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Potential for Biological Control of Dendroctonus and Ips Bark Beetles

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Potential for BIOLOGICAL CONTROL of Dendroctonus and Ips BARK BEETLES

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CONTENTS

PART ONE—BIOLOGICAL CONTROL: Concepts and Implications

PART TWO—CLASSICAL BIOLOGICAL CONTROL: Practical Considerations and Applications

PART THREE—Natural Occurrences of Biological Control

PART FOUR—The Potential for Insect Enemies of Allied Species

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PREFACE

The potential for biological control of *Dendroctonus* and *Ips* bark beetles (Coleoptera: Scolytidae) is examined in four parts: Part One, Biological Control: Concepts and Implications examines the potenial for biological control of *Dendroctonus* and *Ips* bark beetles and alternatives for sucessful biological control in theory and practice. Part Two examines Classical Biological Control: Practical Considerations and Applications, including the olfactory basis for insect enemies of allied species; bark beetles, natural enemies and current management strategies; biological control of *Ips grandicollis* in Australia; and the interaction of *Rhizophagus grandis* with *Dendroctonus micans*, the French and British experiences. Part Three diagnoses natural occurrences of biological control including *Ips typographus* in Central Europe; *Dendroctonus armandi* in China; *Ips* spp. in the southern United States Gulf Costal Plain; and the impact of natural enemies on *Dendroctonus frontalis*. Part Four examines the potential for insect enemies of allied species including inoculative release of *Rhizophagus grandis* for *Dendroctonus terebrans*; cross-attraction surveys for insect enemies of the southern pine beetle; and responses of insect associates of allied species to *Dendroctonus* and *Ips* aggregation pheromones. An administrative perspective and an overview of biological control research in the USDA Forest Service conclude the book.

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The potential for the biological control of bark beetles is a varied and complex issue. Perhaps the most intriguing section of the book is the recurring theme of *Rhizophagus grandis* as both an example of classical biological control and an example of its potential as an insect enemy of an allied species. Cross-attraction surveys provide a method to possibly identify potential biological control agents. This one volume will not answer all the questions but will perhaps provide a framework for examination of this complex and intriguing issue.

PART ONE

BIOLOGICAL CONTROL:
Concepts and Implications

SECTION ONE

Potential for Biological Control of *Dendroctonus* and *Ips* Bark Beetles: The Case For and Against the Biological Control of Bark Beetles

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INTRODUCTION

To evaluate the potential for the biological control of *Dendroctonus* and *Ips* species, it is necessary to examine the case from several perspectives. Starting with general concerns then moving to specifics of bark beetles in forested environments, much of the information discussed here can be found in several recent reviews on bark beetle natural enemies and their potential use (Dahlsten 1982, Mills 1983b, Moeck and Safranyik 1984).

Opportunities for biological control, through importation, augmentation or conservation, vary depending on the environment and the species involved. Each specific situation must be examined carefully since there are great differences among urban, agricultural and forest environments. Some of these differences will be discussed below.

Basic to any biological control attempt, regardless of the type of environment, is scientifically sound evaluation and documentation procedures. Unfortunately these are not always present in biological control programs so that generalization becomes difficult; however with this in mind we will speculate on the case for biological control of bark beetles.

The first step in any biological control program is to determine the distribution of the target pest and then to set up a statistically valid sampling procedure. Reliable population sampling is the foundation upon which any biological control program is built. Sampling methods must be flexible enough to adjust to variation in the distribution and abundance of the natural enemies. This is fundamental to the evaluation of the role of the natural enemy in the dynamics of the host insect.

The winter moth, *Operophtera brumata* (L.), program in eastern Canada (Embree 1971) and the larch sawfly *Pristiphora erichsonii* (Hartig) (Ives and Muldrew 1984), are good examples of well documented programs. However, because many of the programs are not like this, generalizations are difficult on some of the hotly debated topics in biological control. Several attempts have been made to examine a number of these issues with the information available (Hall and Ehler 1979, Hall et al. 1980, Hokkanen and Pimentel 1984). Debate over the approach to be taken in any biological control program is not new (Embree and Pendrel 1986). Some of the important questions that should be considered are as follows: 1) single vs. multiple species introductions, 2) introducing generalist (polyphagous) or specialist (monophagous) natural enemies, 3) attempts against introduced or native pests, 4) introduction of co-evolved (old) associations of natural enemies with their prey vs. new associations (see Hokkanen and Pimentel 1984, also Pimentel in these Proceedings), 5) introduction of parasitoids or predators, 6) introduction of "r" vs. "K" selected natural enemies (see Pschorn-Walcher 1977), 7) biological control programs on islands vs. continents, 8) success of programs against cryptic feeders (such as bark beetles) vs. open feeders (e.g., defoliators). In the following discussion we will address only a few of these interesting issues with respect to the natural enemies of bark beetles.

BIOLOGICAL CONTROL IN FORESTS

The approach or tactics of biological control may be quite different with forest pests as compared to agricultural or urban pests. These differences are due to some distinct attributes of forests. Urban problems are by and large aesthetic, which is not the case in forestry or agriculture. Some important aspects of the forest environment in comparison to agricultural systems follow.

One of the most important distinctions between forestry and agriculture is that the forest is a multiple use resource. Whereas the management goal of agriculture is a crop that is harvested one or more times per year, the management goals of forestry besides that of the timber crop may have other considerations such as wildlife, grazing of livestock, watershed and recreation. Thus, pest management decisions are frequently complicated by multiple goals and often competing interests. When timber is a goal of management, the time to harvest must be taken into consideration. Multiple treatments may be economically feasible for a cash crop harvested annually (such as cotton), but would not be so in a forest with a rotation time of 30 years as in the softwood forests of the southeastern United States. With a common rotation time of 50 to 100 years in other forested regions, the carrying costs of multiple protection attempts would be entirely impracticable.

Another important difference is that the size of contiguous forested regions which in general are much larger than that of agricultural areas even though farms have increased in size in recent years. In addition, forested areas usually have gradual boundaries or transition zones, whereas boundaries in agricultural areas tend to be abrupt, going from cotton to alfalfa to pasture, etc. As will be discussed below, the vastness of forest regions can be a limitation to the tactic selected and is particularly troublesome to the development of a biological control program.

Complexity is greater in the forest environment and has an important effect on pest control strategies. Forests vary from single species conifer plantations to multi-storied forests with great plant diversity. Some of the important factors lending to this complexity are: the depth or height associated with some trees (up to 75 meters); a mixture of age classes from seeds to mature trees; a mixture of tree species; and a number of plant canopy levels ranging from herbaceous plants to mature trees. This complexity affects the distribution of target insects as well as natural enemies and poses many problems in terms of sampling, coverage, and evaluation.

The approach to pest control in coniferous seed orchards and plantations is perhaps more similar to that in field crops than in natural forests, the complexity of which poses other dimensions in the development of pest control tactics. In agriculture plants with similar or the same genetic composition, are evenly spaced, and are watered and fertilized. To attain the level of sampling accuracy commonly found in agricultural systems requires far more work in forests. These difficulties are also an impediment to the development of pest control tactics.

Finally, the frequency of perturbation is much less in forestry than in agriculture. In agriculture there is as least an annual harvest and sometimes several harvests per year, as with alfalfa. The rotation time of a forest can vary from 30 to over 100 years and, depending on the silvicultural system, stand entries of once every 5 to 10 years would be considered frequent.

These differences in the forest add up to a different perspective with respect to pest control. Economic levels of damage will be much higher, as much more damage can be tolerated in a complex ecosystem. Costly, frequent pest control tactics would be unaffordable because of the large land areas involved and the cost of carrying the investment in control through to the time of harvest.

In contemporary biological control there are several options such as importation, augmentation, and conservation of natural enemies. Augmentation may be very difficult in most cases because of the vastness of the forested regions. In Europe, however, nesting boxes for insectivorous birds have been used with some success (Bruns 1960). Inundation would be a problem for the same reason. In China, inundative releases of *Trichogramma*, egg parasitoids, have been made in forested regions for control of defoliators but a large pool of labor and production via cottage industries made this possible (McFadden et al. 1981).

Conservation of natural enemies may be one of the most important approaches to biological control in forests. The vastness, complexity and reduced perturbation lends credence to this approach since it does not involve direct handling of the natural enemies. Conservation has not been carefully evaluated to date, and the effects of the various silvicultural systems, and pesticide use on the distribution and abundance of natural enemies of forest pests should be considered as part of any forest management tactic.

Pschorn-Walcher (1977) reviewed classical biological control (importation) in forestry and evaluated the potential based on ecological attributes of forests. As was pointed out above, forest environments are long lived and therefore relatively stable in space and time which leads to greater diversity in the animal and plant community. Diversity is an advantage in exploration for natural enemies, as there is usually a rich complex of parasitoids and predators from which to choose. On the other hand, this would be a disadvantage for importations as there may be fewer empty niches, particularly if the target is a native pest.

Importation and inoculative releases of natural enemies may be one of few biological control tactics available to the forest pest manager. This approach has dominated forest pest biological control attempts (Pschorn-Walcher 1977). Inoculative releases of natural enemies have been the standard of biological control programs in forests, because of their complexity as discussed above. Unfortunately, as with most biological control programs, documentation has been weak. Two cases well documented and studied are the larch casebearer, *Coleophora laricella* (Hübner), in the western United States (Ryan 1986) and the winter moth, *Operophtera brumata*, in eastern Canada (Embree 1971). Insects with a localized distribution or of recent introduction may be handled quite easily and quickly with inoculative releases, such as the winter moth. The same approach with the larch casebearer, which had a much wider distribution, took several years before success was achieved. Beirne (1975) analyzed inoculative releases in forest environments up to 1958 in Canada and found that the number of individuals per release was also important in establishment of natural enemies. He showed that approximately 60% of the species that averaged over 800 individuals per release became established. On the other hand, only 15% of the species that averaged less than 800 per release became established.

There have been some mass propagation release attempts, however, such as with the European spruce sawfly, *Diprion hercyniae* (Hartig) in Canada, where over 800 million eulophid wasps, *Dahlbominus fuscipennis* (Zetterstedt) were released between 1932 and 1942 (McGugan and Coppel 1962). Other notable mass release programs have been with parasitoids of the gypsy moth, *Porthetria dispar* (Lymantria) in the eastern United States (Leonard 1974) and a nematode, *Deladenus siricidicola* Bedding, for control of *Sirex noctilio* (F.), in Australia (Bedding and Akhurst 1974). Difficulty in rearing the natural enemies of many forest insects and the vast treatment areas preclude the use of this approach to biological control in forests and in particular to bark beetles, as will be discussed below.

At one time only introduced pests were considered to be the targets of the classical importation approach. However, there may be considerable opportunity for importation of natural enemies against native forest pests (Carl 1982). The chances for success would depend on the native insect pest to be controlled. For example, Moeck and Safranyik (1984) concluded after a careful review of the literature that the best tactic for biological control of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, was inundative releases of native predaceous clerid beetles at low outbreak levels of bark beetle populations. This conclusion was based on amenability to immediate experimental evaluation and operational trials and that much greater knowledge was needed than is currently available of the taxonomy and biologies of the native natural enemies to employ the other tactics.

Pschorn-Walcher (1977) concludes that forests are rather uniform over large areas and therefore parasitoid and predator complexes exhibit only minor differences. This would be an advantage for exploration but a disadvantage for importation and release which would be a long-term venture because of uniformity and vastness. Relative to agriculture, forests are not as frequently disturbed and therefore highly structured and well balanced natural enemy–host complexes have evolved and have been preserved. The response of bark beetle natural enemies to the bark beetle aggregating pheromones (kairomones) is a good example of one of these co-evolved systems. Borden (1982) lists 25 species in four orders

(Coleoptera, Hymenoptera, Diptera, and Hemiptera) that have been shown to orient to pheromones of their bark beetle hosts.

Because of the uniqueness of forest insect pests Pschorn-Walcher (1977) argues for a different approach to the biological control of forest insects. He emphasizes the importance of detailed pre-introduction studies of the parasitoid–predator complexes. He feels that there is higher degree of predictability in forests with natural enemies and this is the rationale for the pre-introduction studies. Agricultural pests have a more erratic make-up of the natural enemy–host associations and lend themselves more to the hit or miss approach. As a result, Pschorn-Walcher (1977) recommends multiple species introduction in agriculture, but for forestry he recommends single species introductions of natural enemies.

Pre-introduction studies would also identify r-selected and K-selected natural enemies. Pschorn-Walcher (1977) argues that r-selected species have some distinct advantages; they attack the early larval stages (vs. K-selected, which attack late larvae and cocoons), they often occur when host populations are low (vs. K-selected at higher population levels), and they are adapted to some degree of inbreeding and thus can stand initial low number colonization and perhaps prolonged laboratory breeding.

To further examine the forest as an environment for biological control tactics and eventually biological control of bark beetles, it is necessary to look at the establishment and success of previous attempts.

Hall and Ehler (1979) looked at natural enemy establishment based on habitat stability. From their examination of the literature, they found the following rates of establishment: 0.28 in unstable environments (annual or short cycle crops such as vegetable and field crops), 0.32 in intermediate environments (comparatively less disturbance such as orchards and other perennial crops), and 0.36 in stable environments (forests and rangeland). The only statistically significant difference was between stable and unstable environments. When the success of natural enemy introductions is examined using the same criteria of habitat disruption, the results show the intermediate habitats to be significantly higher than either stable or unstable environments (Hall et al. 1980). From this it is difficult to conclude whether biological control attempts would be more successful in forests or stable environments than in other types of habitats. The weak link in all these analyses of literature is the poor documentation of previous programs, as has been stressed above.

ENTOMOLOGICAL PERSPECTIVES

In the preceding discussion we focused on the forest as an environment for biological control attempts. In this section we will focus on the insect in relationship to the target pest in order to gain further insight into the biological control tactic as it may be applied to bark beetles.

An examination of the establishment and success of natural enemies by the Order of the target insect is interesting but may not be too meaningful. Natural enemies released against Homoptera had one of the highest rates of establishment (0.43) but against the Coleoptera it was the lowest (0.23) (Hall and Ehler 1979). The success of releases showed the Homoptera to be the highest in two categories, complete success (0.30) and any success (0.80) while the Coleoptera were the lowest (0.04) in the complete success category and near the lowest (0.36) in the any success category, being higher than only two other Orders (Diptera 0.31, and Thysanoptera 0.10) (Hall et al. 1980). Although the results of these analyses may be skewed due to multiple successes of one natural enemy against a host (e.g. the cottony cushion scale programs), it does appear that the beetles generally are not good candidates for biological control programs.

Releases of natural enemies have been made against native as well as exotic pests. There have been cases of establishment and success against both categories of pests. In analyzing the literature Hall and Ehler (1979) found natural enemies to establish at a significantly higher rate on exotic pests than on natives. With respect to complete success of natural enemies, the rate was higher for exotics (0.17) than natives (0.06), but the differences were not statistically significant. For all successes, however, the rate for exotics was significantly higher than with natives (Hall et al. 1980). Although this lends support to the classical biological control approach of introducing natural enemies from the native area of the pest (Huffaker et al. 1971) it is encouraging that the approach has applicability against native pests.

Recently the idea of new associations of natural enemies with their hosts has been proposed as the preferred method in selecting biological control agents (Hokkanen and Pimentel 1984, also Pimentel in these Proceedings). New associations could be formed when exotic natural enemies are released against native pests, and old associations when exotic natural enemies are released against exotic pests, as discussed above. Importations against native pests would always be new associations; it is also possible to have new associations of natural enemies with exotic pests.

The theoretical basis for the controversy stems from the opinion of Huffaker et al. (1971) that in the evolution of natural enemies with their prey that the more efficient species have a close association with their hosts. Therefore the chances for success in biological control programs would be greater with those natural enemies that had co-evolved with their hosts. Pimentel (1963) speculated that old associations among natural enemies and their hosts might prevent the natural enemies from being effective control agents. He stated that the benefit of the new association is based on avoiding the tendency of parasites and hosts to evolve some degree of balance (Pimentel 1961).

Just considering the analysis of natural enemy releases of native versus exotic pests (Hall and Ehler 1979, Hall et al. 1980) the proposal by Hokkanen and Pimentel (1984) that new associations be the preferred method appears weak. The analysis of the literature in all cases is based on a review of beneficial insect introductions by Clausen (1978). Hokkanen and Pimentel analyzed the number of releases per success and using Chi-square analysis came up with a figure that new associations yielded 77% more successes than old associations and thus their conclusion that this should be the preferred method. This is contradicted by the results of Hall and Ehler (1979) and Hall et al. (1980). Goeden and Kok (1986) also disagreed with the new association principle with respect to the biological control of weeds. Many of the examples used by Hokkanen and Pimentel (1984) came from programs against weeds. Goeden and Kok (1986) contend that the analysis was biased towards cactaceous insects, and that cacti are not representative of target weeds. They additionally believe that several of the new associations referred to by Hokkanen and Pimentel (1984) were inaccurate.

We reanalyzed the Hokkanen and Pimentel (1984) data using a Chi-square table (Table 1) and came to a different conclusion. It is curious that the authors did not discuss why 42% of the successes for old associations were complete successes while only 29% of the new associations were complete successes. Conversely, 22% of the old and 34% of the new were partial successes. An examination of the successful biological control data for 286 cases chosen by the authors shows an advantage ($p = 0.061$) for old associations in terms of complete versus intermediate versus partial success.

It is clear that arguments can be made for both approaches, native versus exotic pests or old versus new associations. A case by case analysis is the most appropriate approach rather than automatically choosing a single approach as a preferred method as Hokkanen and Pimentel (1984) have done with new associations. Because the forest environment has unique attributes, (as discussed above) and bark beetles have special biologies, as will be discussed below, these factors must be taken into consideration in the development of the biological control tactic to be used. Although the natural enemy complexes of many native forest insects may be known, their role in the population dynamics of their host are generally poorly known. The importance of documenting the impact and biology of natural enemies cannot be stressed enough.

Table 1

Tabulation of degree of biological control success (rows) by new and old associations (columns) showing frequency, row percent and column percent.

	New	Old	Totals
Complete	26	82	108
	24.07	75.93	37.76
	29.21%	41.62%	
Intermediate	33	71	104
	31.73	68.27	36.36
	37.08%	36.04%	
Partial	30	44	74
	40.54	59.46	25.87
	33.71%	22.34%	
	89	197	286
	31.12%	68.88%	

Statistics for table of success by association
Chi-square (2 df) = 5.5832 (p = 0.0613)
Cramer's V = 0.1397
Contingency coefficient = 0.1384

BIOLOGICAL CONTROL OF THE SCOLYTIDAE

Finally we come to a consideration of biological control as a tactic for the Scolytidae and in particular the three most economically important genera, *Dendroctonus*, *Ips*, and *Scolytus*. The general discussion of the forest environment and of insect pests was intended to serve as a background in order to evaluate the pros and cons of this tactic for the Scolytidae.

Although there appears to be renewed interest in the biological control of bark beetles (Berisford, Grégoire, Evans, Miller et al. in these Proceedings, Mills 1983b, Moeck and Safranyik 1984), there have been few attempts with the Scolytidae or with wood boring insects generally. The only partially successful program for a wood boring insect has been with a hymenopteran, *Sirex noctilio* in Australia, where parasitic wasps and a nemotode have been used (Bedding and Akhurst 1974, Turnock et al. 1976). There have been no successful biological control attempts against scolytids with either predators or parasitoids (Dahlsten 1982). A possible exception is the use of the predator *R. grandis* against *Dendroctonus micans* in Russia (Evans in these Proceedings). An unsuccessful attempt was made with a parasitoid on *Dendroctonus rufipennis* (Kirby) in Canada (Baird 1938). Parasitoids have been released in the United States for control of the smaller European elm bark beetle, *Scolytus multistriatus* (Marsham) and although there has been establishment, this has not been a successful program (Peacock 1975). *S. multistriatus* may not have been the best candidate for biological control since it is a disease vector (Dutch elm disease) and therefore requires a high degree of control. There have been other attempts worldwide but with no notable success (Mills 1983b). There are good reasons for the few attempts of biological control against scolytids and perhaps for the lack of success as well (see below).

Currently there are two active biological control programs against bark beetles that show promise. One is against *Ips grandicollis* (Eichhoff) in Australia (see Berisford and Dahlsten in these Proceedings) and the other is against *Dendroctonus micans* (Kugelann) in Britain (Evans in these Proceedings) and in France (Grégoire in these Proceedings). With *Ips grandicollis*, parasitoids and predators from the native range of the bark beetle in the southeastern United States are being introduced as well as natural enemies of *Ips* spp. that attack Monterey pine in California. This, then, is a test of a combination of new and old associations. The natural enemies are released one species per site so that establishment and success can be evaluated (Berisford and Dahlsten in these Proceedings).

The efforts with *D. micans* have concentrated on a predaceous beetle, *Rhizophagus grandis* Gyllenhal, which appears to be highly specific to and co-evolved with *D. micans*. In Britain (Evans in these Proceedings) and France (Grégoire in these Proceedings) the approach has been to mass rear the predator to keep pace with *D. micans* as it has spread across continental Europe and into Britain. This predator appears to do well in normal situations with *D. micans* in Denmark but not in rapidly expanding outbreaks (Bejer 1985). Mass rearing and inoculative releases appear to be a sound approach with this bark beetle. This often effective predator of *D. micans* is also being proposed as a potential control for several North American bark beetles (a new association) (Miller et al. in these Proceedings). Taking a highly co-evolved species and using its efficiency against its normal host as an argument for a new association appears illogical and serendipitous. It is interesting that Moeck and Safranyik (1984) after a careful review of the literature concluded that the best approach with the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, was to work with native predaceous beetles.

As with the development of any control strategy, a good understanding of the biology of the target pest is necessary. The Scolytidae have a number of biological attributes that must be considered. The fact that they occur in a relatively stable forest environment is certainly a factor, but perhaps more importantly they are cryptic insects and therefore present a special challenge to the investigator. In general, the natural enemy complexes of cryptic insects are smaller than with open feeders and those of Coleoptera less than Lepidoptera. For example, compare the Douglas-fir tussock moth, *Orgyia pseudotsugata* (McDunn.), with 45 primary and 18 hyperparasitoids (Torgersen 1981) and the spruce budworm, *Choristoneura fumiferana* (Clem.), with over 70 species of insect parasitoids (Mills 1983a) to the small natural enemy complexes of the bark beetles (Dahlsten 1982, Mills 1983b). Although the community of organisms that occur with bark beetles beneath the bark is rather large (Dahlsten 1982), it is also a very specialized, highly co-evolved community with perhaps few vacant niches. In addition, the beetles have co-evolved with the trees that they attack and often only attack trees that are predisposed by other biological or physical agents (Wood 1982). The beetles have evolved a close association with fungi and have specialized structures (mycangia) that facilitate this mutualistic relationship. Finally, the beetles have aggregating pheromones as an important part of their biology and these pheromones (kairomones) are used by the natural enemies of the bark beetles (Borden 1985). Many of these complex coevolutionary relationships have been reviewed in detail (Mitton and Sturgeon 1982).

There is a large but scattered literature on the natural enemies of bark beetles (Dahlsten 1982, Mills 1983b, Moeck and Safranyik 1984). In most cases information that is gathered on the natural enemies is secondary to that which is being taken for their bark beetle hosts (Borden 1982, Dahlsten 1982). From the studies that have been done, percent parasitization has been shown to be highly variable. This variability may be due to such things as bark thickness, tree species, host insect, silvicultural system, time of year and weather (Dahlsten 1982). The predators are more difficult to evaluate but are often abundant on bark beetle infested trees. There is no question that there is evidence for efficacy in some situations and that natural enemies may be important in the dynamics of bark beetles. Difficulty in rearing and studying these cryptic organisms may be one of the reasons that there has not been more effort in the development of biological control tactics with scolytids.

Whether or not predators or parasitoids should be the focus of a biological control program has been examined for other target insects. Hall and Ehler (1979) showed that there is no difference between the two types of natural enemies with respect to establishment and Hall et al. (1980) found this to be true for all successful biological control programs. From an examination of the literature, then, there is no reason to believe that parasites are superior to predators or vice versa for biological control programs (Hall et al. 1980).

In the case of the bark beetles there is not much previous information to go on with respect to selecting the tactic to be used in biological control. Parasitoids have been established on *Scolytus multistriatus* but they are not very effective (Peacock 1975). Parasitoids and predators have been introduced and established on *Ips grandicollis* in Australia but it is too soon to evaluate the success of this project (Berisford and Dahlsten in these Proceedings). Mass rearing and release of a predator, *Rhizophagus grandis*, on *D. micans*, appears to be successful on a limited basis in France (Grégoire in these Proceedings). In each of the above cases there has been an attempt to reestablish the contact between natural enemies and their host bark beetles using parasitoids and/or predators.

Currently there are two different approaches being proposed for the biological control of native bark beetle species in North America. Moeck and Safranyik (1984) recommend inundative releases of native predaceous beetles as a tactic against the mountain pine beetle, *D. ponderosae*. They came to this conclusion based on an analysis of the literature and some preliminary laboratory rearing experiments. The beetle predators were the easiest to handle and rear and they also felt that synchronization of parasitoids with the suitable life stage of the beetle could pose a problem. They also recommend further study of native and exotic natural enemies to provide the basic knowledge for further development of the biological control tactic for bark beetles. The use of exotic natural enemies against a native was not excluded by Moeck and Safranyik (1984) and was recommended by Mills (1983b) as a possibility.

The second approach is based solely on the new association concept (Miller et al. in these Proceedings). This involves only predaceous beetles and there are currently two different tactics proposed. The first is to use *Rhizophagus grandis* against southern U. S. pine bark beetles based on this predator's efficacy against its normal host, *D. micans*, in Europe. The rationale is that *R. grandis* would be a new association and therefore more effective (see Hokkanen and Pimentel 1984). Also, *R. grandis* has been found to respond to the pheromones (kairomones) of other *Dendroctonus* species in the U. S. (Miller et al. 1987) and a means of mass rearing is available (Grégoire 1986). Miller et al. (these Proceedings) propose using bark beetle pheromones as a means of selecting natural enemies (essentially predaceous beetles) for use in biological control programs. With this procedure the pheromones of several different species of bark beetles are set out in different regions of the world, and whatever predator responds in significant numbers is a potential candidate for introduction against the beetle that it responded to. This obviously would mean a new association.

There is no question that aggregation pheromones of bark beetles may be a useful way to collect and redistribute the native predators of bark beetles. However, using kairomones to select exotic natural enemies may be a questionable practice. There are often problems with the laboratory prepared mixtures, such as the proportion of the different compounds or the enantiomeric composition of a compound (Borden 1985, Wood 1982). Is it possible to determine what the field or laboratory response to a prepared mixture means? Is it the same response as that elicited by naturally occurring mixtures of pheromones and host tree odors? There are enough difficulties in studying the response of the bark beetles themselves, much less their natural enemies, and in most cases the natural enemy response has not been well studied (Borden 1985). Without a large scale, careful laboratory and field study of the response of exotics to the pheromones of various native bark beetles, this approach should not be encouraged. As a quick, shot-gun approach to select candidates for study, it may be adequate, but any such study should be preceded by in-depth studies of the natural enemies of the target bark beetles.

CONCLUSION

In the preceding discussion we have tried to evaluate the pros and cons of the biological control of bark beetles from several perspectives. There are several important attributes of bark beetles that should be considered in the development of a biological control program that perhaps dictate a somewhat different approach from what might be followed with urban or agricultural pests.

Biological control in forest environments should be approached differently because forests are vast and relatively stable. Bark beetle biologies have a number of unique aspects that must be taken into consideration—they are cryptic, are closely associated with fungi, attack in mass on predisposed trees, have a well developed chemical communication system that is used to focus their attack on certain trees and that is used by some of their natural enemies to find their beetle prey. They have small natural enemy complexes, and exist with a number of other organisms beneath the bark in a relatively structured manner.

The approach to be taken should depend on the target bark beetle and whether it is a native or an introduced species. In either case there should be sound preintroduction population studies with emphasis on the natural enemy complexes. In the case of introduced bark beetles this would help in the selection of the natural enemy. Single species releases would make evaluation of the introductions easier and may, in fact, be superior to multiple species releases in forested environments (Pschorn-Walcher

1977). Native species should also be evaluated carefully because of the structured nature of the natural enemy complex, and it should be determined whether there are available niches or greater competitive capacities for exotic natural enemies (new associations) before any introductions are attempted. The introduction phase should not be taken lightly.

With native bark beetles other approaches such as augmentation and conservation of natural enemies may be superior to importation of exotics. Inoculative releases of native predaceous beetles may also be an effective tactic for biological control of bark beetles. Critical evaluations such as with *D. ponderosae* in Canada (Moeck and Safranyik 1984) should be made in all cases and in this situation they selected inundative releases of native predators.

The bottom line in all cases is the detailed study of the natural enemies of bark beetles. This has been largely ignored in most bark beetle research. Studies with natural enemies as the focal point will help to solve the rearing, handling, collection and redistribution problems that confront bark beetle biological control workers. Because of the necessity to work with logs, the work is often labor intensive and requires considerable space. Collection of natural enemies using kairomones is a labor saving technique as is the vacuum technique used by Berisford (these Proceedings) to collect parasitoids from beetle infested trees.

There are many facets of natural enemy biology and behavior that remain to be discovered and the key to the development of successful biological control programs with bark beetles, particularly natives, may well lie here. For example, little is known of the effects of silvicultural systems or other forest practices on bark beetle natural enemies. As has been pointed out by Borden (1985), much remains to be done to understand the role of bark beetle kairomones. Looking to the natural enemies, primarily parasitoids, that arrive after the mass attack phenomenon, little is understood about parasitoid host finding. In this structured, co-evolved system it is possible that fungi, various microorganisms or tree decay compounds may play a role in parasitoids finding their hosts. Other factors such as host tree or characteristics of the host tree like bark texture and thickness (Ball and Dahlsten 1973) and specificity to the host beetle (Kudon and Berisford 1980) may also be critical to host finding.

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SECTION TWO

Alternative for Successful Biological Control in Theory and Practice

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ABSTRACT

Biological control can be made more effective in theory and practice by employing new parasite (predator) associations than by employing "old" associations typical of classical biocontrol. New parasite associations were found to be 3 times more effective than classical biological control. The ecological principle of this alternative avoids the evolved commensalism that generally takes place in parasite–host systems that have evolved over a long period. Another major advantage of new parasite associations is to provide a unique opportunity to control native pests, which constitute 60 to 80% of all pest species.

