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Review Article

Biological control of *Dendroctonus micans* (Scolytidae) in Great Britain

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ABSTRACT

The European spruce bark beetle *Dendroctonus micans* was discovered in Britain in 1982. Although its potential to damage spruce plantations had been recognized for many years, this potentially damaging beetle had been present in the country for at least 10 years before being detected. This paper describes all aspects of the integrated pest management strategy that was carried out by the UK Forestry Commission, and in particular the role of the specific predator *Rhizophagus grandis*, the main tool in the biological control programme. There is now good evidence that the predator has established in Britain and is important in regulating the endemic levels of *D. micans*. Thirteen years after its discovery, *D. micans* is now considered under control within the infested area of Britain, and its management is now part of normal forest operations.

INTRODUCTION

The genus *Dendroctonus* Erichson (Scolytidae) has over 20 species, worldwide. Most of these occur on conifers in North and Central America, where they are the most destructive natural biological factors. *Dendroctonus micans* (Kugelann), the great European spruce bark beetle, is the principal Eurasian representative of the genus and is present from the island of Sakhalin and northern Japan in the East, to northern and western Europe. The only other Eurasian species is *D. armandi* Tsai & Li, a Chinese species. *Dendroctonus micans* is closely related to *D. punctatus* LeConte, found in western Canada and Alaska; the suggestion has been made that these two may be the same species (Bright, 1976).

THE BIOLOGY OF *DENDROCTONUS MICANS*

Adult and egg stages

The adult *D. micans* is a large black beetle, 6-9 mm in length, which exhibits several life cycle characteristics that are atypical of most other scolytid species. Mating takes place under bark, prior to emergence and before the adult beetles are fully chitinized, the females normally being fertilized by sibling males (incestuous mating). This explains the low number of males (typically one to every 10 females, but as low as one to 45) found in this species. Pre-emergence mating avoids the need for female beetles to attract males and therefore there is no adult aggregation pheromone (Grégoire, 1983). Adult beetles can remain under bark for long periods of time if conditions for emergence are not suitable. They often mine in large groups among their original excavations, chewing the larval frass and sometimes forming ‘nose to tail’ columns within the brood system tunnels. Emergence holes are cut through the thin bark covering the brood system, often well ahead of actual emergence, and large quantities of powdery frass are often ejected at this time. Emergence can take place over a protracted period with many beetles using one emergence hole.

The emergent, fertilized females attack new trees or unattacked parts of the existing host tree. Flight, and more commonly walking, play important parts in this dispersal, typically leading to small groups of attacked trees within forest blocks. Sometimes no emergence takes place and new brood areas are established along the margins of the old brood system. Although flight is rare it is important for the natural dispersal and territorial expansion of this beetle. The flight threshold is stated to be 21-23°C (Vouland *et al*., 1985), although in Britain we have observed initial flight at 20°C with secondary take off at 18°C leading to sustained flight at 14°C.

Attacks often occur around areas of damage on a tree and are associated with decreased resin pressure, being found commonly in forked or multiple stemmed trees and often just below branch nodes. In some countries there is thought to be an association between attack and infection by the fungi *Heterobasidion annosum* (Poriales) and *Armillaria* sp. (Agaricales) (Grégoire, 1988). However, this is not necessarily the case, as perfectly healthy trees are just as commonly attacked. Different provenances within tree species may exhibit differential susceptibility to attack and ability to support larval development. This is thought to be associated with the degree of lignification in the bark that prevents the larvae from exploiting the cambium fully (Wainhouse *et al.*, 1990).

Table 1. *Dendroctonus micans* attack frequency on *Picea abies* at five height categories as a percentage of total attacks. Percentages of attacks leading to successful brood establishment are given in parentheses.

Site	Height categories*				
	Root/stump	Stump to BH	BH to crown	Crown to 75 mm	75 mm to leader
Wyre 1	8 (14)	9 (5)	64 (45)	19 (36)	0
Wyre 2	11 (9)	16 (36)	63.5 (55)	9.5 (0)	0
Dean 1	2.3 (8.1)	11.8 (4.1)	48.5 (33.3)	36.8 (51.5)	0.6 (3)
Dean 2	17	3.5	76	3.5	0
Clay pits	5 (0)	21.5 (7)	53.5 (46.5)	2 (46.5)	0

*BH: breast height; 75 mm: 75-mm stem diameter.
Sample size at Dean 2 was too low to allow estimation of percentage of successful attacks.

Once suitable host material is located, the female bores through the bark to reach the cambium layer where she attempts to establish a brood chamber and subsequently to oviposit, clearing resin, the tree's first line of defence, which accumulates in the chamber. When mixed with the beetle's frass, this resinous mixture is typically a purple-brown colour. The female beetle uses her body to expel this frass/resin mixture through the entrance hole, in turn giving rise to the resin tubes characteristic of this beetle. Once she reaches the cambium the female beetle bores upwards for about 2 cm and constructs an egg chamber, in which she lays between 100 and 150 eggs. These she covers with frass and wood dust. She may then go on to produce other egg chambers leading to a mixture of larval stages within a single family group, or she may leave the original chamber and attack other areas of the same tree, or occasionally other trees.

Larvae and pupae

Newly hatched larvae start to feed gregariously, side by side, in a brood area that grows larger as the larvae feed. Similar behaviour is recorded in two North American *Dendroctonus* species, namely *D. valens* LeConte and *D. terebrans* (Olivier) (Grégoire, 1988). This strategy is thought to help the larvae overcome resin defence reactions of the host tree. The size of the brood area varies according to the number of larvae present, larger broods reaching areas of up to 30-60 cm long and 10-20 cm wide. When several females oviposit close to one another, individual brood systems frequently coalesce, extensively wounding the tree.

Within the brood chamber the larval feeding front moves upwards and outwards from its origin, larvae only leaving this front to defaecate or moult. Frass, detritus and even the dead bodies of their siblings are tightly packed into 'islands' behind this feeding front, a behavioural trait that may help to limit the spread of disease. Larvae manipulate the resinous faecal pellets with their heads, forming these 'islands' which give the characteristic 'quilted' appearance to the brood system. Larvae produce an aggregation pheromone (*trans*- and *cis*- verbenol, verbenone and myrtenol) which sustains the single feeding front (Grégoire *et al.*, 1982). If the tree dies while larvae are still feeding, they often feed in the outer phloem, engraving the wood surface.

