Biological control of weeds with insects: A dynamic phenomenon of insect-plant interaction

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Abstract. Extrinsic causes affecting the performance of insect enemies of weeds including climatic unsuitability, parasitism, predation and disease pathogens are discussed, giving examples of both weeds and their insect enemies selected with special relevance to India.

Keywords. Biocontrol; weeds; insect enemies.

1. Introduction

Biological control of weeds is one of the better known alternatives to chemical control and involves the deliberate use of target-specific destructive organisms to check the economic losses caused by terrestrial and aquatic weeds and other undesirable, particularly noxious, plants that occur in various parts of the world. Parasitic plants like witchweed (Striga), dodder (Cuscuta) and broomrape (Orobanche) are also notorious destroyers of useful vegetation. Manual and mechanical removal of weeds, cultural practices and growing of resistant strains of cultivated plants are other control methods used with varying degrees of success, depending on the severity of the weed problem and the manpower, material and monetary resources available to deal with the situation. When successful, biological control is self-sustaining, effective, economical and ecologically sound.

The biological control of the cottony cushion scale insect Icerya purchasi Maskell (Hem., Margarodidae) by the predacious vedalia beetle Rodolia cardinalis Mulsant (Col., Coccinellidae), both native to Australia, in California, USA, by the end of the 19th century led to the application of the same concept to weed control. The first weed to become a suitable target for biological control was lantana, Lantana camara L. (Verbenaceae), in Hawaii. This aggressive and hardy plant, originating from subtropical and tropical Central America, is now almost cosmopolitan in distribution, having been initially introduced purposefully as an ornamental shrub in most areas on account of its attractive and colourful inflorescence. However, the plant has proved toxic to livestock and even to human beings. Several insect enemies of lantana attacking various parts of the plant were found during surveys carried out at first in central Mexico during 1902 and continued from time to time later in several areas of the neotropical region for over half a century. Many of these have been introduced not only in Hawaii but in numerous other countries with partial or substantial control of the weed.

In Australia, prickly pears (Opuntia) were cleared over nearly 60 million acres of infested land during the 1930's by the larvae of a moth, Cactoblastis cactorum (Berg.) (Lep., Pyralidae) imported from Argentina. About the same time outstanding control of prickly pears was also witnessed in India but the control agent responsible for it in this country was Dactylopius opuntiae (Ckll.) (Hem., Dactylopiidae).
These early successes led to increasing worldwide interest in biological control of weeds. By 1980, projects covering 86 weed species and 192 biocontrol agents had been completed or were in progress in many parts of the world. More or less successful biological control has been reported with 48 different weeds in 23 locations (Julien 1982). A notable development is the utilization of native insects (and, of course, other organisms) to control indigenous as well as exotic weeds.

Sankaran (1973, 1974) reviewed the work on biological control of weeds in India. Subsequent efforts and progress and also the significant achievements made over the past one decade under the national biocontrol project of the Indian Council of Agricultural Research are summarised in a recent bulletin (Singh 1989).

A wide range of organisms from microbes to vertebrates have been used in the biological control of weeds but the present study will be restricted to insects. Further, most of the examples given here will be of special interest to entomologists and weed scientists in India who may wish to follow up the research with fresh ideas of their own.

2. Choice of phytophagous insects for weed control

Generally, alien weeds are especially amenable to biological control because of the lack of effective and host-specific natural enemies to keep them under check in the new area(s) which they have colonised. Many a wild plant species is hardly ever treated as a weed in its native distribution range, occurring at low densities, often in scattered stands, and being attacked by an assortment of insects and other natural control agents. However, when the same species invades a new area unaccompanied by its natural enemies it is able to spread and build up its population density very fast, particularly if other ecological conditions are also favourable to it. In India *Parthenium hysterophorus* L. (Compositae) is one of the best examples of such an alien weed.

