Proc. VI Int. Symp. Biol. Contr. Weeds, 19–25 August 1984,
Vancouver, Canada. Delfosse, E.S. (ed.). Agric. Can., pp. 13–26 (1985)

Ecological Theory and Choice of Biological Control Agents

John H. Lawton

Department of Biology, University of York, Heslington, York YO1 5DD, U.K.

Abstract

From many possible topics, three are selected for discussion: the population dynamic characteristics of successful control agents in theory and practice; host shifts and the risks inherent in biological control; and the possibility of using exotic insects to control native weeds. (i) One group of population models proposes that successful control agents show strong aggregative responses to high density host patches. More recent studies cast doubt on this theoretical insight; pertinent field data are virtually non-existent. Whether better understanding of this problem would lead to better practical weed control is a moot point, but it deserves attention. (ii) Worries about biological control agents switching to non-target plants are persistent, but unjustified. Studies on native insect faunas suggest that in general, the probability of an insect used in a biological control programme unexpectedly switching to a non-target host is of order of 1×10^{-8} to 1×10^{-7} insect species, plant species^{-1} year^{-1}. Despite these minute risks, further studies on the genetical, physiological and behavioural changes involved in host shifts would be helpful when selecting biological control agents. (iii) Finally, the use of exotic insects to control native weeds is addressed. Successful application demands detailed theoretical and practical studies on the ecology of native insects feeding on the target weeds. Plans for the biological control of bracken fern, *Pteridium aquilinum*, in Britain are outlined, using exotic, apparently bracken-specific insects from South Africa, selected to occupy vacant niches in the resident British insect community on bracken.

Théorie Écologique et Choix des Agents de Lutte Biologique

Sur un vaste choix de sujets, trois domaines ont été retenus aux fins de l'étude: (1) les caractéristiques de la dynamique des populations des agents biologiques efficaces: théorie et pratique; (ii) la substitution d'hôtes et les risques inhérents à la lutte biologique; (iii) les possibilités d'utilisation d'insectes exotiques pour lutter contre les plantes nuisibles indigènes.

D'après les modèles 'classiques' des populations, pour réussir les agents biologiques doivent être fortement attirés en masse sur les touffes denses des plantes hôtes. Des modèles plus récents remettent cette théorie en question, et il n'existe pratiquement aucune donnée pertinente sur le terrain. Une meilleure compréhension de ce problème permettrait-elle d'arriver à des méthodes plus pratiques de lutte contre les plantes nuisibles? C'est là un sujet à controverse, mais qui mérite plus d'attention.

De temps à autre, on s'inquiète de l'infestation des plantes non-cibles par les agents biologiques. D'après les études théoriques et expérimentales sur la substitution d'hôtes des insectes indigènes, les risques à long terme associés à ce phénomène dans les programmes de lutte biologique modernes n'existent qu'à peine ou pas du tout.

Finalement, l'auter traite de l'utilisation d'insectes exotiques pour la lutte contre les plantes nuisibles indigènes. Pour réussir de telles tentatives, il faut procéder à des études théoriques et pratiques sur les insectes indigènes. Il présente aussi le programme de lutte biologique contre le plèridium des aigles (*Pteridium aquilinum*) que l'on prévoit mettre en oeuvre en Grande-Bretagne par l'introduction d'insectes exotiques d'Afrique du Sud, dont l'unique hôte est la fougère, et qui ont été choisis pour combler les lacunes de la communauté d'insectes indigènes de Grande-Bretagne qui fréquentent les fougères.

Introduction

Data from biological control programmes have undoubtedly contributed more to theoretical ecology than theoretical ecology has contributed to biological control (see, for example, Beddington *et al.* 1978; Ehler and Hall 1982; Caughley and Lawton 1981; Hassell 1978, 1980; Murdoch *et al.* 1984). Reasons for this asymmetry are not hard to find; it is often too expensive, or impossible, to gather information that theoreticians suggest would improve the practice of biological control, or appropriate theory is poor, unconvincing, or absent. Nevertheless, this should not prevent us from trying to improve the practice of biological control by careful use of existing theory (e.g. Harris 1981*a*; Price 1981), or from nurturing the development of more and better theory. An encouraging recent development is the Silwood International Project on the Biological Control of Weeds, a comprehensive theoretical and practical analysis of biological weed control programmes, currently being undertaken by a group of biocontrol workers and ecologists centred on Imperial College and CIBC at Silwood Park in England.