INTRODUCTION

Biological control is a highly effective method of pest control for many reasons. First, when the biocontrol of a pest is complete, no further investment is necessary to maintain control of the target pest species. This was the case when the Vedalia beetle was introduced from Australia for control of the cottony-cushion scale in California. When biological controls are as effective as the Vedalia beetle, the economic return per dollar invested is enormous. Several million dollars in crop savings are provided each year without further investments. Overall, biological controls return about $30 per dollar invested in control, and this includes all the research costs (Pimentel 1986a). This is a handsome return compared with pesticidal controls, which return only about $4 per dollar invested in control (Pimentel et al. 1978, Pimentel 1986a).

The prime difficulty with biological control has been the relatively small number of successes in controlling some of the 10,000 world pests. About 260 pest species have been effectively or completely controlled by biological controls (Huffaker 1986). Although the number of successes has been relatively low, we are convinced that opportunities exist to improve biological control and make it more successful through the use of alternative approaches.

Advances in knowledge of ecology, genetics, behavior, and other sciences offer new ideas and approaches for successful biological control. For example, in classical biological control only introduced pests were targets of biological control. Classical biological control was based on the fact that natural enemies of the introduced pest should be sought in the native home of the pest species. Thus, native pest species attacking the crop were not targets of classical biological control. However, the great majority of pest species in the world are in fact native organisms that moved onto introduced crops and became pests (Strong et al. 1977, Hokkanen 1984, Pimentel 1986b). In the United States, for example, about 60% of the insects, 50% of the weeds, and 45% of the plant pathogens are of native origin (Pimentel 1986b). In Europe, an estimated 70 to 80% of the pests are of native origin (Hokkanen 1985a).

In biological control there is a clear need to seek new information on the ecology of pests as well as natural enemies. In this paper we will further discuss the ecological principles behind the use of new associations in biological control. We will also answer some of the criticisms targeted at our previous analysis on the topic (Hokkanen and Pimentel 1984), and will present further data to support our approach, including fresh examples of ecologically new, effective exploiter–victim relationships. Furthermore, the interrelationships between genetics and ecology in pests and natural enemies will be examined with the goal of improving our understanding and the successes of biological control.

PARASITE/PREDATOR POPULATIONS AND HOST CONSERVATION

About half of all species in nature are parasitic or predaceous and obtain their food resources directly from living hosts (Pimentel 1968, Price 1975). The sugarcane plant, for example, has 1645 parasitic insect species feeding on it (Strong et al. 1977) and at least 100 parasitic disease microorganisms (Martin et al. 1961). Also, oaks in the United States have over 500 known insect species and closer to 1000 that feed on oak trees (Packard 1890, de Mesa 1928, Opler 1974). One of the major insect herbivore parasites of the oaks in the Northeast is the gypsy moth, which has about 95 parasitic and predaceous species feeding on it (Nichols 1961, Campbell and Podgwaite 1971, Podgwaite and Campbell 1972, Campbell 1974, Leonard 1974). Clearly, parasitism and predation are important ways of life in natural systems.

Although parasitism and predation are important ways of life, seldom in nature do these populations increase in number sufficiently to destroy their host populations. Various biological mechanisms function to conserve host populations. These include: patchiness, competition, other natural enemies, and feedback evolution (Andrewartha and Birch 1954, Pimentel 1961a, Nuorteva 1963, Pimentel et al. 1975, Strong et al. 1984, Rhoades 1985, Pickett and White 1985, Faeth 1986). Elton (1927) was the first to point out that " the whole structure and activities of the community are dependent upon the questions of food supply." Conservation of hosts (food) is clearly vital to parasite/predator survival. The stable food supply-demand economy in parasite/predator–host systems appears to be maintained often by genetic feedback evolution (Pimentel 1961a).

The relative stability in parasite/predator–host systems is achieved primarily with individual selection and probably rarely by group selection. Conservation in nature is generally an accepted ecological principle because parasites/predators do not usually destroy their host populations (Hairston et al. 1960, Slobodkin 1961, Pimentel 1961a, Coley et al. 1985, Rhoades 1985, Janzen 1985). This has direct applicability to biological control because our goal is to have the parasite/predator populations reduce their host (pest) numbers to a suitably low level and to keep them at a stable low level.

Most host populations can not tolerate much feeding pressure from their parasite/predator populations. Host resources are limited and thus they must be conserved for themselves. A host utilizes most of its energy and other resources for its own growth, maintenance and reproduction. Roughly only 10% of the host's resources are passed on to parasites and predators (Slobodkin 1960, Phillipson 1966, Odum 1971, Pimentel et al. 1975, Pimm 1982). Plants use 38 to 71% of their energy resources just for respiration; poikilotherms about 50%; homeotherms 62 to 75% (McNeill and Lawton 1970, Odum 1971, Humphreys 1979). Because hosts utilize most of their energy resources for themselves and their progeny, even a small amount of parasite/predator feeding pressure can influence the abundance and distribution of host populations.

In a recent survey of 93 cases of the interactions of herbivores and plant hosts, an average of 7% (range 0.1 to 30%) of the productivity of terrestrial plant–hosts were consumed by parasite/predator (herbivore) populations (Pimentel 1988). These data tend to confirm that hosts can give up only a relatively small percentage of their resources to parasite/predator populations and remain at some stable equilibrium level. Thus, host conservation is important. Of interest is how parasite/predator feeding pressure is limited to less than 10% of the resources of the host.

FEEDBACK EVOLUTION AND DEFENSES IN HOSTS TO PARASITES/PREDATORS

An evolutionary feedback mechanism appears to play a role in limiting herbivore/parasite feeding pressure to some limited level of energy and other resources in the host (Pimentel 1961a, Pimentel et al. 1975). To achieve this economy individual hosts either evolve defense mechanisms (Figure 1), or the parasite/predator populations evolve to only moderately exploit their host population (Pimentel 1961a, Levin and Pimentel 1981). The defenses that evolve in hosts include nutritional, chemical, and physical resistance factors and combinations of these factors (Pimentel 1968, Whittaker and Feeny 1970, Levin 1976, Segal et al. 1980, Berryman 1982, Rhoades 1985, Coley et al. 1985). Note, if parasite/predator numbers are limited by other parasites and predators feeding on them, then the parasites/predators probably exert little or no selective pressure on their host, including plants (Hairston et al. 1960, Lawton and McNeill 1979, Price et al. 1980, Schultz 1983a,b,c).

Evolutionary feedback probably functions as a density–dependent control. Thus, when parasite/predator numbers are abundant and the feeding pressure on the host is relatively intense, selection in the host population will favor allelic frequencies and defenses in the host population that reduce parasite/predator rates of increase and eventually parasite/predator numbers. When slugs and snails, for example, feed heavily on bird's-foot trefoil, the proportion of resistant alleles and level of cyanogenesis increase (Jones 1966, 1979). This tends to reduce feeding pressure on the trefoil.

This relationship can be illustrated further. For simplicity, assume that at one locus in the host there are two alleles, A and A'. The rate of increase of the parasite or predator on a susceptible-type host with AA is >1, whereas on a resistant-type host with A'A'-defenses the rate of increase is <1. Thus, depending upon the proportion of the two alleles in the host population, parasite/predator numbers will increase or decrease — eventually some equilibrium ratio of the two alleles may be approached (Pimentel 1961a).

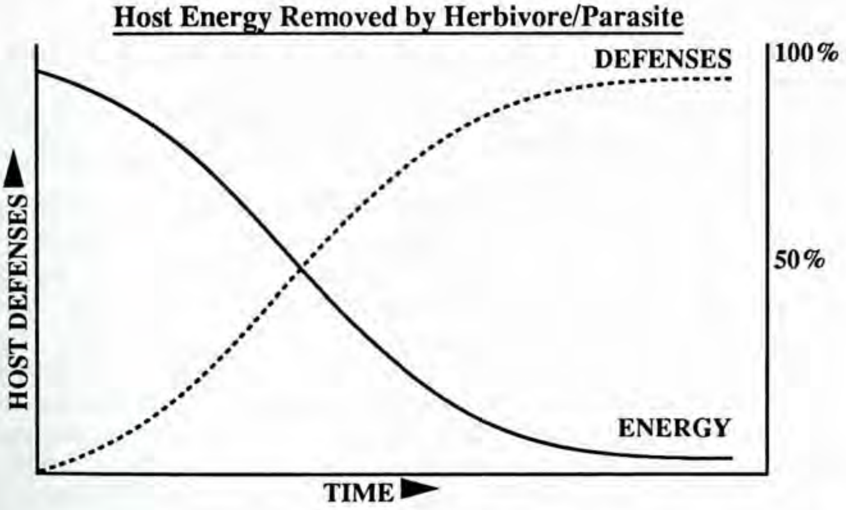
Host Energy Removed by Herbivore/Parasite

Fig. 1. With time, as host defenses increase, the portion of host energy removed by the herbivore/parasite population declines as some equilibrium is achieved in the system.

When the parasite/predator population is exerting heavy feeding pressure and there is intense selection on the host, the frequency of resistant A'-type allele will increase in the host. Natural selection acting on the host favors the retention of a sufficient proportion of the A'-defense allele (Levin 1976, Pimentel et al. 1975). Then, parasite/predator numbers will decline and their feeding pressure on the host will be restricted. The host population probably can never develop 100% effective defensive mechanisms against all parasites/predators exerting the selective pressure on it because of the cost of production and maintenance of defensive mechanisms (McKey 1974, Cates 1975, Krischik and Denno 1983, Rhoades 1985, Rosenthal 1986). At the point when parasite/predator numbers have declined to a suitably low level, the host will no longer benefit from spending energy and other resources to increase its level of resistance to its parasite.

The costs of defensive factors are an essential part of the functioning of the genetic feedback mechanism and equilibrium in the food economy of parasite/host systems (Pimentel 1961a). In the model, when parasite numbers decline sufficiently, then the frequency of defensive alleles will also decline because these alleles cost the host and are usually at a disadvantage in an environment without the parasite (Pimentel et al. 1954, Crow 1957, Pimentel 1961a, Levin 1972, Krischik and Denno 1983). A balance in the economy of the parasite and host is achieved when the costs for host defenses approximately equal the benefits of defenses that reduce parasite feeding pressure. At this point, there is maximal fitness for the host. The costs of the defensive mechanisms utilized by hosts depend on the types of defenses—including nutritional deficiencies, toxic chemicals, tolerance, and various physical factors.

Much evidence supports the proposition that parasite populations are controlled by a wide array of combination defenses, including nutrients, chemical toxicants, physical factors, behavioral avoidance plus natural enemies and other factors (Lawton and McNeill 1979, Price et al. 1980, Schultz 1983a,b,c, Parlevliet and Zadoks 1977, Fleming and Person 1982, Crute 1985, Bremermann and Fiedler 1985, Fraser 1985). The defensive characters, which spread through the host in response to parasite feeding and selective pressure, limit parasite feeding to some level of harvest that conserves the host. The costs of the developing defensive characters prevent the host from accumulating a sufficient level of resistant characters to eliminate completely parasite populations — optimal fitness results from a trade-off of the benefits and costs. Then, levels are such that a relatively sustainable equilibrium exists between host and parasite populations.

EVOLUTION OF PARASITE/PREDATOR POPULATION CONTROLS

In nature, parasite/predator population controls are highly complex. Although numerous factors interact to limit the numbers of parasite/predator organisms in nature, frequently efforts are made to seek general principles that contribute to the control of natural populations. This discussion gives particular attention to the density-dependent parasite/ predator population controls of feedback evolution, natural enemies, competition, and patchiness.

The hypothesized relationship between parasite populations and the factors limiting their numbers are diagrammed in Figures 2 and 3. In favorable environments, and after a supply-demand equilibrium evolves in parasite/predator–host systems, competition and patchiness appear to play a relatively minor role in controlling parasites (Pimentel and Al–Hafidh 1965, Pimentel et al. 1975). Under these conditions, natural enemies and feedback evolution appear primarily to dominate as control agents by individual selection of parasite/predator populations (Figure 3). The degree of control exerted by each density-dependent factor varies for each species, and in addition these often vary in space and time for each population. This emphasizes the complex picture that exists with herbivore populations and their plant hosts in nature and why we have trouble gaining insight into the factors governing the dynamics of natural herbivore–plant systems (Janzen 1985). This is especially true after the systems have evolved for millions of years. Our view of the system is but an instant in time and it becomes a challenge to interpret how the system evolved this relationship.

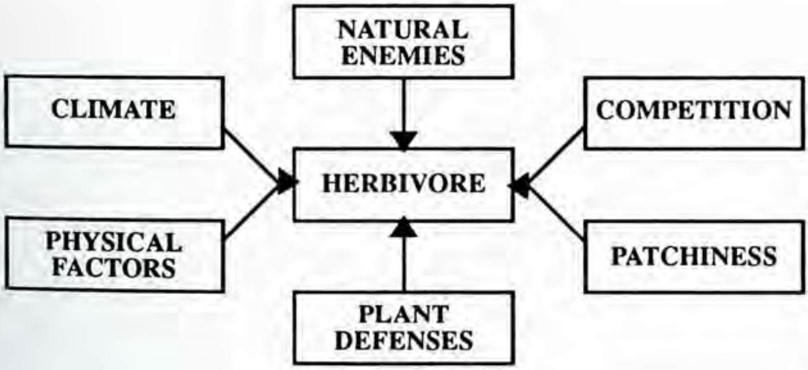

Fig. 2. Feedback evolution and natural enemies play a relatively major role in controlling herbivore numbers in natural systems. Other density-dependent factors, competition and patchiness, contribute to the stability of the herbivore/parasite–host interactions.

created patchiness (increased distance between hosts as host numbers declined).

One of the clearest examples of the evolution of different population controls in a parasite–host system is the myxomatosis virus parasite that was introduced for the biological control of the European rabbit in Australia. The European rabbit, introduced into Australia about 1859, increased rapidly and reached outbreak levels within 20 years. Natural vegetation and pastures were devastated and farmers requested the rabbit pest be controlled (Stead 1935). The myxoma virus was brought from South America where it was associated with the tropical forest-rabbit in which the parasite had minimal effects (Ratcliffe et al. 1952, Fenner and Marshall 1957). The fact that the myxoma virus had little effect on the South American rabbit suggests the viral parasite and South American rabbit had evolved some degree of balance. Certainly, the amount of harvestable energy being removed by the parasite population from the South American rabbit population appears to be relatively small.

In the new association between South American rabbit virus and the European rabbit, the rabbit evolved some defense against the parasite and the virus evolved genotypes (strains) of decreased virulence (Fenner and Myers 1978). In the trend toward a stable equilibrium, the less virulent virus strains evolved and dominated the virus population. At present these viral strains have decreased their impact on the rabbit population and are removing less energy (Levin and Pimentel 1981).

The evolution of population control mechanisms in parasite–host systems was also investigated in a wasp parasite–house fly host system and a simulated parasite–host system also using the house fly (Pimentel and Al–Hafidh 1965, Pimentel et al. 1975). Initially, more than 90% of the control of the two parasitic populations was achieved by competition (Pimentel and Al–Hafidh 1965, Pimentel et al. 1975). Eventually the hosts evolved sufficient defenses to reduce parasite population numbers and their feeding pressures. After major evolution had taken place in the host population, during which significant defenses had developed in the host, about 80% of the mortality and control of the parasite population was by feedback evolution while competition accounted for only 20% of the control. Thus, after evolution, control of parasite numbers shifted from being based on competition to genetic feedback (Pimentel and Al–Hafidh 1965, Pimentel et al. 1975).

In this laboratory population system, when feedback evolution dominated the control of parasite numbers, the amplitude of population fluctuations in the parasite population was dampened and the systems were noticeably more stable than when competition was the dominant control. Af-

1984). About 72% of the natural enemy species introduced for biocontrol came from the native habitat of the pest.

Table 1

A comparison of the number of complete, intermediate, and partial biocontrol successes of introduced natural enemies representing new and old exploiter–victim associations[a] (Hokkanen and Pimentel 1984).

Biocontrol	Exploiter–Victim Association	
Success	New	Old
Complete	26	82
	(22)[b]	(86)
Intermediate	33	71
	(22)	(82)
Partial	30	44
	(15)	(59)
TOTAL	89	197
	(59)	(227)

[a]Each species pair is considered only once.

[b]The figures in parentheses are the expected numbers of successes in each category, if there were no differences in biocontrol success between natural enemies representing new and old exploiter–victim relationships. Because of the method of calculating the expected numbers of success (Hokkanen and Pimentel 1984) the χ^2 values can be given for each success category separately.

χ^2 complete = 0.93, df = 1, not significant.
χ^2 intermediate = 6.98, df = 1, $p < 0.01$.
χ^2 partial = 18.81, df = 1, $p < 0.001$.
χ^2 total = 18.90, df = 1, $p < 0.001$.

The remaining 28% do not represent the proportion of new associations. In 46% of the biocontrol projects listed in Table 2, new associations were never tried. When a new association was tried, previously an average of 2 species representing an old association was tried first (Hokkanen and Pimentel 1984). Most often, 6 to 7 trials with old associations were tried before a new association was attempted.

Even when 6 to 7 trials with old associations were attempted before a new association was employed, there have been numerous successes using new associations (Pimentel 1963, Hokkanen and Pimentel 1984). For example, two prickly pears, *Opuntia inermis* and *O. stricta*, were introduced from Texas and Florida into Australia. They spread widely and

Table 2.

The proportion of new species associations of the total in 95 biocontrol projects that were targeted against 50 pest species (Hokkanen and Pimentel 1984).

Projects	Individual species introductions targeted against 50 pests		95 individual biocontrol	
No. of biocontrol agent species introduced n	% of all target pest species against which n number of natural enemies were used (Number = 50)	% of new species associations of all natural enemy species used	% of biocontrol projects terminated after introduction of nth species (Number = 95)	Avg. % of new species assoc. of the total no. tried in each proj. ending at step n
1	14.0	14.3	25.3	16.7
2	10.0	21.4	20.0	18.4
3	22.0	28.3	21.1	26.3
4-5	16.0	16.3	11.8	14.6
6-10	18.0	6.6	10.8	7.3
>10	20.0	40.8	10.8	43.5
WEIGHTED AVERAGE	–	22.3	–	20.7

rendered millions of hectares useless for cattle and sheep production (Dodd 1940). Several attempts were made to introduce effective biocontrol agents from Florida and Texas, but these failed. Later, the moth *Cactoblastis cactorum*, which was distributed in Argentina, Uruguay, Paraguay, and southern Brazil feeding on the tiger pear, *O. aurantiaca*, was introduced into Australia for biological control. The moth provided exceptional control of *O. inermis* and *O. stricta*, the two most serious pests (Dodd 1940). Interestingly, the moth was ineffective against its native tiger pear.

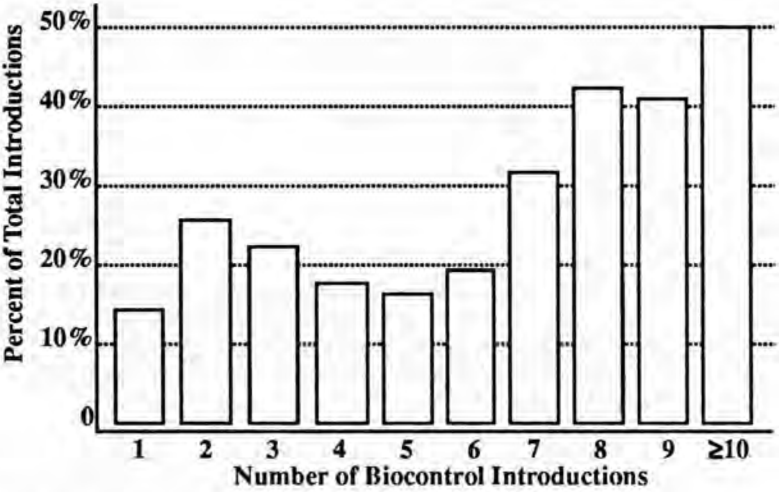

Fig. 4. The frequency with which old-association biocontrol agents were introduced before one new-association biocontrol agent was introduced. For example, for Column 7 biocontrol introductions, a total of 6 old association biocontrol agents was introduced before 1 new association was introduced. This ratio accounted for 31% of the total number of introductions (n = 447). Only 15% of the total introductions was a new association initially tried, and it was the only introduction. The sample included a total of 447 biocontrol agent introductions to control 50 pests (Clausen 1978, Hokkanen and Pimentel 1984).

Another example is the Egyptian fluted scale, *Icerya aegyptiaca*, which was introduced into the Carolina and Marshall Island groups where it seriously damaged citrus and other fruits. This scale was eventually controlled by importing a coccinellid from the Saipan and Palua Islands, although the predator appears to have come originally from China and Formosa (Beardsley 1955).

Recently, Dr. Arnold Drooz and others (1977) employed the principle of seeking new associations of natural enemies with a pest. They introduced a parasitic wasp (*Telenomus alsophilae*) obtained from the fall cankerworm moth in Virginia and introduced to Colombia, South America for control of the pine moth (*Oxydia trychiata*). The biological control of the pine moth was spectacular with this single new association biocontrol introduction.

There are numerous other examples of successful biological controls employing new associations (Pimentel 1963, Hokkanen and Pimentel 1984). It should be noted that when all biocontrol projects targeted against particular pest species are considered, the proportion of new species associations of the total control effort was 22.3% (Table 2). This information was used to calculate the proportion of successes that have resulted from new and old associations (Hokkanen and Pimentel 1984). Based on this, parasites that were newly associated with a host had a 77% greater success rate than using a parasite from the native region of the pest (old association).

Goeden and Kok (1986) would have preferred Hokkanen and Pimentel to exclude all 30 of the cacti biocontrol projects because Goeden and Kok believe that the cacti influenced the results and conclusions "since there were so many *Opuntia* species." However, if one makes an analysis of Laing and Hamai's data on the 30 *Opuntia* spp. biocontrol associations, the results agree with the overall results of all the other cases analyzed (Table 3). Of the 30 cases of cacti, 8 were new associations and 22 were old associations (27% vs. 73%). The ratio for all other data in Hokkanen and Pimentel (1984) was 28% vs. 72%. Thus, if anything, the analysis and statistics would have strengthened our arguments had we left out the *Opuntia* species from the analysis.

Table 3

Biological control of 30 *Opuntia* spp. from Laing and Hamai (1976) for "new" and "old" associations.

		Degree of Biocontrol		Subst.		
Assoc.	Part.	Subst.	Comp.	Comp.	Total	n
New	12.5%	25.0%	32.5%	25.0%	100%	8
Old	13.6%	26.7%	31.8%	27.3%	100%	22
Total	13.3%	26.7%	33.3%	26.7%	100%	30

Goeden and Kok (1986) also suggested that data on new associations and specificity were distorted because biocontrol data on cacti (*Opuntia*) were used in Hokkanen and Pimentel's (1984) study. Are cacti really any different for biological control as indicated by Goeden and Kok than any other pest organism? No! In the analysis made by Hokkanen and Pimentel (1984) of Laing and Hamai's (1976) data on biological control, Hokkanen and Pimentel assessed all the exploiter–victim relations listed. No attempt was made to exclude any data to avoid bias in the statistical analysis.

SPECIFICITY IN PARASITES FROM "OLD" VS. "NEW" HOSTS

Because parasite and predator species introduced from one host to a new host are thought to be generalists, there have been questions about the needed specialization for the control of pests, like weeds, when employing new associations for biological control (Goeden and Kok 1986). Specificity in parasites/predators for hosts depends on the ecology of the parasites/predators and their hosts and the other species making up the "old" and "new" biotic community. The only case of an introduced biological control agent for weed control moving to feed on crops was the classical biocontrol introduction of the lace bug to control a weed pest in Mauritania (Pimentel et al. 1982). The lace bug began feeding on the sesame crop. However, there has not been a single case of an environmental problem with new biocontrol associations introduced for weed control (Pimentel et al. 1982)!

The "newly associated" biological control agents have demonstrated similar specificity for pest–host control as other classical biocontrol introductions. For instance, the *Cactoblastis cactorum* moth introduced for control of two *Opuntia* species fed in the target area only on these two cacti species (Hokkanen and Pimentel 1984). Also the virus from the South American rabbit specifically controlled the European rabbit both in Australia and Europe (Levin and Pimentel 1981). Similarly, the accidental introduction of the Dutch elm disease attacked only the American elm in the United States and Canada, thus further confirming the type of host specificity that "newly associated" parasites may have.

For further assessing the host specificity and the pattern of host switching in biocontrol agents that have successfully been used to control a new host species, the data of Hokkanen and Pimentel (1984) were used as a starting point. The original host species of the control agents were determined based on published information. For 46 species of parasites this could be determined, whereas for 12 parasites the original host is not known. Polyphagous predators were excluded from the assessment.

In general, the newly associated biocontrol agents listed by Hokkanen and Pimentel (1984) do not differ in host specificity from old associations used in biological control. Some of them show host specificity to such an extent that the biocontrol host is the only known host (i.e., the original host is not known at all). Such agents are, for example, *Lecaniobius utilis* (Hymenoptera, Eupelmidae) for the control of black scale, *Metaphycus helvolus* (Hymenoptera, Encyrtidae) for the control of the black and nigra scales, *Tetrastichus brevistigma* (Hymenoptera, Eulopidae) for the control of elm leaf beetle, *Allotropa utilis* (Hymenoptera, Platygasteridae) for the control of apple mealybug, and *Hypena strigata* (Lepidoptera, Noctuidae) for the control of lantana (Hokkanen and Pimentel 1984).

Of the 34 other parasites of insect pests, for which reasonably reliable host specificity data were available, 5 (15%) are restricted in their feeding to 2-4 different species within the same genus. Furthermore, 8 (24%) species feed only on hosts within a specific subfamily, 14 (41%) can utilize many hosts within one family, 5 (15%) are able to parasitize hosts from different families within the same superfamily, and only 2 (6%) species can parasitize hosts from different superfamilies.

Table 4

Taxonomic distance in host switching by biocontrol agents that have successfully controlled an evolutionarily new host species. Figures are the numbers of biocontrol agents in each group, W = agents for weed control, I = agents for insect pest control.

	Original host vs. new host of agent					
	Different species in same genus		Different genuses in same subfam.		Different subfam.	
Biocontrol Success	W	I	W	I	W	I
Complete	5	2	0	5	0	1
Intermediate	5	10	0	6	0	0
Partial	1	10	0	7	0	5
Total	11	22	0	18	0	6

Regarding the pattern of actual host switching in effective biocontrol of evolutionarily new hosts, as a whole the majority of the successful newly associated biocontrol agents were transferred from closely related hosts within the same genus as the target species (Table 4). However, as all the cases in the biological control of weeds were in this category, the data for data for insect pests show, in fact, a tendency for longer taxonomic "jumps" to a new host: over half (52%) of the cases were transfers from a different genus or even from different families of host insects (Table 4). In fact, considering the different success categories as well, it seems that for insect pest control the most successful new association biocontrol agents on the average have not been from species very closely related to the target host (= within the same genus), but from allied species within the same subfamily or family as the target pest. This might be explained by the probable similarity of defense reactions within very closely related species.

The longest jump providing a spectacular biocontrol success was the use of *Telenomus alsophilae* (Hymenoptera, Scelionidae) to control *Oxydia trychiata* (Lepidoptera, Geometridae, Eunominae) in Colombia (Drooz et al. 1977). The natural host of *T. alsophilae* in North America is *Alsophila pometaria* (Lepidoptera, Geometridae, Oenochrominae). Several spectacular successes by biocontrol agents originating from a different host genus exist, e.g., the use of *Apanteles flavipes* (Hymenoptera, Braconidae) to control the sugarcane borer *Diatraea saccharalis* (Lepidoptera, Pyralidae) in Barbados is a well-documented, complete biocontrol success (Alam et al. 1971).

Other target pests completely controlled by agents switching from hosts in a different genus include *Levuana iridescens* in Fiji, *Nezara viridula* in Hawaii, *Chrysompalus dictyospermi* in Greece and California, and *Aonidiella aurantii* in Australia.

In only two cases a natural enemy attacking an insect host species within the same genus as the original host has produced a complete biocontrol success: *Promecotheca coeruleipennis* (original host *P. nuciferae)* was controlled in Fiji, and *Brontispa mariana* (original host *B. longissima*) in the Mariana Islands. In both cases the control agent was a hymenopterous wasp from the family Eulopidae. These two eulopiids also demonstrate a very narrow host range (3-4 different species the same genus), whereas the tachinids *Bessa remota* (for controlling *Levuana iridescens*) and *Trichopoda pennipes* (for *Nezara viridula*) are examples of very successful new association biocontrol agents with a wide host range (host species in different families and superfamilies, respectively).

FURTHER EVIDENCE SUPPORTING THE USE OF NEW ASSOCIATIONS IN BIOLOGICAL CONTROL

In addition to the theoretical and empirical evidence presented from actual biocontrol work, more relevant examples from various ecological situations can be presented to illustrate the fundamental principle and practical applications supporting the potential superiority of newly associated natural enemies in biological control. For example, in the studies on phoretic mites and bark beetle communities, J. C. Moser and co-workers (Moser and Roton 1971, Moser 1975, 1976) discovered that the closeness of association between the mites and the beetles was inversely related to the predatory ability of the mites. In essence this is the same evolutionary phenomenon as the new association/evolution of host conservation as discussed.

Another approach, relating the severity of major plant diseases to the native areas of the pathogens and their cultivated hosts, suggested that most of the really severe plant diseases do not occur on the native continent of the host plant, i.e., the pathogen–host association necessarily is evolutionarily new (Hokkanen 1985a). Also, M. W. Service (1981) in a discussion about ecological considerations in biocontrol strategies against mosquitoes states this same principle quite clearly (p. 184): "Generally, it is better to introduce suitable exotic pathogens and parasites that laboratory trials have indicated have potential for killing mosquito larvae than to try to utilize those that are already coexisting with the mosquitoes."

T.R.E. Southwood (1973) points out while discussing the evolutionary perspective of insect/plant relationships that most of the relationships we now observe are based on millions of years of coevolution. "Even today when a phytophagous species first attacks a new host it often inflicts a disproportionately heavy damage." A good example of this is the introduction of the cedar scales *Lepidosaphes newsteadi* and *Carulaspis minima* into Bermuda around 1940, which almost exterminated the endemic conifer Juniperus bermudiana (Thompson 1954, Bennett and Hughes 1959).

