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Comparing the population dynamics of broom, *Cytisus scoparius*, as a native plant in the United Kingdom and France and as an invasive alien weed in Australia and New Zealand

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Abstract. Broom, *Cytisus scoparius*, is a leguminous shrub native to western Europe that is a serious invasive weed of pastures, forests and natural habitats in Australia and New Zealand. The International Institute of Biological Control, Imperial College, CSIRO and Landcare Research have set up comparable, large-scale field experiments and surveys on broom in the United Kingdom, France, Australia and New Zealand, representing a new level of collaboration between these organizations. The invasiveness of broom as an alien weed could be due to a number of differences between the environments encountered by the plant in Europe in contrast to Australia and New Zealand. Most of the specialist natural enemies attacking broom in Europe are not present in New Zealand or Australia, but there are many other differences between these regions that could be important, including effects of climate, local habitat types, land management and fundamental differences between the levels of interspecific competition in plant communities. This paper will give an overview of, and present preliminary results from the extensive ecological field experiments and surveys being undertaken across the four countries, which are designed to help disentangle the influence of these various factors on the population dynamics of broom. Understanding why broom performs so differently in native compared with exotic environments is a fascinating ecological puzzle and will improve our chances of achieving successful classical biological control of broom as an alien invasive weed.

Introduction

Broom (*Cytisus scoparius* (L.) Link) is a member of the Fabaceae, native to western and central Europe. Whilst broom may occasionally become invasive in poorer pastures in parts of its native range, it is not a major weed. However, in countries where it has been introduced, such as Australia, Canada, Chile, India, Iran, New Zealand, South Africa and the United States of America, it has overrun large areas of land used for recreation, forestry, pastures, orchards, and invaded natural habitats, displacing indigenous species in the process (Parsons and Cuthbertson 1992). On the South Island of New Zealand, broom covers nearly 1% of the land suitable for agriculture (Syrett 1987) and, in Australia, broom has infested about 200000 ha. In both countries broom is still spreading, hence the interest in its biological control. Broom is also an important weed along the west coast of North America, where it infests more than 250000 ha in California alone (Bossard and Remánjek 1994). There is increasing interest in resuming a biocontrol programme against broom in this region.

The International Institute of Biological Control has operated a biocontrol programme against broom for New Zealand since 1981 (with Manaaki Whenua - Landcare Research) and for Australia since 1991 (with CSIRO and New South Wales Agriculture). These programmes, together with the collaboration of the Leverhulme Unit (Imperial College, United Kingdom) have enabled extensive ecological studies to be initiated to determine what makes broom a problem in exotic habitats. An improved ecological understanding of broom as an alien invasive weed is expected to increase the likelihood of achieving successful biological control. As well as the substantial collaborative efforts against broom, the current studies have the advantage of building on pioneering work on the ecology of broom and its associated insect fauna in the UK during the 1950s and 1960s (Waloff 1968; Waloff and Richards 1977).

Broom and its natural enemies

In the UK, the insects attacking broom are well known: at Silwood Park (near Ascot) these comprise nine lepidoteran, five dipteran, one hymenopteran, seven coleopteran and 13 hemipteran species (Waloff 1968). Furthermore, a large scale insecticide-check experiment, operated at Silwood Park from 1966-1977 (Waloff and Richards 1977), compared the performance of broom plants in one plot treated regularly with insecticide, with a nearby unsprayed plot. The unsprayed bushes had higher numbers of most insect herbivores, did not attain full growth and had higher rates of mortality. Seed production by the unsprayed bushes, over the average 10-year life-span, was reduced by 75% compared with the sprayed broom. This impact on broom could not be attributed to particular species of phytophagous insects, but it was observed that high population levels of the aphid, *Acyrthosiphon pisum*, and two psyllid species (*Arytainilla spartiophila* and *Arytaina genistaei*) occurred in particular years, apparently stressing the plants. In addition, the experiment did not take account of plant pathogens (or their possible interactions with insect herbivores) nor of the impact of natural enemies during the establishment of seedlings. The recent ecological work was therefore designed to provide further information on these issues.

The current biological control programmes have included substantial surveys of the natural enemies of broom in France and Spain (Fig. 1). The insects attacking broom in the UK and mainland Europe are similar, although several species are restricted to southern Europe. The pathogens attacking broom are less well known, but damage attributable to plant pathogens can be widespread and can cause mortality of plants of all ages. In contrast, there are few insects or pathogens attacking broom in New Zealand and Australia (Syrett 1993).