My aims in this paper are considerably more modest than the Silwood Project! Theoretical ecology is a broad church, and from among many possible topics I have selected three for consideration. They are deliberately very different. The first addresses the question of whether successful biological control agents have similar population dynamics, and whether these dynamics account for their success. Section two of the paper then moves to the question of risks in biological weed control, and measures the probability of host shifting to non-target plants by insect control agents. Finally, the problems and possibilities for biological control of a native weed *Pteridium aquilinum* (L.) Kuhn. (bracken fern; Dennstaedtiaceae) in the U.K., using exotic insects are discussed. Between them, these three topics allow discussion of a range of theoretical problems of interest to biological control workers, and highlight places where ecological theory might help in the choice of biological control agents.

Population Dynamics Theory and Selection of Biological Control Agents

The hallmark of successful biological control is a persistent, marked reduction in the pest population. A useful measure of the magnitude of this reduction is:

$$q = N^*/K, \tag{1}$$

where q is the ratio of the density of the pest population, N^*, in the presence of a controlling agent, divided by the density of the pest, K, prior to control. Estimates of q are available both for insect pests successfully controlled by parasitoids (Beddington *et al.* 1978; Strong *et al.* 1984) and plants controlled by herbivores (Caughley and Lawton 1981; Strong *et al.* 1984).

Interpreting q*-values*

As a basis for developing theoretical understanding, more and better estimates for q in biological weed control programmes would be valuable. However, existing data are sufficient to establish that q-values of order 0.01 or less, are not uncommon. Theoretical interest in low q-values is considerable, because stable q-values less than 0.1 are surprisingly difficult to generate in population models (Beddington *et al.* 1978; Caughley and Lawton 1981; Crawley 1983). The most complete theoretical framework exists for insect host–parasitoid systems, where detailed mathematical models of the interaction (see Beddington *et al.* 1978; Hassell 1978, 1980; Hassell and Waage 1984) suggest that successful biological control of insect pests (i.e. $q \approx 0.01$) by parasitoids hinges on two phenomena: (i) high parasitoid searching efficiency, generating strong host depression; and (ii) a spatially aggregated host population, on which aggregating parasitoids impose spatially density-dependent mortality. It is aggregation by the parasitoids in regions of high host density that generates stability in the interaction, particularly at very low q-values.

Arguing largely by analogy from these host–parasitoid models, Caughley and Lawton (1981) suggested that spatial heterogeneity in the distribution of weed populations, and non-random, spatially density-dependent mortality induced by herbivores may also be crucial for population stability in successful biological weed control. Unfortunately data to test this suggestion are virtually non-existent. Moreover, realistic but tractable models of insect–plant interactions are considerably more difficult to construct than parasitoid–host models (Crawley 1983). Indeed, Crawley's (1983) models imply that herbivore aggregation alone is not sufficient to guarantee a low, stable q. Under some circumstances, *reducing* herbivore aggregation leads to a dramatic reduction in plant abundance, for example when herbivores reproduce on their host, but have rather poor powers of dispersal between hosts (Crawley 1983, pp. 274–7).

Very simply, we do not understand the crucial dynamic processes involved in the successful control of weeds by insect herbivores. Whether such knowledge would itself lead to the selection of better control agents in the future is debatable. For example, it may simply be too expensive, time consuming and difficult to discover whether a potential agent has the 'right' dynamics. However, we cannot judge whether this will be the case until we know whether successful control agents do indeed share a suite of characteristics lacking in unsuccessful species. In passing, note that we are not concerned here with the timing and type of damage inflicted by successful control agents; these may determine levels of host depression (Harris 1981*b*; Schroeder 1983), but not the stability of the interaction. It is no good devastating a weed one year if it flares up again in subsequent years.

Questions About the Population Dynamics of Successful Control Agents

A better understanding of the mechanisms preventing unstable oscillations in biological weed control programmes might emerge from the following.

How are patterns of herbivore attack and host mortality spatially distributed in successful, and equally important, in unsuccessful control programmes? Clumped distributions of herbivore attack are known to occur in some successful cases of control (Caughley and Lawton 1981; Zwölfer and Harris 1984), although patterns may vary with climate and other variables (Zwölfer and Harris 1984). Moreover, the responses of insect herbivores to host plant density and distribution are many, varied and poorly understood (reviews in Kareiva 1983, and Strong *et al.* 1984). Many Lepidoptera, for example, differentially oviposit on isolated rather than clumped hosts. Which patterns of behaviour, if any, are characteristic of good biological control agents?

