RESTORING THE NATURAL BALANCE: BIOLOGICAL CONTROL OF *DENDROCTONUS MICANS* IN GREAT BRITAIN

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ABSTRACT

Great spruce bark beetle, *Dendroctonus micans*, is an introduced pest to Britain. A strategy, based on importation and release of the predatory beetle, *Rhizophagus grandis*, has been adopted as the cornerstone of management against *D. micans*. *R. grandis* has a range of attributes, including specificity, rapid reproduction and effective dispersal capacity, that make it an ideal biological control agent. In combination with surveys and restrictions on the transportation of wood from infested forests, management of the pest through use of this imported natural enemy is proving effective.

INTRODUCTION

Great spruce bark beetle, *Dendroctonus micans* (Kug.) (Coleoptera: Scolytidae) is one of a number of major bark beetle pests affecting conifers in the northern hemisphere. The genus *Dendroctonus* contains over 20 species, their most destructive effects being noted in North America where extensive tree mortality and recurrence of infestations are a normal part of forest dynamics (Mitton & Sturgeon, 1982). European forests are also subject to bark beetle attacks, but here the dominant genus is *Ips*, particularly the eight toothed spruce bark beetle *Ips typographus* (L.) which has regularly killed large numbers of trees and is a pest of quarantine significance to both the UK and Ireland (Evans, 1995).

D. micans is the only *Dendroctonus* species of significance to Western Europe, having extended its range gradually from its natural Eurasian distribution to give rise to recent new infestations in the Georgian Republic, Turkey, south and west France and Great Britain. It is significant that infestations in these new geographic regions have initially been more serious than in those areas where the bark beetle is endemic. This has been variously attributed to exploitation of susceptible trees at the advancing front of new infestations (Carle *et al.* 1979) or to the tendency for infestations to be concentrated in areas suffering repeated droughts (Bejer, 1985). However, a common feature of all new infestations has been the absence of the specific predatory beetle *Rhizophagus grandis* (Gyll.) (Coleoptera: Rhizophagidae) that is invariably associated with well established populations throughout the range of *D. micans*. This has led to a number of programmes where introductions of *R. grandis* to new infestations of *D. micans* have been carried out, with the aim of restoring the natural balance between predator and prey.

Such an approach has been the objective of the present programme in the United Kingdom, where *D. micans* was first discovered in 1982 and was found, following extensive survey, to have established in most of Wales, the bordering counties of England and at a separate area in Lancashire (Fielding *et al.* 1991a). This paper describes the process of evaluation of the new infestations, the introduction to the UK of *R. grandis* and the impact of the predator on *D. micans* populations in the years since the predator was first released.

ESTABLISHING THE BASELINE: SURVEYS AND FOREST MANAGEMENT

Discovery of an exotic pest, such as *D. micans*, inevitably carries with it the possibility that the impacts of the organism may be different to those observed in its native range. There is also the possibility that, if the infestation has been discovered sufficiently early, aggressive intervention could result in eradication of the pest. Both these possibilities were considered in setting up an intensive survey regime centered on the initial discovery near Ludlow in Shropshire.

Visual surveys, commencing in 1982 over three years, for the presence of dead trees and for indicators such as canopy browning and resin tubes arising from entry of adult beetles to the bark, quickly confirmed that most of Wales and the bordering counties of England were infested, thus ruling out the possibility of eradication. It was also apparent, from assessment of European literature and discussions with scientists working on *D. micans* in Europe, that the bark beetle was behaving slightly differently to its normal attack patterns in its native ranges. In particular, attacks at all heights up the tree were noted, in contrast to the tendency for beetles to concentrate brood establishment on the lower 2-3 m of the trunk in most areas of western Europe (Gregoire, 1985; Evans *et al.* 1985). It was also noted that Sitka spruce (*Picea sitchensis* (Bong.) Carr.), was killed more rapidly than Norway spruce (*P. abies* (L.) Karst), even though *D. micans* tended to prefer the latter for oviposition (Evans & Fielding, 1994). This was a particularly worrying finding, considering that Sitka spruce is the principal commercial tree species in Britain occupying an area of over 650000 ha (Evans, 1987).