There are five larval instars that in Britain require from six to 12 months to develop, depending upon the time of egg-laying. Mature larvae move back into the frass 'islands' behind the feeding front where they construct single pupal chambers. In Britain the total *D. micans* life cycle varies from 10 to 18 months, depending on when eggs are laid and on temperatures; eggs laid in late summer or autumn remain dormant over winter and hatch during the following spring (King & Fielding, 1989).

Attack patterns

In dense spruce plantations where *D. micans* is well-established, attacks are usually characterized by scattered groups of infested trees, representing local foci of infestation. Such groups usually consist of a few dead or partly dead trees, surrounded by others with varying degrees of successful colonization. By contrast, in widely spaced, heavily thinned crops, attacks are more general and widespread with scattered individual dead and dying trees. Inspection of infested plantations will often reveal copious resin bleeding on the stems of heavily attacked trees and the presence of many resin tubes, the main external diagnostic feature of *D. micans* attacks. The consistency of the resin tube varies considerably. Those of pure resin, varying in colour from white to pale pink or brown, often denote an abortive attempt at colonization. Other tubes, consisting of a mixture of resin and bark particles, coloured purple-brown to dark brown, suggest successful entry to the cambium but not always successful brood establishment. Resin tubes may occur singly or in large amalgamations of many tubes sometimes with attendant resin bleeding down the trunk. Those that are crusty and hard are normally old; fresh attacks have soft, malleable resin tubes. However, breeding beetles sometimes successfully re-enter old resin tubes. In such cases, fresh bark particles can be seen at the entry hole. If attack occurs below ground level the resin particles are pushed to the surface in granular form. Destroyed areas of cambium are characterized by concentrations of resinous frass interspaced with tunnels.

In Britain, attacks may occur anywhere from the root system to the upper crown. This is in contrast to the situation found in mainland Europe, where attacks tend to occur near the base of trees (personal observations in Belgium, France and Finland). Investigations into the vertical distribution of *D. micans* attacks were carried out in Britain during 1982 to 1984 (Evans *et al.*, 1985). After felling, tree height categories were selected, namely root/stump, stump to breast height (BH), BH to base of live crown, live crown to 75-mm stem diameter and 75-mm diameter to leader, and attacks in these categories were recorded. The results of these investigations are given in Table 1.

Attack frequency was greatest between BH and base of live crown which, in well-growing trees, represents the main portion of the trunk. It is of interest to note the position of attacks that were successful. These were also mainly between BH and base of live crown but tended to be relatively more successful in the crown itself. Thus, at least at the sites studied, our experience is that attacks, and particularly successful attacks, occur in the upper portions of the tree above BH, including the live crown. Although attacks were concentrated on areas of the tree above BH they were not distributed at random within the various height categories. Positions of attack are summarized in Table 2 which takes account of the various features of a typical spruce trunk.

Most attacks were located at branch nodes or wounds, although the amount of wounding varied from site to site. Selection of branch nodes for entry into the trunk indicates

Table 2. Position of *Dendroctonus micans* attacks on *Picea abies* expressed as percentage of total attacks.

Site	Open bark	Branch node	Wound	Fork	Drought crack
Wyre 1	35.0	52.0	12.0	*	1.0
Wyre 2	56.5	32.5	5.5	5.5	*
Dean 1	10.6	75.6	2.2	*	11.6
Dean 2	24.0	62.0	14.0	0	*
Clay pits	18.0	66.0	9.0	7.0	*

*No data available.

a strong preference by adult beetles for some discontinuity in the trunk, which may aid beetle entry. The mechanism acting to assist entry at these locations is unknown but from our observations it would appear to be reduced resin pressure. It is therefore possible that the greater success of attacks higher up the tree into the crown may be attributable to the greater numbers of branch nodes at this height.

WORLDWIDE DISTRIBUTION AND STATUS

Eurasian distribution

Dendroctonus micans, originally of a northern Eurasian distribution, has spread steadily over the last 100 years or so, probably because of increased trade in roundwood timber. Today it occurs throughout the spruce-growing areas of the European and Asian land masses (Figure 1), showing a well-developed ability to adapt to many climatic and forest conditions. *Dendroctonus micans* is established in Austria, Belgium, Czechoslovakia, Denmark, Finland, France, Germany, Netherlands, Sweden, Rumania, Turkey, Great Britain, the former USSR and former Yugoslavia (Grégoire, 1988). The only limit to its spread would appear to be the distribution of susceptible conifer species.

Throughout its range, *D. micans* is recorded as exploiting a range of conifer genera including *Abies*, *Larix*, *Picea*, *Pinus* and *Pseudotsuga* (all Pinaceae). Norway spruce, *Picea abies*, is the main host in western Europe, whereas oriental spruce, *P. orientalis*, is preferred in the East. Adults show preferences for particular spruce species but this does not necessarily coincide with suitability for successful oviposition and larval development. Bejer (1985) proposed that the adult range of preferences within the genus *Picea* was: *abies* > *pungens* > *sitchensis* = *alba* > *omorika*, while successful attacks were ranked: *pungens* = *orientalis* > *sitchensis* = *alba* > *abies* > *omorika*. The two most important host species in western Europe are *P. abies* and sitka spruce, *P. sitchensis*. *Dendroctonus micans* was discovered on *P. abies* in 1794 (Brichet & Severin, 1903) but it was not until 1852 that the destructive potential of *D. micans* was recognized fully. After this time there was gradual spread and an increase in numbers of reported outbreaks, particularly among the *P. abies* plantations in western Germany. In 1897 *D. micans* appeared in Belgium, where heavy spruce losses were caused by the beetle in the four years 1897-1900 (Severin, 1902). South-westerly dispersal through Belgium was attributed by Brichet & Severin (1903) to the prevailing north-east winds. *Dendroctonus micans* was first recorded in Denmark in 1861, but the first serious outbreak did not occur until the early 1900s. In 1935 it appeared simultaneously at two sites in Holland (Brown & Bevan, 1966).