In what is commonly known as classical biological control the first step is to trace the native range of the alien weed, investigate the biotic agents that regulate its population, select the most promising natural enemies, subject them to a strict protocol of host-specificity screening tests, and then to introduce the successful candidate species into the new area for field evaluation. Many of the insects attacking a potential weed in its native home may be expected to be polyphagous, which will automatically disqualify them for use in biological control in other areas in view of the risk of their attacking useful plants. In this context it should be pointed out that even in a newly colonised area an alien weed will soon be subject to attack by various polyphagous, native insects that may also be crop pests, such as *Aphis fabae* Scopoli (Aphidae) and *Ferrisia virgata* (Ckll.) (Pseudococcidae) on *P. hysterophorus* in India. It is preposterous to treat these insects as beneficial biotic agents that warrant conservation or augmentation. Host-specificity is the most essential requirement for a biocontrol agent used in weed control.

Some native insects that attack indigenous weeds and exhibit monophagy or oligophagy have been studied and used in weed control by breeding them in the laboratory and releasing them to augment the otherwise low natural populations at critical stages in the life-cycle of the weed. *Bactra erutana* Zeller (Lep., Tortricidae) has been used against *Cyperus rotundus* L. (Cyperaceae) in the USA (Frick and Chandler 1978) and periodical releases of the noctuid *Episamea pectinicornis* Hamp. are now a standard control method against *Pistia stratiotes* L. (Araceae) in Thailand (Napompeth 1982).
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The use of native biotic agents may be of value against weeds for the control of which there is little or no scope for introduction of additional, more effective, biocontrol agents from other geographical areas. Although in some instances insects obtained as biocontrol agents from a climatically similar area in the native distribution range have done particularly well in the release area, this is not an indispensable condition for success because some insects have proved to be remarkably effective control agents in climatically different regions. Genetic diversity in the introduced insect population will enhance and improve the chances of success.

3. Aspects of insect-plant interaction determining host-specificity

According to Zwolfer (1973) host-specificity is largely a function of orientation stimuli. These stimuli originate from the host-plant and elicit characteristic responses from the insect acting through various types of sensory structures that have co-evolved in the course of long association and constant interaction between the insect on the one hand and the host-plant and its habitat on the other. Pieterse (1979) has cited Russian work on Phytomyza orobanchiae Kalt. (Dip., Agromyzidae) which demonstrated the ability of the insect to locate Orobanche over a radius of 3 km. With the advances made in the techniques of study on many aspects of insect-plant interaction the morphological, physiological and biochemical bases of host-specificity are being understood much better now than was possible in the first half of this century. Several valuable contributions to our knowledge of this subject have emanated from the Entomology Research Institute, Madras (Ananthakrishnan 1977, 1986).

Some groups of insects contain genera and species that have very specialised host-plant associations and correlated adaptive mechanisms. However, very little is known of all the factors responsible for such insect-plant affinities. For example, why are many species of the weevil genus Smicronyx restricted to parasitic plants such as Cuscuta (Convulvulaceae) and Striga (Scrophulariaceae)? Species of another weevil genus, Nanophyes, that produce and breed in the fruit-galls of their host-plant also exhibit a high degree of specificity as evidenced by a complex of species that occur on various Ludwigia spp. (Onagraceae) in India (Sankaran and Rao 1972). The biology of Nanophyes sp. nr. nigritulus Boh. studied by Sankaran and Krishna (1967) revealed a remarkable synchronisation between the phenology of its host-plant Ludwigia adscendens (L.) Hara (=Jussiaea repens L.) and the ontogeny of the insect.

Insects selected for use in biological control of weeds may be restricted to their host-plants by their oviposition habit, nutritional needs as well as larval developmental requirements, and pupation habit.

Morphological peculiarities or physiological or biochemical cues of the host-plant (actual oviposition site) may attract the mature female to lay eggs and it is sometimes possible to induce a female to oviposit on unnatural plants simulating natural conditions but larval development will not be completed on or within such plants. In screening tests at CIBC, Bangalore, the weevil Neochetina eichhorniae Warner, which has now been so successfully used in the control of water hyacinth Eichhornia crassipes (Mart.) Solms. (Pontederiaceae) in some parts of India and in many other countries, oviposited on water chestnut, Trapa bispinosa Roxb.
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(Trapaceae) but the larva failed to complete its development on it although it fed slightly on the leaf for 10 days.