Unfortunately, measuring spatial patterns of herbivore attack is not straightforward. Patterns may vary with the scale of measurement; i.e. single plants, small groups of plants, patches of a few square metres, etc. (Heads and Lawton 1983). Moreover, insect mortality between the egg and larval stages may mean that patterns of host attack generated by ovipositing adults are not the same as those produced by feeding larvae (e.g. Zwölfer and Harris 1984), adding a further layer of complexity to an already difficult problem.

All this presupposes that spatially density-dependent mortality imposed on the plant population by herbivores is the key to persistent, stable biological control. But alternative theoretical scenarios are possible. For example, spatial refuges, where enemies cannot or do not go, may allow the weed to repeatedly reinvade the rest of its habitat. Outside the refuge, victim and enemy interactions may be unstable (in a formal, population dynamics sense) with frequent local extinctions of both weed and enemy. The woodland refuge for *Hypericum* (Clusiaceae) against *Chrysolina* (Coleoptera: Chrysomelidae) (Huffaker 1964) may be one such example. This particular theoretical scenario, one of repeated local extinctions and reinvasions, appears to be the one favoured by Murdoch *et al.* (1984, 1985) to account for cases of successful biological control of insect pests.

Alternatively, introduced biological control agents may simply depress pest numbers so much that the pest's depleted population becomes susceptible to density-dependent regulation by a second agent, a polyphagous predator (if the pest is an insect) or generalist herbivore, effective at low but not high pest densities (Beddington *et al.* 1978; Hassell 1978; Southwood and Comins 1976; Price 1981). This hypothesis has something of a *deus ex machina* quality about it, but it cannot be ignored simply because it invokes the help of an outside agent to maintain the stability of the interaction. A variant on this hypothesis would be to suggest that steps to improve and restore the habitat by reducing overgrazing (e.g. Goeden and Ricker 1980) are sufficient to prevent the weed from recovering after biological control agents have reduced its population.

Finally, it is possible that one or more of the large number of elements that go to make up a 'typical' plant–herbivore interaction (Crawley 1983) generates stable, density-dependent persistence of the plant and its herbivore control agent at low q-values, but not via the original hypothesis of spatial density dependence. One recent, unexpected discovery in host–parasitoid models is that variable parasitoid sex ratios contribute markedly to the stability of the interaction (Hassell *et al.* 1983). Whether a creative theoretician can discover some equally surprising, stabilising process in the dynamics of insect–plant interactions remains to be seen.

In sum, we do not understand the population dynamics of successful biological weed control. We cannot even hazard a guess as to whether a similar mechanism promotes stability in all successful programmes, or whether each case is unique. Hence, population dynamics theory cannot help us pick better control agents. But as a long-term strategic objective, I believe that this problem deserves more attention.

The Problem of Host Shifts

One of the most frequent worries raised against biological weed control is that it might not be safe; that even after careful and comprehensive screening (CIBC 1978; Schroeder 1983) biological control agents might still eat something else. There are at least two facets to this problem. First, what is the probability of an insect biological control agent making an unexpected host switch? Second, how might ecological theory help us to evaluate starvation screening trials that reveal some ability by proposed control agents to feed on plants other than the target weed?

As Schroeder (1983) points out: 'Biological control of weeds has been practiced for more than 75 years and introductions of control agents have been made against more than 86 weeds in some 20 countries (Julien 1982). In all instances where host range tests ... have been undertaken there have been no adverse or unpredictable results'. Batra (1981) makes much the same point; indeed all biological control workers know that their science has an excellent and enviable safety record, but it may nonetheless help when arguing with legislators and administrators to have a quantitative assessment of risk, to underpin what we all know is true.

The Risk of Unexpected Host Shifts

'Host shift' is a widely used term of convenience. It does not imply that an insect population abandons an old host to take up occupation on a new host species. Rather the new host is simply added to the insect's dietary repetoire. Clearly, the probability of insects shifting hosts is not zero. If it was zero, there would be no host races of one species of insect exploiting different food plants in different geographical regions;

in fact, geographical host races are common (Fox and Morrow 1981; Strong *et al.* 1984; Zwölfer and Harris 1984). Nor would plants accidentally or deliberately introduced into a new region recruit an insect fauna; most introduced plants recruit herbivores surprisingly quickly (Strong *et al.* 1984).

