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Biological Control of Bracken in Britain: Constraints and Opportunities [and Discussion]

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Biological control of bracken in Britain: constraints and opportunities

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Bracken (*Pteridium aquilinum*) is native to this country, but has become a major weed of marginal and hill land throughout western and northern Britain. Estimates suggest that the plant now occupies 3000–6700 km^2 and is spreading at 1–3% per annum. It is a serious weed for several reasons. It causes direct loss of grazing land, is poisonous to stock, and makes shepherding very difficult. It also acts as a reservoir for sheep ticks, causing problems for farmers and managers of grouse moors (ticks transmit louping ill to grouse chicks). The plant is carcinogenic, and has been implicated in higher than average incidences of cancers in people living in bracken-infested areas. Finally, invasion by the plant leads to a loss of plant and animal communities that conservationists regard as more desirable than dense stands of bracken, for example heather moorland. Total costs to agriculture caused by bracken invasion are unknown, but probably run into several million pounds a year. The plant can be controlled by herbicides, or by cutting and rolling, but these methods are often too expensive or too labour intensive for use in many upland areas. One solution may therefore be biological control, although this has rarely been attempted against native plants anywhere in the world. This paper explains why biological control of bracken by using exotic insects from the Southern Hemisphere has a reasonable chance of success. Several potential control agents have now been found on bracken growing in temperate parts of South Africa. They include two moths: *Conservula cinisigna*, a folivorous noctuid, and one or more species of *Panotima*, pyralids that first mine the pinnae, and then bore into the rachis. Both appear to be bracken-specific. Their biologies, and those of other possible control agents are described, and constraints and problems encountered in trying to rear them under quarantine conditions are outlined. Over and above the biological and technical problems that have been encountered, and now largely overcome, are a host of political, legal, environmental and socio-economic problems that must be confronted before biological control of bracken in Britain can be attempted. The ecological and economic consequences of controlling bracken biologically need to be carefully weighed against the effects of its continuing spread, and against alternative solutions, for example, harvesting for biomass or control via markedly increased use of herbicides in upland areas.

Introduction

Biological control has been attempted much more frequently against aliens than it has against native plants. Julien (1982), for example, documents biological control programmes against 86 naturalized weeds and 25 native species. In part, such data merely reflect the fact that many important weeds are aliens, but they are also indicative of a widely held view that native weeds are unsuitable candidates for biological control. Yet biological control of native plants can work; witness the success of *Dactylopius* released against *Opuntia* on Santa Cruz Island, California (Goeden & Ricker 1980).

This paper discusses the prospects for biological control of a British native plant, bracken fern (*Pteridium aquilinum*), by using exotic insects imported from the Southern Hemisphere. There is no tradition of biological control of either native or introduced weeds in Britain. An attempt to control the native thistle *Cirsium arvense* by using the exotic chrysomelid beetle *Haltica carduorum* failed (Baker *et al.* 1972), and did little to encourage further research on biological control of any British weeds. Yet there are good reasons for believing that well-researched programmes against specific weeds may have a reasonable chance of success, bringing with them large economic and potential environmental benefits. Bracken is a good example.

The account that follows amplifies and modifies information on constraints and opportunities that exist for the biological control of bracken in Britain, already published in Lawton (1986*a*, *b*) and Heads & Lawton (1986). The status of bracken in Britain, and reasons for regarding it as an important weed are reviewed, followed by an evaluation of biological control as a possible solution. The first thing we need to know is why native British bracken-feeding insects fail to control the plant. Consideration of this problem leads logically to the ideal characteristics of potential, exotic control agents, and then to a search for suitable species on bracken in the Southern Hemisphere, particularly South Africa. The biologies of several possible control agents are described, including two moths, *Conservula cinisigna* and *Panotima* sp., that look particularly promising. Finally, over and above the biological constraints and opportunities that exist for bracken control in Britain, there are legal, political, environmental and socio-economic factors to take into account before biological control can be attempted. These constraints are dealt with at the end of this paper.

Bracken as a weed

Bracken is an invasive weed of marginal land, particularly hill farms in northern and western Britain. The plant's biology, ecology and status as a major weed are reviewed in Smith & Taylor (1986). According to Taylor (1986) bracken now covers approximately 6720 km^2 of the U.K., approximately equivalent in area to the county of Devon. Other estimates (see, for example, Lawson *et al.* 1986) put the area of infested land at about half this. What is clear is that in Britain as a whole, the plant is spreading vegetatively at about 1.3% per year, with rates as high 3% or more in some areas. Taylor (1986) estimates that between 1985 and 2000, at least another 1500 km^2 of land will be lost to bracken invasion. Put another way, for every two hectares of farming land lost each year to urban development and forestry, somewhere between half and one hectare are lost to bracken invasion. Some of the reasons for bracken encroachment are discussed by Page (1976), who summarizes the history of the plant in Britain from the Pleistocene. Originally a woodland plant, its spread can be traced to the clearance of forests by Neolithic man. More recently, a series of factors have contributed to its continuing expansion (Taylor 1986). For example, sheep rather than cattle are now the most important livestock on upland farms, but this was not always the case. Bracken is sensitive to trampling by cattle, both as dormant rhizomes (MAFF 1983) and in spring when the croziers first emerge. Sheep, with their smaller feet and lighter bodies, do much less damage. Moreover, many farmers no longer have the manpower or the money available to cut and roll bracken regularly in the spring when it is most susceptible to mechanical damage (MAFF 1983; Lowday 1986). Uncontrolled, or poorly controlled, moorland fires also encourage its spread (Brown 1986), as does improved drainage of hill land; bracken grows poorly in waterlogged soil.

Problems caused by bracken

Bracken is a problem for several reasons:

1. It is poisonous to domestic animals (see, for example, MAFF 1983; W. C. Evans 1986; Hannam 1986). Consumption of as little as 1 kg dry mass of bracken per day for a period of 2–4 weeks causes acute, fatal bracken poisoning in cattle; the symptoms include severe and extensive haemorrhages, ulceration of the intestinal mucosa, and leukaemia-like failure of the white blood cells. A similar condition has been described in sheep on the North York Moors, but in general sheep are more resistant than cattle to acute bracken poisoning. Instead, they tend to succumb to 'bright blindness', a progressive degeneration of the retina, and may also develop tumours, particularly in the jaw, but also in the rumen and elsewhere. In horses, eating bracken causes acute thiamine deficiency accompanied by loss of coordination and paralysis, so-called 'bracken staggers'. Invasion by the plant therefore represents not only a direct loss of grazing, but also a serious threat to livestock.

2. Dense bracken makes shepherding very difficult, because it hides both sheep and dogs, and impairs access.

3. The plant acts as a reservoir for sheep ticks (*Ixodes ricinus*) (see, for example, Hudson 1986) and hence acts as a focus of infection for two viral diseases of sheep, louping ill and tickborne fever (Hannam 1986; Johnson 1986).

4. As well as causing problems for farmers, bracken is also a serious weed on grouse moors. Red grouse (*Lagopus lagopus scoticus*) depend upon heather (*Calluna vulgaris*) as their major food, so that invasion by bracken leads directly to loss of grazing for an important upland animal. Worse, the nymphs of sheep ticks also feed on grouse chicks, to which they transmit louping ill virus disease; louping ill is implicated in the long-term decline of grouse in North Yorkshire and probably elsewhere in Britain, and its spread is linked ultimately to that of bracken (Hudson 1986; Dobson & Hudson 1986).

5. As effects on farm animals show, bracken contains one or more carcinogens (I. A. Evans 1984, 1986). There are unsubstantiated suggestions that these compounds may affect humans via milk and water supplies from bracken-infested land (Salazar 1985; Galpin & Smith 1986). Alternatively, higher than average regional incidences of human gastric and other cancers among farming communities in North Wales may be linked to inhaling or ingesting bracken spores; certainly the spores are carcinogenic in mice (I. A. Evans 1986).

6. The continuing spread of bracken poses complex and poorly studied problems for wildlife conservation. Dense stands of bracken have little to commend them in natural history or conservation terms. The plant threatens more valuable plant communities on some nature reserves (see, for example, Marrs 1985; Marrs *et al.* 1986), and on a larger scale is one of the factors contributing to the march of commercial forestry across grouse moors. The replacement of moorland by conifer plantations results in the total disappearance of grouse and other upland animals valued by conservationists (Dobson & Hudson 1986).