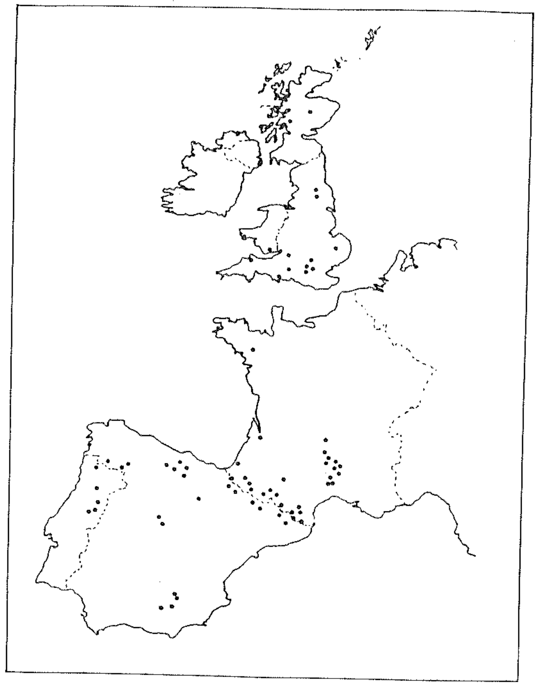

Fig. 1. Sites from which broom insects have been surveyed (closed circles) in Great Britain, France, Spain and Portugal, by the authors, and by Hosking (1990).

What makes broom an exotic weed?

Reduced impact of natural enemies

The low impact of natural enemies on broom in exotic habitats clearly offers one explanation for the status of broom as an invasive weed. The assumption that the specialist natural enemies attacking broom in its native range have a substantial impact on the population dynamics of the plant also underpins the current classical biological control programmes. Of course, natural enemies of broom selected for use as biocontrol agents may have more impact on broom in an exotic habitat because they can be separated from many of their own natural enemies. For example, the twig mining moth, *Leucoptera spartifoliella*, was accidentally introduced into New Zealand at least 45 years ago. In New Zealand, now, the moth is more abundant, and causes more damage to broom, than it normally does in its native range in Europe (Syrett and Harman 1995). High levels of parasitism are thought to prevent *L. spartifoliella* populations reaching such high levels in Europe, and the moth is not attacked by any parasitoid species in New Zealand (Syrett and Harman

1995). In contrast, *L. spartifoliella* was also accidentally introduced into the USA, but accompanied by one of its main natural enemies in Europe, the eulophid, *Tetrastichus evonymellae* Bouché. The presence of this parasitoid probably explains why the moth is reported to have little impact on broom in the USA (Julien 1992).

The hypothesis that the lack of natural enemies results in broom becoming an invasive weed is not the only explanation for the differences in the status of the plant in its native and introduced ranges. We propose some further hypotheses which are not necessarily mutually exclusive.

Abiotic factors

Factors such as the climate or soil types in countries where broom has been introduced could be more favourable for broom than in its native range. So broom might grow more vigorously in these areas regardless of other factors.

Genetic differences in broom

Genetic differences between broom in its native and introduced ranges could arise because of founder effects. For example, the original introductions of broom may have been small in size and, or, selected to be particularly vigorous. There may also have been selection for more vigorous broom in the exotic habitats because of the absence of many natural enemies that may otherwise select for resistance rather than vigour (Blossey and Nötzold 1995).

Reduced interspecific plant competition

Competition between broom and other plant species could explain the weed status of broom as an introduced plant:

a) The native plants typical of natural and semi-natural habitats that broom invades in the USA, Australia and New Zealand may be less competitive than plants typical of such habitats in broom's native range (Frick 1962; Partridge 1992; Memmott *et al.* 1993). Broom may find it easier to establish and dominate these plant communities because of innate features of the native flora, regardless of the influence of natural enemies.

b) The natural and semi-natural habitats that broom invades may have higher levels of natural disturbance. This could favour early mid-successional species such as broom which are strongly associated with disturbance in their native range (Memmott *et al.* 1993). For example, the braided rivers of New Zealand are an inherently highly-disturbed habitat not found in the native range of broom. Broom regenerates rapidly after fire, so this is another potential natural disturbance that could encourage its invasion.

c) In habitats more strongly influenced by human activities such as agricultural grazing or commercial forestry, there may be differences in land management methods, perhaps as a consequence of differences in climate or economic circumstances, that encourage the spread of broom. Even in the native range of broom, land management methods (such as regular burning) are blamed for the relatively minor problems that broom causes in, for example, upland grazing areas in the Massif Central in France (Rousseau and Loiseau 1982). In countries with an impoverished or unusual native mammal fauna, introduced species, such as feral pigs in New Zealand and Australia, can cause additional disturbance that encourages broom to invade.