Over 12000 sites were examined during surveys carried out from 1982 to 1984, revealing over 85000 infested trees. Although relatively few (1000+) of these trees had been killed by *D. micans* activity, knowledge of the bark beetle under British conditions was so scant that it was decided to carry out selective felling of infested trees or clear-felling in the more heavily infested sites. This strategy was designed to reduce the rate of increase of the *D. micans* populations and, combined with regulations requiring movement of infested spruce only to sawmills having the capacity to debark the logs, to prevent accidental transfer of the pest from the infested area to the rest of the country. This strategy, initially under the 1967 Plant Health Act and more recently as part of a European Union Protected Zone requirement, is still in force in order to retain freedom from infestation in the major spruce growing areas of northern England and Scotland.

The 1982-84 surveys established the extent of the *D. micans* outbreak in Britain and also provided valuable information on the biology of the bark beetle in this country. For example, analysis of tree rings cut from felled infested trees demonstrated that *D. micans* had been in the country since at least 1973 and, thus, had developed here for approximately 10 years without detection. Information on the life cycle of the pest also indicated a relatively slow rate of increase, each generation taking between 10 and 18 months depending on temperature and time of year for oviposition (King & Fielding, 1989). There is no synchrony of emergence or oviposition and, therefore, any stage of the life cycle (egg, instars 1 to 5, pupae or adults) could be present on the tree at any time. The above information indicated that a maximum of 10 generations of the beetle had been completed since its initial establishment in Britain. Assuming that the initial infestation was small and restricted to one or very few sites, this implies a maximum per generation rate of increase of less than 3.0, based on an accumulated total of approximately 90000 infested trees during that period. Each tree can be assumed to have been attacked by at least one female, although it is known that up to 80% of attacks are abortive. There is, therefore, a considerable degree of natural mortality affecting the beetle populations, considering that each female produces up to 300 eggs in a number of separate brood chambers (King & Fielding, 1989). Some information is available on natural enemies, primarily predation by greater spotted woodpecker (*Dendrocopos major* L.) and parasitism by the ichneumonid *Dolichomitus terebrans* Ratz., but, being generalists, none have been shown to respond specifically to changes in density of *D. micans* (King & Fielding, 1989). Recently Mills (1983) analysed the natural enemy complexes of a wide range of European bark beetles and listed 21 species of Coleoptera, Diptera, Hymenoptera, mites and nematodes known to affect *D. micans* but, of these, only *R. grandis* was specific. Not all these natural enemies are present in Britain, thus contributing further to the potential for *D. micans* to exhibit greater population increase in this country relative to that observed in its natural range on the European mainland. One of the facets for potential long term management of *D. micans* was, therefore, to identify the most promising candidate natural enemies and to consider their introduction and release within Britain.

RESTORING THE NATURAL BALANCE: INTRODUCTION OF *RHIZOPHAGUS GRANDIS* FROM CONTINENTAL EUROPE

Methods of *R. grandis* rearing developed in Georgia and Belgium/France

Pioneering work carried out by scientists in the Republic of Georgia during the 1960s has provided a strong basis from which to consider the use of *R. grandis* as an introduced natural enemy against *D. micans* (Kobakhidze, 1965; Kobakhidze *et al.* 1970). Using a system of predator rearing in spruce logs in 18 laboratories, Georgian scientists released over 4 million *R. grandis* adults over an area of 129000 ha of oriental spruce (*Picea orientalis* (L.) Link). Monitoring of population changes following introduction indicated that stable populations of *D. micans* below the local economic threshold were achieved in 5-7 years (D. Zharkhov, personal communication). Personal observations by H F Evans in Georgia substantiated this view.