7. The impact of bracken on recreational use of upland areas is poorly studied and complicated (R. W. Brown 1986; I. W. Brown & Wathern 1986). In autumn, golden, bracken-covered hillsides may look nice (Heads & Lawton 1986), but walking or running through dense stands is very difficult and unpleasant; orienteers hate it (Borodino 1986)!

Estimates of economic costs

Together, the real and potential problems are more than enough to show that the continuing spread of bracken cannot be ignored. Yet remarkably, national figures for the economic costs directly attributable to the plant are not available. The current national average rate of spread of over 1% per annum is the net rate after attempts at control. Economic costs include not only obvious things such as stock poisoning, lost grazing, and resources invested in existing control technology, but also less obvious 'secondary costs' such as enhanced mortality of lambs from tick-borne diseases, some of the costs of tick control by dipping, and a fall in the value of bracken-infested land. They also include things that are difficult, if not impossible, to price, such as the wildlife and conservation interests of upland areas.

Some idea of the economic costs of bracken can be obtained by reading the accounts in Smith & Taylor (1986). For example, a combination of MAFF and North York Moors National Park grants, and private investment in bracken control in the north of England in 1984 cannot have been less than £110000 (Johnson 1986). Nationally, the costs of control, lost grazing and stock poisoning must run into several million pounds a year. As Taylor (1986) points out, at current prices, the value of hill land that will be lost to bracken invasion between 1985 and 2000 amounts to some £6 million. By any criterion, bracken is an important weed.

Biological control as a possible solution

Biological compared with other means of control

Bracken can be controlled by repeated cutting (MAFF 1983),or with herbicides. Asulam has been used for several years to good effect (McKelvie & Scragg 1972–73; Soper 1986), and several promising new herbicides are currently being tested (see, for example, Oswald *et al.* 1986). The problem is that hill farming and grouse shooting have precarious economies; it is difficult for individual landowners to justify investment in bracken control with average costs estimated at about £40 per ha† (Taylor 1986), and out of the question on many areas of steep and inaccessible hill land where aerial spraying is the only answer, and costs are over £100 per ha (Soper 1986). Nor do cutting and spraying provide permanent solutions. Four to ten years after spraying with Asulam, bracken has often completely regained its former dominance (Horsnail 1986; Lowday 1986; Robinson 1986; Soper 1986), although careful 'aftercare' helps to prevent reinvasion (MAFF 1983).

Against this background, biological control is attractive because it holds out the prospect of a cheap, permanent reduction in the abundance of bracken over large areas of hill land where more conventional techniques are uneconomic or impossible to apply.

Where might suitable exotic insect control agents be found?

Paradoxically, our capacity to adapt the techniques of classical biological weed control and use them against a native plant rests upon bracken's phenomenol success. The plant's potential Achilles heel is its world-wide distribution; it grows naturally on every continent except Antarctica (Page 1976), and may well be one of the five most abundant plants on earth (Harper 1977). In common with all other widely distributed plants (Strong *et al.* 1984), very

† 1 hectare = 10^4 m^2.

different species of insects exploit bracken in different parts of its range (see, for example, Kirk 1982; Lawton 1982, 1984*a*, unpublished observations). This large pool of exotic insects can be regarded as a 'toolkit', from which, with time and patience, we might reasonably hope to select one or more appropriate biological control agents for use in Britain.

Why do native, bracken-feeding insects fail to control the plant?

There is little point in searching for exotic insect control agents for bracken if they prove to be as ineffective as the plant's native British herbivores. Why do the 27 species of insects that regularly exploit the above-ground parts of the plant in Britain (Lawton 1982) cause it so little damage? Long-term studies (see, for example, Lawton 1982, 1984*a*, *b*, 1986*a*; Lawton & MacGarvin 1985; Lawton *et al.* 1986, 1987; MacGarvin *et al.* 1986) show that most of these herbivores are rare relative to the biomass of plant material available to them. Only very occasionally do native herbivores become common enough to cause heavy defoliation of bracken (Lawton 1976; M. F. Claridge, personal communication). However, it is possible to generate outbreaks of bracken herbivores by experimentally uncoupling them from their own enemies, broadly defined to include predators, parasitoids and diseases. Preliminary accounts of experiments on two species (the delphacid bug *Ditropis pteridis* and the sawfly *Aneugmenus padi*) are in Lawton (1984*b*), Lawton *et al.* (1986) and Lawton & MacGarvin (1985). The most dramatic results were obtained with a population of *Aneugmenus padi* established on an isolated, enemy-free experimental patch of bracken grown in plant pots on the University of York campus. Here, caterpillars of this species reached population densities ten times those of all the sawflies (seven species, including *A. padi*) at our long-term study site at Skipwith Common, near York, and bracken in the experimental patches was completely defoliated for two consecutive years. Because the bracken in the experiment was originally transplanted from Skipwith, the outbreak of *Aneugmenus* is unlikely to have been due to differences in the plants, something that we confirmed by taking half the bracken back to Skipwith with its sawflies. The population collapsed completely, whereas *Aneugmenus* on the campus continued to flourish.

Although we cannot do similar experiments with all 27 native species, a reasonable working hypothesis is that most native, bracken-feeding insects are kept rare, relative to the abundance of the host plant, by their own natural enemies. Hence, relieved of such control, exotic insects could cause extensive, permanent and ultimately debilitating damage. There is nothing particularly novel about this suggestion. A prime requisite for successful classical biological control of any insect pest or weed is to uncouple the control agent from limitation by its own predators, parasitoids and diseases (Huffaker 1974;Schroeder 1983; Goeden 1983). Hence, exotic insects released in Britain against bracken do not have to cause heavy damage to the plant in their own country; at home, they too presumably have specific enemies. What is vital is that agents are established in Britain, free from constraints imposed by higher trophic levels. Only then can we hope to damage the plant sufficiently to bring it under control.

The search for possible control agents

General principles

Potential insect biological control agents for use against bracken in Britain should ideally have the following characteristics.

1. They must come from a cool-temperate, seasonal climate, similar to the British Isles.

2. There are two major subspecies of bracken in the world, *aquilinum* and *caudatum*; British bracken is subspecies *aquilinum* variety *aquilinum* (Page 1976). Morphological and biochemical differences between the two subspecies could, though not inevitably, make it more difficult to establish insects from *caudatum* on *aquilinum* (see, for example, Harris 1984; Hokkanen & Pimentel 1984). In the first instance it would therefore seem wise to search for insects that normally exploit subspecies *aquilinum*.

3. The insects must be taxonomically and ecologically distinct from any of the British native bracken-feeding species. That is, they should exploit a 'vacant niche' (Lawton 1982, 1984*a*), because the more similar potential control agents are to species already resident on the plant in Britain, the more likely they are to suffer attacks from native parasitoids, predators and diseases (Goeden & Louda 1976; Jeffries & Lawton 1984; Lawton 1986*b*, *c*; Lawton & Brown 1986; Briese 1986), and the less likely they are to establish and control the plant.

4. The insects must be specific to bracken.

5. Finally, a search for control agents should not be confined to the above-ground parts of the plant. Little work has been done on rhizome-feeding insects on bracken in Britain (see Lawton 1982), but this should not rule out the possibility of looking for exotic rhizome feeders that also conform to characteristics 1–4. The large underground rhizome is one of the reasons why the plant is so difficult to control; a serious assault below ground could prove to be very effective.

Climatic mismatch almost certainly rules out the use of bracken feeding insects from Papua New Guinea, where the plant has a rich and varied herbivore fauna (Kirk 1982). Nothing ecologically or taxonomically distinct enough has yet been found in North America (Lawton 1982, unpublished data), and the most likely source of potential control agents therefore becomes the temperate Southern Hemisphere. South America and Australasia have the 'wrong' subspecies of bracken (*caudatum*), which leaves southern Africa. It is here that we have concentrated our search. Bracken in South Africa is not only the same subspecies, but it is also the same variety (*Pteridium aquilinum* subsp. *aquilinum* var. *aquilinum*) as British bracken (Page 1976) and grows in a similar climate, particularly in the mountains of Cape Province.