However, habitual oviposition by an insect on or within a plant species is not by itself an exclusive proof of host-specificity. Gesonula punctifrons (Stal.) and Paulinia acuminata (De Geer), both grasshoppers, have been studied for their host-specificity and evaluated as biocontrol agents. G. punctifrons makes tunnels in the soft tissue of the petiole of water hyacinth and lays eggs inside but the nymphs and adults feed not only on water hyacinth but also on Arum (Araceae), Colocasia (Araceae) and Monochoria (Pontederiaceae) and some unrelated economic plants (Sankaran et al 1966). In laboratory tests it was also found to make oviposition tunnels in the stem of Canna (Cannaceae). It is an Oriental species that has become adapted to the alien (neotropical) water hyacinth. The neotropical grasshopper Cornops longicorne (Bruner) has oviposition habit similar to that of G. punctifrons, a good example of convergent evolution. P. acuminata is another neotropical grasshopper that oviposits on the submerged undersides of the leaves of Salvinia molesta D S Mitchell (Salviniaecae) and the eggs do not develop normally and hatch if continuously exposed to the atmosphere. This habit confines it to an aquatic environment, where it may also feed on a few other aquatic plants.

Dietary needs of even host-specific insects may be satisfied not only by the food-plants preferred by them in nature but also by one or more other species of plants. This faculty has helped in the development of artificial diets to breed several species of insects in the laboratory. In screening tests carried out with some phytophagous insects that have eventually been introduced into new areas for weed control the larvae or adults were found to feed on a few related or unrelated plants. However, the adults failed to reproduce after feeding on such plants. In very rare instances the candidate insect fed and also reproduced on the test plant, for example the lantana bug Teleonemia scrupulosa Stal. (Hem., Tingidae) on Tectona grandis L. (Verbenaceae). The lantana bug has, nevertheless, not become a pest of teak although it has co-existed with teak in India since at least 1951. Davies and Greathead (1967) reported that T. scrupulosa attacked Sesamum indicum L. (Pedaliaceae) in Uganda but the bug is not known to be a pest of sesame in India and Mexico (its original home) where this crop is widely cultivated. Three other lantana insects, Leptobyrsa decora Drake (Tingidae), Octotoma scabripennis (Guerin) and Uroplata girardi Pic. (both Col., Hispidae) are also capable of feeding on sesame (Harley 1969; Harley and Kassulke 1971).

An aspect of host-specificity that merits much closer investigation is the occurrence of more than one congeneric species feeding on different parts of the same plant. The larvae of the noctuid Eulocastra argentisparsa Hmps. feed on the ripening seeds of Striga spp. while those of the closely related Eulocastra undulata Snellen feed on the leaves. The larvae of these two species differ in their colouration but the moths reared from them were at first identified by the Commonwealth Institute of Entomology as E. argentisparsa (Sankaran 1973). The water hyacinth weevils N. eichhorniae and Neochetina bruchi Hustache are both able to thrive together because although the larvae have similar feeding habits the adults show different feeding preferences and temperature tolerances and the oviposition behaviour of the females of the two species also differs (Singh 1989).

The mature larvae of some insects used against aquatic weeds seek specific niches as pupation sites that are characteristic of their host plants. Agasicles hygrophila Selman and Vogt (Col., Chrysomelidae) successfully introduced into Australia and
the USA from Argentina to control the alligator weed *Alternanthera philoxeroides* (Mart.) Grisebach (Amaranthaceae), though an external feeder in its larval stages (and also as adult), chews its way as mature larva into one of the apical internodes above the water level and pupates inside. The newly formed adult feeds on the internal side of the stem wall for a short while and then emerges. Full-grown larvae of the two *Neochetina* spp. come out of their feeding tunnels and pupate in submerged cocoons covered over by a ball of root hairs of water hyacinth. Similarly *Cyrtobagous salviniae* Calder and Sands, another weevil that has controlled *Salvinia molesta* in India, Australia etc. pupates within a submerged cocoon in close contact with the plant tissue. Ability to pupate in a non-aquatic medium may render a species suspect and necessitate additional host-specificity studies. The tuber weevil *Bagous affinis* Hustache, introduced recently into the USA from India to control *Hydrilla verticillata* (L.f.) Royle (Hydrocharitaceae) feeds on hydrilla stems but the larvae later complete their feeding and pupate within the tuber although pupation may also take place in soil with adequate moisture (Buckingham 1988).