In the present context, we can learn a great deal from insects recruited onto introduced plants. In biological control work, an introduced insect is exposed to a novel flora of native plants and crops, with a small but finite probability that it may unexpectedly shift hosts and attack one or more of these non-target species. Some idea of the magnitude of the risk of this occurring can be gauged from the analogous 'experiment' in which novel (introduced) plants recruit insects from a native fauna. The best data are for insects known to have colonised introduced trees in Britain (Kennedy and Southwood 1984). The pertinent data are: (*a*) the length of time a tree has been present in Britain; (*b*) the number of insect species now feeding on each species of alien tree; and (*c*) the total numbers of herbivorous insects in appropriate taxa in Britain. (When defining the pool of potential colonists, I have made no distinction between herb- and tree-feeders, because many recorded host shifts have been between plants of very different growth forms; e.g. Winter [1974].)

An estimate of the annual probability, or risk, of one species of insect shifting to a novel host, is $b/(a \cdot c)$.

Appropriate data are summarised in Table 1, giving the individual probabilities of host shifts for various insect taxa × tree combinations summarised in Fig. 1, and an overall probability of one insect species shifting onto one new host plant of 3.6×10^{-6}year^{-1}. (A total of 104 documented host shifts, from a pool of 6175 British insects, over 4700 tree-years.)

This is a very small risk, but for biological control agents it is a serious overestimate. Successive corrections to make the risk assessment more realistic are as follows. (i) Most of the insects colonising introduced plants are externally feeding polyphages (Strong *et al.* 1984). Host shifts are rarer, but not unknown amongst oligophages and monophages. Of 103 cases involving colonisation of exotic trees and shrubs in Europe (Strong *et al.* 1984), 10 were by stenophagous insects, normally feeding on native plants in the same genus as the introduced plant; 8 were stenophages from plants in the same family but different genera; 68 were polyphages, attacking plants in more than one family; and 17 were stenophagous insects attacking a narrow range of hosts in a different family to the introduced plant. One may safely assume that screening in biological control programmes would prevent all but the most unexpected shifts, i.e. those in the last category (Schroeder 1983), reducing estimates of apparent risk by a factor of 17/103; i.e. to $0.165 \times (3.6 \times 10^{-6})$ or to 5.9×10^{-7} insect species, plant species^{-1} year^{-1}. (ii) Trees are much larger 'targets' than other plants for colonisation by insects, over both ecological and evolutionary time (Lawton 1983, 1985). In other words, probabilities of host shifts onto trees are enhanced compared with most plants. In general, trees have insect faunas an order of magnitude richer than herbs (Lawton 1983, 1985); if half this difference in faunal richness is simply attributable to their larger size (Lawton 1985) this suggests that general risks of host switching should be half an order of magnitude less than the figure of 5.9×10^{-7}, i.e. risks of host shifting should, in general, be a number of order 1×10^{-7} insect species, plant species^{-1} year^{-1}. (iii) Finally, newly introduced plants are full of vacant niches. Native plants, and well-established crops should in principle be much harder for introduced insects to colonise. A biological control agent may be unable to successfully shift to a non-target host because it is competitively excluded by resident insects. Two mechanisms of exclusion are possible, conventional interspecific competition for limiting resources such as food or oviposition

Table 1. Documented host-shifts by native British insects onto introduced trees, from Kennedy and Southwood (1984). All data in the table are from this study, except as indicated in the footnotes. Although no Agromyzidae, Cecidomyidae, or Thysanoptera have colonised any of the seven species of introduced trees, each of these insect groups has representatives feeding on native trees.

Insect group	Tree Species							Herbivorous insects: total species in British 'pool'
	Acer pseudoplatanus	*Aesculus hippocastanum*	*Castanea sativa*	*Juglans regia*	*Larix decidua*	*Quercus ilex*	*Robinia pseudoacacia*	
Diptera: Agromyzidae	0	0	0	0	0	0	0	313[2]
Diptera: Cecidomyidae	3	0	0	0	1	0	0	622[3]
Hemiptera: Heteroptera	1	0	0	0	3	0	0	283[1]
Homoptera	10	5	1	2	6	1	1	976[1]
Hymenoptera: Symphyta	2	0	0	0	5	0	1	473[3]
Hymenoptera: Cynipoidea	0	0	0	0	0	0	0	118[3]
Lepidoptera	20	2	9	2	16	4	0	2 233[1]
Thysanoptera	0	0	0	0	0	0	0	183[1]
Coleoptera	2	0	1	0	6	0	0	975[1]
Years since tree introduced to Britain	650	400	1 900	600	350	400	400	—

[1] From Price (1980).
[2] From Spencer (1972).
[3] From Kloet and Hincks (1964–1975).