The fauna of bracken in South Africa

The geographic range of bracken in South Africa is a broad band, from the coast inland until it becomes too dry (roughly coincident with areas that have more than 500 mm annual rainfall); that is, from the Cape, through Cape Province, and then via Ciskei and Transkei into Natal and the Transvaal, more or less parallel to the South Atlantic and Indian Ocean coasts, but extending rather further inland in the wetter Transvaal. With the exception of the Transvaal, which we have not yet searched because it is climatically very different from Britain, the rest of this area has now been reasonably thoroughly surveyed for bracken-feeding insects, commencing with preliminary work in 1983, and then detailed annual surveys in the Southern Hemisphere summers of 1984/85, 1985/86, and 1986/87 (Lawton *et al.* 1988). We have sampled bracken throughout the spring and summer in as many different habitats as possible, including various types of woodland, open sites on fynbos ('heathland'), roadside verges, burned areas, etc. At each site, the above-ground parts of a minimum of 20 fronds have been searched carefully for insects and signs of damage. In addition, in 1985–86, we collected rhizomes from four sites in the eastern Cape, and others from the southern Cape (digging up rhizomes is very hard work and time consuming, restricting the number of sites that could be

TABLE 1. SPECIES OF PHYTOPHAGOUS INSECT (AND ONE SPECIES OF PHYTOPHAGOUS MITE) FEEDING ON BRACKEN IN SOUTH AFRICA (V. K. RASHBROOK, S. G. COMPTON & J. H. LAWTON, UNPUBLISHED OBSERVATIONS OVER FOUR FIELD SEASONS)

(The stages found are indicated by +, either eggs laid on the plant, or feeding larvae and nymphs, or feeding adults.)

species	life history stage found: eggs	larvae/ nymphs	adults	number of sites	distribution of sites
Thysanoptera					
Mycterothrips sp.	–	+	+	12	Cape Province Natal
Hemiptera					
Cicadellidae *Eupteryx maigudoi*	–	+	+	33	Cape Province Natal
Cicadellid sp. 1	–	+	+	1	Natal
Cicadellid sp. 2	–	+	+	3	Natal
Psyllidae					
Psyllid sp. 1	–	+	–	7	Natal
Pseudococcidae					
Mealybug sp./spp.	–	+	+	†	Cape Province
Aphididae					
Miscellaneous aphids	–	+	+	‡	Cape Province Natal
Homopteran sp. 1	–	+	+	2	Cape Province
Pentatomidae					
Erachtheus spinosus	+	+	+	8	Natal
Anthocoridae					
Orius sp.	–	+	+	17 §	Cape Province Natal
Coleoptera					
Curculionidae					
Holcolaccus sp.	–	–	+	1	Natal
Lepidoptera					
Pyralidae					
Panotima sp./spp.	+	+	–	45	Cape Province Natal
Noctuidae					
Conservula cinisigna	+	+	–	53	Cape Province Natal
Conservula minor	+	+	–	7	Cape Province Natal
Hadeninae sp. 1	–	+	–	2	Cape Province
Arctiidae					
Dionychopus amasis	–	+	–	3	Cape Province
Diacrisia eugraphica	–	+	–	1	Cape Province
Geometridae					
Nopia saxaria	–	+	–	1	Cape Province
Epigynopterix maeviaria	–	+	–	3	Cape Province
Acari					
Eriophyidae sp. 1	+	+	+	46	Cape Province Natal

All the taxa dealt with in the following notes have been omitted from the list of 13 species, found more than once, definitely feeding on the above-ground parts of the plant in South Africa (see text).

† Mealybugs occur regularly on potted bracken in cultivation, and we have occasionally found single mealybugs on wild bracken, although it is unclear whether the same species is involved, or whether the 'wild' specimens are feeding and established on the plant.

‡ At least three species of aphids have been found, but we have no evidence that any species forms permanent colonies on the plant.

§ Although *Orius* sp. are common on bracken in some localities, this genus is not normally regarded as phytophagous. The relationship of this species with bracken remains to be determined.

examined). As expected after more than 3 years of field work, we are now finding new species at a very slow rate, and feel reasonably confident that we know all the important herbivores (table 1).

Thirteen species have been found more than once, feeding on the above-ground parts of the plant. (There are 12 insects and 1 mite; in the analyses that follow, the phytophagous mite has been included with the insects). No rhizome-feeders were discovered in the limited below-ground samples. There may be more than one species in the genus *Panotima* (see below); if so, this will raise the number of definite species of herbivores accordingly. At least seven other species (or more correctly, taxa) probably or possibly feed on the plant in South Africa.

Widespread plants are fed on by more species of phytophagous insects than are rare plants. Examples of these species–area relations are now many, both for different species of plants within any one region, and for the same species of plant in different regions (Strong *et al.* 1984). Bracken is no exception, with richer insect faunas in parts of the world where it is more common and widespread (Lawton 1982, 1984*a*). Figure 1 shows the geographic species–area relation

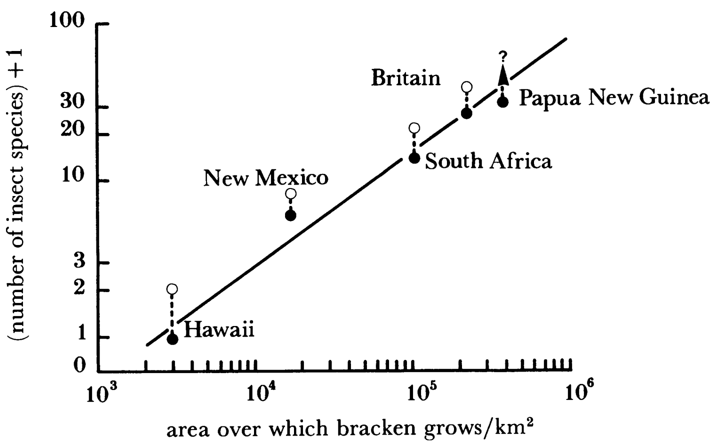

FIGURE 1. Species–area relation for the number of insect species definitely (●) feeding on bracken in different parts of the world, from previously published data in Lawton (1984*a*), with the addition of new information from South Africa (see text for a description of the areas surveyed in South Africa, and table 1 for a list of insects found). Also shown (○) are numbers of species including doubtful or very infrequent associates of bracken. Species + 1 has been used on the ordinate to allow the inclusion of a zero count in Hawaii. Bracken in South Africa has been recorded from 156 grid squares (average area 660 km^2) (W. B. G. Jacobsen, personal communication to V. K. Rashbrook, plus additional records from V. K. Rashbrook and S. G. Compton), giving a total area within which bracken grows of *ca.* 103000 km^2. Similar methods were used to calculate the areas within which bracken grows elsewhere in the world. The area for South Africa is certainly an underestimate, because records of the plant's distribution are incomplete. However, the insect list may also be incomplete, because the Transvaal has not been surveyed in detail for insects, and *Panotima* may contain more than one species (see text). Hence the close relation between area and number of species apparent in earlier plots (Lawton 1984*a*), and now reinforced by the South African data may be weakened by further work. It is extremely unlikely, however, that further work in South Africa, either on the distribution of bracken, or on its insect herbivores, will alter the relation enough to make it no longer statistically significant. The fitted regression line on the definite records is:

$$\log_{10}(\text{species}+1) = 0.696 \log_{10}\text{area} - 2.33, \quad r = 0.987;\ f = 112.1;\ 0.005 > p > 0.001.$$

for bracken and its herbivores, incorporating the new South African data. It suggests that our surveys are now reasonably complete and that further searches are unlikely to be a good investment in time or money (see Lawton & Schroeder 1978).

Among the species that have been discovered in South Africa, two stand out as potential biological control agents for bracken in Britain: *Conservula cinisigna* and *Panotima* sp. (spp.?). Some of the other species may also be suitable, particularly the unidentified mite. I now consider what is known about each.

Studies on potential control agents

Conservula cinisigna

Adult *Conservula cinisigna* are typical, brown noctuids with a wing span of about 2.5 cm. Identification of our material was made by the Commonwealth Institute of Entomology Identification Service, and by V. M. Swain at the National Collection of Insects, South Africa. Taxonomic details are in Lawton *et al.* (1988).