Serious damage and tree mortality resulting from attack by *D. micans* is, however, uncommon, despite the presence of the insect throughout most of the natural range of spruce in Eurasia. Carle *et al*. (1979), studying new outbreaks of *D. micans* in the Massif Central in France, proposed that epidemic populations of the beetle are associated mainly with the front of an expanding population. While there is evidence to support this view, most outbreaks elsewhere appear to have been associated with periods of extreme drought that extended over at least two consecutive seasons. Periods of drought severely weaken the host trees making them less able to withstand beetle attack. The best-documented studies of this association have been in Denmark where outbreaks during 1947-1949 and 1960-1961 have been linked to periods where both summer and winter drought followed each other (Bejer, 1985). This author considered the following factors important during this period: (a) rapidly increasing areas of *P. sitchensis* of appropriate age and dimension, (b) greatly improved opportunities for dispersal with timber and, especially, (c) reduced host resistance owing to the extreme drought at the time. During the outbreaks in Denmark, losses were concentrated in *P. sitchensis* rather than the naturally occurring *P. abies*, although the latter species was also widely attacked. The planting of *P. sitchensis* on sandy soils also contributed to the problem because of large soil moisture deficits on these sites. An exception to the generally short periods of intense *D. micans* activity in western Europe has been the continuously increasing infestation in the Georgian Republic from the first record in 1957. By 1963 over 100,000 ha of *P. orientalis* were heavily infested (Khobakhidze *et al*., 1970).

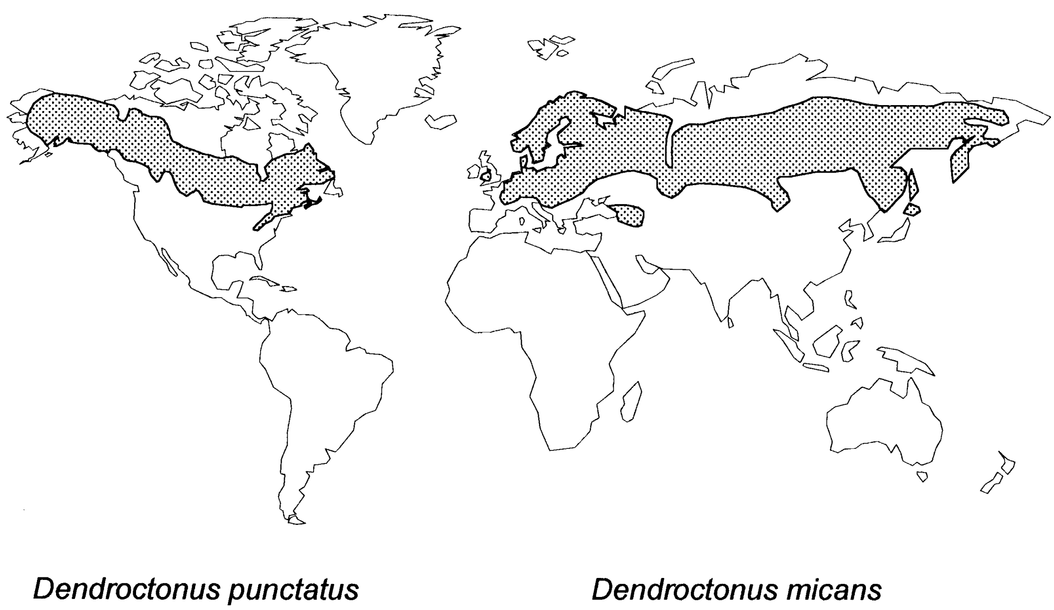

Figure 1. Worldwide distribution of *Dendroctonus micans* and *D. punctatus*.

Table 3. Results of surveys conducted in Britain from 1982 to 1984, showing the numbers of *Picea* spp. trees attacked by D*endroctonus micans*. The mean attacked spruce trees per site reflects the increase in the number of sites surveyed and the effect of sanitation felling.

Year of survey	No. sites surveyed	No. sites infested	No. trees attacked	Mean attacked trees per site
1982	411	290	35173	121.3
1983	3548	1357	29790	22
1984	8123	1554	21985	14.1

The gradual spread of *D. micans* from East to West, with recent southerly extensions into Georgia and Turkey, shows that the beetle has a well-developed capacity to move to, and exploit, previously unattacked spruce forests. There is little reliable information concerning the mode of dispersal but it is clear, from data available on natural flight behaviour, that beetles are only capable of sustained flights at relatively high temperatures. Since adult *D. micans* require temperatures of 21-23°C for initial take off (Vouland *et al.*, 1985), it seems unlikely that the observed rates of colonization in Europe can be attributed to natural dispersal alone. Such temperatures within shaded, closed canopies of spruce forests are infrequent and flight can only be expected during exceptionally hot summers. There are no reliable data on distances flown by beetles, so that even the well-documented history of the appearance and spread of *D. micans* does not distinguish between natural and trade-assisted movement. It is probable that only local dispersal takes place following adult beetle flight. It follows that much of the long-distance spread must have resulted from transport of timber with intact bark. This is almost certainly the means by which *D. micans* circumvented natural barriers to reach Georgia (crossing the Caucasus Mountains) and Great Britain (crossing the North Sea and the English Channel).

Initial British distribution

The potential of *D. micans* as a pest of spruce had, for many years, given cause for concern in the UK (Brown & Bevan, 1966). A review of the literature and direct observations in Denmark and Schleswig-Holstein led these authors to warn of the potential risks from *D. micans*. Although *D. micans* has never been intercepted during plant health inspections at British ports, the fact that the even more damaging bark beetle *Ips typographus* (L.) (Scolytidae) and several north American *Dendroctonus* species have been found frequently amply shows that bark beetles can reach the UK through timber imports (Winter & Burdekin, 1987). Marchant & Borden (1976), in assessing the plant health risks of the major bark beetles worldwide, rated *D. micans* third behind *I. typographu*s and *I. amitinus* (Eichhoff). It was only the low frequency of interception in wood imports that placed *D. micans* behind the other two species in their list.