4. Insect damage potential and its impact on weeds

Insects that damage different parts of the same weed may kill a weed or contribute to an overall reduction in its growth, vigour and reproductive potential. Therefore, if one species fails to control a weed adequately others may be used to enhance the level of control. Synergistic action by two species may also inflict more damage on the weed than that possible by either species working alone, as with *N. eichhorniae* and the water hyacinth mite *Orthogalumna terebrantis* Wallwork (Del Fosse 1978). Species that severely damage the root system or the main stem may kill the plant within a short time while defoliators and flower feeders are less drastic in their effect. Both annual and perennial weeds have been successfully controlled biologically by employing insects. However the intrinsic damage potential of every species may not be fully realised in all situations. Environmental constraints may operate against them. Most of the phytophagous insects themselves are subject to parasitism, predation and pathogenic diseases, and as a result many species occur at low populations, particularly at the most vulnerable stages in the life-cycle of the weed. With annual weeds that only propagate by seed, fruit- and seed-feeding insects are likely to be more effective control agents than they are with weeds that propagate vegetatively as well as by seed.

Larvae of the noctuid *Eulocastra argentisparsa* cause complete loss of seed in individual *Striga* plants but their natural populations are always very low. A microsporidian disease is known to infect them. Moreover *Striga* is an annual weed and its seed-maturing phase is short. *Eulocastra* is unable to build up its population early enough to reduce the total seed output in an infested area significantly. It has been suggested that the insect may be mass-bred on an artificial diet in the laboratory for use in biological control after the necessary screening tests.

A gall-forming weevil, *Smicronyx albovariegatus* Fst. attacks *Striga* spp. in India but most of the galls are produced on the root, stem and branches and yet do not impair the vigour or reproductive capacity of the host-plant. The host-plant is able to withstand, if not resist, the weevil attack. Some other *Smicronyx* occurring in Africa produce fruit galls and thereby arrest seed production. However, parasitism limits their value as control agents.
Larvae of the tortricids *Bactra (Nannotbactra) minima minima* Meyr. and *Bactra (Chiloideas) venosana* Zeller bore into the stem and occasionally into the rhizome of *Cyperus rotundus* L. in India but, since even a partially damaged rhizome can produce a fresh shoot, the insect is not able to kill the plant. The new shoot may also be infested by the borer. Such plant regeneration and insect counter-attack have the final effect of dwarfing the plant by keeping it under constant stress, which gives cultivated plants a competitive advantage over the weed in crop fields. Here again various parasites reduce the effect of these borers (Sankaran and Rao 1972).

The gall-fly *Procecidochares utilis* is widely established on *Eupatorium adenophorum* in many parts of India but its control action is weakened by native parasites.

Harris (1973) has discussed many of the diverse interspecific and intraspecific mechanisms that contribute to low or high vulnerability of weeds to damage by biocontrol agents, with particular reference to photosynthetic activity and carbohydrate reserves in the plant, and to flowering, plant density and competition.

5. Success or failure of insect enemies in biological control of weeds

Many species of insects introduced from one part of the world into another for weed control that have failed to become established have hardly received any further attention although there is much to learn from the negative results of biological control attempts. Several others that are established but do not exert significant levels of control on the target weed in some area(s) have been tried elsewhere with better success. A number of species have performed remarkably well in different areas wherever they have been tried. The latter two categories are preferred for use in newer areas without or after additional testing. However, taking insects and all other biocontrol agents into account, 60–75% of the introductions for weed control are considered to be ineffective (Julien 1982).