Eggs are laid singly or in groups, tucked and glued tightly into crevices on the tips of new bracken fronds; they are further protected by a light covering of small hairs, presumably from the female's abdomen. The newly hatched caterpillars are green; later instars are dramatically polymorphic in colour, either vivid green, olive brown, or almost black, with white, longitudinal stripes. The significance of this larval polymorphism is unknown. Final instars are large (up to 4 cm long), with voracious appetites. All instars are typical, free-living, chewing folivores, exploiting the pinnae ('leaves') of bracken. Eggs are laid very early in the spring on newly emerging fronds, and caterpillars become abundant soon after. However, there appears to be at least a partial second generation later in the year; some eggs and caterpillars can be found throughout the growing season, and fresh adults emerged in the laboratory only 19–36 ($n = 15$) days after larvae from the spring generation had pupated. The mechanisms controlling voltinism are not yet known. *Conservula* is abundant and widespread on bracken throughout South Africa (table 1), and tolerates a wide range of climates, including high-altitude sites with frost and snow in winter.

Although there are several free-living Lepidoptera among the 27 'core species' feeding on bracken in Britain, and several others that do so very occasionally (see, for example, Lawton 1982), and although several of these species are noctuids, there are reasons for believing that *Conservula cinisigna* may make a good biological control agent. First, its main feeding period is much earlier in the year than any native British species, with the exception of the much smaller geometrid *Petrophora chlorosata*. It could therefore occupy a 'temporally vacant niche', and hence avoid enemies, particularly parasitoids, known to attack such species as *Ceramica pisi*, *Laconobia oleracea*, *Euplexia lucipara* and *Phlogophora meticulosa*, all noctuids found on British bracken later in the season. A spring-feeding control agent also attacks the plant when it is most vulnerable to damage (see above). Secondly, and much more important, unlike these British noctuids, all of which are polyphagous on a wide range of plants, *Conservula* appears to be virtually monophagous on bracken in the laboratory and totally so in the field (table 2). The only fern other than bracken on which newly hatched *Conservula* larvae grew and developed in the laboratory was *Pellaea viridis*, but we have never found *Conservula* eggs or caterpillars on this, or any other ferns in the field in South Africa (table 2). A reasonable conclusion from these field surveys is that adult female moths will not oviposit on anything other than their normal host plant, bracken.

The final reason for thinking that *Conservula* may sufficiently damage the plant to make a good biological control agent in Britain is the heavy frond damage sometimes observed in South Africa. Large populations of caterpillars are not uncommon despite attacks by

TABLE 2. LABORATORY AND FIELD OBSERVATIONS ON USE OF SOUTH AFRICAN FERNS BY *PANOTIMA* AND *CONSERVULA*

(Fern species after Jacobsen (1983). No eggs, larvae or feeding damage of either *Panotima* or *Conservula* were found on any ferns examined in the field, except bracken.)

	laboratory trials†							
	Panotima			*Conservula cinisigna*				
fern species and families	no. of larvae tested	feeding damage	no. of larvae surviving beyond first instar	no. of larvae tested	feeding damage	no. of larvae surviving beyond first instar	no. of fronds examined in field for both species	notes
Schizaeaceae								
Mohria caffrorum	22	trace	0	30	trace	0	75	—
Gleicheniaceae								
Gleichenia polypodioides	—	—	—	—	—	—	31	—
Cyatheaceae								
Alsophila dregei	—	—	—	—	—	—	10	—
Dennstaeditiaceae								
Pteridium aquilinum	45	heavy	41	62	heavy	58	not applicable	—
Hypolepis sparsisora	30	1–5 %	0	30	trace	0	40	—
Adiantaceae								
Adiantum poirettii	27	trace	0	25	0	0	0	British genus
Pteris dentata	30	trace	0	30	trace	0	5	—
Cheilanthes hirta	—	—	—	20	trace	0	3	—
Pellaea calomelanos	—	—	—	—	—	—	8	—
P. viridis = *Cheilanthes viridis*	23	1–5 %	0	35	extensive	7	238	—
P. quadripinnata = *C. quadripinnata*	—	—	—	—	—	—	30	—
Davalliaceae								
Nephrolepis cordifolia	27	1–5 %	0	30	trace	0	0	—
Aspleniaceae								
Asplenium aethiopicum	24	trace	0	30	0	0	0	British genus
Thelypteridaceae								
Amauropelta bergiana = *Thelypteris bergiana*	24	1–5 %	0	30	1–5 %	0	10	British genus
Athyriaceae								
Cystopteris fragilis	—	—	—	25	1–5 %	0	0	British species
Aspidiaceae								
Dryopteris inaequalis	20	trace	0	30	trace	0	76	British genus
Polystichum lucidum	26	trace	0	30	1–5 %	0	37	British genus
Rumohra adiantiformis	24	trace	0	30	0	0	378	—
Blechnaceae								
Blechnum punctulatum	—	—	—	—	—	—	67	British genus
B. australe	—	—	—	—	—	—		British genus

† Laboratory feeding trials were done by dissecting eggs from bracken and placing them on test fronds, including bracken. Only healthy eggs that hatched are included in the analyses. Dissected eggs were placed singly on excised, fresh pinnae, maintained on damp filter paper in a petri dish. Experiments were inspected at least once a day, and fresh pinnae provided as required. 'Trace' signifies that the newly hatched larvae attempted to feed; '1–5 %' is the area consumed, given *ca.* 3 cm^2 of frond material; 'extensive' is less feeding damage than 'heavy'.

parasitoids (table 3), and what is from our point of a view a very unwelcome enemy in the form of an unidentified, but quite devastating infectious disease (Heads & Lawton 1986). We have repeatedly lost laboratory stocks of *Conservula* to this disease, and in consequence, with only one main generation a year to work with, have not been able to import enough material into quarantine in Britain to establish experimental cultures. Accordingly, it has not yet been possible to repeat the encouraging screening results in table 2 by using British ferns. However, many of the species tested in South Africa are in the same genus as, or in genera very close to, British ferns. The host-specificity tests in table 2 are therefore very encouraging.

TABLE 3. PARASITOIDS REARED FROM *CONSERVULA CINISIGNA* AND *PANOTIMA* IN SOUTH AFRICA (DATA OF S. G. COMPTON, PERSONAL COMMUNICATION)

stage attacked	parasitoid life history	parasitoid taxonomy	status
Conservula			
eggs	solitary	Trichogrammatidae, genus indeterminable	rare
larvae	solitary	Ichneumonidae, ?*Ophion* sp.	rare
larvae	gregarious	Eulophidae, *Euplectrus* sp.	common
larvae	solitary	Braconidae, genus indet.	widespread
larvae	solitary	Braconidae, genus indet.	uncommon
larvae	solitary	Ichneumonidae, genus indet.	rare
Panotima			
eggs	solitary	Trichogrammatidae, genus indet.	locally common
small lv.	solitary	Eulophidae, genus indet.	uncommon
larvae	solitary	Ichneumonidae, genus indet.	rare
larvae	solitary	Braconidae, genus indet.	uncommon
larvae	gregarious	Braconidae, genus indet.	locally common

Panotima sp./spp.?

Panotima is referred to as *Parthenodes angularis*, or a species very close to it, in earlier publications (Lawton 1986*a*, *b*; Heads & Lawton 1986). Unfortunately, the taxonomic situation is now confused. L. Vári (personal communication) has informed us that a photograph of an adult reared during our work 'is a perfect match' with a series of *Parthenodes angularis* in the Transvaal museum (actual specimens have not yet been compared). However, the genus is poorly known taxonomically, and the Commonwealth Institute of Entomology recently transferred our material to *Panotima* and suggested that more than one species may be involved. Difficulties in rearing adults in the laboratory mean that material for taxonomic work is very limited, and the specific identity of the moth and the number of species feeding on bracken in South Africa have yet to be resolved. Because of these difficulties we have kept separate material from bracken in different localities, and ensured that all our experiments have been conducted on animals of known origin. If more than one species is involved, we have so far found nothing to indicate that their biology differs sufficiently to influence their use as biological control agents. The discussion that follows therefore treats all our material as one species. However, these taxonomic problems will have to be resolved before there can be any question of employing *Panotima* as a biological control agent in Britain.