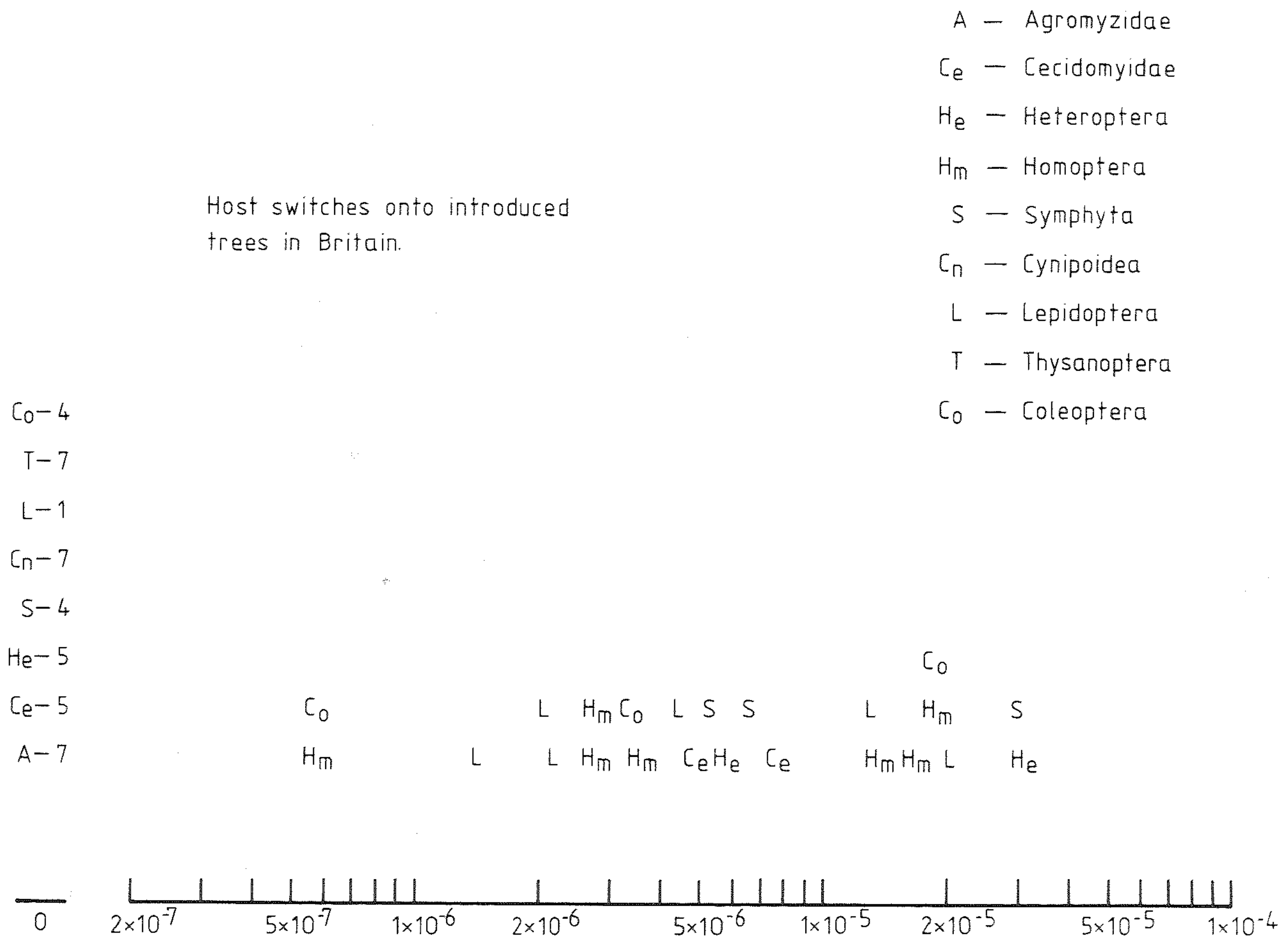

Fig. 1. Probabilities of a host-shift (insect species, plant species^{-1} year^{-1}) calculated from the data in Table 1 (see text for details).

sites, and 'apparent competition' from polyphagous enemies (Holt 1977) or what Jeffries and Lawton (1984) called competition for 'enemy-free space' (see also Price 1981). For insects feeding on plants, competition for enemy-free space seems more likely than conventional competition (Lawton and Strong 1981; Strong *et al.* 1984). The concept of competition for enemy-free space is elaborated in more detail below. Here it is sufficient to note that invasion of native plants by introduced biological control agents may be greatly impaired by the natural enemies of resident insects, just as some biological control agents have failed to establish on target plants because of the ravages of resident enemies that 'spill over' from other prey and plants (Goeden and Louda 1976). It is difficult to estimate by how much risk should be adjusted for the enhanced difficulty of switching to native plants and well-established crops. A conservative guess is that probabilities of attacking such hosts lie in the range 1×10^{-8} to 1×10^{-7} insect species, plant species^{-1} year^{-1}.