The same basic methodology of log rearing of the predator was employed by Belgian and French scientists in a joint venture to establish populations of *R. grandis* in new infestations of *D. micans* in the Massif Central area of southern France (Gregoire *et al.* 1985). Employed up to 1983, the system proved effective but very labour and material intensive and allowed only limited numbers (4100) to be reared for the first phase of the programme in France.

Introduction of *R. grandis* to Britain

Contact with Dr J C Grégoire of Brussels Free University was made soon after the British outbreak was discovered and arrangements commenced for the potential importation of *R. grandis* to Great Britain. Although importation and rearing of the predator could be carried out without licencing (it is not classified as a plant pest), any release of *R. grandis* required to be sanctioned under the Wildlife and Countryside Act (1981) which deals with release into the wild of non-indigenous organisms. This Act is administered by the Department of the Environment (DOE). Discussions commenced with DOE staff as soon as a decision was made to attempt to use *R. grandis* as part of the British management strategy against *D. micans*. The strongest point in favour of release of *R. grandis* was its reputed specificity against *D. micans*. Discussions with Belgian and French scientists and examination of the literature indicated that oviposition by the predator takes place only in the presence of *D. micans*, whereas the larval stages will feed on virtually any prey. This evidence was presented to the DOE who gave initial agreement for limited releases, under annual renewable licencing, from 1983. A requirement of licencing was that tests on possible oviposition by adult *R. grandis* should be carried out using a range of other potential prey likely to be encountered in the spruce forests where the predator was to be released. These tests, carried out over a three year period to include a number of bark beetle and weevil (Coleoptera: Curculionidae) species, from both conifers and broad-leaved trees, all proved negative, confirming that oviposition by the predator is initiated only by presence of suitable stages of *D. micans*. Later work by Wainhouse *et al* (1991) on the long distance attraction of *R. grandis* to *D. micans* broods and by Grégoire *et al* (1991) on the chemical cues required for oviposition, indicated that a complex and specific mixture of tree- and *D. micans*-derived volatiles determined the specificity of the adult predator.

Rearing and release of *R. grandis* in Great Britain

Rearing methods for *R. grandis* were based initially on the log rearing system employed by Georgian and Belgian/French scientists. This has been described in detail by Evans & King (1989). Specialised rearing units were constructed at Ludlow, Shropshire which facilitated the gathering of *D. micans* adults and spruce logs from the field and also fulfilled the legal requirement that no *D. micans* infested material could be moved from the Scheduled Area under the *Restrictions of Spruce Movement Order (1982)* under the 1967 Plant Health Act. The method involved placing *D. micans* adult females onto logs in small containers that encouraged them to burrow into the bark and oviposit. Around 40 days later the resultant *D. micans* larval broods were infested with one pair of *R. grandis* adults which oviposited among the prey larvae. Thirty days later, predator prepupae emerged from the logs and fell through collecting funnels to trays from which they were transferred to containers of moist peat and sand mixtures. A further 40 days were required for emergence of predator adults for use in the field or for further breeding purposes. Although effective, this method proved to be very labour intensive and was very wasteful of material. In addition, it became apparent that losses from disease, especially the fungus *Beauveria bassiana*, and a general decline in viability of adults, were severe limiting factors to production. Despite these limitations, a total of over 120000 adult *R. grandis* were produced during the period 1984 to 1986.

The limitations of the log rearing method had also been recognised by Grégoire *et al* (1985, 1989) who developed a method in which female *R. grandis* were encouraged to oviposit in containers containing *D. micans* larvae on fresh bark and rehydrated bark powder. The emergent predator larvae fed initially on the *D. micans* larvae and were then transferred to feed on muscid larvae. This method had the advantage of natural oviposition cues (the mixture of *D. micans* larvae and spruce bark) and the ready availability of muscid larvae as the main prey items. It also removed the dependence on spruce logs thus being labour and space efficient. Tests of the procedure were carried out in the British programme and refined for full scale mass rearing from 1986 to the present time. The success of the new system can be measured in the reductions in costs from approximately £2 per pair of predators in 1984 to <2 pence per predator under the present procedure.