Recent ecological studies

We give only an overview of the experimental approaches here: detailed methods will be described elsewhere. The basic experimental design comprised pairs of 10x20 m plots, one fenced to exclude vertebrate herbivores, one unfenced. Where possible these were replicated for each country in an area with existing broom stands, in an area with no existing broom (but with a history of broom, so a large seed-bank was present) and in an area with no history of broom. Treatments were randomly allocated to 5x5 m subplots within each plot: (a) one subplot cultivated, then left undisturbed; (b) one subplot cultivated annually; (c) one subplot undisturbed (control); (d) one subplot with simulated grazing (cutting) once per year; and (e) one subplot with the existing mature broom cut at ground level, removed and regrowth killed with spot applications of herbicide.

Within the fenced plots only, the following invertebrate/pathogen exclusion treatments, and treatments manipulating intra- and interspecific plant competition, were added: (f) insecticide application (tau-fluvalinate 3x/year and azinphos-methyl 1x/year); (g) fungicide application (chlorothalonil 3x/year); (h) molluscicide application (metaldehyde pellets 3x/year - and sprayed with water); (i) control - sprayed with water; (j) reduced interspecific competition : herbicide and manual weeding; and (k) reduced intraspecific competition : manual removal of broom seedlings.

Further specific experimental treatments have been added within several of the subplots, for example: (j) quadrats (0.5x0.5 m) were sown with broom seed to test whether the recruitment of broom seedlings is seed limited. Vertebrate seed-feeders were excluded using 1-cm-mesh cages. The controls for this experiment had slightly raised cages to allow access by rodents which we have shown in separate experiments to be major feeders of broom seed on the ground (Paynter *et al.* this Volume).

Sampling methods

In each 5x5 m subplot, broom plants in six 0.5x0.5 m quadrats were recorded. Two quadrats were permanent, allowing individual broom plants to be monitored through time. The remaining four quadrats were randomized on each sampling date to give statistically independent data through time for each subplot. In the permanent quadrats each broom plant had an individual tag and, for each plant, height, girth and growth form were recorded. Any obvious insect herbivores or plant pathogen-damage were also recorded. Only the number of broom plants present was recorded for the random quadrats. On all quadrats, the percentage cover of bare soil, litter, moss, grass, rosette forming plants, and broom was noted on each sampling date. The censusing of the plots was carried out in spring, summer and autumn. The quadrats with extra seed sown were sampled five months after the treatment was applied and then abandoned. The soil seed-bank was sampled by taking soil cores from all the subplots at the start of the experiment, and at intervals of 1-3 years subsequently. Seed-rain on the plots was measured using small pots placed around the permanent quadrats. The fate of broom seed falling onto the soil surface was also investigated after pilot experiments revealed very high levels of destruction by rodents (further details in Paynter *et al.* this Volume).

Results

The experiments outlined above are still producing large and complex data sets which we intend to analyse and publish in a range of papers over the next two years. Here we present an overview of the results to date.

Basic life-history comparison

When considering why broom can be an invasive weed, its life-cycle can be divided into a series of stages (Fig. 2). Where broom has been introduced, the plant can have a much longer lifespan than in its native range, and can grow to a much larger size. In Europe, broom plants grow as tall as 2-3 m, but in New Zealand and Australia some individual plants reach heights of 5-6 m. Seed production is also higher in open habitats in broom's exotic range (Paynter *et al.* this Volume).