The discovery in August 1982 of *D. micans* breeding in sitka spruce near Ludlow, Shropshire was followed by further finds in nearby woodlands (Bevan & King, 1983). Further surveys within the next month showed that the beetle was established in Britain over a large part of the Welsh Marches and eastern and central Wales. These in turn led to intensive surveys that were undertaken between 1982 and 1984 to learn the distribution and attack intensity of *D. micans* in Great Britain (Fielding *et al.*, 1991a).

All spruce trees located within the known infested area, without regard to the size or status of the planting, were inspected for the presence of *D. micans*. The scale of the inspection, which was effectively 100%, was unprecedented in comparison to other European surveys. Selective surveys were later carried out throughout Britain outside the known infested area, where the need for vigilance was also important. Early in 1983, infestations were discovered in Lancashire on Forestry Commission land in the Trough of Bowland. Intensive surveys were subsequently carried out within a 50-km radius of these more northerly sites. This northerly infestation is considered very important owing to its proximity to the large spruce-growing areas of northern England and Scotland. Table 3 gives the result of the surveys over the three years to 1984 and Figure 2 shows the known distribution by the end of 1984.

PEST MANAGEMENT STRATEGY

Towards the end of 1982, the Dendroctonus micans Working Group (DMWG) was set up, comprising representatives from the Forestry Commission and the private forestry sector. The aim of the group was to develop a comprehensive management strategy that then evolved over the early years following discovery of *D. micans*, and was essentially made up of three interrelated elements.

Survey and sanitation felling

Up to and including 1984, a 'seek and destroy' policy was adopted in an attempt to reduce the existing *D. micans* populations to more acceptable and potentially manageable levels. All infested trees located during surveys were marked, felled, debarked and treated with insecticide to kill any live stages of *D. micans*. Felling was always carried out before the end of March in the year following survey; after this time adult beetles can become active. Dates of initial attack were determined by examination of occluded attacks in relation to tree age. This exercise enabled the first appearance of *D. micans* in a given location to be worked out, showing the rate of spread away from the earliest

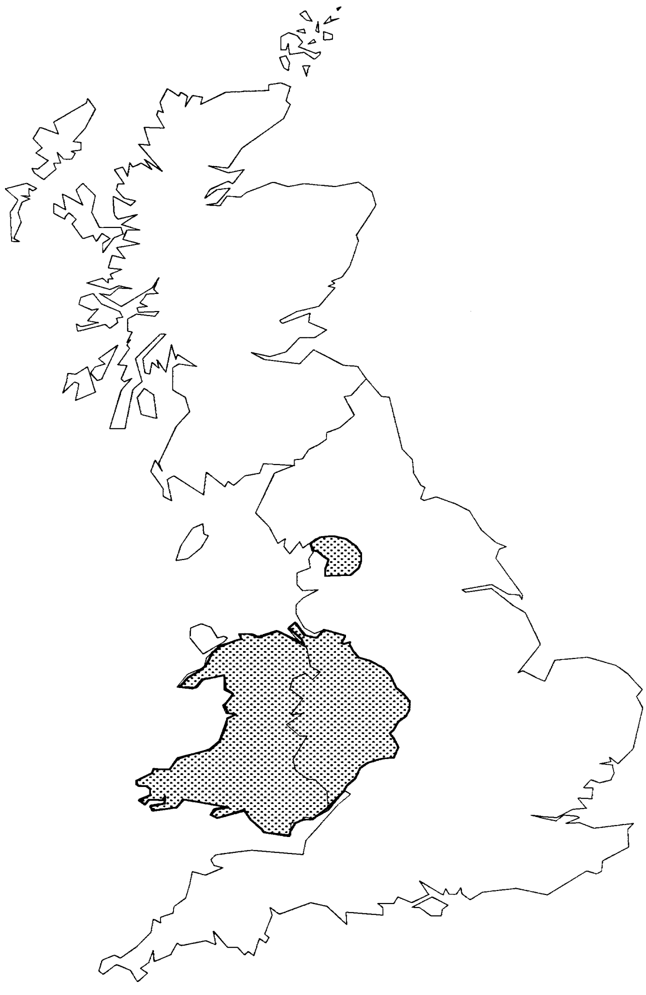

Figure 2. The 1995 distribution of *Dendroctonus micans* in Britain.

known occurrence in 1973, near Ludlow, Shropshire. The 1983 surveys showed very little extension to the known limits of the infested area but, as was to be expected in an exercise of this nature, many older infestations overlooked during the 1982 surveys were found.

The results of the surveys between 1982 and 1984 (Table 3) showed a reduction in the number of infested trees found over the three years, despite the large increases in the numbers of sites examined. Sanitation felling, which sometimes involved clearfelling of infested sites, dramatically reduced the mean number of infested trees per site over the three years. Although difficult to quantify precisely, this felling, by reducing the whole *D. micans* population, was thought to be a sound basis upon which to build other control measures.

Restriction of movement of infested spruce

Although surveys and sanitation felling were seen as a useful means of reducing the identified populations of *D. micans*, it quickly became apparent that the strategy could, at best, only partially control any population increase. While active control measures were being concentrated in the main outbreak area, management strategy had to take account of the fact that, at that time, the outbreak was confined to central Wales and the Marches area of the English / Welsh border. The pattern of establishment of new infestations described by Carle *et al.* (1979) indicated that long-distance spread resulted mainly from trade in poorly debarked timber. This conclusion suggested a possible method for reducing the probability of aided spread to the major spruce forests in the remainder of Britain.

The Forestry Commissioners, under the powers of the 1967 Plant Health Act, introduced 'The Restriction on Movement of Spruce Order (Statutory Instruments 1457)' that defined, for control purposes, a 'Scheduled Area' (essentially the infested area and a non-infested boundary) around the known infested area. No spruce wood from an infested forest (or sawmill to which this wood had been taken) could be moved outside this area unless all traces of bark were removed. The order restricted the movement of spruce from infested stands, requiring that, within the Scheduled Area, two conditions had to be fulfilled. Firstly, all spruce wood felled had to be licensed before it could leave the forest. Secondly, infested spruce could only be moved to approved sawmills, equipped to peel and / or make safe any wood products and / or residues. It was expected that as *D. micans* spread naturally, the boundaries of the Scheduled Area would be moved as necessary.