Release strategy and mass release programme

One of the features of *R. grandis* that makes it so attractive as a potential biological control agent is the very strongly developed host finding capability of the adult predators. This has been studied in detail by Wainhouse *et al* (1991) in laboratory wind tunnel experiments in which various host and tree derived volatiles were compared to *D. micans* frass for their ability to attract adult *R. grandis*. They showed that a mixture of (+)-α-pinene, (-)-β-pinene, β-phellandrene, *dl*-limonene and 3-carene was 80+% as attractive as the natural frass. Later field tests confirmed this finding, using various traps and mixtures of volatiles compared with frass (Wainhouse *et al.* 1992). Depending on concentration of the mixture, captures close to those achieved with *D. micans* frass were achieved using known numbers of released *R. grandis* adults.

The above information, combined with the knowledge that numbers of predators being reared using the log system were limited, that a minimum of 1200 sites over a wide geographic area were infested and our increasing knowledge of the slow rate of increase of *D. micans* populations in the field, contributed to design of the release strategy for the predator. The following facets were taken into account in deciding to employ inoculative releases with low numbers of predators at all sites:

- It was felt that the selective sanitation felling programme being carried out during the 1982-83 period would contribute to slowing the rate of increase of *D. micans*, particularly by removing the largest known infestations. Combined with the early information that generation time was slow (10-18 months), this indicated that massive population increases were unlikely.

- Although over 1200 sites were infested, the majority of these had low numbers of trees attacked (mean number of attacked trees per site 121, 22 and 14 in 1982 to 1984 respectively (Fielding *et al.* 1991a)).

- *R. grandis* was known to have effective host finding capability that enabled it to retain predatory activity even at very low *D. micans* population densities (Gregoire, 1985).

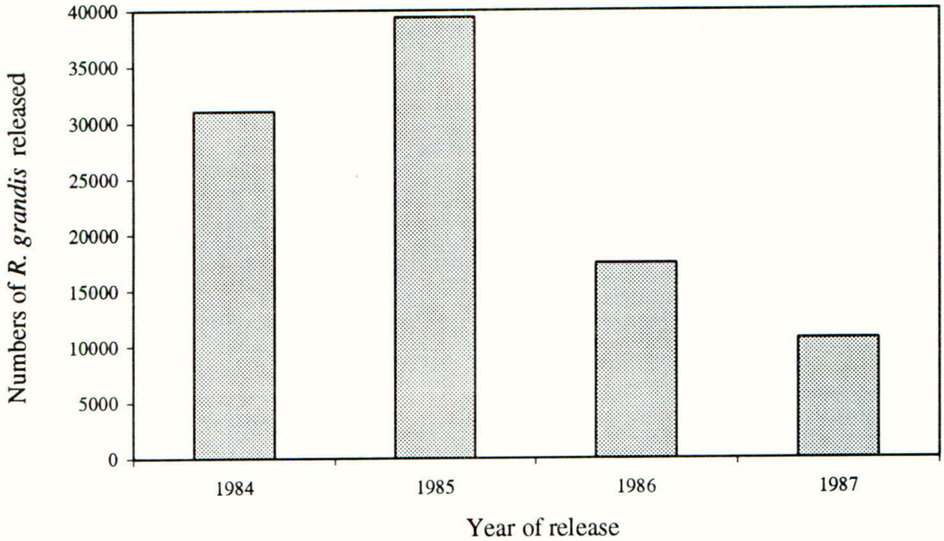
- *R. grandis* has a considerably faster life cycle than *D. micans*, completing each generation in as little as 6 months if eggs are laid during the period April to July (King *et al.* 1991). It, therefore, has the capacity to respond numerically to the presence of its specific prey.