Adult *Panotima* are golden-brown moths, with silver marks on the fore-wings and a wing-span of about 2 cm. No pyralids feed on bracken in Britain, and its life history is totally different from anything found on the plant in this country. Eggs are laid early in the season, singly on the underside of expanding fronds, and the newly hatched caterpillars tunnel and feed in surface mines protected by folds at the edge of the pinnae, with a mixture of silk and frass spun over the back of the frond. They spend the first two or three instars there, often causing very heavy damage to the undersides of the pinnae before migrating to the rachis ('stem') of the plant, into which they tunnel to complete their development. The rachis is usually mined between ground level and the first pair of pinnae. Each larva occupies a single mine, but there can be several mines per stem (the maximum we have found is nine; some typical figures are in table 4). Frass is expelled through an exit hole, and the larvae eventually leave the mine to pupate. Mines cut through vascular bundles in the rachis, and if several larvae occupy one frond, damage is severe; growth of the plant is restricted, and all but the basal pair of pinnae usually die.

Table 4. Representative samples of *Panotima* mines in bracken fronds from sites in southeastern Cape Province, South Africa

(Hogsback and Katberg are mountain sites. Samples taken in the autumn and winter (March–July) represent cumulative attacks on fronds over the previous Southern Hemisphere spring and summer.)

locality	date	fronds examined	no. of *Panotima* mines: occupied	unoccupied	mines per frond
Featherstone Kloof, Grahamstown	25.III.83	20	0	28	1.40
	26.III.83	15	0	25	1.67
	17.XII.84–4.II.85	80	5	—	0.06†
Mountain Drive, Grahamstown	1.IV–9.VII.85	67	0	4	0.06
Hogsback	28.XII.84	20	11	7	0.90
	30.III.85	126	2	13	0.12
Katberg	11.XII.84–3.II.85	180	23	11	0.19
	31.III–5.IV.85	344	356	53	1.19

Distribution of attacks in representative samples (unpublished data of J. H. Lawton, S. G. Compton & V. K. Rashbrook)

		mines per frond: 0	1	2	3	4	5	6	7
Featherstone Kloof, Grahamstown	25.III.83	11	2	0	3	3	1	0	0
Grahamstown	26.III.83	8	1	2	0	1	2	1	0
Katberg	31.III.85	6	11	11	2	1	0	0	1
Katberg	11.XII.84–3.II.85	153	22	3	2	0	0	0	0
Hogsback	28.XII.84	9	5	5	1	0	0	0	0

† Unoccupied mines not counted.

Because *Panotima* is so different biologically and taxonomically, it is unlikely to be heavily attacked by any specific natural enemies of British bracken-feeding insects. The only vaguely similar species is a gelechiid, *Paltodora cytisella*, whose larvae attack bracken early in the spring by mining into the costa ('main stems' of the pinnae) and rachis, where they often induce gall-like swellings. *Panotima* larvae enter the rachis later in the season, feed much lower down, and do not induce swollen galls. There are also at least two species of rachis-mining fly larvae in Britain (Lawton 1982; McGavin & Brown 1986), but these are unlikely to share enemies with *Panotima*.

Panotima is widespread in South Africa (table 1), and common over a wide range of climatic conditions. (If more than one species is involved, it may be that each does best under different climatic regimes, something that will require further investigation.) The main generation is in spring, but in the laboratory a small number of adults emerged 14–19 days ($n = 3$) after larvae from the spring generation had pupated, and in the field small numbers of larvae occur in stem-mines in late summer (e.g. table 4), suggesting that there is a small, second generation. The control of voltinism is not understood.

Panotima seems a very promising control agent. It attacks the plant most heavily in spring and early summer when damage has the greatest impact, but unlike *Conservula*, it causes two kinds of damage (first it defoliates, then it attacks the rachis). It also appears to be bracken-specific. We have been unable to rear it on anything else in the laboratory (table 2) and have never found either eggs, larvae, or its highly characteristic feeding damage to fronds or stems, on any other ferns in the field (table 2). Populations occasionally reach high levels (e.g. table 4), despite some parasitoids that attack it in its own environment (table 3). Without such enemies in Britain, the effects of *Panotima* could be dramatic.

Panotima's peculiar life-history has made it very difficult to rear in the laboratory. Small larvae are easy to culture on cut pinnae, but the rachis-mining larger instars are very difficult to keep. Cut sections of rachis do not stay fresh long enough for caterpillars to complete development; they either dry out, or go mouldy when in water, and because the rachis is hard and tough, it is extremely difficult to remove larvae for transfer to fresh material without damaging them. A few pupae reared on cut stems were small and often mishapen. Most failed to emerge. Caterpillars can be reared on pot-grown bracken, but this needs much space, and they tend to kill the plants! With only one main generation a year, progress in the laboratory has been slow and we have not been able to rear sufficient material either to solve the taxonomic problems or to establish cultures in quarantine in Britain. However, we now appear to have solved the rearing problems by the simple device of making artificial bracken 'stems' from tightly rolling and clipping sections of pinnae to make crude, green 'cigars'. The larger instars readily burrow into these, and the rolls stay fresh much longer than stems. Moreover, when they eventually dry up or go mouldy, they are easily undone, and the larvae rehoused in fresh rolls. This technique has now produced nearly 100 large, healthy-looking pupae, and when applied on a larger scale, should make possible the establishment of good, quarantine stocks of *Panotima* in Britain.

Eriophyid mites

Bracken at many sites in South Africa (table 1) is attacked by a gall-forming mite (Acari, Prostigmata; Eriophyidae). The pinnae, costae and rachis of galled plants are badly swollen and distorted, and photosynthetic tissue is greatly reduced on heavily attacked plants. The species is undescribed (S. Neser, personal communication), but it appears to be bracken specific; nothing resembling its highly distinctive and conspicuous galls has been found on other ferns in South Africa (e.g. table 2, and during many more casual inspections of ferns throughout the southern and eastern Cape). Most eriophyids are extremely host-specific (S. Neser, personal communication), so failure to find it on other ferns is not surprising. We know little else about the biology of this herbivore, nor have we done laboratory specificity tests. However, we know that some bracken patches in South Africa are heavily attacked (e.g. 39 from 67 fronds in a sample near Grahamstown in 1985) and severely damaged, whereas others are apparently mite-free. Dispersal may be a problem, and this, combined with the potential difficulties of working with animals as small as eriophyids, may make them less than ideal as a biological control agent. However, the damage caused may well compensate for these disadvantages.

An eriophyid gall-mite has been reported on bracken in Britain (*Phytopus pteridis*) (Lawton 1976), but I have not seen it during more than 15 years of field work on the plant. (C. Rigby reported few galls that she identified as this species on the North York Moors (Rigby & Lawton 1981). I did not see the specimens then, nor since. Perhaps Rigby's specimens were abnormal *Dasineura* galls.) Descriptions of the damage caused by *Phytoptus* vary (see Lawton 1976), but none resemble the large swollen galls formed by the South African species. On present evidence, therefore, the latter would appear to be another possible biological control agent for use in Britain.

Other South African species

With one exception, either too little is known about the other taxa in table 1 to evaluate them as possible biological control agents or they are ecologically too similar to species already on the plant in this country. The exception is the homopteran *Eupteryx maigudoi*. This feeds only on bracken in South Africa (J. G. Theron, personal communication) and in the Katbergs may cause heavy damage, giving the fronds a silvery appearance presumably by removing most of the cell-contents from the epidermis. Moreover, some Homoptera are important vectors of plant disease, so *Eupteryx* may possibly be exploited in this way. (The control of bracken by diseases has been explored by Burge *et al.* (1986), so far without success.) Against these positive characteristics of *Eupteryx* must be set the presence of native British species in the genus, including *E. filicum* on several ferns, but not bracken (Ottosson & Anderson 1983). That introduced *E. maigudoi* might recruit parasitoids or other enemies from native congeners could greatly reduce its efficiency.