Many other insect pest/host plant associations are in fact evolutionarily new, just as was the case with the major plant pathogens. A well-known example is the Colorado potato beetle (*Leptinotarsa decemlineata*) and its South American host plant. The European corn borer (*Ostrinia nubilalis*), another of the most destructive pests in the world, originally fed on the mugwort *Artemisia vulgaris*, along with wild hop (*Humulus lupulus*) and wild hemp (*Cannabis sativa*), before being brought into contact with maize, now its principal host plant (Hudon and LeRoux 1986). Interestingly, the extensive work on the biological control of neither of these two key insect pest species with control agents from the native area has resulted in any real success. However, the most promising candidate at the moment for the biological control of the Colorado potato beetle in Europe is the microsporidian disease *Nosema* sp. isolated from the bean leaf beetle *Cerotoma trifurcata* (Lipa 1985).

The Asian mite, *Varroa jacobsoni*, is worldwide the most destructive pest on the honey bee, *Apis mellifera*. On its original host, *Apis cerana*, native to Southeast Asia, the mite causes little damage. *A. mellifera* is native to Africa, and only since the 1960's has it been associated with the Asian mite (Crane 1968, Culliney 1983).

Some recent biocontrol successes and research also support the new association approach. For example, the successful biological control of the Mexican bean beetle *Epilachna varivestis* in the United States has been obtained through inoculative releases of *Pediobius foveolatus* (Hymenoptera, Eulopidae), a parasite of destructive coccinellids *Henosepilachna vigintioctopunctata* and *H. sparsa* in South Asia. Another new association biocontrol agent, showing promise in the control of the California red scale *Aonidiella aurantii*, is *Aphytis riyadhi*, a parasite of *Aonidiella orientalis* in Saudi Arabia (DeBach 1979).

Some of the most interesting data with respect to evolution of exploiter–victim systems and its application to biocontrol come from the research on insect pathogens. For example, it can be generalized that old virus/insect host associations have led to an evolutionary balance, whereas new associations often cause severe epidemics (Krieg 1973). There is plenty of evidence that pathogens from a distant source are more damaging to an insect host population than the local pathogens (Krieg, 1973, p. 153, Magnoler 1970). For example, Ossowski (1960) showed that the nuclear polyhedral virus (NPV) of wattle bagworm *Kotochalia junodi* from plantations far (150-200 miles) from the experimental areas caused significantly higher mortality than pathogens from closer locations. This pattern is not always clear (e.g., Stairs 1964, Martignoni and Schmid 1961), as many viruses are also virulent at the location of occurrence (e.g., *Neodiprion sertifer* NPV and *Carpocapsa pomonella* [granulosis virus]).

The codling moth granulosis virus (GV) is, however, interesting in this respect. The host is native to Eurasia (Lloyd 1960) and was established in North America about 150-200 years ago. The *Carpocapsa* GV was discovered in 1963 in Mexico (Tanada 1964), and is therefore most likely a new virus/host association. Interestingly, this is one of the most virulent baculoviruses known so far (Huber 1986), with enormous biocontrol potential. Besides the codling moth, only a few closely related tortricids (which do not belong to the orchard fauna) are susceptible to it (Huber 1986).

Much of the biocontrol research with the insect pathogenic bacteria *Bacillus sphaericus* and *B. thuringiensis* points to similar results to those discussed with insect viruses. Davidson (1976) reported *B. sphaericus* SSII-1, isolated from *Aedes aegypti*, as much more virulent to *Culex* and *Anopheles* larvae than *Aedes*. Reeves (1970) reports similar data on *B.*

thuringiensis BA068 and states that "the enhanced susceptibility of genera other than the host from which a parasite is isolated indicates an evolved accommodation, a less pathogenic host/parasite relationship with the original host."

More recently Langenbruch et al. (1985) reported a new strain of *B. thuringiensis* (var. *tenebrionis*), isolated from *Tenebrio molitor*. Its effectiveness against *Tenebrio* was limited but was highly pathogenic to *Leptinotarsa decemlineata*. Also the first *B. thuringiensis* strain was isolated from a storage pest (*Ephestia kuehniella*), but was most effective against lepidopterous pests in the field.

Clearly, from the above there is no one approach or rule based on the principle of new associations, such as "old associations always fail," or "new associations guarantee a success," as suggested by some critics of the "new association approach." The data on new and old associations indicate that the probability of success will be higher employing new associations rather than old ones. Many researchers have found some relevance in the approach (e.g., Drooz et al. 1977, Legner 1986, Briggs 1986), whereas some have completely refused to consider the approach (e.g. Goeden and Kok 1986, Harris 1986). The number of successes utilizing this method confirms that it can be used successfully, including against native pests!

VIRULENCE AND PATHOGENICITY IN PARASITE–HOST SYSTEMS USED FOR BIOLOGICAL CONTROL

When a parasite is feeding on a host and the host is its only source of food, there is some logic that the parasite and host should co-evolve such that the parasite does not destroy the host population. Clearly, if the parasite destroys its host, it destroys its food supply and itself. A parasite that destroys its host is considered virulent to its host. Virulence, however, is generally a relative term to identify the severity of attack of parasites on their hosts. In addition, we suggest that virulence has to be analyzed in terms of individuals and populations.

For example, if a parasite is virulent (high rate of population growth in the individual host) and kills the individual host in a short period, then this parasite in the individual host can be described as virulent. However, if only a few individual hosts in a population are attacked and infected, then on a population basis the same parasite can be described as avirulent. A parasite can be virulent to individuals and the host population. Certainly this was the case when the myxoma virus was first introduced into the European rabbit population in Australia and Europe. A virulent parasite that attacks only a few individual hosts in the host population acts like a predator in the host population, that is the sparse parasite infects and kills only a small number of hosts in the total host population. Frequently, however, one normally thinks of a parasite (virus, bacteria, fungi, etc.) as infecting a large number of hosts but being relatively harmless to the individual hosts (May and Anderson 1983a,b, Levin and Lenski 1983, Barrett 1983).

In biological control we do not care whether a parasite is virulent or avirulent, as long as the host population is reduced sufficiently that it is no longer causing economic damage to crops. This points up another important factor related to biological control and natural control. A parasite–host system can achieve a state of equilibrium in nature; however, this does not mean that a suitable level of biological control exists. Biological control depends on low pest (host) numbers relative to the target crop. Thus, biological control is strictly an economic evaluation in contrast with natural controls.

Earlier we mentioned that at some level of equilibrium the parasite population removes a relatively small portion of the energy and resources from its host population. This situation is true for both natural and biological controls. If the feeding pressure of the parasite is high such that it is harvesting a relatively high portion of the resources of the host, then the host population will have a rate of increase that is less than 1 and it will be declining in number. At a stable equilibrium, host increase and parasite increase should be approximately 1.

At this point, it would be profitable to examine the relationship that exists among some parasite–host systems in nature that are virulent and avirulent and some of their ecological characteristics. Some bacterial organisms, like *Bacillus cereus* and *B. subtilis* can infect large numbers of certain host insects but are relatively avirulent and nonpathogenic (Steinhaus 1949). At equilibrium, the parasite is harvesting a relatively small portion of resources from the host population despite the fact that most individuals in the host population are infected with the parasites.

In contrast, a virulent virus, like the nuclear polyhedral virus that infects the cabbage looper, is highly pathogenic to individual larvae. However, only a relatively small portion of the looper population is infected at any one time in nature (Pimentel, unpublished). This points up another interesting relationship in the ecology of the parasite and host in these two situations. With the avirulent parasite, transmission takes place relatively easily by contact between abundant larvae; however, transmission is more complex with the virulent virus. Host loopers in a natural population with the virulent virus are widely scattered, which prevents the virus from spreading rapidly and destroying large numbers of the host population (Pimentel, unpublished). Widely scattered hosts reduce the opportunity for rapid parasite transmission (Anderson and May 1982). The nuclear viral organism solves the problem of transmission using a resting stage that can survive outside of the host for 5 to 20 years. Thus, being present in the soil the viral organism can wait many years for a looper to finally come in contact with some of the viral organisms. The resting stage in the virus is essential to its transmission survival.

When a new parasite is introduced into a pest (host) population, ideally we expect the parasite to feed heavily upon the pest population and greatly reduce its numbers. We also hope that when the stable equilibrium is achieved, pest numbers are low and remain at a sufficiently low level that "complete" biological control results. However, evolution may take place, as occurred with the myxoma virus and the European rabbit. The result of evolution may be that the effectiveness of biological control is reduced — like that of the virus–rabbit association. Although evolution has probably taken place (even though undocumented) in other biological control situations, this evolution does not affect the effectiveness of the parasite in keeping the pest population at a suitably low level.

This then raises an interesting question, how do we select parasites for biological control in new associations? At this stage in our knowledge, we really do not know precisely just as we do not know how to select agents in classical biological control. An avirulent parasite in the native host may become virulent when introduced into the new host (e.g., myxoma virus in European rabbit). A relatively virulent virus in the native host might also be virulent when introduced for biological control into a new host.

Some guidelines can, however, be derived from the analyses presented in this paper (on host-switching) and earlier (Pimentel 1963, Hokkanen 1983, 1985b), as well as from other similar assessments. A complete, up-to-date data base on biological control and its skillful analysis should reveal yet much more specific suggestions regarding the choice of best natural enemies for each particular biocontrol situation.

CONCLUSION

As we have stated before, employing new associations will increase the probability for success in biological control compared with classical biological control; however, we can not predict with 100% certainty complete success in all new associations — despite the success of Drooz et al. in introducing a parasite as a new association for biological control (1977).

Based on our knowledge of the genetics and population ecology of parasite–host systems, we can suggest which parasites might be more successful in classical biological control and "new association" biological control. With classical biocontrol, we propose that the best parasite to select in the native habitat of the host is the parasite that is relatively sparse. The reason for selecting the relatively sparse parasite is that the native, wild host would have a low level of natural resistance to this parasite under these circumstances. It is assumed under these circumstances that the pest (host) that was introduced also had few or no evolved defenses to this parasite. Ideally, the parasite of interest is rare because it is controlled at low levels by a hyperparasite. Leaving the hyperparasite behind results in a "new association" between the introduced parasite and the pest. The pest should not have evolved a high level of resistance to the parasite because the parasite was relatively sparse in the native habitat. Thus, the introduced parasite from the native habitat should function effectively in keeping the pest (host) population under control in the new crop ecosystem.

The results support the conclusion that the new association approach is ecologically and statistically sound. One of the major advantages of this approach is its capacity to control native pests, which make up 60 to 80% of all pests. Host specificity of new association biocontrol agents also is similar to other biocontrol agents. In addition, the new approach is as safe as the classical approach in terms of environmental risks. Recent trials in the use of this new approach have been most encouraging, and suggest that this approach should contribute to the future success of biological pest control worldwide.

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PART TWO

CLASSICAL BIOLOGICAL CONTROL: Practical Considerations and Applications

SECTION THREE

Olfactory Basis for Insect Enemies of Allied Species

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ABSTRACT

The evolution of olfactory communication in bark beetles brought with it the parallel or coevolution of kairomonal systems in the natural enemy complexes. Entomophagous insects developed olfactory receptors and behavioral patterns responsive to insect and host-produced volatiles in the ecosystems of bark beetles. The phenomenon has both positive and negative implications for efforts to employ natural enemies in pest management.

Obviously, natural enemies find their prey and hosts. The mechanisms by which they accomplish that end may be less obvious. Olfaction plays a role, but to what extent we know only a little. It is important, however, to understand the olfactory bases of the relationships of predators and parasitoids to their preys and hosts in order to effectively consider the role of the natural enemies in biological control, and to determine the potential impact of pest-oriented, olfactory-based suppression tactics on them.

BEHAVIORAL ASPECTS

The sequence of arrival of natural enemies on bark beetle-infested trees shows a high degree of synchrony with the arrival of their prey or hosts (Camors and Payne 1973, Stephen and Dahlsten 1976, Dixon and Payne 1979). For example, predators of the southern pine beetle, *Dendroctonus frontalis*, tend to arrive on the beetle-infested trees during the first 15 days after initiation of attack by the bark beetles (Fig. 1). This is not surprising since, as adults, predators mostly feed upon adult bark beetles which are most prevalent on the bark of the tree early in the attack. In addition, eggs laid by the predators at that time yield immatures which feed upon the immature stages of the bark beetle. Parasitoids, on the other hand, arrive on attacked trees later when the larval and pupal stages of the bark beetles they parasitize are present (Fig. 2).

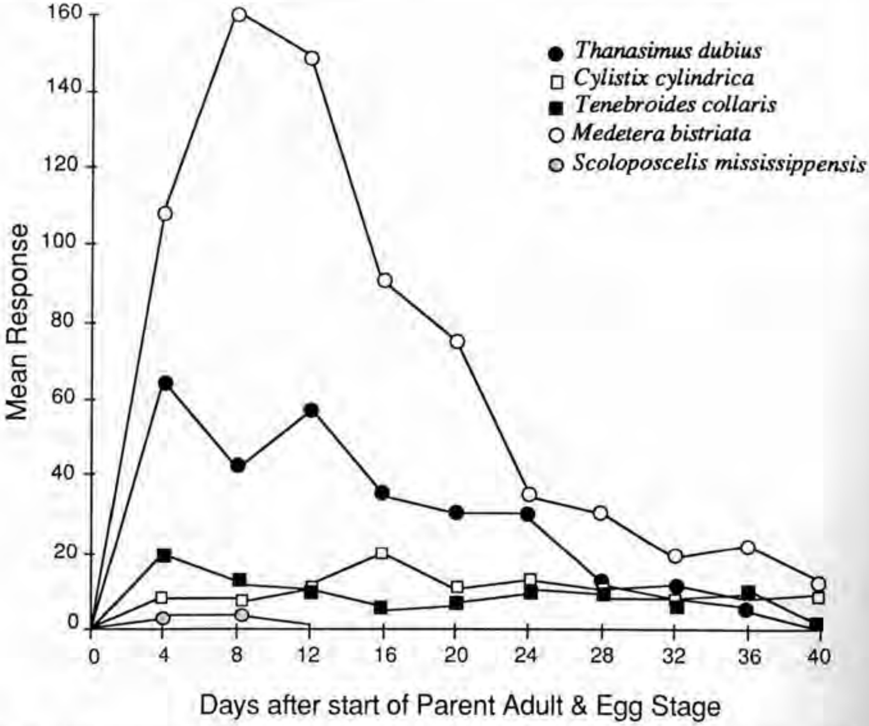

Fig. 1. Sequence of arrival of predators to southern pine beetle-infested trees. Data from 5 trees (modified after Camors and Payne 1973).

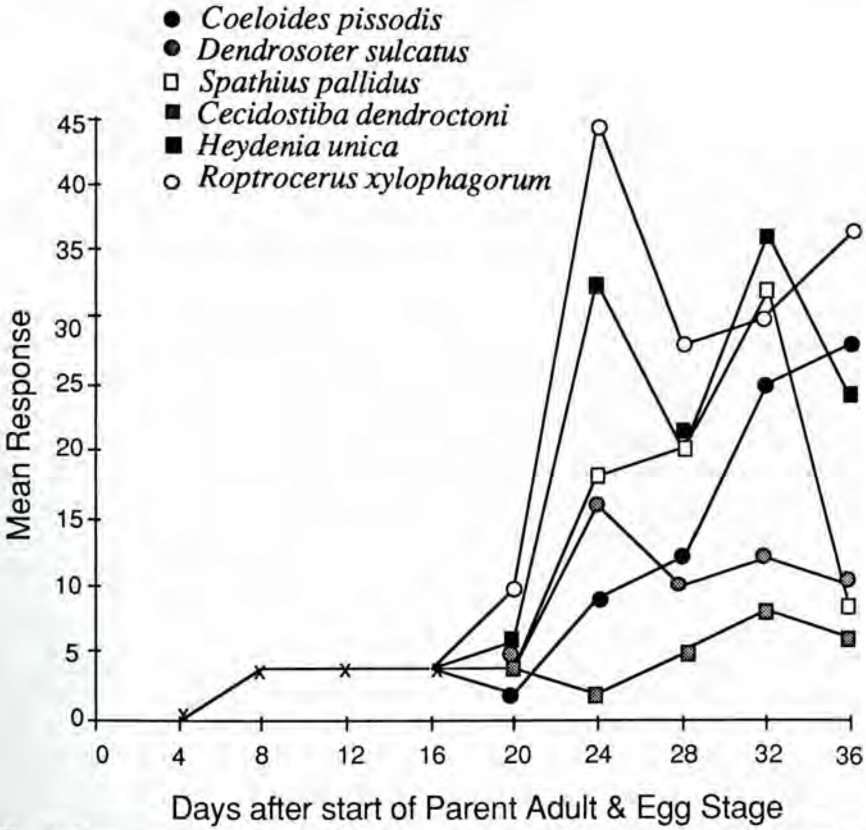

Fig. 2. Sequence of arrival of parasites to southern pine beetle-infested trees. Data from 5 trees. X = average response of parasites at low levels (modified after Camors and Payne 1973).

This seemingly well evolved relationship between natural enemies and bark beetles has some basis in the interaction of bark beetles and their host trees. In fact, it is well recognized that olfactory stimuli associated with bark beetle/host tree interactions are commonly used by various natural enemies in locating their prey and hosts. For example, major aggregations of predators on host trees tend to correspond with the time of peak pheromone production by the attacking bark beetle adults and the presence of increased amounts of host volatiles released from the tree, as a result of the beetle attacks (e.g. Camors and Payne 1973, Dixon and Payne 1979, 1980). In fact, Wood et al. (1968) provided the first conclusive data that bark beetle predators are attracted to the pheromones not their prey. As kairomones the compounds are most likely the olfactory cues used by the predators in locating beetle-infested trees and the beetles themselves. They found that the clerid beetle, *Enoclerus lecontei*, was attracted to two pheromones (ipsdienol and ipsenol) of *Ips paraconfusus*. They also reported a similar phenomenon for the ostomid, *Temnochila virescens chlorodia*. *E. lecontei* was also found to be attracted to host volatiles (Rice 1969), as were the clerid species, *Thanasimus formicarius* in Czechoslavakia (Rudinsky et al. 1971) and *Thanasimus* spp. in Scandinavia (Bakke and Kvamme 1981). Conclusive data of an olfactory basis for the location of bark beetle prey by predators has been reported for several other species (Table 1).

In comparison to the large response of predators to trees containing predominantly the parent adult and egg stages of bark beetles, many parasitoid species tend to respond in peak numbers when the larval stages of the beetles are most abundant in the tree. Generally, peak pheromone production by adult bark beetles has ended when the majority of the parasitoids arrive on the tree; therefore, it is somewhat surprising to find that parasitoids may utilize pheromones released by adult beetles as cues to aid them in locating the host habitat (i.e., infested stand) rather than a specific host tree or the host itself. The parasitoids may use other olfactory cues to aid them in locating host trees and hosts. For example, they may rely on pheromones remaining in the frass after initial attack by the bark beetles (Berisford and Franklin 1971, Dixon and Payne 1980), host tree volatiles (Camors and Payne 1972), and/or olfactory stimuli from larvae feeding under the bark (Kudon and Berisford 1981). A notable exception to the above may be *Tomicobia tibialis*, a rather specific parasitoid of *Ips* species (Bedard 1965). It oviposits on adult beetles and apparently responds to the pheromones of male *Ips* in order to locate the hosts (Rice 1968, 1969).

SENSORY ASPECTS

Although detailed information is limited on the behavioral aspects of an olfactory basis for insect enemies of allied species, data for three species of natural enemy are available on the sensory aspects which provide added, conclusive evidence for the phenomenon.

Hansen (1983) was the first to report on the response of antennal olfactory receptors of a natural enemy of bark beetles to olfactory cues from its prey. The predator, *T. formicarius* feeds on numerous species of European bark beetles (Gauss 1954) and was found to be attracted to various host tree volatiles as well as to prey-infested logs (Rudinsky et al. 1971). It was also found to be attracted to host tree logs baited with pheromones of a prey species, *I. typographus* (Bakke and Kvamme 1978).

Table 1

Response to bark beetle-associated olfactory stimuli by natural enemies (modified after Borden 1982).

Natural enemies	Olfactory Stimuli	Response Information
COLEOPTERA		
Enoclerus lecontei (Cleridae)	ipsenol ipsdienol *cis*-verbenol *Pinus ponderosa* logs infested with *Ips pini*	Trapped in California to mixture of the 3 pheromones (Wood et al. 1968). In California and Idaho field tests, more attracted to odor of boring *I. pini* males from New York than from California or Idaho (Lanier et al. 1972). Attraction to logs infested by male *I. pini* enhanced when ipsenol added as as a stimulus (Furniss and Livingston1979). Response to logs infested by *I. paraconfusus* and *Dendroctonus brevicomis* greater than to logs infested by *I. paraconfusus* alone (Byers and Wood 1980).
Stigmatium nakanei (Cleridae)	*P. densiflora* logs infested with 0, 10, 50 or 150 females *Taenioglyptes fulvus*	Responds to traps baited with logs infested by female *T. fulvus* greater than to control log. Number of predators caught increased markedly to logs infested with 50 or 150 females (Sasakawa et al. 1976).
Thanasimus dubius (Cleridae)	frontalin *trans*-verbenol verbenone	Responds in same diel rhythm as its prey, *D. frontalis*, to frontalin alone or with oleoresin or *trans*-verbenol; verbenone raised male:female response ratio, but lowered overall response (Vite and Williamson 1970, Dixon and Payne 1980). Greater aggregation in low density host populations attributed to kairomone response (Reeve et al. 1980). Males predominate during first 3 days of attack, suggesting that they attract females (Dixon and Payne 1979).
Thanasimus formicarius (Cleridae)	Norway spruce log baited with methylbutenol, *cis*-verbenol & ipsdienol	Response to baited logs in field tests significantly greater than to unbaited control logs (Bakke and Kvamme 1978).

Natural Enemies	Olfactory Stimuli	Response Information
Thanasimus rufipes (Cleridae)	Norway spruce log baited with methylbutenol *cis*-verbenol & ipsdienol	Response to baited logs in field tests significantly greater than to unbaited control logs (Bakke and Kvamme 1978)
Thanasimus undatulus (Cleridae)	frontalin	Attracted in large numbers to frontalin-baited spruce trees (Dyer1973, 1975) or traps (Kline et al. 1974).
Lasconotus pusillus (Colydiidae)	frontalin loblolly pine turpentine	Response baited traps in field tests (Dixon and Payne 1980
Abraeus sp. (Histeridae)	frontalin	Response baited traps in field tests (Dixon and Payne 1980.
Cylistix attenuata (Histeridae)	frontalin	Response baited traps in field tests (Dixon and Payne 1980).
Plegaderus sp. (Histeridae)	*endo*-brevicomin	Response baited traps in field tests (Dixon and Payne 1980).
Leptacinus paurumpunctatus (Staphylinidae)	*frontalin* *exo-brevicomin* *loblolly pine turpentine*	*Response baited traps in field tests (Dixon and Payne 1980).*
Corticeus glaber (Tenebrionidae)	frontalin *exo*-brevicomin *endo*-brevicomin loblolly pine turpentine	Response baited traps in field tests (Dixon and Payne 1980).
Temochila chlorodia (Trogositidae)	*exo*-brevicomin frontalin myrcene verbenone *trans*-verbenone	Responds to traps baited with *exo*-brevicomin alone (Bedard et al. 1969, Pitman and Vite 1971) or with frontalin and myrcene (Bedard and Wood 1974). *Trans*-verbenol with verbenone apparently int response to*exo*-brevicomin (Bedard et 1980).
Rhizophagus grandis (Rhizophogidae)	Frass of *D. micans* larvae	Responded to traps baited with frass of *D. micans* larvae (Gregoire et al. 1982).

Natural Enemies	Olfactory Stimuli	Response Information
HYMENOPTERA		
Dendrosoter protuberans (Braconidae)	*alpha*-multistriatin methylheptanol *alpha*-cubebene	Responds to traps baited with binary or ternary combinations of multilure components (Kennedy 1979).
Dendrosoter sulcatus (Braconidae)	*P. taeda* logs infested with *D. frontalis* larvae.	Response in laboratory olfactometer (Kudon and Berisford 1981).
Coeloides pissodes (Braconidae)	frontalin loblolly pine turpentine	Response to baited traps in field tests (Dixon and Payne 1980).
	P. taeda logs infested with *D. frontalis* larvae	Response in laboratory olfactometer (Kudon and Berisford 1981).
Spatihius benefactor (Braconidae)	*alpha*-multistriatin methylheptanol *alpha*-cubebene	More individuals captured on multilure-baited than on unbaited traps (Kennedy 1979).
Spathius pallidus (Braconidae)	*trans*-verbenol *exo*-brevicomin *endo*-brevicomin loblolly pine turpentine	Response to baited traps in field tests (Dixon and Payne 1980).
Entedon leucogramma (Eulophidae)	*alpha*-multistriatin methlheptanol *alpha*-cubebene	Responds to traps baited with multilure components alone (except methylheptanol) or in binary or ternary combinations Kennedy 1979).
Cerocephala rufa (Pteromalidae)	*alpha* multistriatin methylheptanol *alpha*-cubebene	Responds to traps baited with multilure components alone or in binary and ternary combinations (Kennedy 1979).
Cheirophachus colon (Pteromalidae)	*alpha*-multistriatin methylheptanol *alpha*-cubebene	Responds to traps baited with multilure components alone or in binary and ternary combinations (Kennedy 1979).

Natural Enemies	Olfactory Stimuli	Response Information
Heydenia unica (Pteromalidae)	frontalin *endo*-brevicomin loblolly pine turpentine	Response to baited traps in field tests (Dixon and Payne 1980).
	P. taeda logs infested with *D. frontalis* larvae	Response in laboratory olfactometer (Kudon and Berisford 1981).
Tomicobia tibialis (Pteromalidae)	*Pinus ponderosa* logs infested with male *I. paraconfusus* or male *I. pinii*	Attracted to odor of boring male I. *ponderosa* (Bedard 1965, Rice 1969). *I.pini* from California or Idaho more attractive than than those from New York (Lanier et al. 1972).
Roptrocerus eccoptogastri (Torymidae)	*Pinus taeda* logs infested with female *D. frontalis*	Response to baited traps in field field tests (Dixon and Payne 1980)
Roptrocerus xylophagorum (Torymidae)	*P. taeda* logs infested with *D. frontalis* larvae	Response in laboratory olfactometer (Kudon and Berisford 1981).
DIPTERA		
Medetera aldrichiii (Doliocopodidae)	3,2-MCH	Reduced attack density on *D. pseudotsugae* when host tree treated with high concentrations of 3,2-MCH (Furniss et al. 1974).
Medetera bistriata (Dolicopodidae)	frontalin *trans*-verbenol verbenone *P. taeda* logs infested with male D. *frontalis* or *I. grandicollis*	Attracted to infested logs, frontalin plus *alpha*-pinene, *trans*-verbenol plus *alpha* pinene but not to frontalin or *alpha* pinene alone; verbenone caused change in sex ratio in favor of females (Williamson 1971).
HEMIPTERA		
Scolopscelis mississippensis (Anthocoridae)	frontalin trans-verbenol exo-brevicomin endo-brevicomin loblolly pine turpentine	Reponse to baited traps in field tests (Dixon and Payne 1980).

In his electrophysiological investigations, Hansen (1983) found that olfactory receptors of *T. formicarius* were as sensitive to ipsdienol, (S)-*cis*-verbenol and 2,3,2-methylbutenol, aggregation pheromones of its prey, *I. typographus* (Bakke et al. 1977), as were the receptors of the prey. The rather low threshold concentrations to which the receptors responded indicated that the predator could be attracted over relatively long distances by the pheromones of its prey. The predator was also found to have receptors sensitive to the primary enantiomer of a prey pheromone. However, in general, individual receptors were not specialized for single compounds but responded to several different compounds, although with different intensities.

T. formicarius is not limited to *I. typographus* as its only prey; it preys on additional *Ips* species and possibly other bark beetles as well (Gauss 1954). The somewhat ubiquitousness of ipsdienol and ipsenol in European *Ips* species (Vité et al. 1972) is likely to provide the kairomonal basis for attraction of *T. formicarius* to those species. In addition, the fact that *T. formicarius* was also found to have receptors for the pheromones of other bark beetles and host volatiles (*trans*-verbenol, verbenone, frontalin and *alpha*-pinene) suggests that those compounds might also function as olfactory cues for the predator in locating its prey and prey habitat.

Data on the antennal olfactory response and behavior of a second predator species, *T. dubius*, provides more evidence for the strong role of olfaction in predator/prey interactions. The behavior of *T. dubius* is so closely aligned to that of its prey that as *D. frontalis* adults attack host trees, adult *T. dubius* arrive simultaneously to feed on their prey (Dixon and Payne 1979). The predator–prey synchrony was found to be the result of response by *T. dubius* to the aggregation pheromone, frontalin, released by female *D. frontalis* attacking host trees (Vité and Williamson 1970).

Frontalin was produced as a mixture of 85% (1S, 5R)- (-) and 15%(1R, 5S)- (+)- frontalin (Stewart et al. 1977). Behaviorally, *D. frontalis* was attracted to both enantiomers, but maximum response was elicited by (-)- frontalin alone (Payne et al. 1982). By comparison, the response of *T. dubius* was highly specific in that the predator responded only to the (-) enantiomer (Payne et al. 1984). In fact, the olfactory receptor system of *T. dubius* was found to be highly specific for (-)-frontalin to the extent that only one specimen was found which responded to the (+) enantiomer. Response to the (+) enantiomer was significantly less than to the (-) and may have been due to the small percentage of (-) enantiomer present in the (+) sample. The apparent high level of olfactory and behavioral specificity for the primary enantiomer of its prey suggests coevolution of the neurophysiology and behavior of prey location in *T. dubius* and the aggregation behavior in *D. frontalis*.

Antennal olfactory and behavioral responses were also obtained from *T. dubius* to pheromones of *Ips* species, which the predator feeds upon as alternate prey (J. C. Dickens and T. L. Payne unpublished data, Turnbow 1979, Mizell and Nebeker 1982). In fact, as with *T. formicarius*, olfactory receptors of *T. dubius* responded to several bark beetle and host tree compounds, including *endo*-brevicomin, verbenone, *trans*-verbenol, *cis*-verbenol, ipsenol, ipsdienol, *alpha*-pinene and myrcene (J. C. Dickens and T. L. Payne unpublished data).