Clearly these calculations are very crude, and could be improved, although they start with excellent data (Table 1) for one of the best studied floras and faunas in the world. Difficulties and uncertainties aside, I think they are sufficient to illustrate why well over 100 insect biological control agents (Batra 1981; Julien 1982) have been exposed to 1000s of species of non-target plants for more than 75 years without anything untoward going wrong.

Starvation Trials

Whilst so low a probability of the unexpected happening is comforting, it is not the only, or even perhaps the main concern of many biological control workers. One of the most vexing problems is how to interpret results from screening trials done under highly artificial conditions, suggesting that potential control agents will eat one or more species of non-target plants, at least when they are starving. These problems have recently been cogently addressed by Andres (1981), Dunn (1978), Harris (1985), Schroeder (1983), and Zwölfer and Harris (1984), amongst others, and I do not propose to repeat their arguments here. The following points do, however, seem worth making.

Successful colonisation of a new host plant (i.e. establishment and maintenance of a population on that plant) requires far more than a willingness for starving insects to eat it. Starving people will eat cats, rats and shoe leather, but this information is not useful for predicting what I normally eat for lunch. Stenophagous insects — the type that make good biological control agents — usually have a suite of morphological adaptations and characteristic behaviours all intimately linked to their host plant(s), fulfilling specific adult mating and ovipositional requirements, as well as determining larval success and adult longevity (Bush and Diehl 1982; Diehl and Bush 1984; Futuyma 1983; Futuyma *et al.* 1984). The mechanisms determining host shifts in such insects are still not well understood, but they *do not* simply involve a willingness to feed when starving. A better understanding of these problems will undoubtedly arise from careful studies on the genetics, behaviour and general biology of host races on different species of plants, currently being carried out by several groups, for example Booij (1982), Claridge and Hollander (1983), Futuyma *et al.* (1984), Singer (1983), and Wood and Gutman (1983).

Futuyma *et al.* (1984) suggested that divergence in host utilization occurs first via genetically determined changes in behaviour, rather than by physiological adaptations to the novel host. It remains to be seen whether their results for fall cankerworm generalise to other species. But there is no doubt that although host selection behaviour in the field deserves more study, a species' behaviour in starvation tests bears little resemblance to its behaviour in the field. Intriguingly, although one of the earliest optimal foraging models (Levins and MacArthur 1969) was developed specifically for herbivorous insects, later studies have focussed almost entirely on predators or seed-feeders (see Krebs and Davies 1984). Exceptions are Lacher *et al.* (1982), Rausher (1978, 1981), and Schultz (1983). Foraging theory developed for predators does not extend easily to herbivores, but virtually all existing data and models, be they for herbivores or carnivores, point to strong evolutionary constraints on foraging behaviour. As a result, animals in the field are invariably choosey about where they feed and what they feed upon, avoiding unprofitable or risky feeding sites (Krebs and Davies 1984). Starvation trials, by putting animals at maximum risk, make it profitable for them to try to eat almost anything rather than die. Not surprisingly, they eat things when starving that they would *never* eat in the field. Sensible feeding trials must therefore incorporate sufficient realism for the animal to exercise choice, preferably both about where to eat (or oviposit) and which plant(s) to select. Dunn's (1978) proposals are admirable in this regard. By totally ignoring existing foraging theory and data, starvation trials give quite the wrong impression of risk, and impose highly artificial and unnecessary constraints on biological weed control.

Using Exotic Insects to Control Native Weeds: The Case of Bracken Fern

Biological control has been attempted much more frequently against imported weeds than it has against native weeds. Julien (1982) for example documents biological control programmes against 86 naturalised weeds compared with 25 native weeds. In part, such data merely reflect the fact that many important weeds are aliens. Nevertheless, the use of exotic insects to control native weeds has been virtually ignored, an important exception being the control of *Opuntia* (Cactaceae) on Santa Cruz Island, California, by *Dactylopius* (Homoptera: Dactylopiidae) (Goeden and Ricker 1980). I propose to devote the remainder of this paper to a native weed that is a prime candidate for biological control, namely bracken fern (*P. aquilinum*) in Britain, outlining how detailed ecological studies have pinpointed at least one, and possibly more, potential exotic control agents.