Potential control agents from South Africa: a review

Biological and technical problems have constrained the work in South Africa. Failure to find a rhizome-feeder is disappointing, although few sites have been searched below ground. Above ground, bracken in South Africa has yielded some potentially promising control agents, but disease and other rearing difficulties have made detailed studies frustratingly slow, as has the predominantly univoltine life cycle of the two most interesting species (*Panotima* and *Conservula*). These difficulties now seem to have been overcome, and should make it possible to establish quarantine populations of both species in Britain. We now need to repeat the encouraging host-specificity trials (table 2) with British ferns, although it seems very doubtful that the results will differ substantially or significantly from those obtained with closely related South African ferns. On biological grounds, therefore, the opportunities for controlling bracken in Britain by using one or more exotic insects from South Africa look hopeful.

Possible biological control agents from elsewhere in the Southern Hemisphere

A search for possible biological control agents on subspecies *caudatum* has been made on my behalf by J. A. Thomson and colleagues in southeastern Australia. The insect fauna is rather disappointing, and, despite herculean efforts, no rhizome feeders have been found. However, they discovered a new species of moth in Tasmania, the larvae of which mine the pinnules of mature fronds, destroying the entire mesophyll and palisade layers. Several caterpillars occupy one frond, and damage is severe. There is nothing similar on bracken in Britain, making this new microlepidopteran another potentially useful control agent. It is not known whether it will feed on subspecies *aquilinum*.

The likelihood of successful control

Looking ahead, and assuming that one or more safe (i.e. bracken-specific) species will soon be available for use in Britain, what are the chances of successful control? The history of biological control is littered with the corpses of very promising agents that failed to live up to expectations. Worse, we often have no idea why some agents fail and others succeed (Schroeder 1983). A potential cause of failure on bracken could be climatic mismatch (see Hokkanen (1986) for a recent review). Cape Province is at the same latitude south as North Africa or southern Spain, and although winters in the mountains bring snow and frost, summers are sunnier and drier than in Britain. Unfortunately, detailed climatic records are not available for Hogsback or Katberg, the two main mountain study sites near Grahamstown (e.g. table 4), but even if they were imperfectly matched with British sites, little further could be done. Africa stops at Cape Aghulas. So we have to make do with the available study areas (Schroeder 1983).

It is equally difficult to predict the impact of resident natural enemies on introduced control agents. Natural enemies have been implicated in the failure of classical weed control programmes (Goeden & Louda 1976), and as pointed out on p. 340, they might be a particular threat to exotic insects introduced to control a native plant. However, the proposed agents are all ecologically and taxonomically distinct from the resident herbivores of the British bracken community. Probably the only way to see if they are distinct enough is to introduce them.

These considerations aside, bracken is such a vigorous plant that it seems unduly optimistic to expect control by a single species of insect. Several agents are often needed in biological weed control (Hokkanen 1986, and references therein). Harris (1986) discusses the idea of a critical damage threshold, arguing that plants must sustain a certain amount of damage before they can be brought under biological control. More than one agent may be neccesary to do this. Whether *Conservula*, *Panotima* and other agents would together impose sufficient stress on bracken to slow down, halt, or even reverse its rate of spread, is impossible to say with certainty. But the signs are hopeful. *Panotima* alone scores well on Goeden's (1983) system for evaluating potential control agents (Lawton 1986*a*), and would appear to have a good chance of contributing to effective control. Both *Conservula* and *Panotima* cause greatest damage in spring and early summer when bracken is at its most vulnerable, another very desirable property for control (Schroeder 1983; Harris 1986). Finally, experience of previous biological control successes suggests that species that 'destroy the vascular support tissue' and that 'damage the plant in several different ways' may, though not always, make the best control agents (Hokkanen 1986, and references therein). Both criteria apply to *Panotima*.

The broader implications of biological control of bracken

In many ways, the constraints and problems encountered during the search for bracken biological control agents are insignificant compared with legal, political, environmental and socio-economic questions that confront us (Heads & Lawton 1986). The opportunity to control bracken biologically looks technically feasible; but do we actually want to do it, and who should decide? The great advantage of biological control is that it could provide a permanent, cheap solution to the bracken problem. But the permanence worries many people, as does the uncontrolled nature of the experiment; a successful agent will spread widely and can potentially reduce or eliminate bracken wherever it occurs. Not everybody will regard this as self evidently good, however appealing it may seem to hill farmers. Conflicts of interest are a feature of biological control programmes anywhere in the world (Schroeder 1983), but may be particularly strong when the target is a native plant.

The legal position and the problem of consultation

Under the Wildlife and Countryside Act 1981, permission to release alien insects into Britain for biological control purposes rests ultimately with the Secretary of State for the Environment, but how is information for and against such a release to be obtained? There are no precedents for the release of exotic biological control agents against a native weed in Britain. For example, there is no obligation under the Act for consultation with the Nature Conservancy Council (Stubbs 1987), although its opinions are obviously important. So are the opinions of other individuals and organizations, from the Ministry of Agriculture, Fisheries and Food, and voluntary conservation bodies, to land owners and other individuals. The Central Directorate for Environmental Protection (CDEP) in the Department of the Environment ultimately has responsibility for coordinating information for and against a release (Stubbs 1987), but how CDEP might get its information is unclear.

One potential legal problem centres on commoners rights of 'estovers', the right to cut bracken for winter bedding (Hughes & Aitchison 1986). Although the practice is not now so prevalent, reflecting the decline in cattle on upland farms, it is still regarded as a valuable right on many Welsh commons (Hughes & Aitchison 1986), and doubtless elsewhere. Would commoners have any redress against a very successful biological control programme that deprived them of their crop? Indeed, would any individual landowner who did not wish their bracken controlled have any legal redress?

Other problems

It is easier to pose other problems and questions that need to be resolved than to answer them. The main problems and questions seem to be as follows.

1. What scale of economic benefits might be expected to follow successful biological control of bracken? These are not difficult to work out for individual farms and estates, assuming various levels of control and no change in the *status quo* of other components, for example, patterns of taxation and government subsidies for hill farms. Likely effects on the economic infrastructure of upland areas, subsidies, taxes, land values and so on are much more difficult to take into account.

2. What effects will successful biological control have on ecological communities? One way to examine this problem is to assume that success will do no more than restore the open, more

bracken-free uplands, forests and heaths of a hundred or so years ago. Yet bracken is not without some benefits, because it provides an important habitat for some British native animals. But it can be argued that its spread excludes many more plants and animals of greater conservation importance. My view, based on evidence that no biological control agent has ever eliminated its host plant and that extermination of bracken in Britain is inconceivable, is that biological control poses much less of a threat to native flora and fauna than the continuing spread of bracken, or massive aerial spraying of herbicide, or blanket afforestation of uplands. None of these alternatives looks very attractive for conservation, but a proper assessment has not been done. What is needed is an 'environmental balance sheet' setting out the ecological pros and cons of biological control of bracken. It would also help to know NCC's Policy and Position Guidelines on introductions into Britain; these have never been made public, but are known to be extremely conservative (Stubbs 1987). The Nature Conservatory Council do, however, maintain an open mind about the use of exotic insects to control the spread of bracken in Britain (Key 1987).

3. Will biological control be safe? Above all, we must be sure that any introduced biological control agent feeds exclusively on bracken. Existing data for several of the potential control agents are very encouraging, but more host-plant specificity tests are needed. If control agents pass these standard tests (e.g. CIBC 1978; Schroeder 1983), there are no grounds for believing that they pose a threat to any other native plants. Whenever the standard protocol has been followed, biological weed control has an excellent and enviable safety record; there have been no adverse or unpredictable effects from introductions made against more than 86 species of weeds, in some twenty countries over the past 75 years (Julien 1982; Batra 1982; Schroeder 1983; Kelleher & Hulme 1984; Lawton 1986*b*).

4. Can anything useful be done with bracken-infested land that does not involve biological control, herbicide control, or commercial afforestation? The answer is a guarded 'yes'. One interesting suggestion is that bracken could be cut for biomass, dried or treated in some other way, and burned as a renewable energy source (Lawson *et al.* 1986, and references therein). On a local scale, the idea looks economically feasible. The problem is that harvesting bracken for biomass on many steep, rocky or remote hillsides is impossible. Here bracken will continue to spread and cause problems. Again, there are no clear answers to questions of alternative land-use strategies, national priorities, and economics.