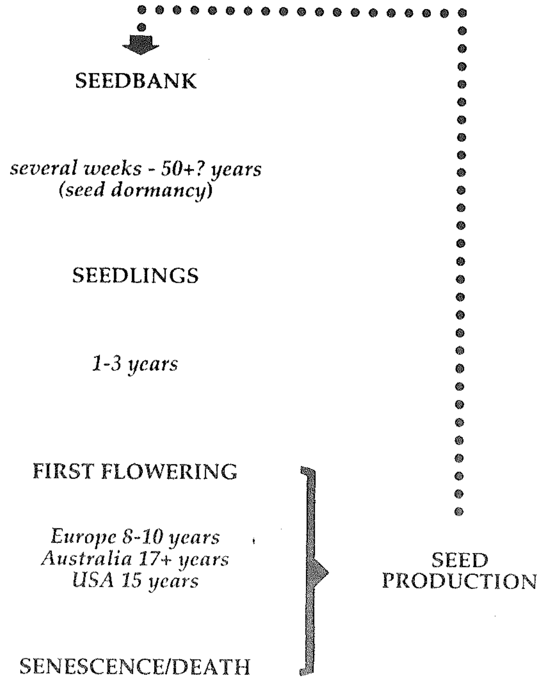

Fig. 2. A schematic comparison of some aspects of the life-history of broom as a native and as an introduced plant.

These observations do not help to explain why broom is a weed in Australia and New Zealand, and differences could be caused by any of the hypotheses presented above. However, our results suggest that the concept of broom growing better in exotic environments is an over-simplification. The most rapid early growth of broom in all four countries occurred in the UK plots, where some plants were over 1 m high after just one calendar year and produced flowers in their second growing season. These results suggest that the weedy attributes of broom in exotic environments are not simply due to differences in the climate or to genetic differences in the broom itself.

A comparison of the effects of natural enemies on broom

Another simple diagram of the life-history of broom is helpful in discussing the possible effects of natural enemies on broom through its life-cycle (Fig. 3). Apart from destruction by rodents, we found no evidence that broom seed on the soil is significantly attacked by any natural enemies (Paynter *et al.* this Volume). Although vertebrate seed-feeders differ in the four countries, the levels of destruction can be extremely high, perhaps explaining the lack of significant differences in the size of the soil seed-bank despite large differences in the overall levels of broom seed production in the native and introduced ranges of broom.

We had expected that the establishment of seedlings, and their performance until they first flowered, could be strongly affected by natural enemies such as insect herbivores or plant pathogens. However, evidence from the plots in the UK and France suggests that these effects are normally minor in comparison to mortality resulting from dry weather. A possible exception occurs when broom seedlings are growing very close to an existing stand, where they receive substantial levels of attack from the specialist insect herbivores present in large numbers on the more mature broom (Fig. 4) (Denton 1994). Such an effect could help to explain why broom stands in Europe seldom persist beyond one generation of plants.

Prior to this study, only the effects of insect herbivory from the seedling stage to maturity had been demonstrated (Waloff and Richards 1977). The

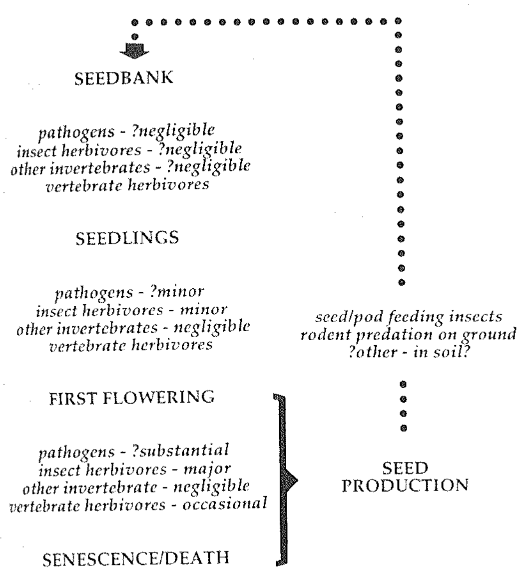

Fig. 3. A diagrammatic summary of the proposed effects of natural enemies on broom in its native range.