This legislation has now been altered because of new legislation drawn up for the 1993 European Union (EU) single market. The Scheduled Area was replaced by the Dendroctonus micans Control Area (DMCA) and the remainder, the uninfested part of Britain, is now the Dendroctonus micans Protected Zone (DMPZ). A Protected Zone is defined under EU legislation as an area in which, despite conditions being favourable for its establishment, an organism present elsewhere in the Union is not present. This new legislation maintains our domestic controls against *D. micans*, while it also buffers our external controls to prevent re-introduction of this, as well as other, potentially damaging pests. The only difference to the legislation is that from 1993, all conifer wood (not just spruce) movement between the DMCA and the DMPZ is controlled and restricted. The purpose of any legislation is to minimize the risk of accidental carriage of *D. micans* to new locations remote from the main infested area, a strategy that is now the cornerstone of management of *D. micans* in Britain.

After the 1984 survey a major review of control options and strategy was undertaken. This included an appraisal of all aspects including control, research findings, survey results and an assessment of a trial biological control programme conducted during 1983. Concurrent with this, a financial assessment was also undertaken, encompassing a range of alternative strategies from 'do nothing' to increasing the controls already in place. It was becoming clear that the two initial policies of 'seek and destroy' and the 'Restriction on Movement of Spruce Order' had stabilized, if not reduced, the *D. micans* populations and as a result lowered the risk of long-distance spread. It was also recognized that, although data showed a reduction in the size of *D. micans* populations, a significant residual population remained and would continue to exist within the infested area; a situation ideally suited to a strategy based on use of natural enemies.

Biological control

During early population assessments it was noticed that *D. micans* mortality was influenced by a variety of natural enemies as well as certain environmental conditions. The most important of these is undoubtedly the great spotted woodpecker, *Dendrocopos major* (Picidae), which was shown to be particularly important during winter months in mixed conifer and broadleaved woodlands. The presence of aggregated larvae and adults, coupled with the flimsy covering of dead outer bark over the brood systems provides these birds with an easily obtainable meal. A parasitoid, *Dolichomitus terebrans* (Ratzeburg) (Ichneumonidae), normally associated with the pupal stages of pine weevils (*Pissodes* spp.; Curculionidae), had adapted well to *D. micans*, and was often found associated with its brood systems. However, neither of these natural enemies is thought to respond quantitatively to changing population densities of *D. micans*. Literature survey and contact with European scientists had, however, suggested that a specific predatory beetle, *Rhizophagus grandis* Gyllenhal (Rhizophagidae), was a significant natural mortality agent in Europe (Kobakhidze *et al.*, 1970; Bevan & King, 1983). Steps were therefore taken to assess its potential for use in Britain.

Rhizophagus grandis is the single most important and potentially useful natural enemy of *D. micans* throughout its Eurasian range. The potential usefulness of this predator as part of Britain's control programme was recognized shortly after the discovery of *D. micans*. Steps were taken to obtain both supplies of the predator and permission for its release in the outbreak area of Britain. The first notable artificial breeding and release of this predator began in 1963 in the Georgian Republic, and is still on going, being regarded as influential in reducing serious outbreaks of *D. micans* in the extensive oriental spruce forests (Kobakhidze *et al.*, 1970). A similar programme began in France in 1983; scientists from Belgium worked with the French forest authorities to introduce *R. grandis* to the various outbreaks of *D. micans* (Grégoire *et al.*, 1984a). In Belgium, naturally occurring populations of *R. grandis* are thought to maintain *D. micans* populations at low endemic levels, such that economic damage occurs only in the large forests of the Ardennes (Grégoire, 1984).

INTRODUCTION AND REARING OF THE PREDATOR

Contact was quickly established with Belgian entomologists, led by J.-C. Grégoire, involved in an European Community / Belgian / French project on artificial rearing and release of *R. grandis*. This led in June 1983 to the importation into Britain of 200 male / female pairs of *R. grandis* adults, to establish a trial breeding and release programme, the latter being under licence from the Department of the Environment (DOE) and in compliance with the Wildlife and Countryside Act 1981. Facilities to breed this insect were established in 1983 at Ludlow, Shropshire, a location convenient to the main *D. micans* populations (King & Evans, 1984).

Early attempts at breeding under artificial conditions met with mixed success. Initial methods of rearing *R. grandis* closely followed those described by Kobakhidze *et al.* (1970)

and Grégoire *et al.* (1984b), and used cut spruce logs as a feeding substrate for *D. micans* larval broods. Female *D. micans* were introduced onto freshly cut *Picea abies* logs in two ways; the first method involved confining free-ranging beetles upon logs within closed boxes, allowing them to initiate attack at will. The second method involved confining single beetles under polythene caps (15 × 8 mm) pinned against the bark, where a small plug of bark had been removed to predispose beetle entry. In controlled conditions (temperature 20°C ± 1°C, relative humidity of 65-75% and 18-hour daylength) a period of 35-45 days is required from *D. micans* introduction to the development of second- to third-instar larval broods. Field-collected larvae were also implanted into spruce logs in the manner described by Kobakhidze *et al.* (1970). A small rectangular piece of bark (about 8 × 4 cm) was removed and approximately 100 larvae were placed in the recess, along with some dried, powdered bark. The 'artificial' brood was then covered with plastic-coated paper that was stapled into position. Larvae rapidly adjusted to and fed in their new environment and, depending upon the larval stage, a period of two to 10 days was allowed before they were utilized in the *R. grandis* breeding system.

Male / female pairs of *R. grandis* adults were introduced into the broods by lifting a small triangle of bark (or waxed paper) directly over the *D. micans* larvae. The triangular section was then replaced and held down by adhesive tape and the logs incubated for 25-27 days, after which they were placed vertically on steel mesh platforms over large plastic funnels. Emerging *R. grandis* prepupae fell into the funnels and were collected *en masse* in shallow plastic trays, from which prepupal collections were made twice daily. Prepupae were incubated for 40 days in closed containers containing a moist, sterilized peat / sand mixture, eventually emerging as adults. Adult *R. grandis* were counted, sexed and stored at 4°C in Petri dishes containing damp sand. Under these conditions adult predators can survive for up to six months without any apparent adverse effects.