In contrast to the *Thanasimus* species, *Rhizophagus grandis* appears to be a specific predator on *D. micans* (Grégoire et al. 1982). In the laboratory and field, adult *R. grandis* responded to frass of *D. micans* larvae (J-C. Grégoire personal communication). They also aggregated quickly on wounded larvae and responded to mixtures of verbenone (known to be present in larval frass), myrtenol and *trans*-verbenol. However, recordings from antennal olfactory receptors showed that *R. grandis* is capable of perceiving more bark beetle pheromones than those to which it was found to respond behaviorally (Tømmerås et al. 1984). The olfactory receptors were most responsive to (+)-ipsdienol and (-)-verbenone and somewhat less responsive to frontalin and *exo*-brevicomin. Separate receptor cells were found which were specific for (+)-ipsdienol and for (-)-verbenone. With the exception of verbenone, the pheromones have not yet been identified in *D. micans*. However, frontalin and *exo*-brevicomin have been found in a related but allopatric bark beetle species, *D. terebrans* (Payne et al. 1986), thus suggesting that the compounds might be present in *D. micans*.

It is surprising that the olfactory receptors of *R. grandis* were highly responsive to the *Ips* pheromone, (+)-ipsdienol, since the predator has not been shown to prey upon *Ips* species. It was hypothesized that *R. grandis* has receptors sensitive to the pheromone so it can avoid trees attacked by *I. typographus*, since the predator is specific for *D. micans* (Tømmerås et al. 1984). It was also hypothesized that *D. micans* itself might produce ipsdienol. Obviously it is not clear what role the various bark beetle pheromones play in the host finding behavior of *R. grandis*. However, it is clear that the predator is sensitive to the compounds, which makes it likely that the pheromones do have significance in the behavior of the insect.

IMPLICATIONS TO IPM

Behavioral chemicals offer considerable potential as tools in integrated pest management through their use in survey and detection, and in suppression and prevention (Payne and Wood 1981). However, depending upon the use, behavioral chemicals could enhance or impair the impact of natural enemies.

As attractants, behavioral chemicals have their greatest potential in traps for survey and damage estimation and prediction. Thus far that potential has not been realized for bark beetles. However, the potential negative impact such an application might have on natural enemy populations is clear. Great numbers of natural enemies are eliminated through pheromone traps. For example, one *T. undatulus* was trapped for every two to seven *D. rufipenis* (Dyer 1973), or four *D. pseudotsugae* (Pitman 1973). Likewise, one *T. formicarius* or *T. rufipes* were trapped for every four *I. typographus* (Bakke and Kvamme 1978). The data available are limited to a few predator species, however, the implication is general.

The negative impact could be magnified when attractant-baited traps or trap trees are used in suppression and prevention applications. For example, in a large trapout program on *D. brevicomis* in California, close to 90,000 *T. chlorodia* were trapped at the ratio of one predator to seven prey (Bedard and Wood 1974). At a ratio of nearly two predators to a thousand prey, over one million *T. formicarius* were trapped in the two year, *I. typographus* mass trapping program in Norway (Bakke 1981). Also, natural enemy populations could be expected to be adversely effected when attractants are used on trap trees to be removed to mills for processing and trap trees treated with pesticides.

Even though the numbers of natural enemies trapped may appear great, it is not known what effect their elimination might have on the pest population and its damage to the forest. Those data are needed before a quantitative measure of the negative impact can be made.

Behavioral chemicals as attractants and repellents do not appear to be detrimental to natural enemy populations when the pheromones are used in disruption tactics. For example, *T. dubius* did not appear to be adversely effected by the use of the attractant frontalure to disrupt *D. frontalis* infestations (Richerson et al. 1980). In fact, the predator remained in close association with the prey when *D. frontalis* was redirected from unattacked trees to those trees that had been attacked and were no longer suitable as hosts. *T. undatulus* was not repelled by 3,2-MCH, the anti-aggregation pheromone used to disrupt its prey, *D. pseudotsugae* (Kline et al. 1974, Furniss et al. 1981). Similarly, there were no significant differences in the numbers of *T. dubius* which landed on *D. frontalis* infested trees whether or not the trees had been treated with repellents (Richerson and Payne 1979). The repellents did not effect the numbers or distribution of the predator.

Beyond the indirect effects of behavioral chemicals on natural enemies as a result of pest-oriented applications, behavioral chemicals should be considered for use in directly manipulating natural enemy populations. It may be possible to capitalize on the kairomonal phenomenon and enhance the impact of insect enemies on allied species.

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SECTION FOUR

Bark Beetles, Natural Enemies, Management Selection Interactions

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ABSTRACT

Management of bark beetles requires more than a knowledge of the elements (biotic and abiotic) which regulate them. An understanding of the interactions associated with the implementation of management strategies and tactics needs to be understood. Specifically, the impacts on the natural enemy community and other non-target objects needs to be understood. It is from this knowledge that we will be better able to assess the success or lack of success in our bark beetle management efforts. Management tactics such as salvage operations remove many parasites and predators from the forest system. Of those that survive the treatment their powers of dispersal will determine if they are able to locate new bark beetle infestations, to survive and hence dampen the impact on the natural enemy community dynamics. Parasites and predators of bark beetles utilize chemical cues similar to the host bark beetle population. Hence, bark beetle management strategies and tactics that call for disruption or inhibition tactics utilizing pheromones will also impact the natural enemy community. It is from this perspective that this paper will be developed and presented.

INTRODUCTION

Bark beetles (*Dendroctonus* spp. and *Ips* spp.) have long been a part of the forest ecosystems of the world. From our current perspective they and their hosts have co-evolved together. In many cases they are considered to be "native" to a particular location and associated with the "native" *Pinus* spp. and other host genera. With tree improvement programs in place these "native" pine species are much different than their ancestors of the past. In fact loblolly pine (*P. taeda* L.) is considered to be somewhat of a plastic species since it can be crossed with other southern yellow pines. It has been manipulated to favor certain marketable characteristics (e.g., straightness, specific gravity, etc.).

Since we have elected, in our management strategies to maintain *Pinus* spp. in our forests we have, in essence, decided to maintain *Dendroctonus* and *Ips* populations by providing them with suitable food resources and habitats within which to live. That is to say, from our current understanding of the resource preferences of these genera, we are perpetuating their preferred hosts throughout their range. One might also speculate that these genera of bark beetles maintain forests in their subclimax state by going through major periodic population fluctuations that insure that resources will be available for future generations through successional changes. On the other hand, bark beetles tend, in some cases, to move a forest towards the climax state by removing the subclimax species, if a hardwood component exists in the stand (Nebeker 1985).

In considering the influence of management strategies and tactics to reduce the impact of bark beetles it is essential that we understand that we are working with a co-evolving system. Further, that many of the factors that influence the buildup of bark beetles, for example in the southern United States, are both a result of natural processes and the influence of man as illustrated in Fig. 1.

In response to the buildup of bark beetle populations numerous management options have been developed and evaluated. The majority of the evaluation effort has been placed on methods (management options) of controlling the bark beetles. However, there are interactions that take place as a result of our efforts to reduce the impact of the bark beetles (Fig. 2) that we may not be aware of or were not considered in the evaluation process. A particular management option directed at the bark beetles may have an adverse effect on the soil, host and/or the entomophagous organisms. The intent of this paper is to discuss, conceptually, the potential effects of the various management options with emphasis on the natural enemy community.

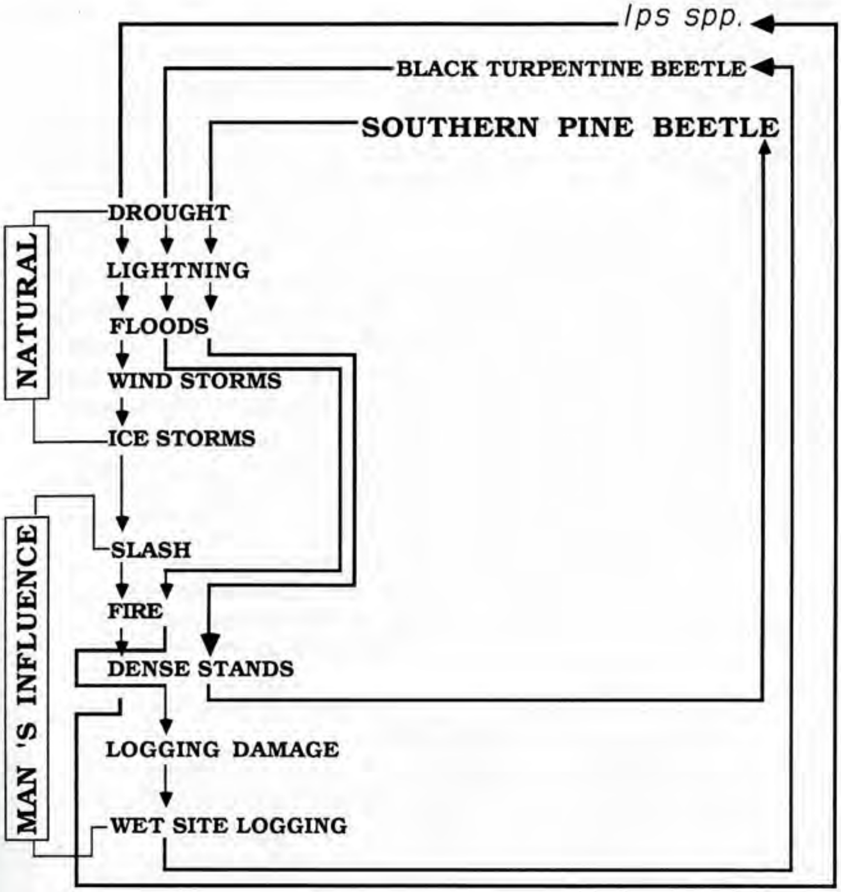

Fig. 1. Factors influencing bark beetle populations are both natural and a result of man's intervention into the forest ecosystem.

MANAGEMENT OPTIONS

Management of bark beetles requires a knowledge of: 1) the elements which potentially regulate them; 2) actions that can be taken to disrupt key population processes; and 3) the interrelationships (interactions) that exists between and among the various management options. These options may be classified, in broad terms, as either doing nothing, direct or indirect (Nebeker et al. 1984).

Doing Nothing

Within the forest management realm, the option to do nothing is a viable one with respect to pest populations. In some situations, it maybe more cost effective to do nothing than to invest in one or more of the other management options. If this option is taken what can be expected? From an historical perspective we can expect that timber losses will be approximately the same as in the past. As the host acreage increases, and directly related to the overall beetle population at a particular point in time, one would predict a proportional increase in tree mortality. That is to say, if the population is in an epidemic state vs. an endemic state, considerably more mortality will occur and acres (hectares) infested as a result of increased host availability. The natural enemy community will respond to these changes in density. As the bark beetle population increases the biotic factors that generate dramatic declines in the beetle population will begin to take effect and the cyclic nature of these populations will be observed.

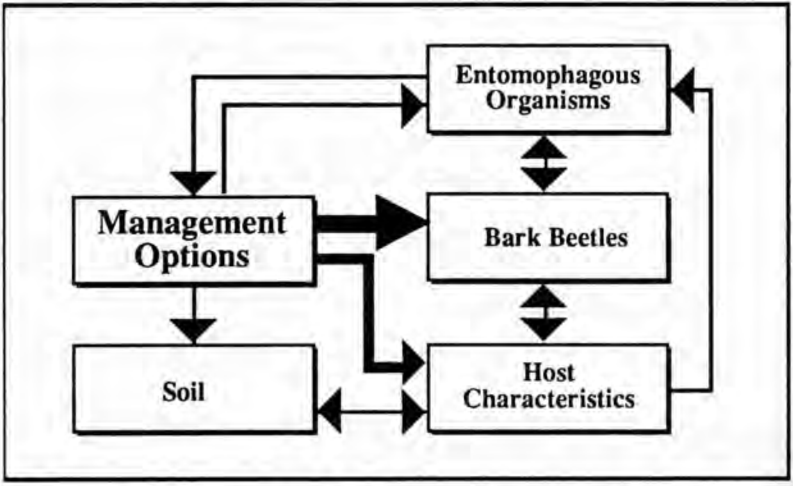

Fig. 2. Major components that are in the decision making process when management of bark beetles is the central theme. Arrow line thickness indicates current areas of thrust. Additional arrows indicate interactions and influences that need to be explored in general.

Direct Control Options

Options considered to be direct controls include: *salvage* (clear cutting and removal); cut and leave; cut, pile and burn; cut and spray; spray standing trees; and *trapping* (via traps or bait trees). Each of these options are aimed at causing mortality to the bark beetle population within a short time period.

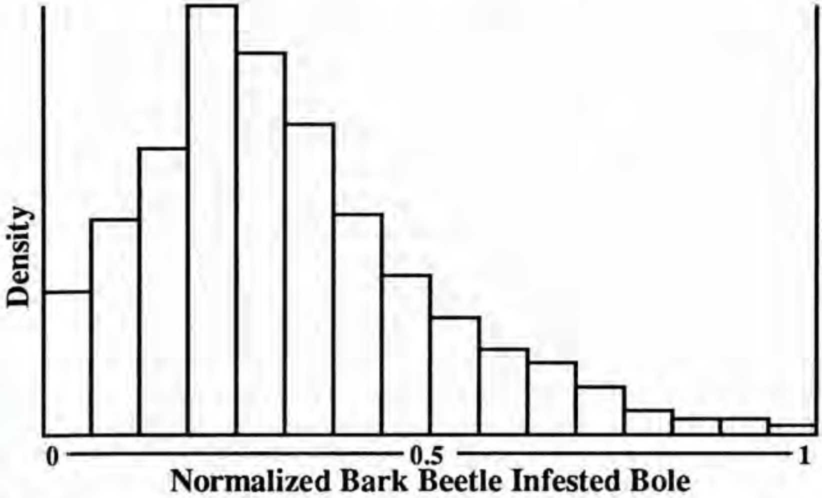

Fig. 3. Generalized distribution of *Thanasimus dubius* pupae in loblolly and shortleaf pine (after Mizell and Nebeker 1981).

Salvage

Salvage is a preferred option because some financial losses may be ameliorated and the site, if large enough, prepared for regenerating the desired species. Unfortunately the natural enemy population is directly effected by the salvage operation in most cases. The removal of infested trees and recently vacated trees includes the removal of some natural enemies. If the natural enemies are able to survive until they reach the wood yard and complete their development, then their power of dispersal will dictate whether they are able to survive such an operation and successfully locate new bark beetle infestations. It is in association with this management option (salvage) that natural enemy conservation should be considered. For example, *Thanasimus dubius* (F.) a clerid predator of the southern pine beetle (SPB), *D. frontalis* Zimmermann, pupates in the lower portions of SPB infested trees. In fact, over 80% of the pupae are found in the basal third (Fig. 3) of a SPB infested tree in the outer bark (Mizell and Nebeker 1981). With this predator having a life cycle approximately twice as long as the SPB many still remain within the tree long after the SPB has emerged. Conservation of this predator can be achieved by letting trees stand until emergence of the predator population is complete or by stripping the bark from the basal portion of the infested bole and leaving it in the forest. After the bark is removed care should be taken to insure that no further disturbance occurs that would cause additional mortality to the remaining population. This is but one example of possible natural enemy conservation. Cut and Leave is not as harmful to the mobile portion of the natural enemy community as are other direct control options. Those that are able to move to the underside of the tree and escape the increased subcortical temperatures of the bark, as a result of its more direct exposure to the sun, will have a better chance of survival. However, competition for prey items will increase as a result of the reduction in foraging area. The less mobile portion of the community will be impacted directly. Mortality occurring as a result of mortality to their hosts and their inability to tunnel through the bark to locate new host material. Cut, Pile and Burn, Chemical Treatment and Baited Trap Trees also directly impact the natural enemy community. Unfortunately, few data are available concerning the impact of such treatments on the natural enemy community. With respect to the baited trap trees, the adult natural enemy population is not as directly effected as the subsequent generation. Survival of the F_1 generation is drastically reduced.

Trapping

The direct control option that possibly has the least impact on the natural enemy community would be *trapping*. Traps can be designed to exclude the parasites and predators of the bark beetle being trapped. Design of the trap is extremely important and if caution is not taken great numbers of the natural enemy community can also be lost. However, the pathogenic microorganisms within the population cannot be excluded. It is possible that in an extensive trapping program, sufficient numbers of beetles could be trapped so as to preclude the density from reaching critical levels for these organisms to cause an epizootic and subsequent decline in the bark beetle population that would occur if such an option had not been utilized.

Indirect Control Options

Options considered to be indirect include silvicultural tactics (e.g. thinnings), and manipulation of chemical cues (pheromone disruption or inhibitors) utilized in host and/or prey location. To prevent or reduce the hazard/risk of bark beetle attack one silvicultural tactic, thinning, is often the option of choice.

The influence of thinning on host-susceptibility to bark beetles has been investigated in the inter-mountain region of the United States (McGregor et al. 1987, Amman and Schmitz 1988, Amman et al. 1988 Bartos and Amman 1989, Schmitz et al. 1989) and in the southern region-Gulf Coastal Plain of the United States (Nebeker and Hodges 1983, Nebeker et al. 1983, Nebeker and Hodges 1985). With specific respect to the southeastern United States, we (Nebeker et al. 1985) have reviewed and summarized thinning research, current field practices, and related the positive and negative aspects of these practices to current or potential destructive agent problems in association with various thinning concepts. Unfortunately, the response of the natural enemy community was not discussed. This is true of almost all studies aimed at reducing the overall (area wide) or local population of bark beetles. The non-target species (e.g. parasites and predators) receive little, if any, consideration in the evaluation process. It is assumed that if the bark beetles can successfully colonize hosts in an altered environment, such as a thinned stand, then the natural enemy community can also. However, this question should be addressed as area wide pest management options are evaluated.

Any thinning strategy must also consider the associated potential hazard(s). Bark beetle infestations are often associated with poor tree vigor which may be altered in response to the thinning. The development of bark beetle outbreaks is therefore strongly influenced by tree vigor. Though vigor is difficult to quantify, recent and/or current radial growth can serve a strong indicator of tree condition or vigor. Other factors that effect vigor include: age, stand density, soil texture and type, drainage patterns, and stand disturbances associated with cultural practices. Poor tree vigor is often associated with densely stocked stands and indicated by declining or slow radial growth. These conditions can be readily alleviated by thinnings. Thinnings tend to eliminate the less vigorous or weakened individuals which are the prime targets for bark beetle attack.

Reduced competition pressure enhances the vigor of residual trees. Thinning stands back to 70-100 ft^2/acre basal area reduces the hazard to bark beetle attack and may also slow spot growth if an attack occurs (Nebeker and Hodges 1983). Timing of the thinning operations is also critical. Thinning during periods of reduced beetle activity (e.g. winter) is recommended except possibly where annosus root rot is a problem. However, one must also consider the impact on the site from rutting and damage to the residual stems during such time periods when the soil moisture levels are high. Growth rates may be reduced if the stand is extensively disturbed through ruttings, etc. Thinnings during periods of beetle activity (spring through early fall) can be done if care is taken in the distribution of the slash material.

Slash distribution patterns vary according to the type of thinning. Slash piled around the bases of residual stems increases the probability that they will be attacked by bark beetles, particularly *Ips* spp. which are attracted to the slash. Hence, it is critical that considerations be given to the slash distribution pattern. Distributing the slash throughout the site increases the bearing strength of the soil and bark removed caused by logging traffic reduces the resources available for bark beetles. It is assumed that since bark beetles are less likely to attack trees in recently thinned stands that the natural enemy community would not be adversely effected. However, some natural enemy mortality might occur in high traffic areas. With extremely limited data one can only speculate as to the amount of mortality.

Thinning normally stimulates radial growth, reduces evapotranspiration, and increases precipitation through fall. Lower evapotranspiration reduces groundwater use and favors continued diameter growth. Low water stress reduces monoterpene concentration and increases resin acid levels which may make stands less attractive to beetles (Hodges and Lorio 1975). Stands which are frequently flooded may be more susceptible to bark beetle attack. In these areas, thinning alone will not correct the problem. Additional forestry practices such as drainage to divert excess water may be needed. Chemical cues (pheromones and kairomones) are important in the aggregation of bark beetles and some associated organisms. Utilization of these behavioral chemicals to disrupt or inhibit bark beetle communication appears to be a potential pest management option. However, these tactics may also impact the natural enemies. Many of the parasites and predators of bark beetles utilize pheromones produced by their prey to locate them. Data are scarce on the influence of such management tactics on natural enemies, but it should be addressed. *Thanasimus dubius* does not appear to be adversely effected by the use of the attractant frontalure to disrupt *D. frontalis* infestations (Richerson et al. 1980). For additional examples see Payne (1987). Synthetic attractants may possibly be used to augment entomophagous organisms as Chaterlain and Schenk (1984) attempted to do.

CONCLUSIONS

It is still extremely important that we understand the ecological consequences of our forest management activities. History has shown that management options have been developed and are currently in place for dealing with bark beetle problems on a local level and in some cases on an areawide basis. However, many of the options for bark beetle control have not been evaluated for their impact on natural enemies. This is of major concern. We are working in direct conflict with natural regulating mechanisms. Therefore, outbreaks could be prolonged because the efficacy of factors (natural enemies) that cause sporadically fluctuating populations to decline is reduced. The impact of bark beetle management strategies and tactics on natural enemies should be evaluated on a local and area-wide basis. An understanding of the roles of associated organisms is necessary to determine why certain tactics succeed or fail.

ACKNOWLEDGMENTS

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SECTION FIVE

Biological Control of *Ips grandicollis* (Eichhoff) (Coleoptera: Scolytidae) in Australia — A Preliminary Evaluation

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ABSTRACT

The engraver beetle, *Ips grandicollis* (Eichhoff), was first discovered in South Australia in 1943 and has since spread to four additional states.

A biological control program, instituted in 1981, has established laboratory colonies of parasites and predators from the United States. Field releases of three hymenopterous parasites and two predaceous beetles have been made since late 1982. The parasite, *Roptrocerus eccoptogastri* (Hymenoptera: Torymidae), has been the most successful release to date with establishment and subsequent rapid spread in several locations. The predaceous clerid beetle, *Thanasimus dubius* (Coleoptera: Cleridae), is apparently established in South Australia and Queensland, but unequivocal proof is not available.

Preliminary impact data show ca. 18 percent parasitism by *R. eccoptogastri* but variation is high, ranging from 0 to over 50 percent.

History of *Ips grandicollis* in Australia

The engraver beetle, *Ips grandicollis* (Eichhoff), was first found attacking Corsican pine, *Pinus nigra calibrica* (London) Schneider, at Wirrabara Forest in South Australia in 1943 although it may have been introduced as early as 1939 (Morgan 1967). It is generally assumed that it was introduced from somewhere in the eastern United States, but the exact point of origin is unknown. The beetle was apparently introduced via infested pine slabs used to make machinery crates. A separate introduction also occurred in Western Australia where it was found infesting Monterey pine, *P. radiata* D. Don in 1952.

Since Australia has no acceptable native tree hosts, the rate of spread from the area where the initial infestation occurred was slow because the pine forests are planted in isolated holdings, mostly on government and forest industry lands. As forests matured and wood products were moved about more frequently, the rate of spread accelerated. Fig. 1 shows the approximate dates of discovery of *I. grandicollis* in South Australian forests. Early control efforts were aimed at preventing movement of infested logs and other wood products into uninfested areas via quarantine. Since the economic viability of the forests in west central South Australia is not high, major control efforts were not initiated. However, when the beetle was discovered in 1979 in a major timber-producing region in the southeastern tip of South Australia near Mt. Gambier, a biological control project was proposed.

In 1982, the presence of *I. grandicollis* was confirmed in Victoria (Neumann, and Morey 1984) and in Queensland near Brisbane. Establishment was reported in New South Wales in 1983.

Biology of *Ips grandicollis* in Australia

The biology of *I. grandicollis* has been studied most intensively in South Australia. In general, its habits are consistent with those reported in the United States, with most attacks confined to logging slash and trees weakened or killed by drought, flooding, lightning strikes, etc. Occasional attacks also occur on healthier trees when *Ips* populations are very high and highly susceptible hosts are not available. There is, however, one striking behavioral difference in the form of common "feeding attacks" as described by Morgan (1967). These attacks are made on saplings or pole-size trees by very large numbers of adults which literally consume all of the phloem and some sapwood. Morgan (1967) found up to 3700 attacking adults per ft^2 of bark surface. Although some breeding and gallery construction often occurs, brood production is very low. Morgan also

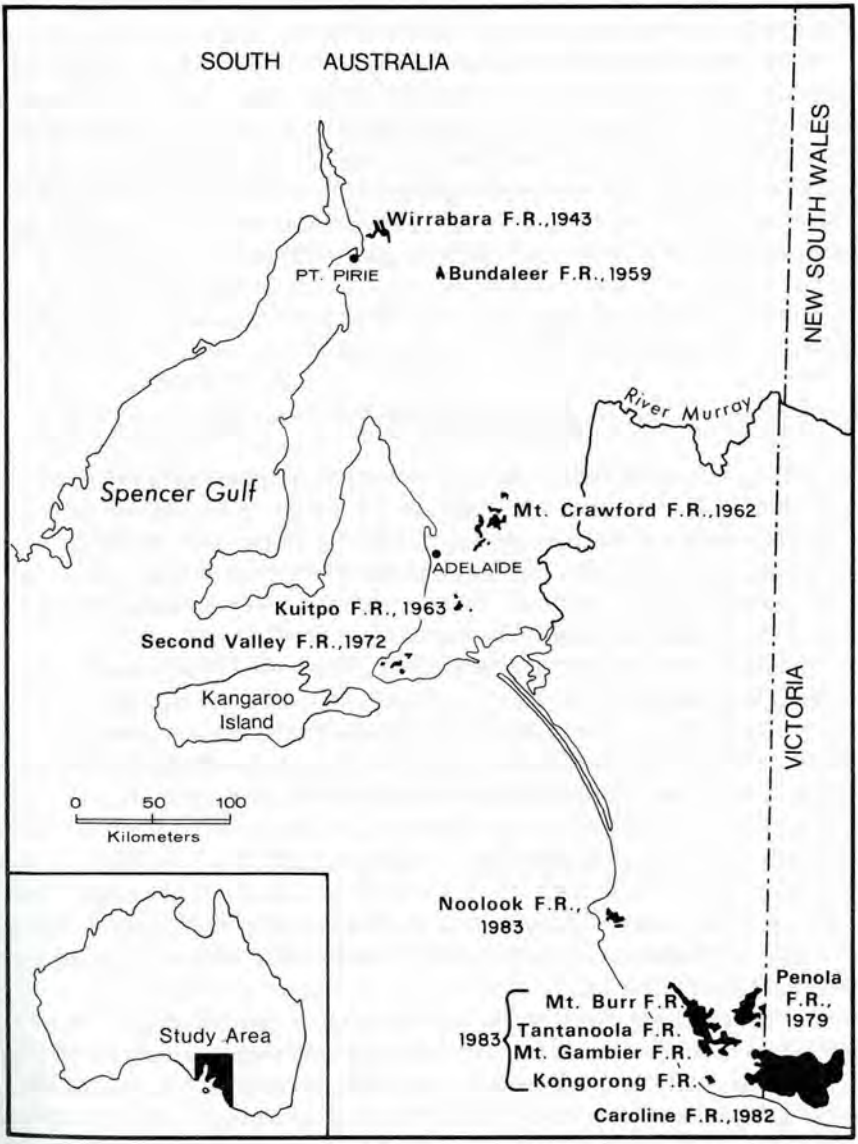

Fig. 1. Movement of *Ips grandicollis* in South Australia from the point of initial discovery at Wirrabara Forest Reserve in 1943. (F. D. Morgan, pers. comm.)

found that the fat bodies of the adults involved in such attacks are depleted, suggesting that feeding attacks may be dictated by the physiological condition of the beetles; i.e., low food reserves.

Brood production of *Ips grandicollis* in South Australia is approximately one-third higher than that in the United States (Georgia) although attack densities and numbers of eggs deposited may be similar (Berisford, unpublished). This relatively high brood production is apparently due to the absence of serious competitors and natural enemies. However, the effect of different tree hosts has not been determined. It is possible that Monterey pine, which is the major pine species in South Australia, is a superior host for *I. grandicollis*. However, loblolly pine *P. echinata* L. and Monterey pines of similar diameters and crown classes have similar phloem thicknesses (Berisford, unpublished).

Initiation of Biological Control Efforts

In 1981, a committee was formed to recommend approaches to biological control and funding was provided by the South Australia Woods and Forests Department and two timber companies, Softwoods Holdings, Ltd. and South Australia Perpetual Forests, Ltd. The program was and is currently administered through the Waite Agricultural Research Institute at the University of Adelaide under the direction of Dr. F. D. Morgan.

Initially, researchers in the United States who had experience in working with natural enemies of *Ips* spp. were contacted as potential suppliers of parasites and predators. Preliminary selection of parasites and predators was based on studies which had documented their abundance, apparent impact on *Ips* populations, potential for laboratory colonization, and apparent low niche overlap to minimize competition. A preliminary visit to Australia during February, 1982 was made by C. W. Berisford to become more familiar with the *Ips* research situation in Australia and to work out details for shipping natural enemies from Georgia (USA). Similar arrangements were made with D. L. Dahlsten for shipments of natural enemies from California.

Hymenopterous parasites selected as possible candidates for introduction from Georgia were *Roptrocerus eccoptogastri=xylophagorum* Ratzeburg (Torymidae) and *Coeloides pissodis* Musebeck (Braconidae). They were initially selected because they are among the most abundant parasites of *Ips grandicollis* (Berisford et al. 1970, 1971, Berisford and Franklin 1972, Berisford 1974), other southern U. S. *Ips* spp. (Riley 1983, Bing 1985, Miller 1986, Kulhavy et al. 1989), and the southern pine beetle, *Dendroctonus frontalis* Zimmermann (Overgaard 1968, Moore 1972, Moser et al. 1971, Dixon and Payne 1979, Kudon and Berisford 1980).

One of the more common parasites, *Heydenia unica* Cook and Davis (Chalcidae) was not selected because females of this species are aggressive and often disturb other parasites, including conspecifics which are attempting to search and/or oviposit (Dix and Franklin 1974). Competition between *Roptrocerus* and *Coeloides* for hosts is apparently relatively low because *Roptrocerus* enters host galleries to oviposit; whereas, *Coeloides* and most other bark beetle parasites oviposit through the bark.