- *D. micans* life stages are present throughout the year, thus ensuring that *R. grandis* have a source of prey whenever they are active in the field.

The inoculative strategy was initially based on release of 50 pairs of *R. grandis* adults at sites with >100 infested trees, 25 pairs for 50-99 trees, 15 pairs for 5-49 trees and 10 pairs for 1-4 trees. Later release strategy was altered to provide 3 pairs per tree.

Total releases per annum for the first four years of the programme (total of around 100,000 predators) are shown in Figure 1. Both Forestry Commission and Private Sector plantations received predator releases, thus ensuring that *R. grandis* was distributed over all known infested sites.

Figure 1: Numbers of *R. grandis* released in Britain during the initial period of the *D. micans* biological control programme.



Releases have continued to the present, but have been concentrated only on new infestations found during the course of surveys around the periphery of the infested area or previously undiscovered in the main infested area. In these cases inundative releases have been used reflecting the increased numbers of predators available from the new rearing system and also the desire to slow the rate of spread at the edge of the infested area as quickly as possible.

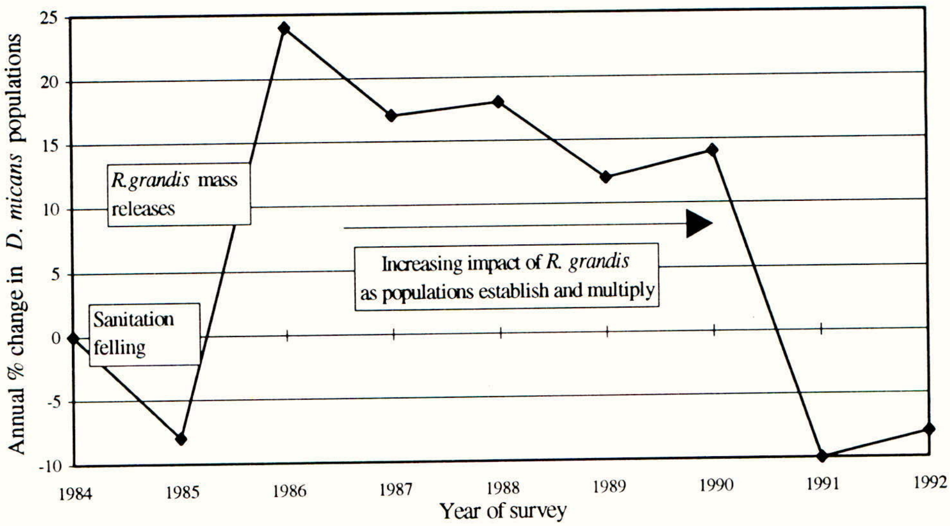
ASSESSING THE EFFECTIVENESS OF *R. GRANDIS* IN BRITAIN

A range of experiments and field observations, both qualitative and quantitative, have been carried out to assess the impact of *R. grandis* on *D. micans* population growth in Britain in the period since 1984. These have been described in some detail by Evans & Fielding (1994) and are summarised below.

Annual surveys of *D. micans* population density

Without felling a tree and examining broods for the presence of *R. grandis* it is not possible to determine with certainty that the predator is present at a particular site. However, whole plot surveys for the presence of *D. micans* can provide data on the rate of change of the prey population which, in turn, provides circumstantial evidence of impact of the predator. Surveys, in which all trees in given plots are examined for symptoms of *D. micans* attack, have been carried out at approximately 60 sites since 1984. Each tree found to be infested was marked and, thus, new attacks could be distinguished from previous attacks during each survey. The data, therefore, provide an accumulative total of trees attacked but, in particular, indicate what the relative rate of population increase has been from year to year. The results are summarised in Figure 2, which shows the percentage change in *D. micans* populations relative to the previous year.