The Nature of the Problem

Dense, more or less pure stands of bracken now cover thousands of hectares of hill land in Britain, land that is used primarily for hill farming, forestry, water catchment areas and recreation. The plant is a major weed for the following reasons: (a) It has spread dramatically during the present century, and continues to do so at between 2 and 4% a year. Reasons for the spread are discussed by Page (1976). Spread of bracken leads directly to loss of grazing, makes shepherding very difficult, and provides a reservoir for sheep ticks. (b) Bracken is a very toxic plant (Jones 1983) and although normally avoided by stock, they occasionally eat sufficient to cause poisoning and death. (c) One of the toxins in bracken is a carcinogen, detectable in milk from cows grazing on hill land, and a potential hazard in human water supplies from bracken-infested catchment areas (Taylor 1980; Hoeven *et al.* 1983). (d) In some areas, e.g. the North Yorkshire Moors, bracken is a serious problem on grouse moors, where grouse shooting for sport is a valuable source of income to landowners (Dr. G.R. Potts, Game Conservancy, pers. comm.). (e) In recreation areas, bracken impedes access by the public, and adversely affects natural vegetation and the appearance of beauty spots.

Bracken control by spraying or repeated cutting (e.g. MAFF 1974; McKelvie and Scragg 1972/3) is expensive, difficult, and usually impermanent. In Scotland, *c.* 2 000 ha are treated each year (a mere 1% of infested land) at a total cost of £200 k. Despite control, bracken in Scotland is estimated to be spreading at 7 000 ha per annum. In 1982 the North Yorkshire Moors National Park (one small part of Northern England) estimated that £35 k was spent on bracken control from the Public Sector, and £40 k from the Private Sector. This control at best is effective for only 3–4 years (Dr. R. Brown, North York Moors National Park staff, pers. comm.). The Yorkshire and Scottish figures suggest that total costs of bracken control in Britain must easily exceed £500 k per annum, not including figures for lost grazing, stock poisoning, etc. Although by the standards of some weed control programmes (Harris 1985; Schroeder 1983) these are not large sums of money, it has to be remembered that most bracken-infested land in Britain goes untreated because existing control methods are too expensive or impossible to use because of the terrain. Under these circumstances, biological control may provide an ideal solution.

The Native Insect Fauna of Bracken

Detailed studies on the ecology of British bracken-feeding insects have been carried out by colleagues and myself at York since 1971. Some 27 species of native insects feed on bracken in Britain, with others doing so occasionally (Lawton 1976, 1982). None significantly damages the plant, not because the plant is toxic to them, but because they are in the main kept rare by their own natural enemies, parasitoids, predators and diseases. Experimentally released from the impact of enemies, some British native insects build up to large numbers and extensively damage the plant (Lawton 1984*a*, *b*). Imported insects similarly released from natural enemy control might reasonably be expected to cause extensive damage to bracken.

Where Might Suitable Biological Control Agents be Found?

The same species of bracken grows naturally on every continent except Antarctica. The herbivore fauna found on the plant is very different in each geographical region (Lawton 1982, 1984*b*); hence there should be no shortage of possible biological control agents feeding on bracken outside the British Isles. Of course, bracken is not identical in all parts of the globe. The taxonomy of the plant is complex (Page 1976), with two major subspecies each with several varieties. In the first instance, suitable control agents should be sought in areas with the same subspecies as Britain (*P. aquilinum*, subspecies *aquilinum*); i.e. in North America, Africa, or Asia and the Far East. This is not to say that insects associated with subspecies *caudatum* (found primarily in South America and Australasia) would not make suitable control agents for subspecies *aquilinum*, but matching subspecies may increase the changes of success (see Harris 1985 for a brief discussion of the problem of host varieties).

The Characteristics of an Ideal Control Agent

An ideal control agent for bracken in Britain must: (a) come from a temperate, seasonal climate; (b) be bracken specific and capable of imposing significant damage to the plant; (c) feed in a way that is different from any native British species; and (d) be taxonomically distinct from native British species.

Requirements *c* and *d* specify that the ideal control agent ought to occupy a currently vacant niche (Lawton 1982). This requirement is not to prevent exclusion of exotic control agents by conventional interspecific competition, which appears to be negligible amongst British bracken-feeding insects (Lawton 1982, 1984*a*, *b*), but to prevent exclusion via 'apparent competition' (Holt 1977) or competition for 'enemy free space' (Jeffries and Lawton 1984) from the natural enemies of resident British bracken-feeding insects.