The efficacy of *Coeloides* and other parasites can be restricted by bark thickness (Ryan and Rudinsky 1962, Demars et al. 1970, Berisford et al. 1971, Ball and Dahlsten 1973, Goyer and Finger 1980, Gargiullo and Berisford 1981). *Roptrocerus* is also influenced by bark thickness although it oviposits from within bark beetle galleries (Gargiullo and Berisford 1981). *Roptrocerus* is also positively density-dependent on the southern pine beetle. Additional parasites which were selected to help stabilize the rate of parasitism included a mixture of Chalcidoid and Braconid candidates. Berisford et al. 1971 found that although the average rate of parasitism was fairly constant, Chalcidoids tended to be seasonally abundant when Braconids were low and vice versa. Other species considered were *Rhopalicus tutela* (Walker), *R. pulchripennis* (Crawford) (Chalcidae), *Dendrosoter sulcatus* Musebeck and *Spathius pallidus* Ashmead (Braconidea).

Two predaceous beetles, *Thanasimus dubius* F. (Cleridae) and *Temnochila virescens* F. (Trogostitidae) were selected for introduction Although *T. dubius* is primarily a predator of the southern pine beetle and responds strongly to the aggregating pheromones (Dixon and Payne 1979, Mizell et al. 1984), it also attacks *Ips* spp. and apparently uses secondary olfactory cues such as *trans*-verbenol to locate host-infested trees (Vité and Williamson 1970). *Temnochila virescens* is commonly associated with both *Ips* and *Dendroctonus* spp., apparently responding to both insect and tree host-produced volatiles (Billings and Cameron 1984). Adults of both species prey on adult Scolytids; whereas, their larvae consume bark beetle larvae plus associated arthropods and nematodes. Representatives of most of these genera were also to be collected in California.

A quarantine facility was designated at the Waite Institute to receive and rear the natural enemies. Adults and larvae of parasites and predators were collected from trees infested with *Ips* spp. or southern pine beetles in Georgia and from *Ips*-infested trees in California and shipped to Australia by air. Australian quarantine authorities required that the natural enemies be reared through one or two generations in quarantine to screen for hyperparasites. Prey acceptance studies on a variety of common and/or beneficial insects were required for the predators.

Colonies of both predators were readily established in quarantine, but they required a very labor-intensive effort because larvae had to be reared individually and fresh food (*I. grandicollis* larvae) was provided 2-3 times

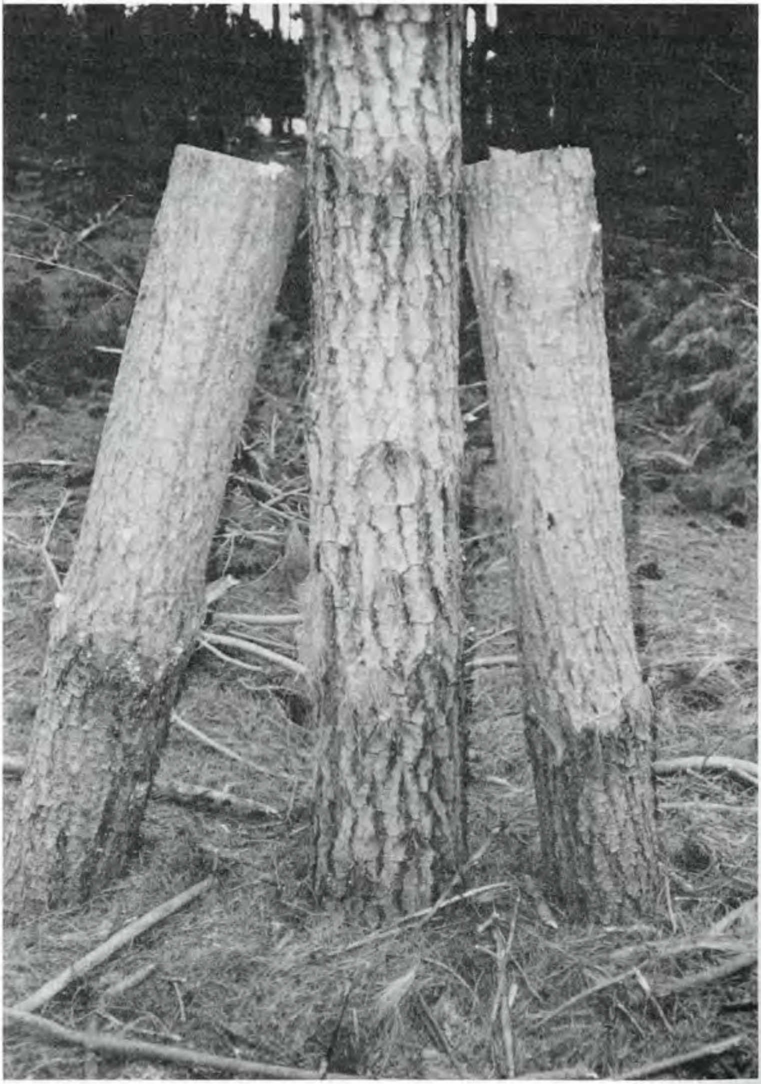

Fig. 2. Billets infested with *Ips grandicollis* prepared for release of *Thanasimus dubius*. (Photo by C. W. Berisford)

per week. Rearing techniques were slightly modified from those reported by Nebeker et al. 1980.

Roptrocerus eccoptogastri (Georgia) was the first parasite to be established in the laboratory and reared in large numbers. Subsequently, cultures of *Dendrosoter sulcatus* (Georgia strain), *Spathius pallidus* (Georgia strain), *Rhopalicus pulchripennis* (California strain), and *Roptrocerus eccoptogastri = xylophagorum* (California strain) were established. *Coeloides* spp. have not been successfully cultured in the laboratory, primarily due to high mortality of males during shipment from the United States.

Table 1

Natural enemies shipped from Georgia[1] and California[2] to Australia, 1982-86, for laboratory propagation and possible field release.

	Culture Established?	Released In Field?	Number of Releases	Established In Field?
PARASITES				
Roptrocerus eccoptogastri[1]	yes	yes	70	yes
Roptrocerus eccoptogastri[2]	yes	yes	1	no
Dendrosoter sulcatus[1]	yes	yes	30	yes[4]
Rhopalicus pulchripennis[2]	yes	yes	1	no
Rhopalicus pulchripennis[1]	yes	yes	1	no
Dinotiscus burkei[2]	no	—	—	—
Spathius pallidus[1]	no	—	—	—
Eurytoma conica[1]	no	—	—	—
Coeloides pissodis[1]	no	—	—	—
Heterospilus sp[1]	no	—	—	—
PREDATORS				
Thanasimus dubius[1]	yes	yes[3]	60	yes[4]
Temnochila virescens[1]	yes	yes	10	yes[4]
Temnochila virescens[2]	no	—	—	—

[3] Includes multiple releases at the same site.

[4] Probably established but unequivocal evidence is unavailable.

Table 1 summarizes the current information on establishment of lab colonies, field releases, and field establishment. *Roptrocerus eccoptogastri* was the first natural enemy to be released from quarantine. The initial field release of 12-15 mated females was made at Wirrabarra Forest Reserve on windthrown trees in September 1982. A larger release was made at Mt. Crawford Forest Reserve near Adelaide in late December 1982. In that

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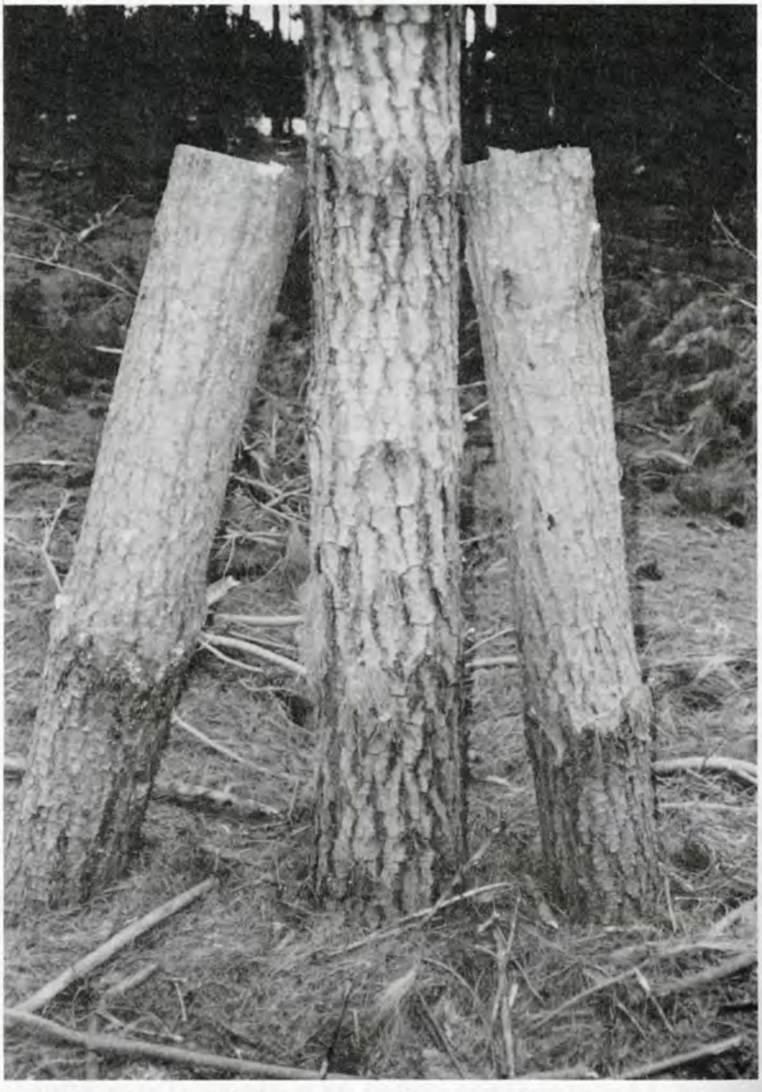

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Coeloides pissodis[1]	no	—	—	—
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Table 1 summarizes the current information on establishment of lab colonies, field releases, and field establishment. *Roptrocerus eccoptogastri* was the first natural enemy to be released from quarantine. The initial field release of 12-15 mated females was made at Wirrabarra Forest Reserve on windthrown trees in September 1982. A larger release was made at Mt. Crawford Forest Reserve near Adelaide in late December 1982. In that area, adult males and females were released on stacks of logs which harbored *I. grandicollis* broods which were in various stages of development.

Establishment of *R. eccoptogastri* was confirmed in late January 1983 at Mt. Crawford, but progress at Wirrabarra was not monitored closely and confirmation came in 1984 when it was found to have colonized much of the forest. Establishment has occurred subsequent to almost every release of *R. eccoptogastri* (Georgia strain) but the lab colony of the California strain eventually died out after only one release in the field. Sampson (1984) presented evidence based on morphology and cross-breeding experiments that the *Roptrocerus* from Georgia and California may be different species. The *Roptrocerus* from Georgia may be better adapted to the field conditions in Australia or perhaps to the rearing conditions in the laboratory. Additionally, the colony of the California strain may have become diseased.

Fig. 3. Billets containing *Ips grandicollis* broods parasitized by *Roptrocerus xylophagorum* deployed to release the parasites into an uncolonized area. (Photo by C. W. Berisford)

Dendrosoter sulcatus has been very successful in laboratory rearing and has been released several times since 1985. Although *I. grandicollis* larvae have been found to be parasitized by *D. sulcatus* at some release sites, positive evidence of establishment and spread beyond the release area has not been found.

A single release of *Rhopalicus pulchripennis* from California was made at Noolook Forest Reserve in 1985, but no evidence of establishment has been found.

The release of the predators from quarantine was delayed due to their long life cycles and the requirements for prey acceptance tests. Permission for initial releases of *T. dubius* was obtained in February 1983. The first field releases were made on February 26 and March 3, 1983 on the Myora Forest near Mt. Gambier in southeastern South Australia (Fig. 2). Releases of males and mated females were made at four sites on felled trees or billets which were under attack by *I. grandicollis* adults. An additional release was made at Tantanoola Forest Reserve on April 12, 1983. Supplementary releases were made in all areas in 1984, 1985, and 1986.

Preliminary evaluations showed that there were *T. dubius* larvae in every log or billet on which adults had been released plus some larvae on other logs up to 80 meters from any release site. Evaluations in 1985-86 indicated that *T. dubius* is established in South Australia because larvae have been found in areas several kilometers from release sites. However, unequivocal proof of establishment is lacking, perhaps due to the high dispersal capabilities and long life cycle of *T. dubius*.

Temnochila virescens has been released at several locations since 1985 and larvae have been found at or near most release sites, but establishment is not yet confirmed.

Impact of Natural Enemies

Since most releases and subsequent establishment are relatively recent, impact data are only preliminary. The only data at this point are for *R. eccoptogastri* in samples taken at Mt. Crawford and Wirrabarra Forest Reserves in 1986. Billets which had been removed at random from *Ips*-infested logging slash generated by thinnings and a few standing trees were evaluated. A 20 X 20 cm. sample was delineated on the bark which was then carefully removed and numbers of *I. grandicollis* and their life stages were recorded as were all *R. eccoptogastri*.

Parasitism was highly variable among 82 samples taken, ranging from zero to over 50 percent but averaged about 18 percent. Only late instar *Ips* larvae and pupae plus a few callow adults were parasitized. Samples with little or no parasitism had high percentages of early instar Ips larvae. We feel, therefore, that the available impact figures are conservative.

Release of Natural Enemies Outside of South Australia

Ips grandicollis became a national problem with the discovery of the beetle in Victoria, New South Wales, and Queensland in 1982 and 1983. State forestry organizations and timber companies outside of South Australia contributed funds to help with the establishment and maintenance of cultures of the natural enemies and interstate shipments of parasites and predators for field release were begun. Releases of *Roptrocerus*, *Dendrosoter*, *Thanasimus*, and *Temnochila* have been made at various locations in Victoria, New South Wales, Queensland, and Western Australia. Establishment of *Roptrocerus* has been confirmed in most release areas and there is good, but not conclusive, evidence for establishment of *T. dubius* in Queensland.

Future of the Biocontrol Program

The program has made substantial progress since its inception. Laboratory rearing of *Roptrocerus* is being de-emphasized in favor of field collection of billets from infested logs for distribution to new areas (Fig. 3). Introductions of *T. dubius* are also being made via billets infested in the laboratory. This will release laboratory space for rearing other natural enemies. Introductions of *Roptrocerus*, *Dendrosoter*, *Thanasimus*, and *Temnochila* are expected to continue.

Additional material is being shipped from the United States. In addition to supplementing cultures of natural enemies already established, further attempts are being made to introduce and culture *Coeloides* from California and Georgia plus introductions of *Enoclerus* spp. (Cleridae) from both regions.

We anticipate that additional data on the impact of *Roptrocerus* and other parasites and predators will be collected as new introductions become established. Plans are also being formulated to determine if reductions in *Ips* populations by natural enemies will be manifested through a reduction in tree mortality.

At this point, we are optimistic that once a small complex of parasites and predators are well established, they will significantly reduce *Ips* populations. There is, however, much work to be done in propagation, establishment, and evaluation before a realistic assessment of the program can be made.

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SECTION SIX

Interactions between *Rhizophagus grandis* (Coleoptera: Rhizophagidae) and *Dendroctonus micans* (Coleoptera: Scolytidae) in the Field and the Laboratory: Their Application for the Biological Control of *D. micans* in France

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ABSTRACT

Studies on *Rhizophagus grandis* and *Dendroctonus micans* in Belgium since 1976 substantiate the earlier claims in Europe that *R. grandis* is a major regulating agent in *D. micans*' population dynamics under endemic conditions.

Field observations showed that the predator has a very high capacity to discover its prey, colonizing up to 90% its brood chambers in every infested stand in the country. Laboratory experiments revealed that the predator has high fecundity, is very voracious at both the adult and the larval stages, and has a significant impact on its prey.

An attempt to exploit fully this predator–prey relationship has been developed since 1978 in the Massif central (France), where *D. micans* had

arrived during the early seventies. A mass-rearing method has been devised for *R. grandis*, a release strategy has been defined and implemented, and early assessments of the predator's establishment and dispersal have been made. Eighty-four thousand predators have been produced since 1983, 67,000 have been released in about 50 sites over an 5,000 km^2 area. The predators established in all sites sampled so far, and colonized up to 75% of the prey's brood systems.

INTRODUCTION

The Greater European Spruce Beetle, *Dendroctonus micans* (Kugelann), one of the only two *Dendroctonus* species of the old world, inhabits the Eurasian coniferous forests from eastern Siberia at the East to central France and the United Kingdom at the West. The pest is still spreading, and presently, an estimated 200,000 ha are suffering from outbreaks in recently invaded territories in the United Kingdom, France, the Georgian S. S. R. and Turkey. In the inner parts of the range, however, *D. micans* generally remains at very low and harmless population levels.

D. micans is a primary pest, mostly of spruce, *Picea* spp., and occasionally of Scots Pine, *Pinus sylvestris* L. It differs from the aggressive American species by its kin-mating, solitary attacks, gregarious larvae and apparent lack of associated pathogenic fungi. Except during outbreaks, the trees are not immediately killed and can survive several bark beetle generations (Grégoire 1985).

Dendroctonus micans seems protected against most competitors and generalist enemies by the defenses of its living host (Everaerts et al. in press). However, one specific predator, *Rhizophagus grandis* Gyllenhal., is very common and abundant in the inner parts of the bark beetle's range, and has been held responsible for the stable, low *D. micans* population levels in these areas (Bergmiller 1903, Pfeffer 1955, Kobakhidze 1965, Ceianu and Istrate 1976, Grégoire 1976). Based upon these claims, a vast biological control program has been developed in Georgia S. S. R. since 1963 (Shavliashvili and Zharkov 1985), and the predator had apparently been unable to follow and had to be introduced. Presently, 200,000 insects are produced each year, and effective control is achieved (H. F. Evans, personal communications).

In Belgium, we took another approach to this problem. *Dendroctonus micans* and *Rhizophagus grandis* had been present in the country for a long time (the former, 80 years; the latter, at least 40 years), and this allowed us to study the relationships between both species under endemic conditions. Field surveys were made in 1971-1972 and in 1976-1984 (Grégoire

1984). Additionally, several aspects of the *R. grandis/D. micans* relationship were studies in the laboratory.

During the same period, *D. micans* was developing outbreaks in the southern Massif central, where it had entered during the early seventies (Carle et al. 1979), ahead of its predator. This provided a very welcome opportunity, both for a practical use of our previous experience and for real-scale experiments. Within the frame of an European Economic Community-funded Programme (Wood as a Renewable Raw Material), close co-operation started in 1983 between the Universite libre de Bruxelles (ULB), the Institut national de la Recherche agronomique (INRA) at Avignon, France, and the Parc national des Cévennes (PNC) at Florac, France, for the development of a full biological control project in the National Park of the Cévennes (Grégoire et al. 1984b, 1985).

EXPERIMENTAL WORK IN BELGIUM

Field Surveys

Surveys in mature Norway spruce stands, *Picea excelsa* Link., revealed that all or nearly all mature spruce stands in the country shelter *D. micans*, although in very low densities (less than 4 attacked trees/ha). *R. grandis* was also found in all these stands, in 148 of the 245 brood systems sampled (60.4%). This global colonization rate corresponds well with records from other countries, 2-42% in Denmark (Gohrn et al. 1954) and 48% in Romania (Istrate and Ceianu 1976), although Tvaradze (1977) observed global colonization rates of 78%. However, if we consider more closely the global data recorded in Belgium, it appears that the actual colonization rate is much higher since prey brood colonization continues as the prey grow older. About 26% of the egg galleries are already found by *R. grandis*, but more brood systems are colonized as they grow older and, when the oldest larvae in the broods have reached the third instar, nearly 90% of the systems contain the predators. This level remains then steady in the older broods. These figures do not vary much between successive years of samplings or between different stands (Grégoire 1984, and unpublished data).

One conclusion is that *R. grandis* has an excellent capacity to locate its prey: each of the few brood systems lost in one ha of spruce has a 90% chance to be discovered by the predator. Another conclusion is that the brood systems remain attractive during their whole life. Although attraction to the egg galleries is probably due to allelochemics produced by the adult bark beetle, attraction to older systems is probably due to odours produced by the prey larvae themselves. Preliminary field verification of this last hypothesis has been made in late 1985 in France: 26 *R. grandis* were caught in 3 Lindgren Funnel Traps baited with *D. micans* larval frass (among which 13 males and 12 females) and 4 were caught in the 3 control traps (unpublished data). These findings suggest that trapping with adult bark beetle synthetic pheromones as a method for screening potential exotic enemies of these pests (Miller et al. these Proceedings) may have but a limited validity, since it was to larval frass that the predators responded in this case.

The field surveys confirmed all the accounts from the literature concerning the narrow specificity of *R. grandis:* never has it been found in the galleries of other bark beetles. The surveys also brought information about the phenology of *R. grandis*. It is very versatile and matches that of the prey. Larval and adults area found throughout the year; pupae, which have to be searched into the litter, were found more irregularly.

There is however one piece of data that the field surveys did not yield. It was impossible to draw any clear conclusion about the impact of *R. grandis* on *D. micans*, for the following reasons:

a) There is no average *D. micans* brood. Egg-laying is protracted over the whole growing season, and variable climatic conditions may influence the number of eggs ultimately laid. Moreover, facing the permanent reaction of the host, the female can interrupt oviposition before her full 150-200 eggs are deposited. On the other hand, several females may oviposit close together and the resulting larval groups may fuse. Retrospective countings are impossible because the eggs are laid in batches.

b) It is impossible to keep track of the predators. They do not leave any permanent sign of their presence, e.g. as parasitoids would leave cocoons. The absence of *R. grandis* in a system during sampling does not mean that they were always absent.

c) The "large" time intervals at play allow interactions of various intensities which left no traces. The life cycle of *D. micans* is particularly long (1 to 2 years), and the predator may invade a yet untouched system at any time, with an impact proportional to the precocity of the invasion, which we have no possibility to estimate.

d) Climatic influences vary for each *D. micans* brood. The very long egg-laying period results in variable climatic conditions influencing the age structure of each different brood. Each brood overwinters at a different state and weather-linked mortality (frost,

> drowning of underground systems) has thus a different impact in each case. Moreover, the predator/prey interactions also vary according to the climate.

These reasons may explain why no significant correlations were found between the numbers of prey and those of predators in 31 systems containing first-fourth instar *D. micans* larvae (r = -0.16), in 35 systems containing fourth-fifth instar *D. micans* larvae (r = 0.20), nor in 23 systems containing *D. micans* pupae and young adults (r = -0.17). Moreover, the average numbers of prey in the systems devoid of predators were not significantly higher than in the systems containing *R. grandis* (unpublished data).

Laboratory Experiments

Experimental results in the laboratory provided complementary information supporting the claim that *Rhizophagus grandis* has a significant impact on *D. micans* in endemic conditions (Merlin et al. 1984, and unpublished data). Some relevant data are reported here.

Pairs of adult *R. grandis* reared in polystyrene boxes (*vide infra*) produce an average number of eggs varying between 30 and 117. When they were transferred four successive times in fresh rearing boxes however, pairs of predators laid a total average of 276 eggs, which is close to figures from the Georgian rearings (Kobakhidze et al. 1968).

Prey consumption of *R. grandis* larvae was measured. Each predator larva consumed an average 41.8 mg (fresh weight) of prey, which is about ten times their own maximum weight, and amounts to the weight of a fully grown *D. micans* larva.

Pairs of predators were introduced each into a *D. micans* brood system in a fresh spruce log, when most of the prey were at the 3rd larval instar. Seventeen logs treated this way yielded an average 58.9 young *D. micans* adults, whereas 19 control broods yielded 153.7 adults. Predation had thus significantly reduced the prey broods by about two-thirds (t test, $p < 0.001$). Earlier introduction of the predators (which is the case in the forest for 50% of the brood systems) is likely to result in even more important brood reduction.

The results of our field and laboratory work support thus well the conclusions of earlier authors, based mostly on casual observations. *R. grandis* has an extraordinary capacity to locate its prey, at any stage of this latter; it has flexible phenology; its fecundity is high, matching that of the prey; its larvae consume each the equivalent of a mature prey larva, which means that they generally eat at more than one prey when these are smaller;

pairs of predators and their broods may reduce a prey's brood by at least two-thirds.

Although further information, from the field and the laboratory, is still urgently needed, these data provided sufficient support for attempting biological control with *R. grandis* in France.

THE BIOLOGICAL CONTROL PROGRAMME IN FRANCE

Background

Coming from the north, *Dendroctonus micans* is progressively invading the southeastern Massif central (Ardeche, Haute-Loire, Lozère, Gard). It soon appeared that the difficulty in detecting new infestation spots, due to the cryptic attacks of the pest and the trees remaining green, made traditional silvicultural control measures (hygiene thinning and clear-cutting) ineffective (D. Schveszter, personal communication). On the other hand, the literature and our own experience suggested that *D. micans* was especially suitable for biological control. There is some evidence that *Rhizophagus grandis* followed its prey to some extent into the Massif central, but the natural populations of this species were restricted to very few and limited spots (Grégoire et al. 1985). Filling the gaps between these spots in areas of ancient bark beetle colonization, and rapidly introducing the predators in areas of incipient attack were the two aims of the INRA - PNC - ULB joint project. Although some preliminary, limited trials were made by both the ULB and INRA since 1978, the real efforts started in 1983 and are still in progress.

Rearings

In 1983, the mass-rearings of *R. grandis* were based on the methods used in Georgia (Kobakhidze et al. 1968). Predators were introduced into logs containing *D. micans* broods, their prepupae were collected when leaving the logs, and pupation occurred in sand-filled Petri dishes. One large unit was built at the ULB, a smaller one in the PNC, at Le-Mazel-du-Bleymard (Lozère). Forty-one hundred predators were produced.

In 1984, a semi-artificial rearing method was used (Grégoire et al. 1984a). Pairs of predators were induced to oviposit in 25 ml glass test-tubes containing each 20 prey larvae, rehydrated spruce bark powder and a strip of fresh bark. The resulting predator larvae were then reared in containers and fed with muscid maggots. Eleven thousand six hundred predators were produced.

In 1985, the glass tubes were replaced by cylindrical clear polystyrene boxes with a tight fitting cover (diameter 49 mm; height 17 mm) (Grégoire et al. 1986); a third, small-scale rearing unit was started at the Office national des Forêt (ONF), on Mount Aigoual (Lozére). Thirty thousand seven hundred insects were produced.

In 1986, the rearings went on in the polystyrene boxes. Fifty-two thousand three hundred insects were produced. Presently, our rearing method has the following characteristics:

Yield: 30-70 young adults per female *R. grandis;*
1.5-3.5 young adult *R. grandis* per *D. micans* larva.

Generation time: 60-80 days at room temperature.

Survival: larvae to prepupae: ca. 90%;
prepupae to adults: ca. 80%;
larvae to adults: ca. 70%.

The fungus, *Beauveria bassiana*, which caused up to 80-90% mortality in earlier rearings (Grégoire et al. 1984b, King and Evans 1984) has been almost totally eradicated, due to the reduced numbers of natural prey used, and to thorough prophylactic methods. Today, *B. bassiana* occurs only exceptionally in rearings with predators collected in the field. Overall, about 1% of the rearing boxes are observed to contain *B. bassiana* and are immediately discarded. Fungal occurrence in further stages of the rearings is extremely rare.

Releases

In 1983, 2,350 predators were released; 8,500 in 1984; 16,350 in 1985; 41,800 in 1986.

The first trial in 1983 had shown that releasing large numbers of predators allowed good establishment of these latter *(vide infra)*. Consequently, similar release criteria were adopted during the following years: 50 pairs of adult beetles at the base of each attacked tree if the site contains less than 10 attacked trees/ha; at least 500-1,000 pairs per site when there are more than 10 attacked trees/ha. These criteria are close to those used in Grégoire (Tvaradze 1977), where 1 pair of predators was released per *D. micans* attack on 50 trees/ha, with 1.5-3 km between each release site.

In 1983, the predators were released in a densely attacked stand (Forêt du Goulet), well behind the limits of *D. micans*' range at that time. During the following years, most the releases were concentrated on the limits of the range, where *D. micans* was still sparse and could possibly be brought under control rapidly. The production of the PNC unit however, is used to fill the gaps in *R. grandis* settlement around the Forêt du Goulet at the vicinity of the unit, so that the impact of predator releases in areas of intensive *D. micans* colonization could also be assessed in the future.

Assessment of *R. grandis* establishment and spreading

One major problem in assessing *R. grandis* establishment in the Massif central is that one is never quite sure of the origin of the insects found during samplings. Some limited natural populations have been observed in the northern parts of *D. micans*' range, and may have spread locally; the earlier releases between 1978 and 1982 may have also led to unnoticed establishment of predators. For example, the day after releasing *R. grandis* in Legoulet in 1983, a tiny pre-existent population was discovered, which none of the previous samplings had revealed. These insects may have come from a local release by INRA in 1978, although no recovery was made in the years after the release.

So far, six release sites have been surveyed to assess predator establishment. *R. grandis* was present in all of them. The lowest colonization rate after one year was 14.4% (14 brood systems sampled). *R. grandis* establishment was particularly studied in two stands: the Forêt du Goulet, well within the range, and the Forêt d'Aire de Cote, on the range's limits when the releases were made.

In Le Goulet (2,350 predators released in 1983), 17% of the prey's systems sampled were colonized in 1984 (n = 60): see Fig. 1a; this proportion had reached 48% in 1985 (n = 54), and the predators had spread to a distance of 1.5 km from the 1983 release plot: see Fig 1b; in 1986, 73% of the brood systems were found colonized in the area sampled in 1985, and 54% in the whole 150 ha of 60-80 years old spruce (n = 59): see Fig. 1c.

In Aire de Copte (6,400 predators released in 1984; 3,200 released in 1985), 44% of the prey's systems were colonized in 1985 (n = 25) and 56% in 1986 (n = 18).

Perspectives

D. micans is still progressing southward and eastward in the Massif central, and still other spruce stands are threatened, towards the Pyrenean Mountains, Brittany and Normandy, respectively on the southwestern and northwestern limits of the spruce range. Mass-rearings and extensive releases of *R. grandis* might thus need to continue for several years.