Figure 2: Annual percentage change in *D. micans* populations (mean of 60 sites)



The results include three phases that can be linked to the control strategy employed against *D. micans*. Initially, *D. micans* populations showed a sharp decline consistent with the sanitation felling policy employed up to 1985. The rate of change then increased rapidly as populations returned to the normal development. Mass releases of the predator took place from 1984 to 1986, established successfully in the field and gradually multiplied. Thus from 1987 onwards there has been a steady reduction in the annual rate of increase of *D. micans* population growth to reach, in 1991, a negative growth rate. Changes in the numbers of sites available (some have been harvested) has prevented us from presenting data on precisely the same basis since 1992. However, the trends observed in the field have continued, with the annual percentage change at the remaining survey sites fluctuating around the -10% to +10% levels. This trend is consistent with the build-up time expected for the predator from inoculative releases and provides strong circumstantial evidence for a regulatory influence by *R. grandis* over *D. micans*, with populations appearing to show relatively small fluctuations around a stable equilibrium below an acceptable economic threshold level.

<u>Quantitative assessment of predator impact in detailed study plots</u>

R. grandis numbers can be assessed only by destructive sampling of *D. micans* broods following the felling of infested trees. This poses considerable limitations on quantitative field sampling because the process removes trees and limits sequential sampling over time. Nevertheless, it provides the only accurate measure of *R. grandis* impact in the field where both predator and prey populations can be scored. Three detailed study plots were established in the main infested area and sampled over a number of years, using 10% stratified random sampling (based on the degree of infestation of the trees). Results from all three sites were similar. Initial sampling took place two years after inoculative releases of *R. grandis*. An average of 34% of broods were colonised two years after release. This rose to 68% in the following year and, at the only site that had sufficient trees for a full quantitative sample in the fourth year after release, 83% of the broods had been colonised. Colonisation alone, of course, does not mean that population regulation is taking place, but in parallel to the increased presence of *R. grandis*, there was a reduction in the numbers of active *D. micans* broods in the plots.

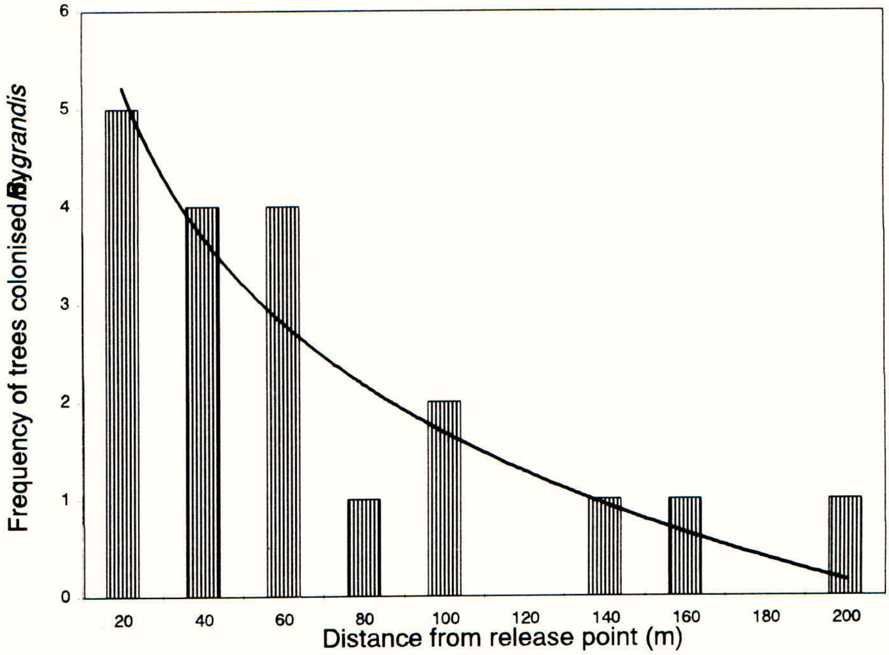
<u>Dispersal capacity of *R. grandis*</u>

