of life-history traits and the damage inflicted to the plants. A review of successes and failures (Crawley 1989) emphasized taxonomy of the agent, intrinsic rate of increase, voltinism, and the distribution and abundance of the agents in their native land.

The selection of potential agents during the last decade has been largely based on experimental data on the population biology of the weed, impact studies of agents on the plant and the combined effect of herbivory and plant competition (e.g. Forsyth and Watson 1985; Müller-Schärer 1990, 1991; Louda *et al.* 1990; Sheppard *et al.* 1990; Cullen 1995).

It is an axiom in weed biocontrol that insect herbivores have the potential to become abundant and devastating when released from their natural enemies, and when ecoclimatically pre-adapted to the area into which they are introduced. Although often claimed, the role of natural enemies in failures has rarely been demonstrated, e.g. through life-table analysis, or exclusion experiments. The role of weather is rather poorly documented, and it mainly concerns failures in establishment (Myers 1987). The role that weather may play indirectly, through plant quality, has been overlooked.

Although little attention has been given to the level of herbivory in successes and failures in weed biocontrol, I assume that the prerequisite for success is that the herbivore reaches high densities. This does not mean that a high level of herbivory will bring about control, but the probability of success will be higher.

Exceptions to this assumption seem to be pre-dispersal seed predators, and in cases where asymmetry occurs between the plant and the insect (Crawley and Gillman 1989). Environmentally controlled compensatory mechanisms at the individual plant or population level may moderate the impact of food-limited herbivores. Moisture availability is known to favour plant compensatory growth of *Senecio jacobaea* after defoliation by *Tyria jacobaeae* (Cox and McEvoy 1983), and of *Hypericum perforatum* when attacked by *Chrysolina quadrigemina* (Williams 1985). In this paper I wish to re-emphasize the role of insect demography and behaviour in weed biological control.

Insect demography and behaviour

Survivorship, development rate, and fecundity are all important components of insect demography (Crawley 1986). The intrinsic rate of increase (*r*), (i.e. the combination of the above-mentioned biological parameters) expresses insect fitness, which I assume to be a key-component in determining the potential effectiveness of weed biocontrol agents. The correlation between feeding rate, body size, and intrinsic rate of increase implies that the amount of damage per individual agent is not important, but the total amount of damage, expressed by the demographic response of the agent on the plant is important. For example, the most obvious attributes of the first four agents selected for the biological control of *Euphorbia esula* were their large size and high *per capita* feeding rate with subsequent visible damage on the host plant. For various reasons none of these agents became successful, in contrast to small chrysomelids which all showed a high numerical response in the areas of release (Gassmann and Schroeder 1995). Dispersal capability, or aggregative behaviour may also be important components of success. Clumped distributions of herbivore attack are known to occur in some successful cases of control (Lawton 1985), and a wave process has been described for *Zygogramma suturalis* on *Ambrosia artemisiifolia* (Kovalev 1989). This may also have happened with *Chrysolina quadrigemina* on *Hypericum perforatum*. A similar advancing front by the agent has been reported with *Aphthona* spp. on *Euphorbia esula* (McClay personal communication).

Comparative studies of the reproductive biology of closely related beneficial phytophagous insect species or biotypes are rare in the literature. However, one example is the comparative study on the intrinsic rates of increase of *Cyrtobagous singularis* and *C. salviniae* on *Salvinia molesta* (Sands *et al.* 1986). At all temperatures tested, *C. salviniae* laid seven times more eggs than *C. singularis*. Differences in population levels attained by the two species, and their different feeding behaviours have thus contributed to the different impacts on the weed by the two species (Sands and Schotz 1985; May and Sands 1986). In the country of origin, comparative demographic studies of selected potential agents are rarely carried out. The oviposition pattern and larval survival of *Agrilus hyperici* on *Hypericum perforatum* were estimated at four sites in its native range in southern France (Briese 1991): generation increases varied between 3.8 to 11.7 fold. Unfortunately comparative fecundity between sites was not included in this study.

Insect life tables

The biological and demographic characteristics of a species are strongly related to various ecological factors, including natural enemies, competition, climate and habitat, and food resources. The natural enemies of insects are believed to be a major reason for failure in the biological control of weeds, but their real importance is not known, although rates of predation or parasitism are often given to support that assumption (e.g. Myers 1987; Müller-Schärer and Goeden 1990). However, rates of parasitism or predation which suggest that entomophagous insects are responsible for the failure of an agent can be misleading because of compensatory mechanisms. For example, egg-predation of *Cactoblastis cactorum* by ants, as well as the effects of climate, considerably reduced the effectiveness of *C. cactorum* in South Africa (Robertson and Hoffmann 1989). However, it is not clear to what extent egg mortality induced by predators in Australia (where the moth is very successful) is compensated for by density-dependent larval mortality. Such supposed compensating factors cannot be evaluated by simple removal from a life table of one cause of death. Removal of the factor under study must occur in the field, in as natural a setting as possible, so that the role of compensating factors can be observed (Price 1987). The main mortality factors can be assessed using a key factor analysis or a probability analysis, as proposed by Carey (1993), where it is not possible to determine experimentally the effect of eliminating a certain cause of mortality.

Crude comparisons of insect fecundities to select for potential effectiveness may be as misleading as rates of predation in explaining failures. For example, the average total fecundities of 29 macrolepidopteran forest pests varied from 58 to 880 eggs per female (Nothnagle and Schultz 1987). They concluded that one of the most influential environmental factors for pest species was likely to be variation in host-plant quality for young larvae. In summary, the comparisons and conclusions based on isolated life-history traits, such as fecundity or predation may be misleading. Experiments and comparative life tables are needed for a better understanding of the dynamic processes of herbivorous insects on weeds.