The presence of the entomopathogenic fungus *Beauveria bassiana* (Hyphomycetes) proved to be a serious problem in this rearing system. The disease first appeared in August 1983 among the breeding stock of *D. micans*, and resulted in up to 80% mortality of incubating *R. grandis* pupae and adults. During the main breeding programme it became a constant problem among both *D. micans* adults and pupae / adults of *R. grandis* where it occasionally caused total mortality. Three fungicides (thiabendazole (TBZ), benomyl (Benlate R) and carbendazim) were tested in an attempt to reduce mortality from *B. bassiana* in both insect species. Results suggested some improvement could be made, but were not statistically significant. In late 1985 and early 1986 stringent hygiene resulted in a far lower incidence of the disease, but a more fundamental appraisal of methods was needed and this led to a review of methodology during summer 1986.

An alternative method of rearing *R. grandis* that involved stimulating oviposition by *R. grandis* in containers of powdered spruce bark containing *D. micans* larvae, as described by Grégoire *et al.* (1986), was assessed and subsequently adopted. Once the *R. grandis* eggs had hatched, the young larvae were transferred to other containers and fed to maturity on alternative insect prey. Although this method had been tried in Britain during the early stages of the rearing programme it had given very poor results. Modifications to the system were developed and incorporated in 1986 and have proved successful. In addition the introduction in the breeding units of ultraviolet lighting at night helped to reduce the incidence of disease by killing fungal spores.

The 'box-breeding' system now in use involves the following procedure. Circular clear polystyrene containers (50 × 25 mm) are half-filled with rehydrated, coarsely ground dried spruce bark. Around 20 *D. micans* larvae in the second- to fourth-instar stages are added and covered with a rectangle of fresh spruce bark, cambium side down, after which two females and one male *R. grandis* are added. The box is closed and incubated in the dark at 20°C for 20 days. After this time the contents of five of the oviposition containers are emptied into larger polystyrene boxes (17.5 × 11.5 × 6 cm) and *R. grandis* larvae are then fed dead larvae of *Calliphora* sp. (Calliphoridae) that have been stored at -20°C. These boxes contain an outer 'wall' of plaster of Paris. After about 25 days prepupae climb onto this 'wall' and are collected daily. Prepupae are incubated in similar boxes containing moist silver sand for 40 days, during which time all moult to adults. The addition of 0.2 ml of α-pinene to these boxes has almost eliminated the incidence of *B. bassiana*. *Rhizophagus grandis* adults are separated from the silver sand using a sieve and water. Yields per female *R. grandis* have been, and still are, variable (range 0-70) but are an improvement on the log breeding method. The method also has the major advantages of requiring less space, fewer *D. micans* larvae, no logs and giving greater control against disease. Up to 80 progeny are regularly produced from each oviposition box, but this figure can be increased by the addition of either α-pinene or a synthetic oviposition stimulant (Grégoire *et al., 19*91). The need for *D. micans* larvae can be temporarily eliminated by using *Calliphora* sp. larvae and an oviposition stimulant, consisting of camphor (racemic), (-)-fenchone, terpinen-4-ol (racemic), (-)-α-fenchol, borneol, (S.vt)-(-)-verbenone and pentane in equal quantities (Grégoire *et al.*, 1991). However, this method cannot be used exclusively as it only works for one to two generations (J.-C. Grégoire, pers. comm.). *Rhizophagus grandis* breeding continues at a low level to the present, but large numbers could be produced within four months of a need being identified, thus enabling us quickly to introduce the predator into any newly discovered *D. micans* outbreaks.

PREDATOR RELEASE PROGRAMME

The first small-scale experimental releases of the predator were made in 1983 and resulted in successful establishment of the predator at two of three sites. At one site some 27 pairs of *R. grandis* were released into an unsanitized area of *P. abies*, after which adults and their larvae were subsequently recovered in October 1983 and June 1984. Two other recoveries of adult *R. grandis* were made in September 1984, one among infested omorika spruce, *P. omorica*, following release of adults in the preceding June, and one in an area where *R. grandis* had been released in a forest stand some 200 m away. These releases were made under licence from the DOE and required, as a condition of issue, extensive testing of the predator against many other species of bark beetles, all of which were unaffected by this introduced predator.

The 1983 survey revealed that 1424 (493 Forestry Commission and 931 privately owned) sites were infested with *D. micans*. Sites varied from an entire forest, through small groups of trees to, sometimes, single trees. The mass-release programme commenced in 1984 and initial releases, intended to cover as many infested sites as possible, were based upon conservative estimates of *R. grandis* production during the first year of mass-rearing (Fielding, 1992). Early in the programme a decision was taken to use low-density inoculative releases, in order to cover as many locations as possible. It was considered that the slow life cycle of *D. micans*, combined with the low residual populations remaining after sanitation felling, would give ample time for *R. grandis* to build up to levels that would exert an effect on the *D. micans* population. To achieve this distribution of predators throughout the infested area, with a projected production of 10,000 pairs of beetles in the first year, the following guidelines were laid down: sites with more than 100 attacked trees received 50 pairs of *R. grandis*; sites with 50 to 100 attacked trees received 25 pairs; sites with five to 50 attacked trees received 15 pairs; sites with one to five attacked trees received 10 pairs.

For release, male / female pairs of *R. grandis* were placed in individual plastic containers on moist sand. Each pair was introduced into the forest at the base of an infested tree at the rate of one pair per tree, and were thus distributed throughout the plantation. If, because of sanitation felling, few or no infested trees could be found, *R. grandis* adults were released in the same manner on uninfested trees, as some *D. micans* broods are always missed during survey and subsequent sanitation felling. Areas clear-felled during sanitation operations did not receive *R. grandis* and release was postponed in forests where thinning or felling was taking place. Care was taken to avoid inclement weather such as high winds or heavy rainfall that might have affected adult mobility and prey detection. Releases were confined to the period May to August inclusive to coincide with maximum activity in the field when monthly temperature maxima in Britain can exceed 22°C. Experiments undertaken during 1987 and 1988 showed that offspring from *R. grandis* adults that lay eggs between April and July will develop into adults before the end of the same year (King *et al*., 1991). Predator releases were concentrated initially along the outer edges of the infested area to try to reduce the rate of spread of *D. micans* and to establish the predator as quickly as possible so it could follow its host during natural dispersal. Once the edge sites had been treated, the most intensely infested sites were dealt with in descending order of priority. By the end of the 1984 programme, a total of 936 sites had been treated with some 16,000 pairs of *R. grandis.* No distinction was made between Forestry Commission and privately owned woodlands.