5. What are the other real or perceived problems? This is not a frivolous question. Release of a biological control agent is essentially irreversible, and therefore to be taken very seriously. How do we consult people in general, and how are their views to be heard? Should we even bother if the experts' considered opinion of is that, on balance, biological control is a good idea? The solution for analogous problems of regional or national concern is a public enquiry. Perhaps, in the end, something similar will be needed before attempting the biological control of bracken in this country. These are deep and uncomfortable waters for a biologist!

Concluding remarks

Constraints on the biological control of bracken in Britain are many and varied, the most difficult being human, not biological. It may seem odd that legal, political, environmental and socio-economic problems were not resolved before spending time and money looking for suitable control agents. But in the absence of promising agents, it made no sense to spend even more time and money exploring a thorny and multi-disciplinary problem embracing everything from the legal rights of estovers, to the economics of hill farming, and the ecology of upland Britain. The problem now is to try and develop both the biological control work and the complementary, but essentially much larger and more complex studies side by side, until either an insurmountable technical difficulty rules out biological control; or it is deemed too risky and the idea has to be abandoned, or permission to go ahead is finally granted. The bracken problem will not be resolved on its own. Continuing with present policies, or lack of them, has a price in economic, social and environmental terms. So does a massive increase in the use of herbicides to halt or reverse the relentless spread of the plant, and so do alternative land use strategies. The prospects for biological control deserve a fair hearing within this much larger context.

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References

Baker, C. R. B., Blackman, R. L. & Claridge, M. F. 1972 Studies on *Haltica carduorum* Geurin (Colepotera: Chrysomelidae) an alien beetle released in Britain as a contribution to the biological control of creeping thistle, *Cirsium arvense* (L.) Scop. *J. appl. Ecol.* **9**, 819–830.

Batra, S. W. T. 1982 Biological control in agroecosystems. *Science, Wash.* **215**, 134–139.

Borodino 1986 *Pteridium aquilinum* – the orienteer's scourge. *Compass sport: the orienteer* **7** (7), October/November, p. 14.

Briese, D. T. 1986 Factors affecting the establishment and survival of *Anaitis efformata* (Lepidoptera: Geometridae) introduced into Australia for biological control of St. John's wort, *Hypericum perforatum*. II. Field trials. *J. appl. Ecol.* **23**, 821–839.

Brown, I. W. & Wathern, P. 1986 Bracken control and land management in the Moel Famau Country Park, Clwyd, North Wales. In *Bracken, Ecology, land use and control technology* (ed. R. T. Smith & J. A. Taylor), pp. 369–377. Carnforth: Parthenon Publishing.

Brown, R. W. 1986 Bracken in the North York Moors: its ecological and amenity implications in national parks. In *Bracken, Ecology, land use and control technology* (ed. R. T. Smith & J. A. Taylor), pp. 77–86. Carnforth: Parthenon Publishing.

Burge, M. N., Irvine, J. A. & McElwee, M. 1986 The potential for biological control of bracken with the causal agents of curl-tip disease. In *Bracken, Ecology, land use and control technology* (ed. R. T. Smith & J. A. Taylor), pp. 453–458. Carnforth: Parthenon Publishing.

CIBC 1978 *Screening organisms for biological control.* Farnham Royal: Commonwealth Agricultural Bureaux.

Dobson, A. P. & Hudson, P. J. 1986 Parasites, disease and the structure of ecological communities. *Trends Ecol. Evol.* **1**, 11–14.

Evans, I. A. 1984 Bracken carcenogenicity. In *Chemical carcinogens* (ed. C. E.Searle), pp. 1171–1204. (American Chemical Society Monograph 182.) Washington, D.C.: American Chemical Society.

Evans, I. A. 1986 The carcinogenic, mutagenic and teratogenic toxicity of bracken. In *Bracken, Ecology, land use and control technology* (ed. R. T. Smith & J. A. Taylor), pp. 139–146. Carnforth: Parthenon Publishing.

Evans, W. C. 1986 The acute diseases caused by bracken in animals. In *Bracken, Ecology, land use and control technology* (ed. R. T. Smith & J. A. Taylor), pp. 121–132. Carnforth: Parthenon Publishing.

Galpin, O. P. & Smith, R. M. M. 1986 Bracken, stomach cancer and water supplies: is there a link? In *Bracken, Ecology, land use and control technology* (ed. R. T. Smith & J. A. Taylor), pp. 147–159. Carnforth: Parthenon Publishing.

Goeden, R. D. 1983 Critique and revision of Harris' scoring system for selection of insect agents in biological control of weeds. *Protection Ecol.* **5**, 287–301.

Goeden, R. D. & Louda, S. M. 1976 Biotic interference with insects imported for weed control. *A. Rev. Ent.* **21**, 325–342.

Goeden, R. D. & Ricker, D. W. 1980 Santa Cruz island – revisited. Sequential photography records the causation, rates of progress, and lasting benefits of successful biological weed control. In *Proceedings of the Vth International Symposium on the Biological Control of Weeds, July 1980, Brisbane, Australia* (ed. E. S. Delfosse), pp. 355–365. Melbourne: CSIRO.

Hannam, D. A. R. 1986 Bracken poisoning in farm animals with special reference to the North York Moors. In *Bracken, Ecology, land use and control technology* (ed. R. T. Smith & J. A. Taylor), pp. 133–138. Carnforth: Parthenon Publishing.

Harper, J. L. 1977 *Population biology of plants*. London: Academic Press.

Harris, P. 1984 *Euphorbia escula–virgata* complex, leafy spurge and *E. cyparissias* L., Cypress spurge (Euphorbiaceae). In *Biological control programmes against insects and weeds in Canada 1969–1980* (ed. J. S. Kelleher & M. A. Hulme), pp. 159–169. Farnham Royal: Commonwealth Agricultural Bureaux.

Harris, P. 1986 Biological control of weeds. *Fortsch. Zool.* **32**, 123–138.

Heads, P. & Lawton, J. 1986 Beat back bracken biologically. *New Scient.* **111** (1525), 40–43.

Hokkanen, H. M. T. 1986 , Success in classical biological control. *CRC Crit. Rev. Plant Sci.* **3**, 35–72.

Hokkanen, H. & Pimentel, D. 1984 New approach for selecting biological control agents. *Can. Ent.* **116**, 1109–1121.

Horsnail, G. B. 1986 A comparison of methods of control of bracken regrowth following aerial application of asulam in northern Britain. In *Bracken, Ecology, land use and control technology* (ed. R. T. Smith & J. A. Taylor), pp. 425–430. Carnforth: Parthenon Publishing.

Hudson, P. J. 1986 Bracken and ticks on grouse moors in the north of England. In *Bracken, Ecology, land use and control technology* (ed. R. T. Smith & J. A. Taylor), pp. 161–170. Carnforth: Parthenon Publishing.

Huffaker, C. B. (ed.) 1974 *Biological control*. New York: Plenum/Rosetta.

Hughes, E. J. & Aitchison, J. W. 1986 Bracken and the common lands of Wales. In *Bracken, Ecology, land use and control technology* (ed. R. T. Smith & J. A. Taylor), pp. 93–99. Carnforth: Parthenon Publishing.

Jacobsen, W. B. G. 1983 *The ferns and fern allies of southern Africa*. Durban and Pretoria: Butterworths.

Jeffries, M. J. & Lawton, J. H. 1984 Enemy free space and the structure of ecological communities. *Biol. J. Linn. Soc.* **23**, 269–286.

Johnson, J. 1986 Current policies on the reclamation of bracken land with particular reference to northern England. In *Bracken, Ecology, land use and control technology* (ed. R. T. Smith & J. A. Taylor), pp. 325–330. Carnforth: Parthenon Publishing.

Julien, M. H. (ed.) 1982 *Biological control of weeds. A world catalogue of agents and their target weeds*. Farnham Royal: Commonwealth Agricultural Bureaux.

Kelleher, J. S. & Hulme, M. A. (eds) 1984 *Biological control programmes against insects and weeds in Canada 1969–1980*. Farnham Royal: Commonwealth Agricultural Bureaux.

Key, R. S. 1987 Bracken control – an open mind. *Farmers Weekly* 6 November 1987, pp. 9–10.

Kirk, A. A. 1982 Insects associated with bracken fern *Pteridium aquilinum* (Polypodiaceae) in Papua New Guinea and their possible use in biological control. *Acta Oecol./Oecol. Appl.* **3**, 343–359.