A further facet of behaviour by an effective predator is the ability to disperse and locate its prey effectively (Luck *et al.* 1988). Experiments to determine the components of *D. micans* frass that act to attract *R. grandis* adults have been described earlier in this paper. Further work on the ability of *R. grandis* adults to locate prey in natural *D. micans* broods were carried out in mark-recapture experiments in the infested area (Fielding *et al.* 1991b). A release of 2500 adult *R. grandis* into a 2 ha Norway spruce site was followed by destructive sampling of those trees over the following month. Results demonstrated the rapid and effective dispersal of *R. grandis* adults to exploit the available *D. micans* population. In summary, 82 *D. micans* broods were located on 34 trees throughout the study area. These were examined for the presence of adult *R. grandis* which indicated that 28 (34.1%) had been located by the predator. Although there was some uncertainty arising from loss of the fluorescent dye used to mark the released adults, 374 *R. grandis* were found in sampling, representing a maximum of 15% of the number released. A frequency histogram, at 20 m intervals, of numbers of trees *D. micans* broods located with distance is shown in Figure 3.

This suggests a declining rate of capture at distances up to 200 m (203 m) from the release point but this is compounded by the slightly greater frequency of *D. micans* infested trees near the release point. However, the overall trend is consistent with a typical dispersal curve in which concentration declines with distance from the source.

There was also a significant linear correlation between the numbers of mature larvae and pupae of *D. micans* in each brood and the numbers of *R. grandis* that had colonised those broods, implying that adults were responding to the greater volatiles produced by larger broods. This is an effective strategy for the predator because laboratory experiments have shown that if eggs are laid in *D. micans* broods that are either small or have very young larvae, there may be insufficient food available for full development of the predator (Evans & Fielding, 1994). A strategy that maximises the chances of survival of the predator by offering abundant prey biomass and the ability of the adult predators to lay more eggs according to the availability of prey within a brood (Evans & Fielding, 1994) is a strong indicator that *R. grandis* is an effective regulator of *D. micans* populations. In the mark-recapture experiments described above, up to 70 adults had colonised a single *D. micans* brood, further demonstrating the capacity for exploitation of available prey. Similar results were obtained during sampling of *D. micans* broods in Belgium, where it was found that the proportion of broods colonised by *R. grandis* was greater (approximately 80%) in mature broods than in immature (eggs and first instars) broods (approximately 30%) (Gregoire, 1985).

Figure 3: Frequency of trees colonised by *R. grandis* adults following release of 2500 predators at a single point in a discrete Norway spruce forest block. Fitted line is $y = -2.192 \ln(x) + 5.21$, $R^2 = 0.80$



One of the most encouraging features of *R. grandis* dispersal capacity is the fact that it is now being found regularly in newly discovered *D. micans* infestations in the field, even when these are several kilometres from the nearest known release site for the predator.

CONCLUSIONS

Accumulating information, some of which has been presented above, is providing convincing evidence for the successful establishment and impact of the predator *R. grandis* as an effective biological control agent against the great spruce bark beetle, *D. micans* in Britain. This is entirely consistent with the principal features of the predator prey interaction observed by a number of research groups in Europe (Gregoire & Pasteels, 1985) and the former Soviet Union (Kobakhidze *et al.* 1970). The combination of rapid establishment, effective dispersal and maintenance of activity at low *D. micans* population densities implies that *R. grandis* will continue to regulate prey populations in the future. It is already moving with the slowly advancing front of the main *D. micans* infestation area and, thus, reduces the dangers of unexpected major bark beetle population increases on the periphery of the current known distribution. However, it is important to maintain an awareness of the natural rate of spread and, through the European Union Protected Zone strategy, to prevent long distance movement through trade in spruce within Britain. We are confident, however, that if a new infestation is found in the major spruce growing areas in northern Britain, releases of *R. grandis* will continue to provide the basis for long term regulation of *D. micans*.

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