Experiments, started during 1984, to investigate the effects of an inoculative release of *R. grandis* adults within an infested plantation, showed that the predator can search for and locate even low densities of prey (King & Fielding, 1989). Further experimentation during 1987 and 1988 (Fielding *et al*., 1991b) showed that *R. grandis* quickly spread through an infested forest area, locating a high proportion of the available host material. Furthermore, our breeding records showed a natural sex ratio of 1:1, thus removing the need for sexing the insects before release. All introductions since 1985 have, therefore, been made *en masse* within infested spruce stands, reliance being placed on natural dispersal of the predator adults. Current releases are now concentrated on new outbreaks found around the edge of the known *D. micans* infested area. This area is surveyed annually and so monitors any outward movement of *D. micans*. Releases also take place in any new infestations within the main infested area. Releases since 1986 have consisted of 50 or 100 *R. grandis* per infested site (Table 4).

ASSESSMENT OF *RHIZOPHAGUS GRANDIS* ESTABLISHMENT IN BRITAIN

Adult *R. grandis* are highly effective at locating their prey, sensing the chemical signals emitted from *D. micans* broods (Wainhouse *et al*., 1991, 1992; Grégoire *et al*., 1992). Once under the bark, if no larval prey is located, *R. grandis* adults can feed on *D. micans* eggs, effecting a considerable population reduction in individual broods (Evans & Fielding, 1994). If *D. micans* larvae are present, the predators mate and lay their eggs, the numbers being in proportion to the density of prey in the brood, presumably reflecting the concentration of the *D. micans* larval aggregation pheromone (H.F. Evans, unpublished data). Parent *R. grandis* wound the *D. micans* larvae to help their progeny in their initial feeding. The predatory larvae aggregate to their victims, mining into and totally consuming the soft body tissues, leaving only the husk of the *D. micans* larva. As they grow through their three larval instars they attack and consume prey directly. When fully fed, *R. grandis* larvae enter a prepupal stage and the majority leave the *D. micans* brood system, dropping from the tree to enter the soil where they pupate and eventually emerge as adults to begin a fresh breeding cycle. Information gained on the life cycle timings and behaviour of the larval, prepupal and adult

Table 4. A summary of *Rhizophagus grandis* releases from 1984 to 1995.

Year	No. sites treated	No. predators released	Mean no. predators released per site
1984	936	31062	33.2
1985	641	39392	61.5
1986	538	20754	38.6
1987	83	10700	128.9
1988	74	7400	100
1989	50	5000	100
1990	57	5700	100
1991	81	8100	100
1992	112	13800	123.2
1993	65	7200	110.7
1994	49	2650	54.1
1995	55	4600	83.6
Totals	2741	156358	57

stages of *R. grandis* show that this species has an excellent survival strategy. The adults can survive for long periods, both under bark and in the soil, and are thus able effectively to exploit *D. micans* populations, most stages of which can be found at any time of the year (King *et al*., 1991).

Inoculative release means that efficacy, in terms of reductions in *D. micans* populations, can be assessed only after the predator has had several generations to reproduce and potentially to reach a dynamic balance with prey populations. Even allowing for the rapid reproductive rate of *R. grandis*, there is little likelihood that significant impact would be observed within the first 12 to 24 months. A policy of sample surveys to assess predator establishment was, therefore, initiated. Establishment was considered successful if *R. grandis* life stages were found after sufficient time had elapsed for them to be second or later generations. In 1985, one year after the first predator releases, 47 sites were sampled by felling five or 10 of the most heavily infested trees. At each site, depending on the level of *D. micans* attacks, each *D. micans* brood was examined carefully for the presence of both predator and prey life stages. In 22 of the 47 sites, representing 47% of those surveyed, *R. grandis* was found at stages ranging from adults to larvae, confirming its establishment under British forest conditions. The labour intensity of this method of sampling limited the number of locations that could be sampled, but the results showed an encouragingly high level of predator establishment in the year after release. Carefully conducted more detailed and random samples were taken at three sites in 1986. These showed that 34% of the available *D. micans* broods were attacked by the predator. By 1987 this figure had doubled to 68%, and by 1988 (at one site) 80% of prey broods were attacked (Fielding *et al*., 1991b). It is now rare to find a site infested with *D. micans* that does not contain *R. grandis.*

Other field observations and experiments show that *R. grandis* has a highly developed host-finding ability and disperses over significant distances. Adult dispersal of up to 200 m was observed within 28 days of release in Britain (Evans & Fielding, 1994), while other field surveys showed that the predator can locate and establish itself in *D. micans* populations in isolated forest blocks 9 km from the nearest infestation.

Information on dispersal and on the increasing incidence of *R. grandis* over time from the first releases in 1993 provides evidence for the developing role of this predator in the regulation of *D. micans* populations in the field. Evans & Fielding (1994) provided a detailed appraisal of the attributes of *R. grandis* as a predator showing, in particular, that population trends in *D. micans* numbers decreased with increasing *R. grandis* numbers in the field. This is illustrated in Figure 3, which shows the trends in population growth

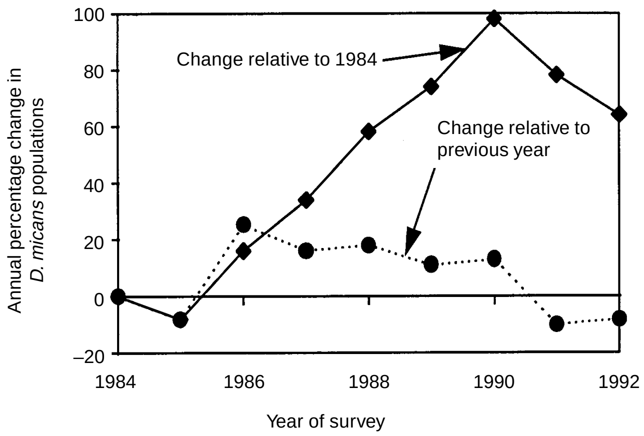

Figure 3. Annual percentage change in trees infested by *Dendroctonus micans*. The lines show the changes relative to the initial population identified during the 1984 survey and also in relation to numbers in the previous year. A regression line has been drawn through the latter data to illustrate the downward trend in *D. micans* population growth since 1986, two years after *Rhizophagus grandis* releases commenced. A total of 65 sites is intensively surveyed each year.