Lawson, G. J., Callaghan, T. V. & Scott, R. 1986 Bracken as an energy resource. In *Bracken, Ecology, land use and control technology* (ed. R. T. Smith & J. A. Taylor), pp. 239–247. Carnforth: Parthenon Publishing.

Lawton, J. H. 1976 The structure of the arthropod community on bracken. *Bot. J. Linn. Soc.* **73**, 187–216.

Lawton, J. H. 1982 Vacant niches and unsaturated communities: a comparison of bracken herbivores at sites on two continents. *J. Anim. Ecol.* **51**, 573–595.

Lawton, J. H. 1984*a* Non-competitive populations, non-convergent communities, and vacant niches: the herbivores of bracken. In *Ecological communities: conceptual issues and the evidence.* (ed. D. R. Strong, Jr, D. Simberloff, L. G. Abele & A. B. Thistle), pp. 67–101. Princeton University Press.

Lawton, J. H. 1984*b* Herbivore community organisation: general models and specific tests with phytophagous insects. In *A new ecology: novel approaches to interactive systems* (ed. P. W. Price, C. N. Slobodchikoff & W. S. Gaud), pp. 329–352. New York: Thomas Wiley.

Lawton, J. H. 1986*a* Biological control of bracken: plans and possibilities. In *Bracken, Ecology, land use and control technology* (ed. R. T. Smith & J. A. Taylor), pp. 445–452. Carnforth: Parthenon Publishing.

Lawton, J. H. 1986*b* Ecological theory and choice of biological control agents. In *Proceedings of the VIth International Symposium on the Biological Control of Weeds, August 1984, Vancouver, Canada* (ed. E. S. Delfosse), pp. 13–26. Ottawa: Agriculture Canada.

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Lawton, J. H. 1986*c* The effect of parasitoids on phytophagous insect communities. In *Insect parasitoids* (ed. J. Wagge & D. Greathead), pp. 265–287. London: Academic Press.
Lawton, J. H. & Brown, K. C. 1986 The population and community ecology of invading insects. *Phil. Trans. R. Soc. Lond.* B **314**, 607–617.
Lawton, J. H. & MacGarvin, M. 1985 Interactions between bracken and its insect herbivores. *Proc. R. Soc. Edinb.* B **86**, 125–131.
Lawton, J. H., MacGarvin, M. & Heads, P. A. 1986 The ecology of bracken-feeding insects: background for a biological control programme. In *Bracken, Ecology, land use and control technology* (ed. R. T. Smith & J. A. Taylor), pp. 285–292. Carnforth: Parthenon Publishing.
Lawton, J. H., MacGarvin, M. & Heads, P. A. 1987 The effects of altitude on the abundance and species richness of insect herbivores on bracken. *J. Anim. Ecol.* **56**, 147–160.
Lawton, J. H., Rashbrook, V. K. & Compton, S. G. 1988 Biocontrol of British bracken: the potential of two moths from Southern Africa. *Ann appl. Biol.* (In the press.)
Lawton, J. H. & Schroeder, D. 1978 Some observations on the structure of phytophagous insect communities: the implications for biological control. In *Proceedings of the IVth International Symposium on the Biological Control of Weeds, August 1976, Gainesville, Florida* (ed. T. E. Freeman), pp. 57–73. Gainesville: University of Florida.
Lowday, J. E. 1986 A comparison of the effects of cutting with those of the herbicide asulam on the control of bracken. In *Bracken, Ecology, land use and control technology* (ed. R. T. Smith & J. A. Taylor), pp. 359–367. Carnforth: Parthenon Publishing.
MacGarvin, M., Lawton, J. H. & Heads, P. A. 1986 The herbivorous insect communities of open and woodland bracken: observations, experiments and habitat manipulations. *Oikos* **47**, 135–148.
MAFF 1983 *Bracken and its control*. Northumberland: Ministry of Agriculture, Fisheries and Food (Publications). (Leaflet 190.)
Marrs, R. H. 1985 The effects of potential bracken and scrub control herbicides on lowland *Calluna* and grass heath communities in East Anglia, UK. *Biol. Cons.* **32**, 13–32.
Marrs, R. H., Hicks, M. J. & Fuller, R. M. 1986 Losses of lowland heath through succession at four sites in Breckland, East Anglia, England. *Biol. Cons.* **36**, 19–38.
MacGavin, G. C. & Brown, V. K. 1986 Variation in populations of mine- and gall-forming Diptera and the growth form of their host plant, bracken (*Pteridium aquilinum* (L.) Khun). *J. nat. Hist.* **20**, 799–816.
McKelvie, A. D. & Scragg, E. B. 1972–3 The control of bracken by Asulam. *Scott. Agric.* **51**, 474–480.
Oswald, A. K., Richardson, W. G. & West, T. M. 1986 The potential control of bracken by sulphonyl-urea herbicides. In *Bracken, Ecology, land use and control technology* (ed. R. T. Smith & J. A. Taylor), pp. 431–439. Carnforth: Parthenon Publishing.
Ottosson, J. G. & Anderson, J. M. 1983 Number, seasonality and feeding habits of insects attacking ferns in Britain: an ecological consideration. *J. Anim. Ecol.* **52**, 385–406.
Page, C. N. 1976 The taxonomy and phytogeography of bracken – a review. *Bot. J. Linn. Soc.* **73**, 1–34.
Rigby, C. & Lawton, J. H. 1981 Species–area relationships of arthropods on host plants: herbivores on bracken. *J. Biogeog.* **8**, 125–133.
Robinson, R. C. 1986 Practical herbicide use for bracken control. In *Bracken, Ecology, land use and control technology* (ed. R. T. Smith & J. A. Taylor), pp. 331–339. Carnforth: Parthenon Publishing.
Salazar, J. V. 1985 Carcinogenicidad del *Pteridium aquilinum* y alta incidencia del cancer gastrico en Costa Rica. *Rev. Cost. Cienc. Méd.* **6**, 131–139.
Schroeder, D. 1983 Biological control of weeds. In *Recent advances in weed research* (ed. W. W. Fletcher), pp. 41–78. Farnham Royal: Commonwealth Agricultural Bureaux.
Smith, R. T. & Taylor, J. A. (eds) 1986 *Bracken, Ecology, land use and control technology*. Carnforth: Parthenon Publishing.
Soper, D. 1986 Lessons from fifteen years of bracken control with asulam. In *Bracken, Ecology, land use and control technology* (ed. R. T. Smith & J. A. Taylor), pp. 351–357. Carnforth: Parthenon Publishing.
Strong, D. R., Lawton, J. H. & Southwood, T. R. E. 1984 *Insects on plants: community patterns and mechanisms*. Oxford: Blackwell Scientific.
Stubbs, D. 1988 *A report on introductions and reintroductions of living organisms into the wild in Great Britain*. Wildlife Link (In the press.)
Taylor, J. A. 1986 The bracken problem: alocal hazard and global issue. In *Bracken, Ecology, land use and control technology* (ed. R. T. Smith & J. A. Taylor), pp. 21–42. Carnforth: Parthenon Publishing.

Discussion

M. J. Way (*Imperial College at Silwood Park, Ascot, U.K.*). In the face of the problems you mention could you indicate the way ahead? How will you deal with the potential environmental issues without evidence from some form of experiment in an ecologically isolated site?

J. H. Lawton. If and when we get to the point of wanting to release one or more agents, the safest and wisest course of action would be to do the introductions on one of the many small, bracken-infested, isolated offshore islands that lie along the west coast of Britain. Several offers from owners or tenants, of such islands have already been received to use their islands as release sites. There is great interest in the project and I do not think finding suitable sites will be difficult.

J. S. Noyes (*Department of Entomology*, *British Museum* (*Natural History*), *U.K.*). In light of the fact that Professor Lawton is introducing an exotic phytophage to control a native plant pest does he not think it is possible or even likely that a native parasite or parasites will switch from native insects on bracken to the introduced phytophage and stop it before it can effectively control the bracken?

J. H. Lawton. As I have explained in the paper, the insects we have chosen as the most suitable potential control agents have been chosen to avoid this possibility as far as possible; i.e. they are ecologically and taxonomically as different as possible to native, bracken-feeding insects. But we cannot rule out attack from native enemies as a possible cause of failure.