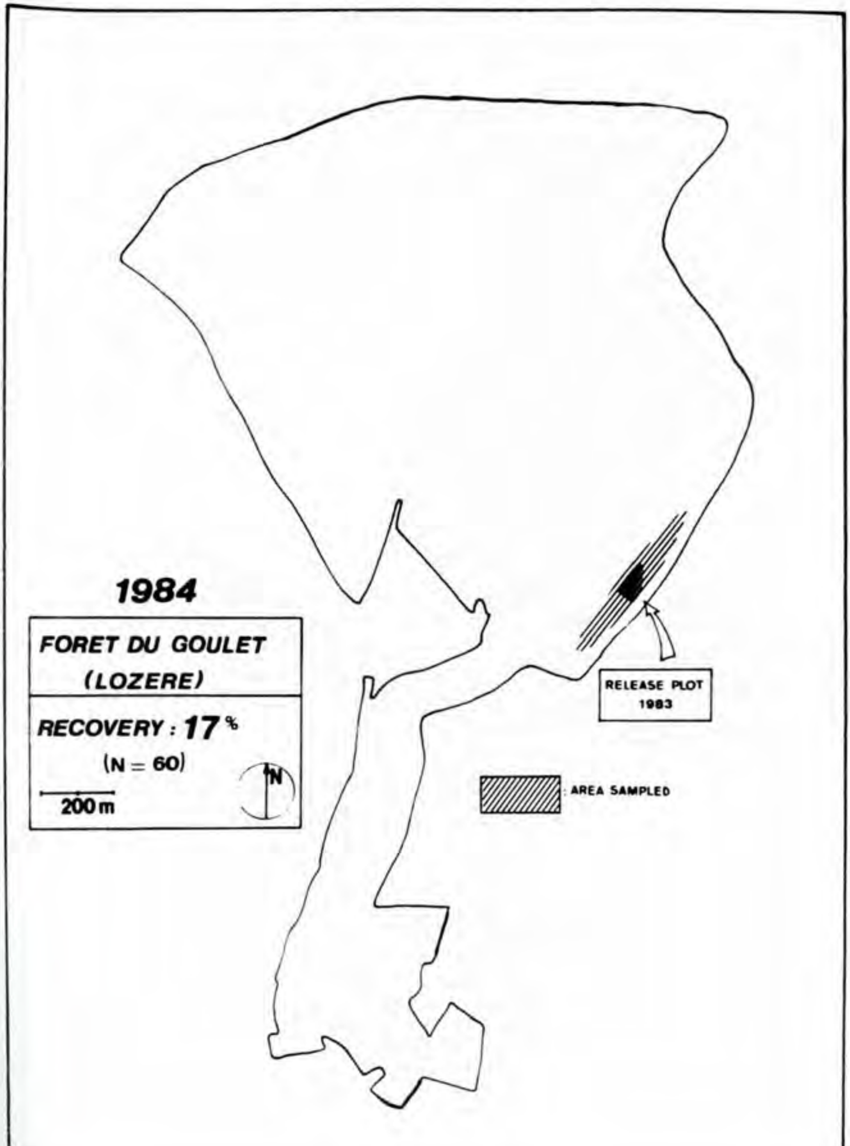

Fig. 1a. Establishment and spreading of *R. grandis* in the Forêt du Goulet, after a release in 1983.

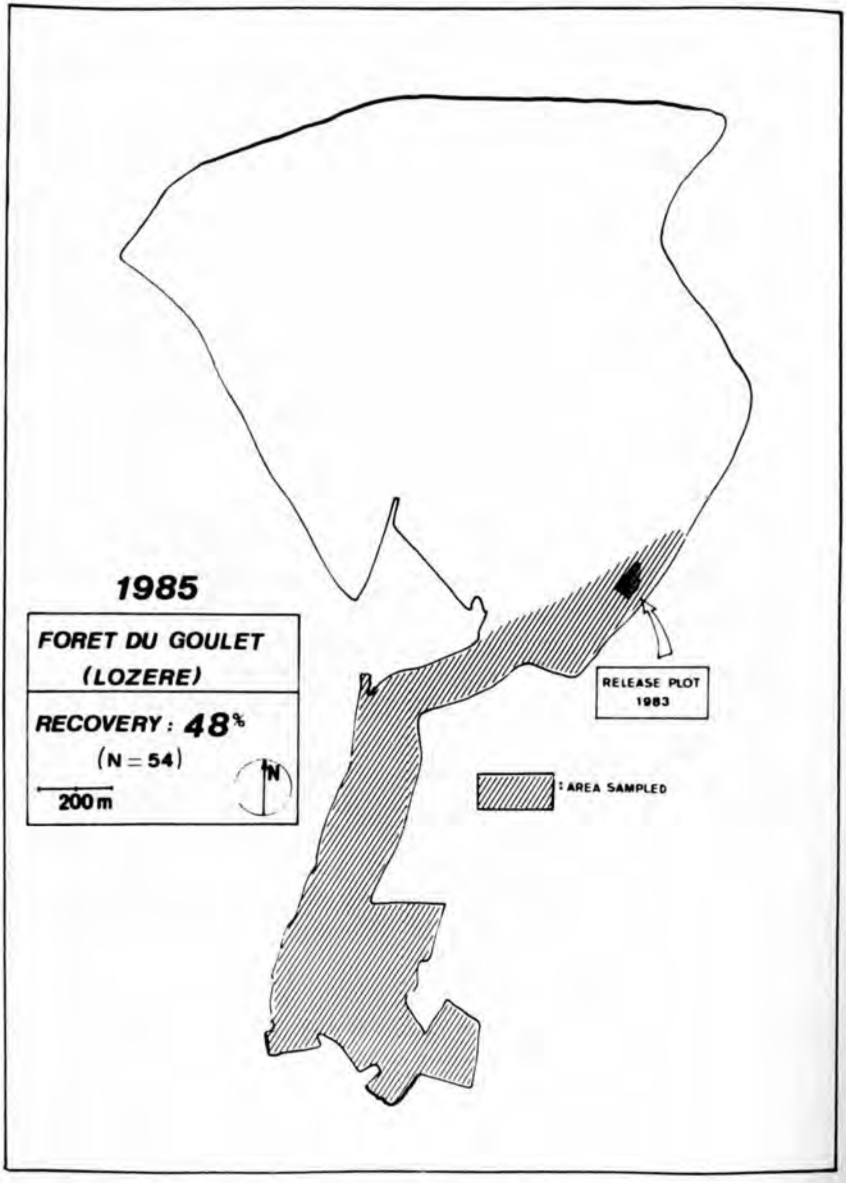

Fig. 1b. Establishment and spreading of *R. grandis* in the Forêt du Goulet, after a release in 1983.

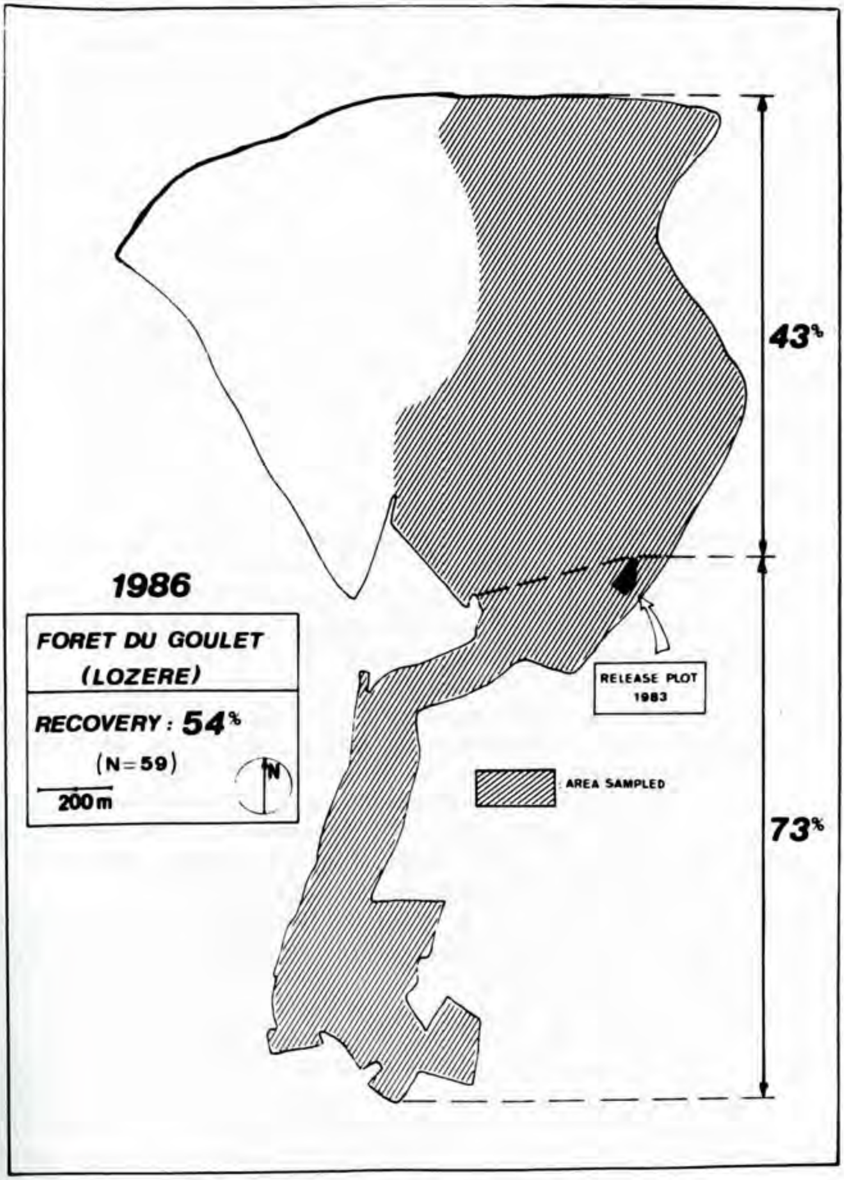

Fig. 1c. Establishment and spreading of *R. grandis* in the Forêt du Goulet, after a release in 1983.

On the other hand, assessments of the predator's impact in treated areas are now urgently needed. Exclusion experiments, comparisons of treated and control plots, artificial introduction of *D. micans* alone or with *R. grandis* in standing trees should be considered as the priorities for the years to come.

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discussion examines the attributes of predators as regulatory agents and assesses the status of *R. grandis* relative to these.

INTRODUCTION

Great spruce bark beetle, *Dendroctonus micans* Kug. has been known as a pest of spruces in Europe for the last 100 years or more. It has spread steadily from its North Eurasian origin, undoubtedly assisted by increased commerce in timber. *D. micans* is the only representative of the genus *Dendroctonus* found in Europe and is regarded as closely related, if not conspecific, with the North American *Dendroctonus punctatus* LeConte (Bright 1976). Most, if not all, of the genus Picea is susceptible to attack by *D. micans* and this is reflected in its association with most of the spruce forests throughout Eurasia. Economic damage is currently causing concern in the Georgian SSR, Turkey and France.

Marchant and Borden (1976), in reviewing the world wide introduction and establishment of bark and timber beetles, rated *D. micans* as potentially one of the most serious bark beetle pests. This was based on its known history of outbreaks and movement between countries. Similar worries concerning possible introduction and establishment of *D. micans* had been expressed in Britain (Brown and Bevan 1966) and plant health inspections were tightened up to minimize the risks of importation. However, despite these measures the beetle was discovered in 1982, following a routine inquiry concerning some killed Sitka spruce, *Picea sitchensis* (Bong.) Carr trees. Its discovery was followed by forest surveys showing that *D. micans* was distributed over much of Wales and central west England. Ring analysis of earlier attacks indicated that it had been present in Britain since at least 1972 (Bevan and King 1983). Immediate measures to more accurately determine the distribution of attacks were initiated. These involved intensive surveys of all spruce including large commercially managed plantations, minor plantings as well as individual trees in gardens and parks. This provided a basis for assessment of the scale of infestation and for determining strategies for control of *D. micans*.

Strategies for control of *D. micans* in Britain.

A review of the literature on attack intensity and options for control of *D. micans* revealed that three main strategies, alone, or combined had been used in Europe and the USSR. These include:

(a) Sanitation felling to remove infested trees or, in severe cases, full clearance of the affected site. This was the normal forest management option for rapid reduction of *D. micans* populations with salvage of the affected timber.

(b) Chemical insecticide treatments of standing trees to kill existing *D. micans* broods or to prevent new attacks. This was adopted mainly in the USSR.

(c) Introduction of the specific predator *Rhizophagus grandis* Gyll. This strategy had been practiced in the Georgian SSR from 1963 (Kobakhidze et al. 1970) and more recently in France (Grégoire et al. 1985).

In Britain, scolytids of pest status are few in number, and with the exception of those associated with Dutch elm disease, are rarely serious. *D. micans* presented new problems to British foresters because it attacked only living and relatively healthy trees. Traditional methods for prediction and control of bark beetle populations did not apply and the control strategy adopted here has been based on the options outlined above with the addition of methods specific to Britain.

The immediate concern was to reduce *D. micans* populations to manageable levels and to allow time to implement a more permanent long term control strategy. To this end a "seek and destroy" policy was adopted in 1982. This involved felling of all infested trees discovered during intensive surveys. Trees displaying symptoms of attack, normally the pitch tube produced following boring by the female beetle, were felled, debarked and sprayed with insecticide (0.5% (AI) Gamma-HCH in water). This strategy was carried out for two years during which time 63,000 trees were felled within the infested forests. At the same time the Forestry Commission brought in legislation to control the movement and fate of spruce felled in infested forests. Thus all spruce required specific felling licenses and could only be moved to approved timber mills capable of removing bark. A scheduled area surrounding the main infested area was established and no movement of infested spruce was allowed between this and the rest of Britain. This strategy was therefore designed to minimize the risks of accidental carriage of *D. micans* to other spruce plantations especially in Scotland. The sanitation felling policy was dropped in 1984, partially because of the high costs in terms of staff, premature felling and destabilization of crops, but mainly because it was incompatible with the biological control strategy using *R. grandis* that was adopted in 1983.

The scheduled area and restriction on timber movement remain in force. Liaison with Belgium scientists (J-C. Grégoire and J. Pasteels) resulted during 1983 in importation to Britain of initial stocks of *R. grandis*. Small scale rearing trials indicated the feasibility of producing sufficient numbers of predators for field release and the decision to use *R. grandis* as the main long term control measure against *D. micans* was taken late in 1983.

Mass Rearing of *Rhizophagus grandis*

Kobakhidze et al. 1970 had reported on the breeding methods of *R. grandis* used in the Georgian SSR. These essentially followed nature as closely as possible and involved infesting cut spruce logs with *D. micans* larvae followed by introduction of *R. grandis* adults. Oviposition and larval predation took place under the bark with eventual emergence of prepupae that dropped into sand below the logs where they molted to adults. A similar method had been successfully adopted by Grégoire et al. (1985) and it was decided to use the same approach in Britain.

Between 1983 and 1985 a number of specialized rearing units were installed at Ludlow, Shropshire, a location convenient to the infestations

Fig. 1. Rearing of *Rhizophagus grandis* in spruce logs. Introduction of an *R. grandis* adult to a larval brood of *Dendroctonus micans*. (Photo courtesy of Forestry Commission.)

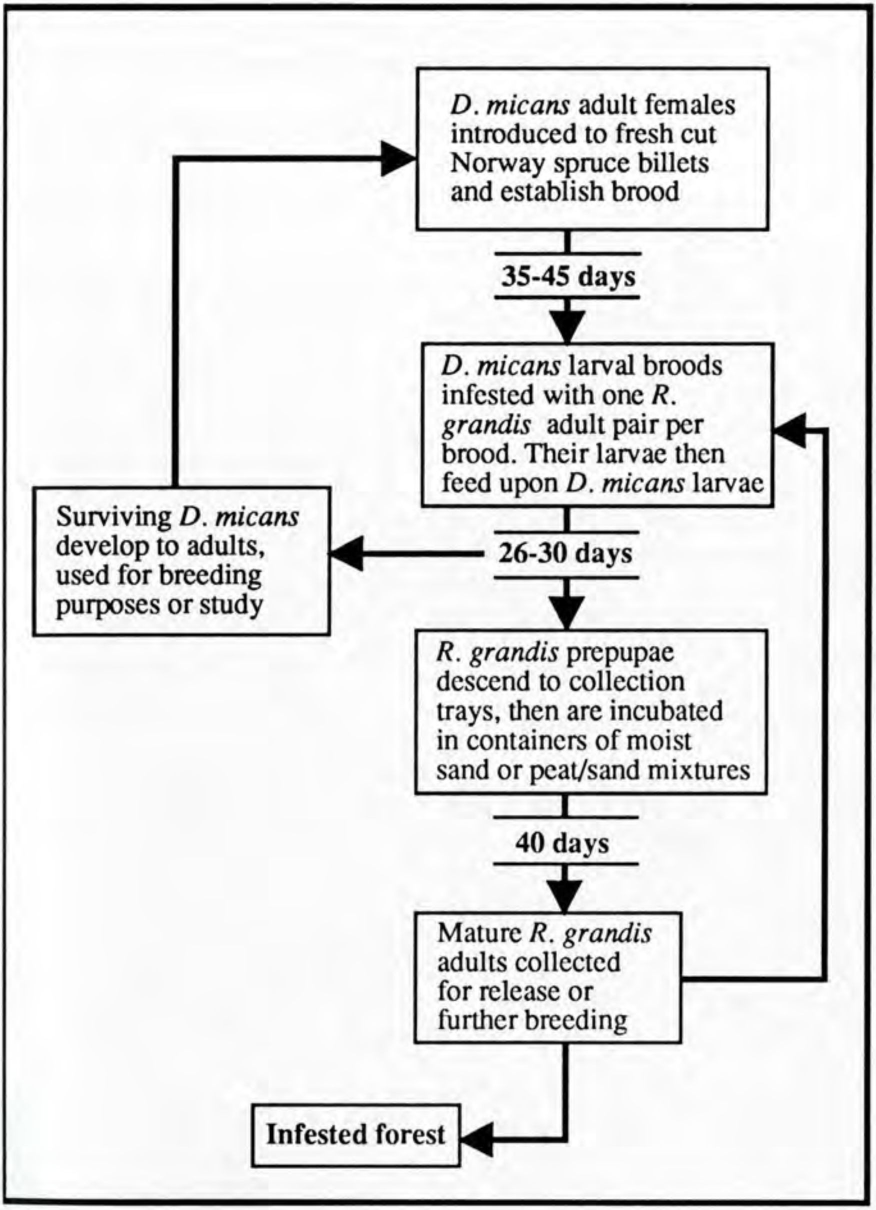

Fig. 2. Schematic representation of the basic *Rhizophagus grandis* rearing process.

and within the scheduled area. The units consisted of prefabricated cabins equipped with temperature and humidity controls maintained at 20°C ± 1°C and 65-75% RH. Cut logs of Norway spruce, (*Picea abies* (L) Karst.), were used as a breeding resource for *D. micans*.

Establishment of *D. micans* broods was achieved using two main approaches:

(a) Introduction of *D. micans* adult females for oviposition and establishment of larval broods.

(b) Implantation of *D. micans* larvae to logs by removing bark and inserting an appropriate number of third instar larvae, the area being covered by waxed paper.

This was followed by insertion of one pair of *R. grandis* adults to the brood chamber (Fig. 1). The whole process is summarized in Fig. 2 which outlines the basic procedures and timings for the conditions pertaining in the rearing chambers. Clearly direct implantation of larvae saves between 35 and 45 days and is more efficient in terms of generations reared per year. However, it does carry a penalty in the labor involved in collecting sufficient larvae from the field. Larval implantation is the only practical method during the winter months when adult *D. micans*, although active, are unable to breed successfully.

Practical Considerations

The process of introducing *D. micans* females to logs was prone to inconsistency in success of establishment. Two methods were used. The first involved placing a number of females in sealed cages containing fresh spruce logs. This enabled the insects to select the site of entry and more closely mimicked the situation in the field. The second relied on confining single females against the bark using small polythene caps pinned over prepared entry holes. Of these two methods the latter was eventually used routinely because the number of successful beetle entries could be observed and the distribution of broods within the logs controlled more readily.

To accommodate the log breeding method each unit was furnished with strong metal racks placed upon steel mesh over funnels leading to shallow trays (Fig. 3). Prepupae descending from the brood logs were concentrated by the funnel to the tray below where they were readily collected and transferred to containers of sterile moist peat/sand for pupation. The tray itself contained moistened plaster of Paris to minimize the possibility of desiccation of prepupae.

Results of the Mass Rearing Program

During the three years of the *R. grandis* rearing program there have been encouraging successes as well as a number of problems that have reduced the numbers of predators available for field release. Table 1 summarizes the main results of the program and serves to pinpoint those stages of the life cycle where breeding success has been most variable.

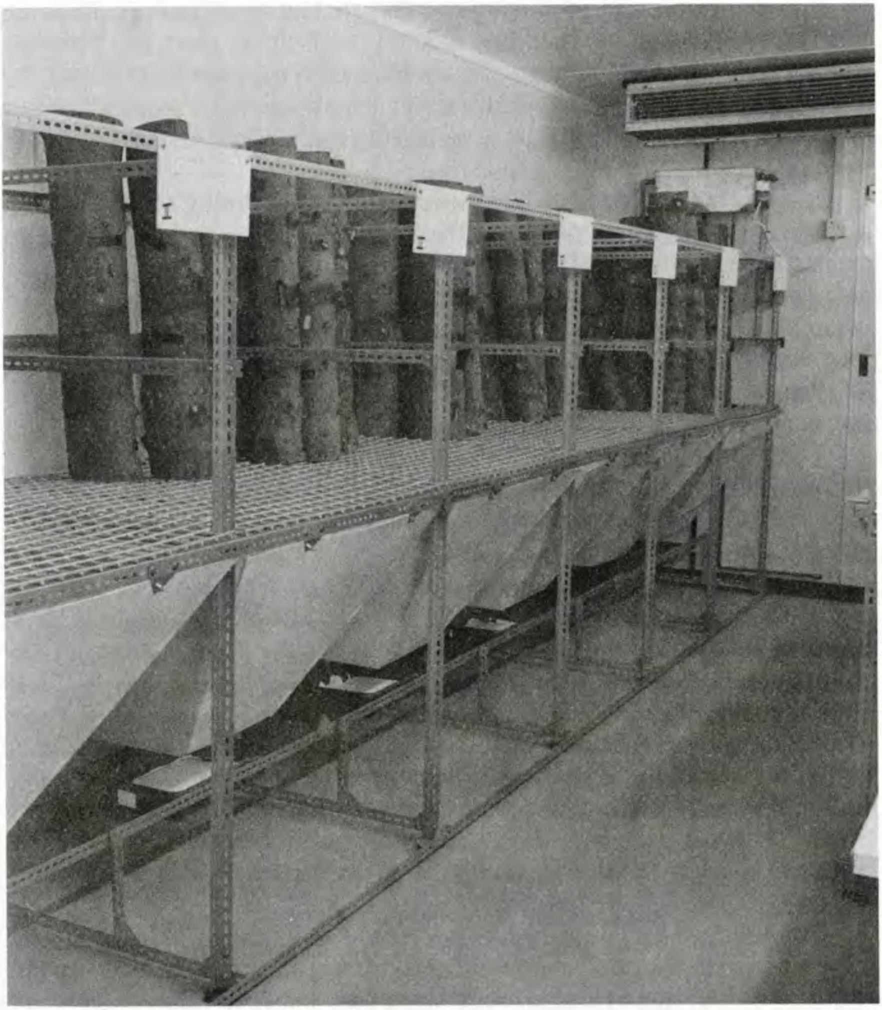

Fig. 3. The log support and funnel system used for rearing *Rhizophagus grandis* in spruce logs. (Photo courtesy of Forestry Commission.)

A total of ca. 102,000 adult *R. grandis* have been reared using the log method. This has been achieved at the expense of a large labor input and, particularly in 1985, a high cost in turnover of logs. There are no reliable data on mean numbers of eggs produced per female using this method. Mean oviposition of 150-230 eggs/female in the Georgian SSR (D. Zharkov pers. comm.) and around 100 eggs/female in Belgium (Merlin et al. 1985) have been reported. The latter data should apply equally to the British *R. grandis* because they were derived from the same origin. An approximation of the egg production per female has been obtained from the recently established box breeding method (see below). Here it is possible to enumerate the larval progeny per female by direct observation during the rearing process. A mean of 39 larvae per female has been recorded with a range of 7 to 131 indicating great variability both in oviposition and larval survival.

It is likely therefore that large losses may occur during the oviposition and larval establishment phases of the *R. grandis* life cycle but these losses cannot be quantified within the logs. Losses from prepupae to adult are also substantial and were particularly serious for natural broods in 1985 when nearly 60% of an already reduced number of prepupae per female were lost. Similarly the mean numbers of adults produced per introduced *R. grandis* female were less than 50% of the 1984 totals for each of the succeeding two years.

The principal limiting factor has been the increasing incidence of the entomopathogenic fungus *Beauveria bassiana*. This disease has affected all stages of both predator and prey especially among adult *D. micans* maintained at ambient temperatures with fresh spruce bark, implying that fungal contamination was derived from the bark. The severe losses between prepupae and adults recorded in Table 1 were attributable mainly to *B. bassiana* infection. Trials with fungicides applied to various stages of the rearing process failed to ameliorate the situation (King and Evans 1985). In 1986 the incidence of *B. bassiana* has been reduced as a result of more stringent hygiene methods. These included fumigation in an atmosphere of formalin vapor of all adult insects, flame sterilization of log surfaces, generally improved handling procedures and early rejection of all infected material. This has been reflected mainly in the improved survival from prepupae to adult of the *R. grandis* reared on natural broods, confirming that adult *D. micans* are significant carriers of *B. bassiana* inoculum.

Other factors affecting rearing success were linked to changes in viability and fecundity of *D. micans* adult breeding stocks. Generally, oviposition by *D. micans* could be relied upon only between January and July after which, with few exceptions, they would not initiate broods. It is not clear why laboratory performance declined so dramatically because in the

Table 1

Rearing of *Rhizophagus grandis* in spruce logs: *D. micans* natural oviposition (N) and impanted larvae (I).

	NUMBERS PER YEAR								
	1984			1985			1986		
Stage	N	I	Total[a]	N	I	Total	N	I	Total
Logs used	300	620	341	-	-	-	-	-	-
D. micans broods	648	293	941	3353	570	3923	933	975	1908
R. grandis prepupae	38232	9376	49583	73139	20644	103417	20526	14625	35330
R. grandis adults	28434	6010	35504	29366	13247	45464	13146	8123	21269
Mean no. prepupae/male	59	32	53	22	36	26	22	15	19
Mean no. adults/male	44	21	26	9	23	12	14	8	11
% Prepupae to adult	74.4	64.0	71.6	40.4	64.2	44.0	64.0	55.5	60.2

[a] Totals include feeding on of immature larvae whose origins (N or I) were uncertain.

Release of *R. grandis* in Infested Forests

Throughout the mass rearing project the distribution and abundance of *D. micans* attacks have been closely monitored by means of intensive surveys. These data have been used as the basis for the release strategy for *R. grandis* in Britain. An early decision was taken to develop a policy of relatively low density inoculative releases over a large number of locations covering the major part of the infested areas. It was argued that the slow generation time of *D. micans* (12-24 month cycle adult to adult) combined with the low populations remaining following the sanitation felling program gave ample time for a relatively rapidly breeding predator like *R. grandis* to build up to levels sufficient to regulate *D. micans*.

Release policy was therefore tailored to known densities of *D. micans* in the field. Survey data were expressed as infested trees per location, the diagnosis of infestation being a combination of visible damage and more frequently, the presence of pitch tubes. The numbers released were related to the intensity of *D. micans* attack using the following scheme.

Sites with > 100 infested trees	50 pairs of *R. grandis* adults
" " 50-99 " "	25 " " " "
" " 5-49 " "	15 " " " "
" " < 4 " "	10 " " " "

Although the numbers of *R. grandis* released at higher density sites were fewer than the recorded infested trees it was known that many *D. micans* attacks were old and did not contain active brood or were abortive. In detailed studies at some sites successful attacks averaged around 22% while the proportion of those containing active brood was no higher than 50% thus giving an overall rate of current successful brood of 10% only (Evans et al. 1985). On this basis the numbers of *R. grandis* females per tree with active *D. micans* brood were probably at least four at the high density sites and proportionately greater at the low density sites.

Releases during the first year were based on placement of one sexed pair of *R. grandis* at the base of each infested tree, a method that was aimed at maximizing the probability of prey encounter. Care was taken to avoid inclement weather such as high winds or heavy rainfall which might have affected adult mobility and prey detection. Releases were confined to the period May to October inclusive to coincide with maximum activity in the field. During this period average monthly maxima in Britain exceed 22C and both *D. micans* and *R. grandis* can be expected to be fully active. Studies of *R. grandis* dispersal, reported in a later section, indicated that flight took place readily during this period and that *R. grandis* adults were able to locate prey at least 200 m from a point release. On this basis it was decided to change methods to release in bulk at one or two points only in each infested location so that the adult predators themselves were relied upon to disperse to infested trees. In this, the second year of release, the numbers of predators averaged three per infested tree at the majority of locations.

Data on the rates of *R. grandis* release are given in Table 3. These represent releases at all locations having more than three infested trees and included complete treatment of sites at the periphery of the infested zone. The distinction between Forestry Commission and privately owned holdings of spruce serves to emphasize the need for a comprehensive logistic approach to releases, since 56% of the sites were in private hands. All *R. grandis* were reared by the Forestry Commission and distribution in the field was carried out in collaboration with the private sector. In this way it has been possible to complete the release program with the knowledge that all sites have been treated on the same basis regardless of ownership, an important factor in ensuring a consistent control strategy. For reasons already mentioned, the 1985 release program did not reach its target and further releases had to be made in 1986 in order to achieve coverage of all infested sites.

Table 3

Numbers of *Rhizophagus grandis* released in Britain in the period 1984 to 1986.

Year	No. *R. grandis* released	FC[a] locations	PW[b] locations	Total locations
1984	31168	528	414	942
1985	39392	206	449	655
1986	17604	319	496	815
Totals	88164	1053	1359	2412

[a] FC = Forestry Commission

[b] PW = Private Woodlands

Assessment of *R. grandis* Establishment in Infested Forests

The concept of inoculative release means that efficacy, in terms of reductions in *D. micans* populations, can only be assessed after the predator has had several generations to reproduce and reach a dynamic balance with prey populations. Even allowing for the relatively rapid reproductive rate of *R. grandis* there is little likelihood that significant impact would be observed within the first 12 to 24 months. For this reason a policy of sample surveys to assess predator establishment was initiated. Establishment was considered successful if *R. grandis* was found after sufficient time had elapsed so that all life stages present must be second or later generations.