The effects of plants on insects

The effects of resource variation on herbivorous insects has been reviewed by Denno and McClure (1983) and Hunter *et al.* (1992). The impact of the nitrogen content of plant tissue on the demography of insects is also well documented (e.g. Mattson 1980; White 1984), and a number of life-table analyses have suggested that variation in fecundity is an important factor regulating population dynamics (see Preszler and Price 1988 and references therein). For example, adults of the cinnabar moth, *Tyria jacobaeae* lay more eggs on individual plants of *Senecio jacobaea* with high nitrogen contents (van der Meijden *et al.* 1989). Price *et al.* (1990) suggested incorporating female behaviour into life tables, using the cohort of eggs as the basis for these tables.

Room *et al.* (1989) showed that nitrogen-rich *Salvinia molesta* grew faster and suffered less damage per individual *Cyrtobagous salviniae* weevil but, because the populations of *C. salviniae* increased more rapidly on host plants containing higher concentrations of nitrogen, such plants sustained more damage. Successful control of prickly pear cactus by *C. cactorum* in Australia was achieved in an area with poor soil only after nitrogen fertilizer improved the nutritional quality of the plants. The dynamics of the cinnabar moth are strongly influenced by plant-nitrogen levels, and artificial defoliation and, or, water stress of *Hypericum perforatum* increased the nitrogen levels of regrowth foliage (Myers 1987). The indirect effects of fire in eucalyptus forest in Australia favoured population build-ups of *Chrysolina quadrigemina* and *Aphis chloris* (released against *H. perforatum*), through increased plant-nutrient levels (Briese 1995).

Abiotic factors (e.g. rainfall, soil drainage, temperature, soil-nutrient status) change the plant-herbivore relationship in many cases, acting to change the carrying capacity for insect populations. For example, water availability to willows can result in a 100-fold difference in survival of the shoot-galler *Euura lasiolepis* (Price 1992). Therefore, the evaluation of the impact of plant resources on insect survival and reproduction (e.g. performance) is a crucial step towards a better understanding of successes and failures in weed biological control.

In common with many environmental factors, plant genotype can influence the capacity of an individual plant to support growth and reproduction of its consumers. A few studies on natural populations have addressed the demographic consequences of host-plant genotypic variation for herbivores. Littlefield (1987) showed the variable host-plant suitability of various clones of *Cirsium arvense* to gall induction and host selection by *Urophora cardui*. Some varieties of *Lantana camara* are more resistant to attack by *Teleonemia scrupulosa* than other forms (Harley *et al.* 1979).

For the last years, the subject of variation within arthropod pests has become a target of intensive research using molecular and morphometric techniques, and over 122 insect pests have been checked for genetic variation (Steiner 1993). Genetic diversity in insects is expressed in numerous biological traits including morphology, sexual behaviour, developmental rate, fecundity, dispersal ability and feeding preference (e.g. in *Drosophila* spp.). However, in many instances, genetic variation is assessed without any knowledge of the corresponding variations in fitness. Much work remains to be done to gather evidence for the genetic basis of such variation and to demonstrate the role of genetic adaptations in the establishment and effectiveness of biological control agents. Crossing experiments appear to be the best source of evidence for the genetic basis of traits likely to affect establishment and effectiveness (Hopper *et al.* 1993). Regarding genetic variation in the weed and in the insect, little has been done so far, with the exception of some work on the suitability of different host-plant races for different hosts (e.g. *Rhinocyllus conicus*) (Unruh and Goeden 1987). Plant suitability is usually estimated by measuring insect growth and survival, but female fecundity and behaviour are rarely considered.

Conclusions

For over 100 years weeds have been controlled by the deliberate introduction of phytophagous insects. For almost as long, entomologists have discussed the necessity of improving success rates. The topic of genetic and phenotypic variability in agents selected for weed biocontrol was first discussed by Sands and Harley (1980) and by Myers and Sabath (1980). These papers reflected on the need to obtain insects that are pre-adapted to a wide range of climates and host varieties, and were concerned more with the establishment of the agents than with their abilities to control the weed. Since then, few weed biocontrol agents have been subjected to infraspecific, phenotypic and genetic variation studies.

Although poorly documented, most failures to control the target weed after successful establishment of the agent seem to be due to low levels of herbivory (with the exception of pre-dispersal seed-feeders), or to selective attack (e.g. on *Lantana camara*). The demographic and behavioural responses of herbivorous insects used in weed biocontrol are therefore crucial issues for a better understanding of successes and failures, whether they are genetically fixed, determined by environmental conditions, or by within-plant genetic or phenotypic variants.

The field of research is enormous, varied and complex. Geographical populations with the best fitness traits should be selected to favour the numerical response of the insect in the area of introduction. We need more information on the phenotypic and genetic variability of weed-biocontrol, herbivorous insects related to fitness/effectiveness. When more data are collected, the debate will inevitably return to whether it is preferable to introduce populations with high genetic variability and let selection operate, or to select, before their introduction, populations with optimal characteristics.

The effect of plant variability on the abundance of a number of insect pests is well documented, as is the effect of environmental stress on plants. In contrast, little is known about host-plant variability and its effect on beneficial herbivorous insects. A few examples in weed biocontrol indicate that host quality may be a crucial component of success. A better understanding of successes and failures will come through a better understanding of the impact of plants on insects, and through an understanding of how environmental factors act on insects through changes in host-plant resources.

The main requirement for research in the area of origin of the target weed is to select insect populations with the best fitness traits, and to see whether these are genetically fixed or determined by environmental conditions. The main requirements for successful releases are the selection of the most suitable weed populations and favourable environmental conditions, all of which aim at optimizing the demographic potential of the selected agents.

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