The causes for failure of a species may be extrinsic, i.e. they are not directly related to insect-plant relationship *per se* but attributable to unfavourable factors of the environment such as climatic rigours, interference from natural enemies, man-made disturbances etc. The gall-fly *P. utilis* well established on *E. adenophorum* in the Nilgiris is handicapped by the high annual rainfall in the area, apart from being parasitised by native chalcidoids.

The critical importance of infraspecific biosystematics to biological control of weeds has been amply demonstrated in recent years. Investigations in Australia have revealed that lantana naturalised there for over a century occurs in some 21 strains or varieties but *T. scrupulosa* has definite preferences for particular taxa, which reduces its control value in areas where other taxa predominate. This is thought to be due to the limited gene pool of the original stock of the insect imported in 1935. Enrichment of the genetic foundation of the local population by incorporating fresh stocks of the bug from various parts of south America resulted in better control of the resistant varieties of lantana (Harley 1973).

*Pareuchaetes pseudoinsulata* Rego Barros (Lep., Arctiidae), previously known as *Ammalo insulata* Walker, introduced from Trinidad into several countries to control *Chromolaena odorata* (L.) (Compositae), presents a puzzling picture of contrasting performance. It failed to get permanently established in Ghana, Malaysia and Nigeria. In Ghana, the larvae were predated upon by insects, lizards and spiders. In
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Sabah (Malaysia) it did not persist for long. The causes for its failure there and in Nigeria are unknown. Large-scale field releases of eggs, larvae and adults in the plantations of Kodagu (Coorg) in Karnataka did not result in success. Native predators, mainly ants, were largely responsible for its failure. The ants were attracted to the weed because of the presence of honey-dew-producing aphids and mealybugs. A granulosis virus of the larva is also believed to have prevented its establishment. In renewed efforts, a strain of the same insect was obtained from Sri Lanka, where it had been introduced from Trinidad in 1973 and become naturalised, and was released in a rubber plantation in Kerala and it became established. Defoliation of the weed has occurred over a small area (Singh 1989). In marked contrast, the same strain introduced from India in 1985 was soon established on the island of Guam (Pacific Ocean) by 1986 and has destroyed the weed over 10,000 acres (CIBC Report, April–December 1986).

The level of biological control resulting from interaction between an agent and the weed can be raised by environmental stresses acting on the plant. Harris (1981) has suggested a 5-fold strategy to increase the stress on the weed: (i) decreasing the mortality factors affecting the control agent, (ii) increasing the number of agents attacking the weed, (iii) increasing the fecundity of the agent, (iv) altering cultural practices to stress the weed while still favouring the agent and (v) selection of agents that inflict a high stress load. These include even unconventional measures such as limited use of insecticides to eliminate predators that interfere with biological control by phytophagous agents and increasing the nutritive value of the weed by correcting mineral and nitrogen deficiencies in the habitat by judicious application of chemical inputs. These measures will make biological control an important component of weed management.

6. Conclusions

Biological control of weeds by insects, whether native species or introduced ones, involves a complex of interacting morphological, biochemical, phenological and other factors in both host-plant and control agent. Host-specificity is the most essential requirement for an insect to be used as a weed control agent. While an insect initially locates its preferred host-plant by responding to various orientation stimuli, eventually it selects and remains on the plant for feeding and breeding by reacting more intimately to one or more of the various factors mentioned above. Oviposition habit and nutritional suitability of the plant for growth and reproduction are important criteria in determining insect-plant association. Insects attacking water weeds have characteristic biological traits that tie them to an aquatic habitat. Some taxa of weeds are resistant to or tolerant of attack by certain insects but may be susceptible to damage by different agents from other areas. More than one species of insect occurring on the same weed at the same time but exhibiting complementary and not competitive feeding and oviposition habits may have a synergistic effect in suppressing the weed. Apart from climate, biotic factors such as parasites, predators and pathogenic organisms, as well as biochemical and phenological changes in host-plant vulnerability are among the major causes that affect the control value of insect enemies of weeds. Measures to eliminate or minimise their adverse impact are known and can be adopted to improve biological control.
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