Early evidence was obtained following a small release in 1983 (27 pairs of *R. grandis*) at three sites. In 1984 the predator was found breeding at one of these sites. Following the main 1984 program a sample survey at 47 sites throughout the infested area was carried out in 1985, 12-15 months after the releases had taken place. At each site, depending on the level of *D. micans* attack, either five or ten of the most heavily infested trees were felled and 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. The labor intensity of this method of sampling limited the number of locations that could be sampled, but the results indicated an encouragingly high level of establishment of *R. grandis* in the year after release in the forest.

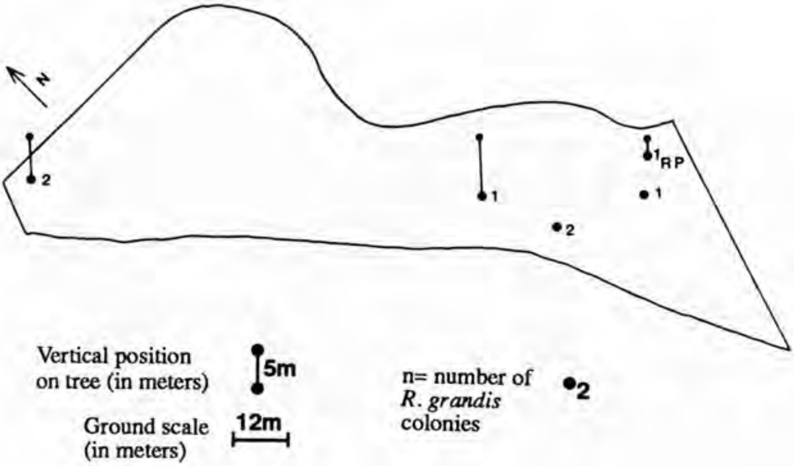

Fig. 4. Plan view of *Rhizophagus grandis* dispersal study site.

Dispersal of *R. grandis*

A study of dispersal of *R. grandis* was made at a single infested stand during 1984. The site consisted of a 50:50 mixture of 26 year old Norway spruce and oak covering an area of 1.1 ha (Fig. 4). Planting density was 1250 Norway spruce trees per ha thus totalling approximately 1375 trees at the site. Of this total 121 trees had been attacked by *D. micans* and 33 trees carried live brood at the time of sampling. Twenty-five pairs of *R. grandis* adults were released at the base of a single infested tree in August 1984 (RP in Fig. 4). Between seven and eight months later all infested trees in the plot were felled and each *D. micans* brood examined for the presence of life stages of predator and prey.

Fig. 4 summarizes the distribution of *R. grandis* up to 8 months following a point release. In view of the warm autumn in the year of release it is likely that the adult *R. grandis* found in two of the *D. micans* broods represented progeny of those released, indicating a generation time of around eight months for the predator when eggs are laid in late summer. A shorter cycle would be expected if eclosion occurred in late spring so that larvae benefitted from the higher summer temperatures. Up to two broods of *D. micans* on individual trees had been colonized and a maximum dispersal of 218 m was recorded. *R. grandis* had also colonized the tree at the release point. Dispersal was directional presumably reflecting the prevailing winds from the northwest during the period of study.

The 33 trees containing live *D. micans* carried a total of 63 live broods, of which seven had been attacked by *R. grandis* at various heights up the trunk, as indicated by the vertical bars in Fig. 4. This result can be assessed in the context of the inoculative release strategy adopted in Britain. The 25 female *R. grandis* released represented less than one per infested tree which is therefore less than the majority of the main release densities. Despite this low ratio of released predators to available prey, at least seven breeding colonies of *R. grandis* had been established thus providing evidence for remarkably well developed prey finding by this predator. The density of *D. micans* attacked trees was moderate relative to those reported by Grégoire et al. (1985) in a similar dispersal study in France. The major contrast between the two studies was the densities of *R. grandis* released at the British (25 pairs) and French (2350 adults) plots. A similar eight month period elapsed between release and sampling. In this time five trees in Britain and ten trees in France were successfully colonized by *R. grandis*. Although not a full measure of establishment it is relevant to a release program to quantify the rate of *R. grandis* colony breeding relative to the numbers of adults released. Thus establishment to release ratios for females of 0.2 in Britain and 0.009 in France would be recorded using this criterion. There are clearly too few data to extrapolate these findings to success of establishment at all release sites but the inference that inoculative release is proving effective provides encouragement that the method is adequate for establishing a breeding base for *R. grandis* in the field.

Other casual observations confirm the well developed dispersal capacity of *R. grandis* adults. A single adult has been found at a small isolated spruce plantation 4 km from the nearest release point while others have been found at distances up to 1.2 km from source. All indications from the various research workers in Britain, Europe and the USSR confirm the dispersal capacity of *R. grandis* and this is likely to be reflected eventually in a close correlation between predator and prey populations in the field.

DISCUSSION

Predators have tended, with a few notable exceptions such as control of cottony cushion scale *Icerya purchasi* Maskell by the vedalia beetle *Rodolia cardinalis* (Mulsant), to take second place to parasitoids in biological control programs. This has often been attributed to the polyphagous feeding habits of many predators that tend to give poor synchrony with the target prey. However, indications from the various attempts at using *R. grandis* for control of *D. micans* are that it is an effective regulatory agent. It is pertinent to examine why this predator appears to be successful when so many others, especially those that have been associated with bark beetles, have not exerted significant control. Rosen (1985) provided an excellent framework for defining the attributes of an effective natural enemy and this will be used to assess those of *R. grandis*:

(a) Searching capacity. This is clearly essential for effective exploitation of a prey resource that may be widely distributed at low densities, as is the case for *D. micans*. The predator must therefore have well developed prey finding behavior both at the adult and, within the brood, at the larval level. The dispersal study reported here confirms that *R. grandis* fulfils the requirement of effective searching capacity. The natural association of *R. grandis* with low density *D. micans* populations throughout Europe further points to this well developed capacity to find prey. Laboratory studies confirm that *R. grandis* adults respond positively to odor cues produced during *D. micans* brood development (Merlin et al. 1985, Tømmerås et al. 1985, D. Wainhouse pers. comm.) and it is through this route that both prey finding and specificity are defined.

Aggregation to concentrations of prey is a further characteristic of an effective predator. There are no quantitative data available on this for adult *R. grandis*. However, observations in the Georgian SSR of brood colonization at extremely high density *D. micans* populations indicate that the great majority of broods are found by *R. grandis* often with many adults (20+) being aggregated in single broods (H.

Evans, personal observation). Larval aggregation by *R. grandis* is a well described characteristic that results in rapid exploitation of prey individuals, the cues for this behavior being aggregation pheromones produced by the *D. micans* larvae in maintaining their distinctive group feeding (Grégoire and Merlin 1985).

(b) Specificity. A specific predator will have co-evolved with its prey and will therefore respond to changes in both prey density and distribution. Specificity is reflected in prey finding (above) and in the ability to exploit low prey populations without switching to more abundant prey. A disadvantage of specificity is the inability to exploit other prey when the prey of choice is at undetectable densities. *R. grandis* fulfils the requirements of specificity and there is no evidence that adult *R. grandis* exploit other species in its natural Eurasian range. However, it would obviously be of interest to assess the potential of this predator against the north American species of *Dendroctonus* (Grégoire and Moser this volume). All evidence from our own observations and others in Europe confirms that specificity is defined by the orientation behavior of the adult. Larval feeding is polyphagous but clearly there is little likelihood of their encountering other prey in the field.

(c) Power of increase. Rapid numerical responses to fluctuations in the densities of prey are important attributes, particularly for specific natural enemies. Preliminary observations indicate that *R. grandis* has a life cycle approximately half as long as that of *D. micans*. In addition, the adult stages of *R. grandis* are very long lived and they can survive periods when prey is either not available or is at an unsuitable stage of development. In Britain *R. grandis* adults placed in *D. micans* broods, both in forest and in prepared logs during September, overwintered *in situ* and oviposited in the following spring.

In addition to short generation time *R. grandis* also has a relatively high potential rate of increase per generation. Up to 300 eggs may be produced under laboratory conditions (Merlin et al. 1985) and a mean of 150 eggs per female was recorded by D. Zarkhov (pers. comm.) in the Georgian SSR. We have calculated that even at a pessimistic productivity of five progeny females per generation and at around 1.5 generations per year a single female *R. grandis* will have multiplied to nearly two million within six years. These calculations have shown that *R. grandis* powers of increase are more sensitive to the number of generations per year than to progeny per female. Thus two generations per year would increase the projected yields from two million to 250 million, while a similar proportionate increase in progeny per female to between six and seven would only result in an increase to around 30 million. *R. grandis* therefore acts as a classical r-strategist and is theoretically capable of responding rapidly to fluctuations in prey density. However, although observations in the Georgian SSR support this view, there are, as yet, insufficient quantitative data to confirm it unequivocally.

(d) Fitness and adaptability in relation to classical programs of predator introduction to new locations. This characteristic is particularly pertinent in Britain where the isolation afforded by its island status precludes the natural dispersal of *R. grandis* with its prey. Observations on successful establishment and dispersal reported here indicate that the predator has adapted well to British conditions of climate and tree ecology.

Taking these attributes as a whole there is accumulating evidence that *R. grandis* fulfils the majority of desirable traits outlined above. It is too soon after the initial introductions to be definitive on the question of whether it will provide long term regulation of *D. micans* in Britain. It is clear from the Soviet Georgian experience that, at least under their conditions, a period of 7-10 years is required following release before populations of *D. micans* are significantly regulated by *R. grandis* (D. Zharkhov, pers. comm.). While there are strong reasons to hope that the same will apply in Britain, the basic studies on predator orientation, response to prey, and interactions with other mortality factors will continue in order to further our understanding of the interactions of this unique predator with its bark beetle prey.

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PART THREE

Natural Occurrences of Biological Control

SECTION EIGHT

The Natural Enemies of *Ips typographus* in Central Europe: Impact and Potential Use in Biological Control

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ABSTRACT

The biological control of native scolytid pests in Canada through the introduction of exotic natural enemies from Europe is considered and investigations on the impact and potential of the natural enemies of *Ips typographus* are reported. The within tree dynamics of scolytid populations in Bavaria and the Graubuenden were studied in 1983-84 and the data obtained indicate the dominant role of competitive interactions and the importance of clerid predation and parasitism. Exotic natural enemies for use against native pests must show, in addition to the general requirements of biocontrol agents, an ability to locate and develop on the target host. Host location mechanisms for predators and parasitoids of scolytids are discussed and observations on the kairomonal action of aggregation pheromones and the role of heat, sound and odour in sub-cortical host location by parasitoids are presented. Preliminary results indicate the importance of volatile odours for host location by scolytid entomophages and point out the necessity for further work on parasitoids to better assess their compatibility with novel target hosts.

INTRODUCTION

While most scolytids can be regarded as secondary forest pests, some species in the genera *Dendroctonus*, *Ips*, *Scolytus* and *Tomicus* are able, through mass attack, to overcome the natural defenses of living host trees. Such scolytids are characterized by eruptive outbreaks (Berryman 1986) and are some of the most destructive forest pests.

Biological control as a strategy of forest pest management has three main advantages over the traditional use of chemical control. Firstly, beneficial organisms have the ability to provide self-perpetuating control following an initial inoculation into the forest environment. Secondly, the forest environment, being relatively stable both in time and space, provides favorable conditions for sustained natural enemy control over wide areas due to the lack of disturbance. Then thirdly, natural control agents are ecologically and socially more acceptable due to their more specific action against a target pest.

While biological control has classically concentrated on introduced pests, Carl (1982) points out that there is considerable agreement that native pests are an equally good, though neglected, target for control by introductions of exotic natural enemies. Indeed, Hokkanen and Pimentel (1984) believe that such an approach is more likely to result in success.

The selection of natural enemies for use in a biological control program is a widely discussed subject (e.g. Greathead and Waage 1983, Cock 1986, van Lenteren 1986). In general, desirable natural enemies should be able to respond to changes in host population densities, to efficiently search for hosts and to synchronize with appropriate host life stages. Pschorn-Walcher (1977) points out the necessity for more detailed investigation of the structure of mature natural enemy complexes, that are associated with forest insects, in selecting candidates for introduction. This is particularly true in the case of exotic introductions against native pests, where host location mechanisms, developmental compatibility with the target host and competitive compatibility with or superiority to native natural enemies are additional requirements.

In Europe, the closest ecological equivalent of North American *Dendroctonus* pests is *Ips typographus* (L.), an aggressive spruce infesting species with similar population characteristics. The natural enemy complex of this species is typical of European scolytids (see Mills 1983 for a review). In this paper, we present results obtained from a program, in collaboration with the Canadian Forestry Service, to assess the impact of the natural enemies of *I. typographus* in central Europe and their potential for use as exotic introductions for the control of native *Dendroctonus* pests in Canada.

HOST DYNAMICS AND NATURAL ENEMY IMPACT

The dynamics of *Ips typographus* populations and the impact of natural enemies were studied within infested trees in a low altitude (450 m), low attack density region in Bavaria in 1983 (Mills 1986) and in a higher altitude (800-1400 m), high attack density region in the Graubuenden, S.E. Switzerland in 1984 (Schlup 1987). In both cases, trees were sampled once only toward the end of the brood development period (i.e. the time of host pupation) and details of the scolytid life stages and associates were determined by examination of the bark. In Bavaria, 8 trees were sampled by collection of 0.7 m length logs from 3-4 height sections and due to the practical difficulties encountered with this scheme, 26 trees in the Graubuenden were sampled by taking three 100 cm^2 bark squares from 4 m height intervals.

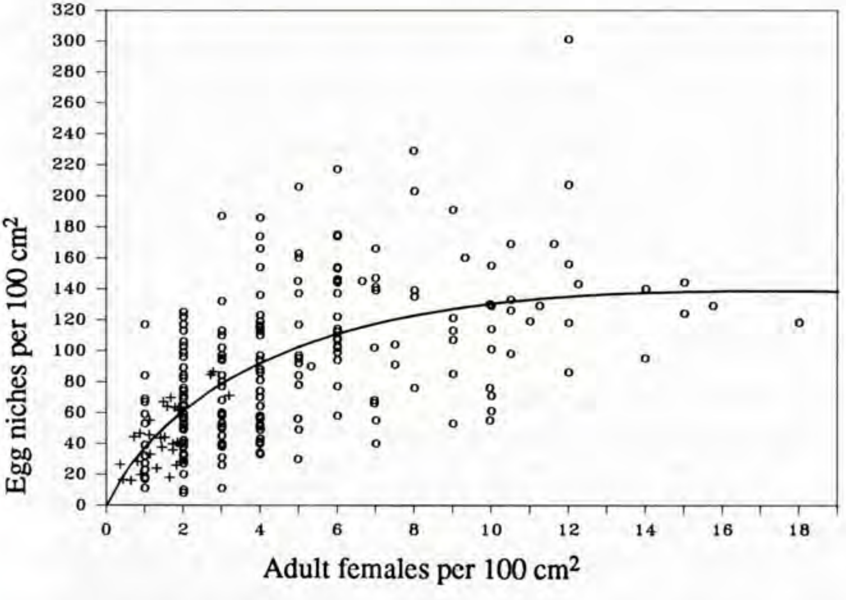

Fig. 1. The reduction in per capita oviposition through competition between colonizing females, described by the multiplication model $y=xa^{\exp(-bx^{0.5})}$, where a=61.55±5.97, b=0.49±0.04. n=232 and r^2=0.39. Symbols (+) = data from individual sample logs from Bavaria 1983; (o) = data from individual 100 cm^2 bark samples from the Graubuenden 1984.

Colonization and Oviposition

One of the main characteristics of scolytid populations is the phenomenon of mass attack, mediated through the use of aggregation pheromones, which enable the beetles to successfully overcome their hosts natural defenses and colonize the sub-cortical habitat. However, mass attack can also lead to competition and in Fig. 1, data from both Bavaria and the Graubuenden have been combined to show the competitive interaction between colonizing adult females. This indicates an asymptotic relation over the range of attack densities observed, suggesting that the scolytids adjust their oviposition, through competition for space, to match the "carrying capacity" of a tree for subsequent brood development. This relation is well described by Berryman's (1974) exponential multiplication model, modified to include egg density.

The pteromalid endo-parasitoid of adult scolytids of the genus *Ips*, *Tomicobia seitneri* (Ruschka), parasitizes *I. typographus* on the bark surface as they aggregate to colonize a host tree. The influence of this parasitoid on the dynamics of the colonization phase could not be determined in this study due to the late timing of the samples. However, Thalenhorst (1958) observed that oviposition by parasitized females was reduced by 30% and that few parasitized females would be able to re-emerge to form sister broods. It is probable that any reduced oviposition would be compensated for by reduced competition between ovipositing females but a reduction in re-emergence could have a greater influence on the development of sister broods.

Egg Mortality

The late timing of the sampling precluded the separation of egg mortality into causal categories. While resinosis remained clear in the bark samples, other losses through failure of females to oviposit in egg niches, predation and parasitism by *Iponemus gaebleri* (Schaars.) (Acarina: Tarsonemidae) could not be distinguished.

The mean egg mortality in the Bavarian region (with a mean egg density of 44.8 per 100 cm^2) was 5.4%, while in the Graubuenden (mean egg density of 88.9 per 100 cm^2) it reached 20.1%. This regional difference is appreciable but it is unknown whether the cause is due to natural enemies responding to the difference in egg densities or due to regional variation in host trees and their sub-cortical microclimate. However, within each region, egg mortality was independent of the density of egg niches (Mills 1986, Schlup 1987).

Larval Mortality

Larval mortality is considered to be that mortality due to competition, predation and disease, occurring between egg hatch and larval maturation and not including parasitism of mature larvae. In Fig. 2, larval mortality is presented in logarithmic form for data from Bavaria and from 10 of the trees from the Graubuenden which were comparable in containing pupae as the dominant host stage at the time of sampling. While the extent of mortality differs between regions, both sets of data indicate a maximal survival rate of the larval brood at initial larval densities of about 30 per 100 cm^2.

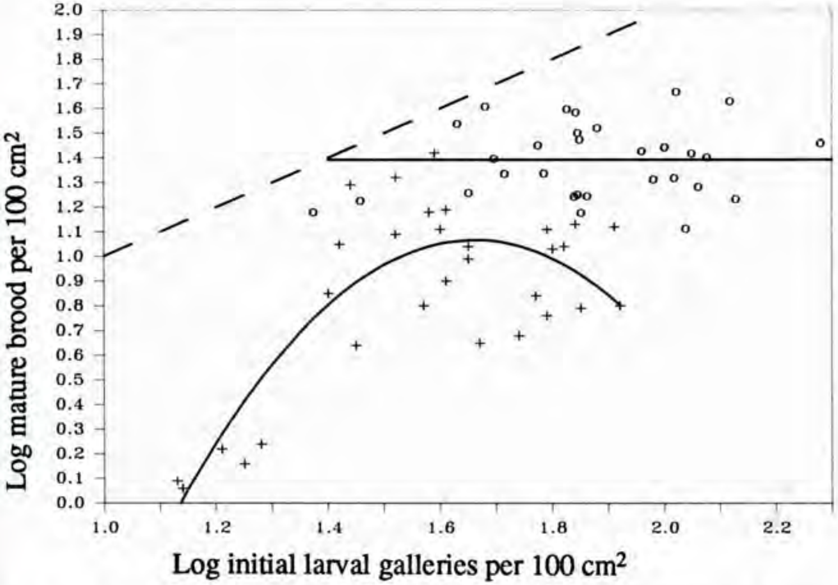

Fig. 2. The larval mortality of the developing brood for (+) individual log samples from Bavaria 1983 and (o) the mean of 3 samples from each height section of 10 compatible trees from the Graubuenden 1984. Bavarian data are described by a polynomial $y=a+bx+cx^2$; a=-9.64±1.85, b=12.91±2.45, c=3.89±0.80, n=30, r^2=0.66 and the Graubuenden data by a constant mean of 1.39±0.03, n=30.

It was not possible to determine the influence of pathogens due to the late timing of the sampling and vertebrate predators, such as woodpeckers, which do not actively forage on infested trees during the brood development period. The density related mortality suggests that insufficient host tree conditioning or poor quality resource reduce larval survival at low densities, while exploitative competition and arthropod predation may be responsible for reduced survival at higher densities.

The two main predators occurring in both regions are *Medetera* spp. (Dolichopodidae) and *Thanasimus* spp. (Cleridae). It was initially thought that all the clerid larvae were *T. formicarius* (L.) but subsequent rearing of material from the Graubuenden indicated that *T. rufipes* Brahm. is equally represented in this region. Other associates such as *Nudobius lentus* (Grav.) (Staphylinidae), *Rhizophagus ferrugineus* (Payk.) (Rhizophagidae) and *Palloptera usta* (Mg.) (Pallopteridae) were found in small numbers but could not have contributed significantly to the host larval mortality. While *Medetera* larvae were more abundant (mean density of 0.14 per 100 cm^2 in Bavaria and 0.44 per 100 cm^2 in the Graubuenden), their limited feeding capacity could account for a maximum of 5% scolytid larval mortality and the total larval mortality was independent of *Medetera* larval densities in both regions (Mills 1985, Schlup 1987).

In contrast, *Thanasimus* larvae have a greater predation potential (Mills 1985) and could account for up to 53% mortality in individual log samples from Bavaria. The mean density of *Thanasimus* larvae in Bavarian samples was 0.13 per 100 cm^2 and at the time of sampling all were near the end of the larval feeding period. The observed densities of this predator were an important factor in explaining the variation in total scolytid larval mortality between sample logs (Mills 1986), although the mean level of predation was estimated at only 13.2%. At the higher altitudes of the Graubuenden, the mean density of *Thanasimus* larvae was 0.56 per 100 cm^2 but the development of the larvae was retarded and less well synchronized with that of the scolytids. Despite a higher mean level of estimated predation (15.9%), *Thanasimus* larval densities did not explain the variation in scolytid larval mortality in this region (Schlup 1987).

Larval Parasitism

The parasitoids obtained in these two studies, in Bavaria and the Graubuenden, were generally collected as larvae and considerable difficulty was experienced in rearing them through to the adult stage. The two families of primary parasitoids, Braconidae and Pteromalidae, were easily separated but this was not the case for individual species, due to the lack of morphological differences. From those larvae that were successfully reared to adult the parasitoid complex in both regions included the braconids *Coeloides bostrychorum* Gir. and *Dendrosoter middendorfi* (Ratz.) and the pteromalids *Rhopalicus tutela* (Wlk.), *Roptrocerus mirus* (Wlk.) and *R. xylophagorum* (Ratz.). In addition, the cleptoparasitoid *Eurytoma arctica*

Thoms. (Eurytomidae), which has an easily distinguishable larval stage, was reared.

Percentage parasitism in Bavarian log samples ranged from 0-93% for braconids and from 0-34% for pteromalids. Neither group of parasitoids showed a correlation between percentage parasitism and bark thickness, although braconid parasitism varied with relative height section (Mills 1986). In addition, a significant negative correlation was found between parasitism by the two separate families of parasitoids, suggesting a possible competitive interaction. In the higher altitude region of the Graubuenden, larval parasitoids also had a similar impact, with a mean level of parasitism of 21%. However, while the exact representation of the two parasitoid families was not determined, pteromalids were the dominant group in this region.

Table 1

Mean partial life tables for *Ips typographus* in Bavaria 1983 (8 trees) and the Graubuenden 1984 (10 trees), from samples containing pupal brood.

Scolytid stages/ 100 cm^2	Bavaria		Graubuenden	
Bark thickness in cm	0.31		0.59	
Females	1.50		4.24	
Potential eggs	92.33		260.97	
% loss through competition		51.48		61.43
Actual eggs	44.81		100.65	
% loss - infertility, predation		5.38		20.45
Initial larvae	42.40		80.07	
% predation - *Thanasimus*		13.23		13.43
% predation - *Medetera*		2.29		5.19
% loss - competition and disease		61.41		48.35
Mature larvae	9.78		26.45	
% parasitism - braconid		22.82		
% parasitism - pteromalid		6.45		22.50
Pupae	7.34		20.50	

Natural Enemy Impact

The results of these investigations on the dynamics of within-tree populations of *I. typographus* and the impact of its natural enemies are summarized in potential life tables in Table 1. This indicates the dominant density dependent influence of competition between colonizing females. Losses through larval competition and disease were greater in Bavaria despite the lower initial larval densities and this is probably the result of the differential mean bark thickness of the trees in these two regions. While adult females construct galleries at the bark-sapwood interface, larvae are able to make use of the full depth of the inner bark and may thus avoid the intensity of competition imposed by thinner bark. Egg mortality in the Graubuenden and parasitism in both regions are also important causes of mortality. Predation by *Thanasimus*, while of lower magnitude appears to have a significant impact on scolytid larval mortality, although this may be influenced by the synchronization of the larger larvae with the final stages of scolytid larval development.

THE POTENTIAL OF EUROPEAN NATURAL ENEMIES AS EXOTIC INTRODUCTIONS

In the use of exotic natural enemies against native pests there are two additional and dominant criteria in the selection of candidate control agents. These criteria are that the selected agent must be able to successfully locate the new target host and then subsequently must be able to successfully use the host for oviposition and development. In the case of scolytid target hosts, the second criterion is likely to be met by many of the potential candidates, since members of the natural enemy complex are oligophagous and attack hosts of various sizes (Mills 1983). However, the insect–host tree relationships of scolytids involve more specific volatile cues that may present greater constraints on the host–natural enemy compatibility.

Cross Attraction

In order to investigate the kairomone response of European scolytid entomophages to synthetic aggregation pheromones, the following field experiment was conducted in 1985. In three different localities, the Graubuenden, Denmark and Austria a set of drum traps combining a sticky surface with a flight barrier and funnel of the same surface area were used from May till September 1985, the catches for each month being stored separately. Each set included four traps baited with the following pheromones used to trap the corresponding scolytid species: 1) Methylbutenol, ipsdienol, *cis*-verbenol (*I. typographus*), 2) *Exo*-brevicomin, *trans*-verbenol, mycrene (*Dendroctonus ponderosae* Hopkins), 3) Frontalin, seudenol, *alpha*-pinene (*D. rufipennis* (Kby.)) 4) Control.

2

traction trapping in the Graubuenden, indicating the numbers of scolytids and associates caught each y sticky or barrier traps.

	Control					*Ips typographus*					*D. ponderosae*					*D. rufipennis*				
	5	6	7	8	9	5	6	7	8	9	5	6	7	8	9	5	6	7	8	9
trap																				
phus	2	0	1	0	1	714	1101	1843	589	106	8	2	0	0	0	0	0	1	0	1
arius	3	0	0	0	0	9	5	3	0	0	21	6	3	0	0	3	0	0	0	0
s	0	0	0	0	0	18	11	2	4	0	0	0	0	0	0	0	0	0	0	0
i	0	1	0	0	0	184	690	260	33	5	0	1	1	0	0	0	0	0	0	0
spp	1	10	3	0	1	11	67	43	15	4	6	14	10	2	1	8	7	8	0	0
barrier trap																				
phus	1	0	0	0	0	2335	2098	1832	97	175	8	0	0	0	0	2	0	0	0	0
arius	0	1	0	0	0	2	3	0	0	0	3	1	0	0	0	0	0	0	0	0
s	0	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0
i	0	0	1	0	0	2	20	8	0	4	0	0	0	0	0	0	0	0	0	0
spp	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0

Unfortunately, the low numbers of insects trapped in Denmark were insufficient to allow for analysis and in addition, no results were obtained from Austria due to technical problems. However, the traps from the Graubuenden provided reasonable data for analysis. The numbers of each species trapped are summarized in Table 2.

A comparison of the two trap types shows clearly that the sticky traps were better suited to catch all insects apart from *I. typographus*, which was caught in higher numbers by the flight barrier trap. The two clerid predators *T. formicarius* and *T. rufipes*, responded to the pheromone of *I. typographus* and *T. formicarius* also responded well to the pheromone of *D. ponderosae*. No attraction of either of the two clerid species was noted to the pheromones of *D. rufipennis*. Bakke and Kvamme (1981) have previously shown a response of the clerids to several of the components of the pheromone of *I. typographus*. The response of *T. formicarius* to the pheromones of *D. ponderosae* is probably due to the *exo*-brevicomin component, to which *T. formicarius* has previously been recorded to be attracted (Kohnle and Vité, 1984).

A strong response to the aggregation pheromones of *I. typographus* was show by the adult parasitoid, *T. seitneri*. It did not respond to either of the pheromones of the two *Dendroctonus* species, which compares well with the fact that parasitoids of the genus *Tomicobia* are only reported from *Ips* species. Together with the two clerids, *T. seitneri* belongs to the group of entomophages that have developed similar mechanisms of host location, involving the use of the scolytid aggregation pheromones as kairomones. Predator species of the genus *Medetera* probably also belong to this group as the North American dolichopodid, *Medetera bistriata* Par., shows a kairomone response to the aggregation pheromone of *Dendroctonus frontalis* Zimm. (Williamson 1971). Although higher numbers were attracted to *I. typographus* pheromones, the exact species composition needs to be determined before any further conclusions can be drawn. However, it is possible that the species caught on the control traps is different from that responsible for the higher catches on the *I. typographus* trap.

A second group of scolytid entomophages, the larval parasitoids, attack their hosts in the late larval stage, a phase of brood development which occurs several weeks after aggregation pheromone production has ceased. Therefore one would not expect them to have evolved host location mechanisms based on host aggregation pheromones. These considerations are fully supported by the results of the pheromone trapping. None of the larval parasitoid species were attracted to the aggregation pheromones. However, Kennedy (1984) reported attraction of several larval parasitoids of *Scolytus multistriatus* (Marsh.) to multistriatin, a component of the aggregation pheromone used by this elm infesting scolytid. This observation suggests that larval parasitoids also use volatiles to aid in host location and that the specific cues are perhaps very similar in composition to the host tree derived scolytid aggregation pheromones.

Thus while cross-attraction, using scolytid aggregation pheromones to identify potential exotic entomophages for use in biological control, is a particularly useful tool in the case of early attacking entomophages it is probably ineffective for the identification of compatible larval parasitoids.

Host Location by Larval Parasitoids

Host location by the larval parasitoids of scolytids can be divided into two phases. In the first phase the parasitoids must locate host trees infested with mature scolytid larvae, suitable for parasitization, and in the second phase the problem of locating individual hosts under the bark is encountered. Preliminary investigations have been conducted to address both these phases of host location.