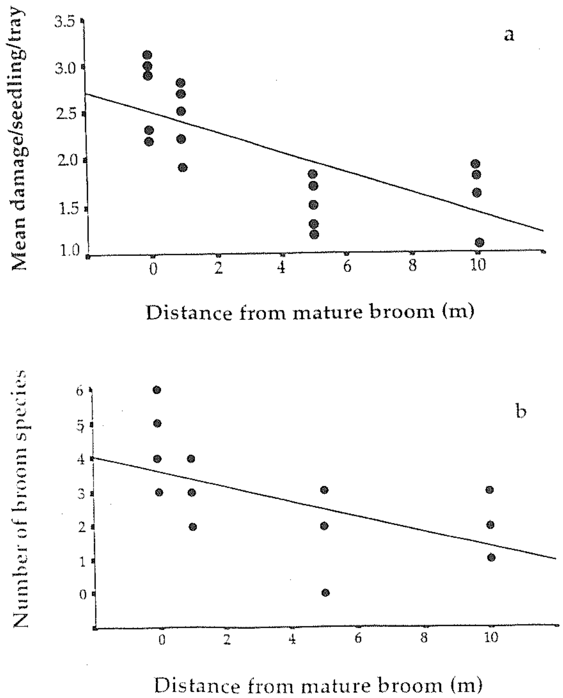

Fig. 4. The decline in the level of damage to broom seedlings (a), and the diversity of specialist broom herbivores that colonized seedlings (b), at various distances from a stand of broom (after Denton 1994).

experimental plots in the UK have now been in place for nearly five years and, although the data have yet to be fully analysed, the build-up in numbers of herbivores and visible stunting of the broom appears similar to that reported by Waloff and Richards (1977). The only natural enemies that caused mortality of broom plants were vertebrates and plant pathogens. In the UK, rabbits damaged all broom seedlings in the unfenced plots and deer occasionally destroyed larger broom plants in the fenced plots. In France, grazing by cattle and uprooting by wild boar is a common cause of seedling mortality. A pathogen, tentatively identified as a *Phomopsis* sp., caused low levels of mortality to broom seedlings in the UK, and *Pleiochaeta setosa* (Kirchn.) Hughes, caused patchy mortality in France. An unidentified plant pathogen has continued to cause low levels of mortality to the broom plants that are now approaching five years of age in the UK.

It is too early to report in detail on the results from the pesticide experiments, but these should provide replicated, quantitative data on the impact of insect herbivores and plant pathogens in the four countries.

Preliminary data from France reveal that only the molluscicide treatment has reduced seedling mortality.

A comparison of the effects of plant competition

Another diagram helps to visualize the effects of plant competition on broom (Fig. 5). A low level of plant competition, usually as a result of disturbance, was essential for extensive germination to occur. In France, the percentage of the seed-bank that germinated was about 100x higher in the cultivated plots than in the control plots, and the number of seedlings appearing was positively correlated with the size of the soil seed-bank (Fig. 6). Similar relationships were noted in Australia. Some of the habitats invaded by broom in New Zealand and Australia typically appear to have less ground cover than in Europe for at least part of the year, probably because of differences in the climate and in the composition of the plant communities. Our experiments are designed to test the importance of this apparent difference, both by manipulating levels of interspecific plant competition and by experimentally sowing extra broom seed.

The experiments measuring inter- and intraspecific competition have been running for less than two years, but it appears that once seedlings have established, interspecific competition from other plant species is often low. However, intraspecific competition (or self-

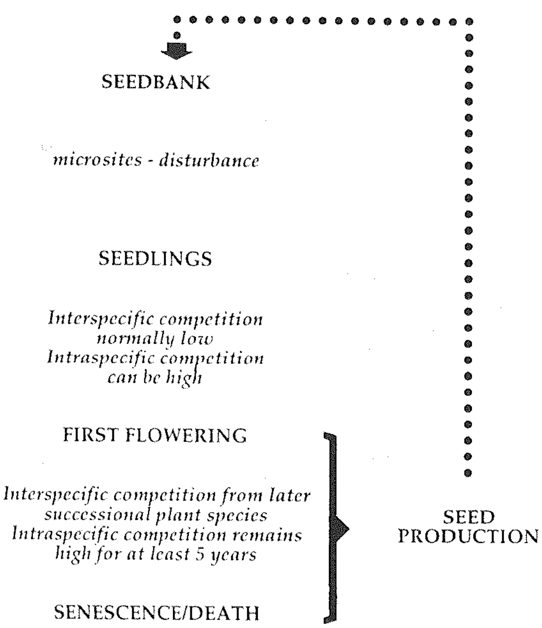

Fig. 5. A diagrammatic summary of the proposed effects of plant competition on broom in its native range.