The conditions for a new species, j, to invade and establish itself in a community where it is subject to attack by resident natural enemies have been formally stated by Holt (1977). They are:

$$r_j > a_j P. \tag{2}$$

where: r_j = intrinsic rate of increase of the invading species j; in this case j is the species to be released as a biological control agent; a_j = attack rate (or area of discovery [Hassell 1978]) of an established enemy population on species j; and P = density of established polyphagous enemies, sustained by resident herbivore species, but capable of attacking the biocontrol agent, j.

Characteristics of species j that reduce a_j, for example their taxonomy or feeding site, will favour j's establishment in the community. Clearly, the more species j differs from victim populations already in the community the less likely enemies are to recognise it as food or hosts, and the more likely species j is to establish and spread.

One species is currently thought to fit all these criteria, a moth *Parthenodes angularis* Hampson (Lepidoptera: Pyralidae) from the Katburg Mountains and elsewhere in South Africa (identity confirmed by Mr. M. Shaffer, British Museum). One or more caterpillars mine the rachis (stem) and by cutting the vascular bundles greatly stunt the growth of the frond. Preliminary field work carried out by Professor V. C. Moran and myself in South Africa suggests that *Parthenodes* is bracken specific; we found it in no other ferns, nor has it ever been reported as a pest of any plants anywhere in South Africa. Yet damage to bracken was often extensive and heavy. No native British insects cause damage to bracken as does *Parthenodes*, and none of the British bracken-feeding Lepidoptera are Pyralidae. Finally, and most conveniently, bracken in the Katburg Mountains is the same subspecies and variety (subspecies *aquilinum* var. *aquilinum*) as British bracken, and the climate is very similar to that in Britain.

Two other possible control agents also live on bracken in the same area, but much less is known about them. They are again very different from native British bracken-feeding insects. They are *Eupteryx maigudoi* Dworakowska (Homoptera: Typhlocybini), apparently bracken-specific, and an unidentified eriophyid mite that causes extensive damage and distortion of the fronds. Bracken is such a persistent, vigorous plant that it will almost certainly be necessary to release more than one species of control agent against it (Harris 1981*b*, 1985).

What Next?

At the moment, permission to import *Parthenodes* into Britain under quarantine has been made in collaboration with CIBC; grant support for the work has been approved by the Agricultural and Food Research Council, and screening will commence early in 1985. We also need to find out more about the other possible control agents, and to search other likely localities. On climatic grounds, Chile looks a suitable area, although bracken there is subspecies *caudatum*. Only when *Parthenodes* has been screened, and other possible control agents located and studied will we be in a position to contemplate releases in Britain. Since biological control of weeds has never been attempted in this country, the decision whether or not to release will have to be taken after the widest possible discussions with all interested parties. Harris (1985) has some exemplary comments to make on these problems, but for the moment, they lie outside the scope of this paper.

Finally, it should not have escaped the reader's notice that *Parthenodes* could make an ideal control agent for bracken elsewhere in temperate regions where native bracken is spreading and causing serious problems; mainland Europe and New Zealand are two such areas.

General Lessons

I do not believe that bracken is the only native weed that is suitable for biological control using exotic insects. The general criteria are: (i) A weed that is native in at least two different parts of the world, or with at least close relatives in other parts of the world from which suitable control agents might be collected. (ii) A distinct insect fauna in different geographical regions, to provide a pool of potential control agents. This condition seems to be typical of most plants (Strong *et al.* 1984). (iii) Good ecological studies on the resident insect community attacking the plant in areas where it is a weed to discover (a) why resident insects are ineffective as control agents and (b) vacant niches suitable for exploitation by control agents.

Of course there is no guarantee that suitable control agents fulfilling all these criteria will exist, particularly insects that are capable of inflicting damaging control on the weed, and are safe. But there is no guarantee, either, that we can continue to develop new and better herbicides for weed control as resistance (Gressel 1984) and economic constraints pose increasing problems. I believe the time is now ripe to pay more attention to the possibilities of biological control of native weeds.

Acknowledgments

I have benefited from, and greatly enjoyed discussions on the ecology of biological control with John Beddington, Mick Crawley, David Greathead, Peter Harris, Mike Hassell, Cliff Moran, Dieter Schroeder and Jeff Waage. The misconceptions are my own.

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