of *D. micans* since 1984, based upon visual surveys of all trees at 64 sites, expressed as an annual rate of increase. The ability of the predator to distinguish the relative densities of *D. micans* within broods is an important characteristic that points to potential density-dependent reductions in prey populations. This is illustrated in Figure 4, also from Evans & Fielding (1994), where the numbers of *R. grandis* adults present per brood is linearly related to the numbers of *D. micans* larvae per pupae. In addition, data by Evans (unpublished) show that, once in a brood, the adult predators lay their eggs in proportion to the prey present and show positive functional and numerical responses in the larval stages. Thus, survival of the predator and, more significantly from the point of view of integrated pest management (IPM), reductions in prey populations are assured by the biological characteristics of the predator.

Tvaradze (1977) stated that, in the Georgian Republic, reduced damage from *D. micans* following release of *R. grandis* was observed only when the proportion of attacked trees was less than 3%. However, in the same region, complete control of *D. micans* took seven to 10 years (Y. Zharkhov, pers. comm. in Evans & King, 1989). Similar trends have been observed in France (Van Averbeke & Grégoire, 1995). On average 60% of the brood chambers are colonized in Belgium at low prey density (Grégoire, 1988). In the Georgian Republic up to 78% of the broods can be colonized during outbreaks (Tvaradze, 1977).

Van Averbeke & Grégoire (1995) showed that although damage within a stand may continue to increase, other less noticeable changes occur as a result of the predator release. They also believe that local tree density and not predator abundance are important, as they found a slightly significant inverse relationship between local tree densities and proportions of attacked stems, a relationship that has been observed by many other authors.

CONCLUSIONS

In Britain, *D. micans* has shown its ability to colonize new forest locations both by its capacity to attack individual, apparently healthy trees, and also in its gradual spread into new locations by either trade-assisted movement or natural dispersal. The appearance of the bark beetle in Britain, without its natural predator, prompted an intensive programme of management, using the specific predator *R. grandis* as the central factor. In its natural range in Europe it is accompanied by *R. grandis* which, with occasional exceptions such as in Denmark during consecutive years of drought (Bejer, 1985), appears to exert significant population regulation to maintain populations below economically damaging thresholds.

Evidence now points to a successful programme of introduction and establishment of *R. grandis* in Britain; a strong link has been shown between the reduced pest population and the increased predator levels now encountered within the main infested area. Coupled with this, the importance placed on reducing long-distance dispersal by preventing movement of infested timber has formed the framework of Britain's integrated control programme. The assumption of success is backed up by recent survey data showing slow population expansion in the field and, coupled with this, low incidence of tree mortality. However, we need to remain vigilant, particularly in those forests outside the current infested area. Early warning of new outbreaks, such as that given by the annual surveys along the edge of the known infested area, will enable inundative releases of *R. grandis* to be carried out before *D. micans* populations can build up to destructive levels. Data on population levels early in the outbreak now show that the infestation in the UK was caused by non-catastrophic *D. micans* population levels, a fact that is in sharp contrast to the situation elsewhere (Carle, 1975; Evans & Fielding, 1994).

We still need to be concerned over the fate of spruce forests elsewhere in Britain (outside the infested area), where the potential of consecutive summer drought and winter frosts, such as occurred in Germany and Denmark during the late 1940s, could upset the balance that appears to be developing between predator and prey, and thus stimulate *D. micans* outbreaks. Such weather conditions have not as yet been recorded in Britain since *D. micans* was discovered. The experiences in Denmark provide a note of caution since the *D. micans* populations there were already subject to natural biological control by *R. grandis*. However, the sandy sites on which sitka spruce was grown and the combination of summer droughts and winter frosts recorded in Denmark are conditions that are not likely to be encountered in commercial forestry in Britain.

Van Averbeke & Grégoire (1995) suggest that biological control of *D. micans* is at present an empirical technique; release rates are set according to priorities such as forecasted predator production, instead of scientific data, and therefore range from 10-50 pairs per site in Britain (King & Evans, 1984) to 50-1000 pairs in France (Grégoire *et al*., 1989). Furthermore, the time

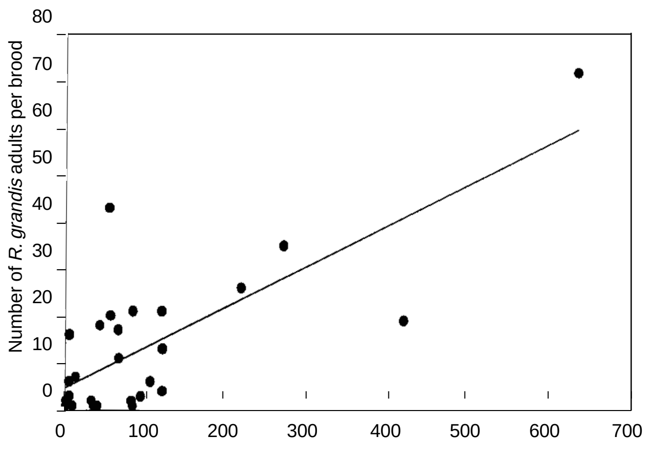

Figure 4. Colonization of *Dendroctonus micans* broods following release of 2500 *Rhizophagus grandis* adults from a single release point during a mark-release-recapture experiment. There is a linear relationship between the numbers of *R. grandis* adults and the numbers of *D. micans* larvae and pupae present per brood.

allowed for 'success' is still unpredictable, and what really happens within this interval is not known. Success has yet to be quantitatively defined. Experience shows us that, several years after predator release, rates of *D. micans* infestation always reduce to, and remain at, harmless low levels (5-10% of the attacked trees), and that 60-80% of the broods will be colonized by *R. grandis* (Van Averbeke & Grégoire, 1995).

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Tables 1 and 2 first appeared in Evans *et al.* (1985) and are reproduced with permission.

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