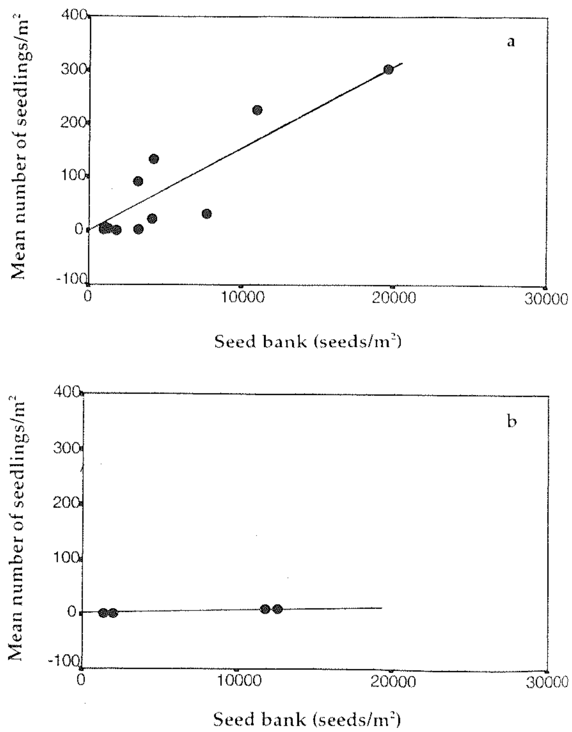

Fig. 6. The relationship between the mean number of broom seedlings that germinated and the size of the seed-bank for cultivated plots (a), and for undisturbed plots (b), in France.

thinning) can be very important if the seedlings are at a high density (Memmott *et al.* 1993). The later effects of interspecific competition appear to be important. Broom plants growing under eucalypt forest in Australia, and under sweet chestnut woodland in Europe, produce fewer seeds than plants growing in open pasture (Paynter *et al.* this Volume). In Europe at least, as broom plants senesce and die, competing species seem better at exploiting these gaps than broom seedlings, and their presence helps prevent the stand from regenerating. However, this may reflect an interaction between the natural enemies raining down on the broom seedlings from the broom plants above, rather than a purely competitive effect (see the 'natural enemies' section above).

Conclusions

A tentative conclusion is that both natural enemies and interspecific plant competition are significant factors influencing the weediness of broom. We can probably dismiss abiotic and genetic factors because growth and survival of broom up to the first flowering was higher in the UK than in exotic habitats. Furthermore, we can begin to see the stages in the life-history of broom when these factors are important, although the system is complex and our understanding of it should benefit from a simulation modelling approach (e.g. Lonsdale *et al.* 1995).

Broom seed-banks do not vary greatly between native and exotic habitats. Moreover, the seed-banks are usually too high for populations to be seed limited (see Paynter *et al.* this Volume). Germination from the seed-bank relies upon disturbances that remove most inter- and intraspecific plant competition. Subsequent survival and establishment of the seedlings does not vary greatly in native and exotic habitats (Paynter *et al.* this Volume). Specialist natural enemies do not seem to have any substantial impact on broom seedlings in the first two years of their life, with the possible exception of broom seedlings growing near larger broom plants in their native range. Subsequent mortality of mature broom plants has been strongly linked to insect attack (Waloff and Richards 1977) and this may help explain why broom appears to live longer in some exotic habitats. This leaves us with two explanations why broom is weedy: (i) periods when interspecific competition is lower, creating ideal germination conditions, are more common in the exotic habitats where broom is a weed; and (ii) stands of broom survive for longer in exotic habitats in the absence of heavy attack by phytophagous insects and plant pathogens. So for a given rate of disturbance, the percentage ground cover of broom will be higher, simply because of the increased longevity of the stands.

It is likely that both are important factors, but what are the implications for biocontrol? If different levels of interspecific competition are the most important factor, then broom is a potentially difficult plant to control. Indeed, Rousseau and Loiseau (1982), considered that the occasional weediness of broom in the Auvergne was a direct result of poor land management - extensive regeneration of broom after deliberate burning cannot be prevented unless the land is very heavily grazed afterwards. However, one weapon that an Auvergne farmer does not have in his armoury is classical biological control. If natural enemies are the important factor, then prospects of control are good, although, depending on how introduced agents perform in the absence of natural enemies, it may take a considerable time for the results to become apparent. We consider that the evidence to date on the impact of natural enemies on broom in its native range suggests that classical biocontrol is likely to be at least partly successful, assuming that the potential agents are sufficiently host-specific for introduction into other countries.

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