In the first phase, the parasitoids must locate host infested trees. However, the sub-cortical habitat is used by *Pissodes* weevils as well as scolytids, and yet the larval parasitoid complexes of these two groups of hosts are quite distinct (Mills 1983, Mills and Fischer 1986), with only marginal overlap. Thus quite different cues must be used by the parasitoids to locate larvae of the two different host insects in the same host tree species. One distinguishing feature of the general biology of these two host groups is that most of the scolytids have associated fungi which are inoculated into the host trees at colonization. One scolytid that has no such associated fungus, *Dendroctonus micans* Kugel., is attacked by parasitoids characteristic of *Pissodes* hosts. Thus it seems possible that the volatile cues used by scolytid larval parasitoids may be produced by the action of the host associated fungi.

A field experiment was conducted in Badgastein, Austria in 1986 to assess the attraction of mature larval brood and associated fungi to the scolytid larval parasitoids. Three sets of sticky drum traps were placed close to *I. typographus* infestations and baited with: a) a spruce log infested with mature larval brood of *I. typographus*; b) the bark and brood of a spruce log as in (a); c) the wood from a spruce log as in (a), containing fungi only; d) a spruce log colonized by adult *I. typographus* to inoculate associated fungi; and e) control. The bait (d) was set up specifically to provide logs inoculated by all fungi associated with *I. typographus* by allowing adult scolytids to colonize the logs for 2-3 days before removing them and destroying eggs laid. However, not all eggs were destroyed and some larval brood developed within the logs and thus bait (d) was rejected for use in this experiment.

CONCLUSIONS

In this study we have looked at the impact of natural enemies on the dynamics of within-tree populations of *Ips typographus* and made some preliminary observations on the host location mechanisms of the dominant entomophages. The natural enemy impact assessment suggests that the clerid predators, *Thanasimus* spp., and the larval parasitoids have the greatest influence on host brood survival. *Thanasimus formicarius* females can oviposit up to 1000 eggs (unpublished observations) and have evolved an efficient host location mechanism, based on the aggregation pheromones of their prey. In contrast, the larval parasitoids have a much lower fecundity, estimated at 20-25 (Ryan and Rudinsky 1962, Samson 1984) and have an as yet unknown host location mechanism.

Thus for the purposes of biological control is would seem that the best candidates for introductions would include *Thanasimus* and selected larval parasitoids. However, while *Thanasimus formicarius* could be considered for exotic introductions against native *Ips* species or *Dendroctonus ponderosae*, due to its proven host location ability, this is not yet possible for the larval parasitoids. Further investigations of the host location mechanisms of the larval parasitoids are required to more adequately assess their compatibility with novel target hosts. The extraction of the source of volatiles used for long range host location would permit the screening of exotic parasitoids through field trap survey and a knowledge of the subcortical host location mechanisms would indicate the suitability of target hosts for oviposition. In addition, it is necessary to investigate the structure of the larval parasitoid complexes to determine the range of possible competitive interactions and to exclude deleterious clepto- or hyperparasitoids from consideration as potential candidates.

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SECTION NINE

Dendroctonus armandi Tsai et Li (Coleoptera: Scolytidae) in China: Its Natural Enemies and Their Potential as Biological Control Agents

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SUMMARY

Dendroctonus armandi Tsai et Li is native to the Qinling and Bashan Mountains in China. Its host tree is *Pinus armandii* Fr. which occurs in previous two mountain ranges and other mountainous areas of Southwestern China. This beetle is a unique species, different from all others in the genus. It mainly attacks apparently healthy trees over age 30, and has recently caused serious damage to the *P. armandii* stands in the Qinling Mountains. The numbers of generations differ with elevation. Two generations appear at elevations below 1700 m per year, three in two years between 1700 m and 2150 m, and one per year above 2150 m. It overwinters in all stages except the egg. Many natural enemies attack the beetle, including entomophagous insects and mites as well as woodpeckers. *Coeloides qinlingensis* Dang et Yang (Hymenoptera: Braconidae) has high potential as a biological control agent for other *Dendroctonus* species. Stand sanitation is the principal control measure.

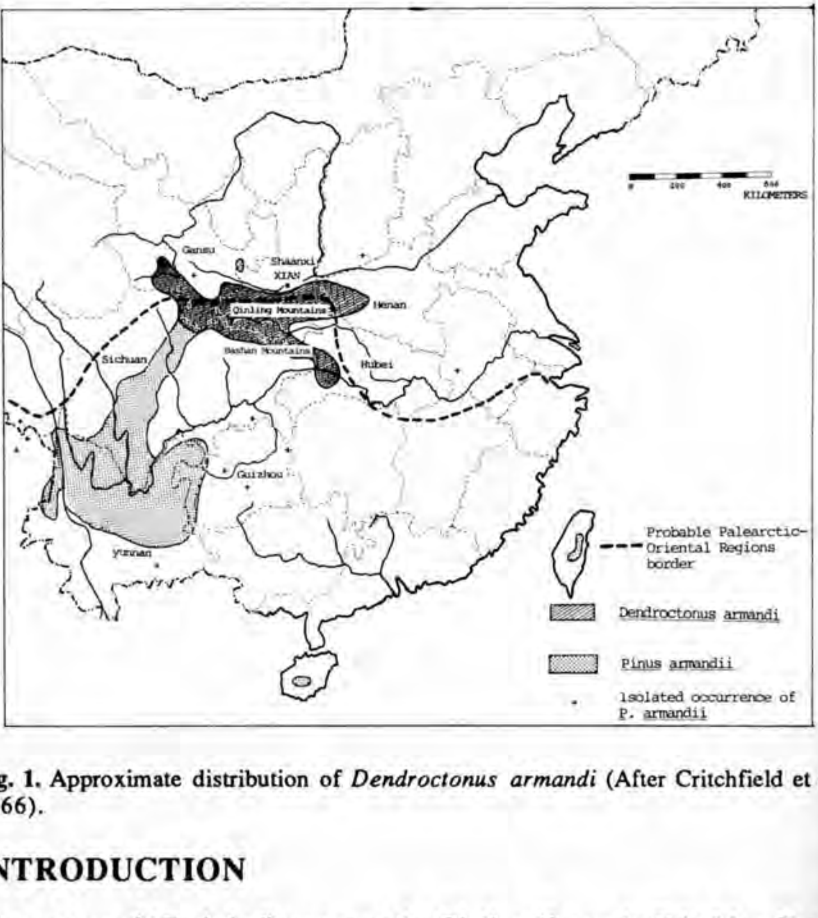

Fig. 1. Approximate distribution of *Dendroctonus armandi* (After Critchfield et al. 1966).

INTRODUCTION

Pinus armandii Fr. is indigenous to the Qinling (formerly Tsin Ling Shan), Bashan Mountains, and certain other mountainous areas in Southwestern China (Fig. 1). This covers parts of Shaanxi, Gansu, Sichuan, Hubei, Henan, Yunan, and Guizhou provinces (Critchfield et al. 1966). The Qinling Mountains provide a border separating the Palearctic and Oriental Regions in China, the dividing line of which runs form west to east along the highest peaks of the range (Chao et al. 1985). The line also serves as a weather demarcation between South and North China. Stands of *P. armandii* in this area not only grow rapidly, but produce a high quality of wood. However, these stands have been recently infested by *Dendroctonus armandi* Tsai et Li in the Qinling and Bashan Mountains. Fig. 1 shows the approximate distribution of this bark beetle. Damage by this bark beetle was first recorded in 1932 (Yin et al. 1984). Prior to this time its damage was light but since then, huge areas of *P. armandii* forests have been killed every year in the Qinling Mountains. Once a stand is killed, regenerating hardwoods (mostly *Quercus* species) quickly dominate and *P. armandii* often fails to regenerate.

Since 1958, entomologists have begun studying this problem (Li 1959, Ren and Dang 1959). In 1959, the beetle was described as *Dendroctonus armandi* Tsai et Li, by the late Professor Tsai Banghua and Professor Li Chaoling of the Zoological Institute, Academica Sinica (Tsai et al. 1959). Before this, it was simply called "the large pitch tube bark beetle" in reference to its damage symptoms. *Dendroctonus armandi* primarily infests *P. armandii* but in rare cases it may also attack *P. tabulaeformis* Carr. in the Qinling Mountains. It mainly attacks apparently healthy trees over age 30.

BIOLOGY AND ECOLOGY

According to Wood (1982) *D. armandi* is a unique species, quite different from the remainder of the genus (Fig. 2a,b,c,d). It is about the same size as the mountain pine beetle, *Dendroctonus ponderosae* Hopkins.

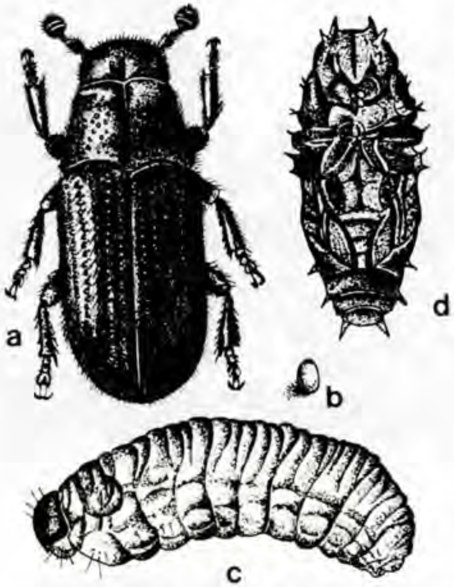

Fig. 2. *Dendroctonus armandi:* a - adult, b - egg, c - larva, d - pupa (Redrawn from Li and Zhou 1980).

The number of generations of *D. armandi* differs with elevation in the Qinling Mountains. At elevations lower than 1700 m, there are two generations a year, between 1700 m and 2150 m, three generations in 2 years and above 2150 m, one generation a year (Ren et al. 1962, Li and Zhou 1980). It overwinters in all stages except the egg. Approximately 295.5 degree days are required to rear a generation, the approximate threshold temperature is 9.6°C. But these figures differ for each stage (Table 1) (Li and Zhou 1980).

Table 1

Developmental temperatures for *D. armandi*.

Stages	Degree Days (°C)	Threshold temperature for starting development (°C)
Egg	64.5	8.1
Larva	178.7	10.2
Pupa	52.3	10.6
Adult	200.0	

Fig. 3. Pitch tubes on the bark of *Pinus armandii* (Redrawn from Li and Zhou 1980).

D. armandi attack symptoms on trees resemble other *Dendroctonus* species. Initial entrance tunnels are surrounded by red- to grey-brown pitch tubes, about 10-20 mm diameter (Fig. 3). The egg gallery is simple and longitudinal, averages from 30-40 cm in length, with extremes of 10-60 cm (Fig. 4a) somewhat resembling the American species, *D. adjunctus* (Fig. 4b). Individual larval mines develop outwards from both sides of the egg gallery. They are usually 2-3 cm long and may attain 5 cm. A conspicuous nuptial chamber occurs at the entrance of the egg gallery. The female bores the initial gallery and nuptial chamber, after which the egg gallery and lays eggs on both sides. One female may lay 20-100 eggs, usually about 50. The distance between egg niches averages 8 mm. After hatching, the young larva initially bores into the phloem. Later, it widens the gallery and begins to engrave the xylem. Pupal chambers are elliptical or irregular at the ends of mines.

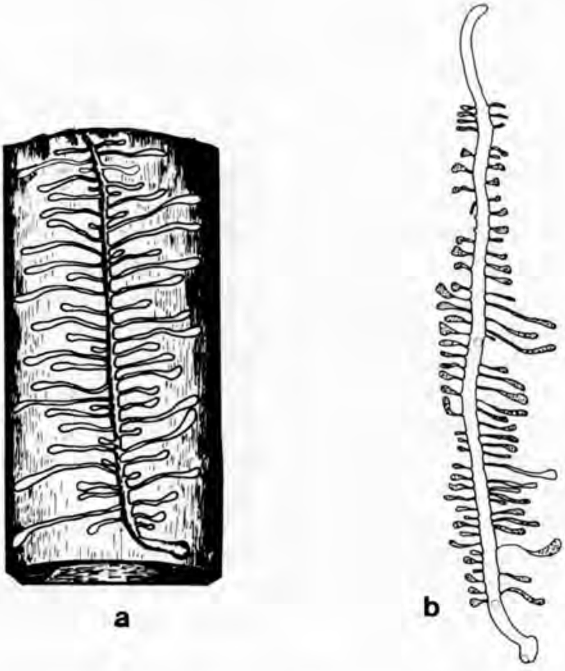

Fig. 4. A. Gallery of *Dendroctonus armandi* in sapwood of *Pinus armandii* (Redrawn from Li and Zhou 1980). **B.** Gallery of *D. adjunctus* (Redrawn from Wood 1982).

The newly enclosed brood adult is light-yellow in color, gradually becoming light-brown, black-brown and finally black. The mature adult feeds on pupa chamber, greatly enlarging it. This feeding enormously increases the area of damage to the phloem tissues. After this, the beetle emerges and flies from 6:00 to 13:00 hours. Very few fly in the afternoon or evening. Brood adults fly directly to new host trees, the flying period on the south slope of the Qinling Mountains begins about July 11-20. July 21 to August 10 is the peak period, ending about September 10.

At first attacking, it is possible that some of the initial intruders may be drowned or trapped by exuding resin of host trees. But beetles of *D. armandi* can overcome this resistance through mass attacks that overwhelm the resistance of the host and they are finally successful. At the onset of winter, larval galleries are still small, not girdling the tree until spring, at this time needles yellow and the tree dies. Weakened trees are quickly invaded also by other scolytids, cerambycids and curculionids which may attack unthrifty trees by themselves, too. There are over 20 species of bark beetles infesting *P. armandii* in the Qinling Mountains, each species may dwell in certain parts of the host trunk (Fig. 5). Most of *D. armandi* occur from the lower 10% to the upper 70% of the tree height.

On the drier north slope of the Qinling Mountains *P. tabulaeformis* predominates and *P. armandii* is very rare. Tree distribution on the south slope is more complex, but *P. armandii* predominates. Both trees and bark beetles are distributed by elevations (Fig. 6).

Outbreaks of *D. armandi* generally begin in pure natural stands of *P. armandii* on south slopes and then expand to stands mixed with *P. tabulaeformis, P. massoniana, Quercus* species and/or deciduous trees. *P. tabulaeformis* is sometimes attacked as mentioned above, but *P. massoniana* never is. Stands on poorer sites are more severely attacked than those on good sites. The bark beetle seemingly prefers sparse stands more than dense ones. Pine stands with low to moderately high density are often severely damaged while others with higher density are lightly infested. Most *D. armandi* attacks occur from 1800 m to 2100 m with lighter attacks below or above these altitudes. Also stands on the upper parts of mountains having thin soil layers are more severely attacked than those in deeper soils on the lower slopes. The infestations are more serious on steeper slopes, too. On the south slope of the Qinling Mountains south and west exposures are drier and more infested than the wetter north and east exposures.

Natural Enemies

D. armandi has many natural enemies. The beetle, *Thanasimus formicarius* L. (Coleoptera: Cleridae), is a common predator. Two staphylinids, one histerid and one raphidiid, are also common. The larvae of all these as well as the adults of the former two species consume the larvae of *D. armandi* in galleries. In addition, a species of *Pyemotes* (Acarina: Pyemotidae) commonly mass-consumes the beetle brood. Many hymenopterous parasitoids have been reared and collected from *D. armandi* (Yang 1986). *Coeloides qinlingensis* Dang et Yang (Dang and Yang 1986), *Spathius* sp. (Braconidae), *Roptrocerus mirus* Walker, *R. qinlingensis* Yang, *Dinotiscus armandi* Yang (Pteromalidae) and *Eupelmus* sp. (Eupelmidae) all ectoparasitize the larvae. *Tomicobia lioli* Yang (Pteromalidae) may be endo-

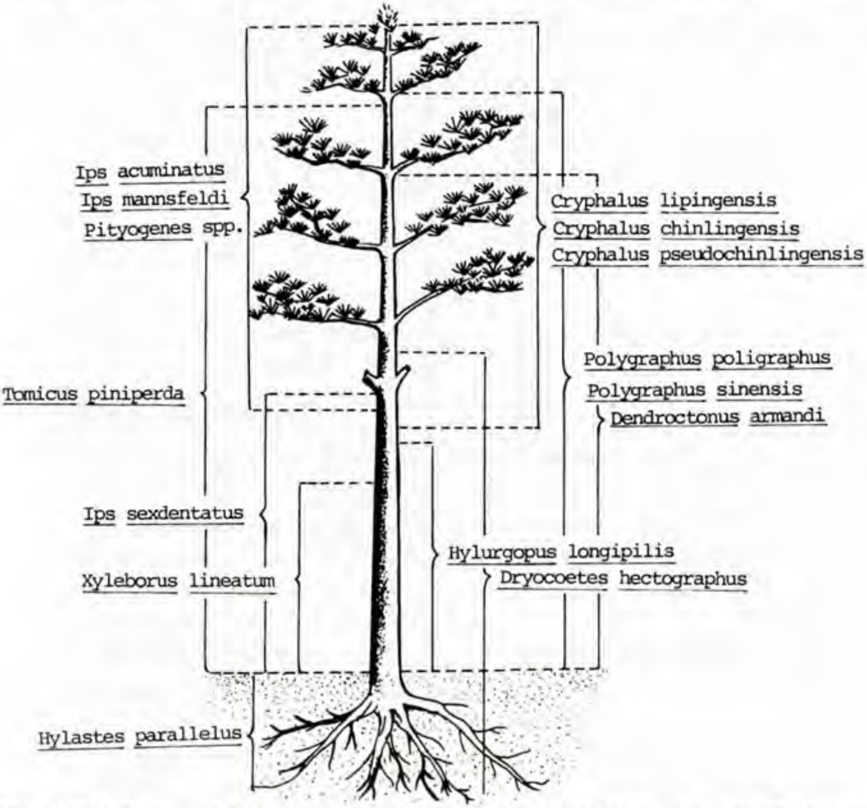

Fig. 5. Distribution of bark beetles on the standing tree of *Pinus armandii* (Redrawn from Li and Zhou 1980).

parasitic in the adults of *D. armandi*. *Coeloides qinlingensis* is a very effective natural enemy; in most cases it can parasitize 30-40% of host larvae and in some cases over 90%. This parasitoid may have high potential as a biological control agent for other *Dendroctonus* species. Some of the other parasitoids unique to *D. armandi* may also have potential although they do not appear to be as aggressive as *C. qinlingensis*. Several species of woodpeckers have been noticed foraging brood with resulting piles of chipped bark around some trees.

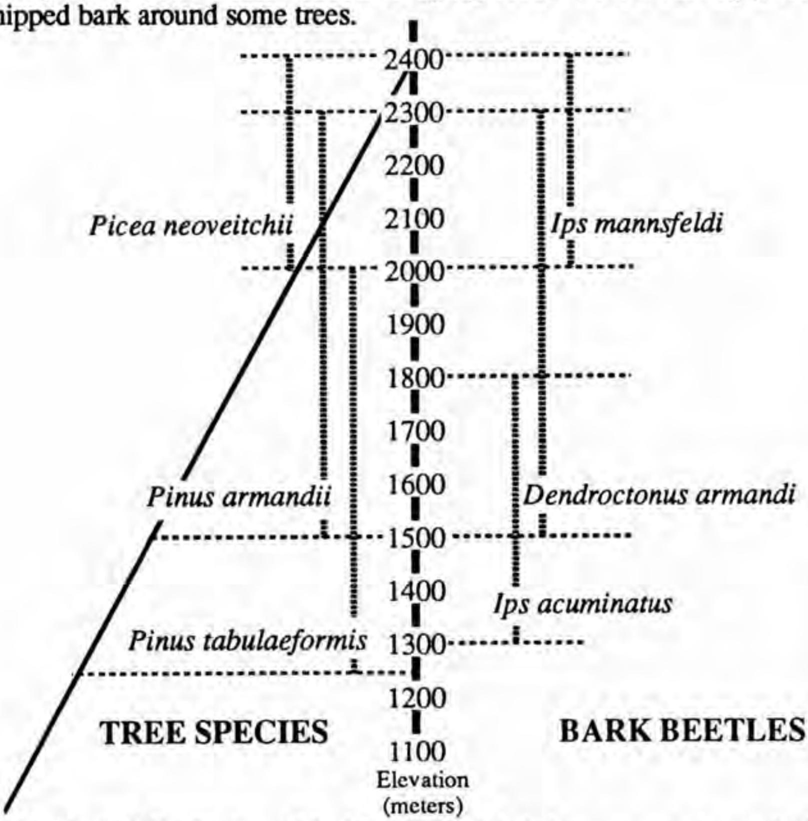

Fig. 6. Vertical distributions of bark beetles and their host trees on the south slope of the Qinling Mountains.

Control Measures

D. armandi is now recognized by local forest managers as the primary pest of forests in the Qinling Mountains. Stand sanitation is the principal method of control (Ren et al. 1965, Zhou 1963). This requires removal of infested trees. Individual infested trees in the mountains can be easily seen from a distance by their distinct yellow or yellow-brown needle color.

It is essential that infested trees should be removed before adults of *D. armandi* emerge by the next July. The best time for harvest is from March to April because of the heavy snow cover in winter.

Debarking tree stems is important to prevent adult emergence. Dusting removed bark with insecticides is combined with debarking because burning is prohibited during winter and spring in all forests in China. Since debarking and transportation from the mountains are difficult, some trees cannot be removed before July. To prevent beetle emergence from these trees, the logs are treated primarily by two methods: soaking them in water (there are many streams in the Qinling Mountains), or exposing them direct to sun light. In the latter case, they are turned over and checked several times to ensure that all the larvae are killed. Because in China timber is scarce, the high cost of this mechanical control is offset by the timber value.

Freshly cut trap logs are also used in treated stands to attract any remaining adult of *D. armandi*. These trap logs are placed before the end of April, and debarked in late June or early July.

The above procedures (sanitation, debarking, dusting bark with insecticides, and use of trap logs) was used for over 15 years on several test stands in the Qinling Mountains and has shown excellent control results. Now the practice is becoming standard for the majority of forest farms within the range of *D. armandi*. When the recommendations are strictly followed over a number of years, control prospects are good.

For restocking *P. armandii*, the measures below should be followed: 1. Manage existing *P. armandii* stands for pest-resistance, such as by permitting hardwoods to regeneration and lowering the rotation age 2. When stands are regenerated on low elevations, *P. armandii* should be mixed with *P. massoniana*, *P. tabulaeformis*, *Quercus* and other deciduous trees. At higher elevation sites, *P. armandii* may be planted with *Populus davidiana* and/or *Betula* species.

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SECTION TEN

Ips spp. Natural Enemy Relationships in the Gulf Coastal States

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INTRODUCTION

Colonization of southern yellow pines by *Ips* spp. bark beetles results in the creation of a habitat utilized by a large complex of insect associates. The beneficial insect component, i.e., predatory and parasitic species, associated with *Ips calligraphus* and *I. grandicollis* is dominated by predators. In the Gulf coastal states of Louisiana and Texas, nearly 99 percent and 95 percent, respectively, of the beneficial complex in terms of numbers of adults obtained from exclusion studies were known predators or facultative predators.

In Louisiana on felled loblolly and slash pines the species composition of *Ips* broods consisted of *I. calligraphus* (80.2 percent), *I. avulsus* (11.2 percent), and *I. grandicollis* (8.2 percent). In Texas on loblolly and shortleaf pines the complex consisted of *I. grandicollis* (72 percent), *I. avulsus* (20 percent), and *I. calligraphus* (8 percent). Studies conducted by Riley and Goyer (1986) revealed that the emergent *Ips* spp. broods were reduced 30.8 percent as a result of insect predators and parasites.

In the two states 32 species of predators representing 15 families and 14 species of parasites representing 7 families were recorded (Bing 1985, Riley and Goyer 1986).

LOUISIANA STUDIES

In Louisiana, the most abundant predators were *Lonchaea* sp. larvae (Diptera: Lonchaeidae) which accounted for 45.2 percent of all predators and 44.7 percent of the entire beneficial complex. The adults and larvae of *Aulonium* spp. (Coleoptera: Colydiidae) accounted for 17.5 percent of all predators. Adults of the family Staphylinidae accounted for 6.8 percent of all predators and the adults and larvae of all histerid species accounted for 6.0 percent. *Scoloposcelis mississippensis* Drake and Harris, (Hemiptera: Anthocoridae), comprised 4.3 percent of all predators while the predatory genera of *Zabrachia* (Diptera: Stratiomiidae), *Corticeus* (Coleoptera: Tenebrionidae), and *Plegaderus* sp. (Coleoptera: Histeridae) accounted for 3.6, 2.1, and 1.0 percent, respectively. *Platysoma attenuatta* (Coleoptera: Histeridae) (LeConte), *Temnochila virescens* (F.) (Coleoptera: Trogositae), and *Thanasimus dubius* (F.) (Coleoptera: Cleridae) comprised 1.5, 1.4, and 1.0 percent, respectively, of all predators (Fig. 1). Several of the predators of *Ips* were recovered in the larval stage at, and identification, in many cases, could not be made below generic or family taxon.

The most abundant species of parasite was *Roptrocerus eccoptogastri* (Hymenoptera: Pteromalidae) comprising 37.3 percent of the total parasite complex but only 0.5 percent of the total beneficial complex. An unidentified wasp in the family Encyrtidae was the second most abundant parasite species accounting for 19.0 percent of all parasites and 0.2 percent of all beneficials.

Stein and Coster (1977), in their study of SPB in loblolly and shortleaf pines in Texas, found that 12 predator and 9 parasite species comprised 99 percent of their natural enemy complex. Parasites in their study were found in much greater abundance than in the present study. Composition of their most abundant predators were similar to ours with the exception of *Lonchaea* sp. (our most abundant species). Moser et al. (1971) also found a greater composition of parasites than we did.

In evaluating the parasite complex of southern bark beetles, several researchers (e.g., Berisford and Franklin 1969, 1972, Stein and Coster 1977, Goyer and Finger 1980) found *Roptrocerus eccoptogastri* (also cited by some workers as *R. xylophagorum*) to be the most abundant parasite

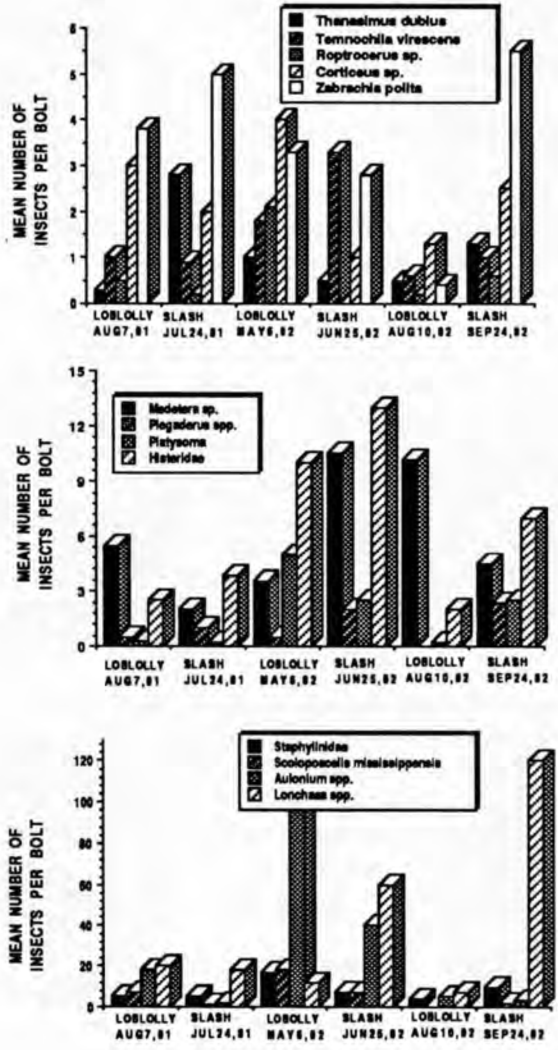

Fig. 1. Mean number of beneficial insect emerging from loblolly and slash pines in Louisiana.

species as in our study. Berisford and Franklin (1969, 1972), studying *Ips avulsus* and *I. grandicollis* associates, found 4 parasite species made up 95 percent of their total insect beneficial complex, with *R. eccoptogastri* comprising 75 percent of all parasites found. Their data reflected insects collected attacking the trees, whereas the numbers in our study reflect those insects emerging from *Ips*-infested bolts (Fig. 1, Fig. 2).

Lonchaea sp. showed two peaks of abundance, one from the September 1981 felling date and one from the June 1982 felling date, Fig. 2. There was no corresponding abundance peak from the previous September felling date. Bing (1985) found *Lonchaea* to be most abundant May through June in Texas.

Several predator and parasite species (e.g. *P. attenuatta*, *S. mississippensis*, *Corticeus* spp., staphylinids, *Aulonium* spp., and *R. eccoptogastri*) appeared to follow an abundance pattern similar to that of *Ips* beetles.

Smith and Goyer's studies (1980) of *Corticeus glaber* from SPB-infested logs showed similar seasonal abundance patterns to those of our study (peaks in spring and fall and lower populations in the summer). They found *C. parallelus* though, to be only abundant in June. Bing (1985) found *Corticeus* spp. to be most abundant in May and July. Stein and Coster's study (1977) showed a peak population of *Corticeus* spp. in spring and a decline through summer. Abundance patterns of *S. mississippensis* as observed by Stein and Coster (1977) revealed a pattern which contrasted from ours. They found *S. mississippensis* populations to build from February through September. Bing (1985) found *S. mississippensis* to peak July through August and in October. Studies of *R. eccoptogastri* (reared from infested boles) by Goyer and Finger (1980) revealed populations of this parasite to be highest in late spring. However, they found a second peak for this parasite in August which is not seen in our data. Bing (1985) and Stein and Coster (1977) found *Roptrocerus* numbers in a pattern similar to ours (a peak in May and low numbers at other times).

Seasonal abundance of histerids as a group, including their larvae, showed maximum numbers from the June felling date, lowest numbers in August, and an intermediate level in the fall. *Plegaderus* sp. adults had three peaks of similar magnitude each coinciding with a slash pine felling date, Fig. 1. Contrasting these results, Stein and Coster's (1977) findings on seasonal abundance for *Platysoma* spp. (including *P. attenuata*, *P. cyclindrica*, and *P. parallelum*) and also for *Plegaderus* sp. showed a gradual rise in populations from spring through September. Populations of *Plegaderus* sp. were higher on shortleaf pine than on loblolly pine.

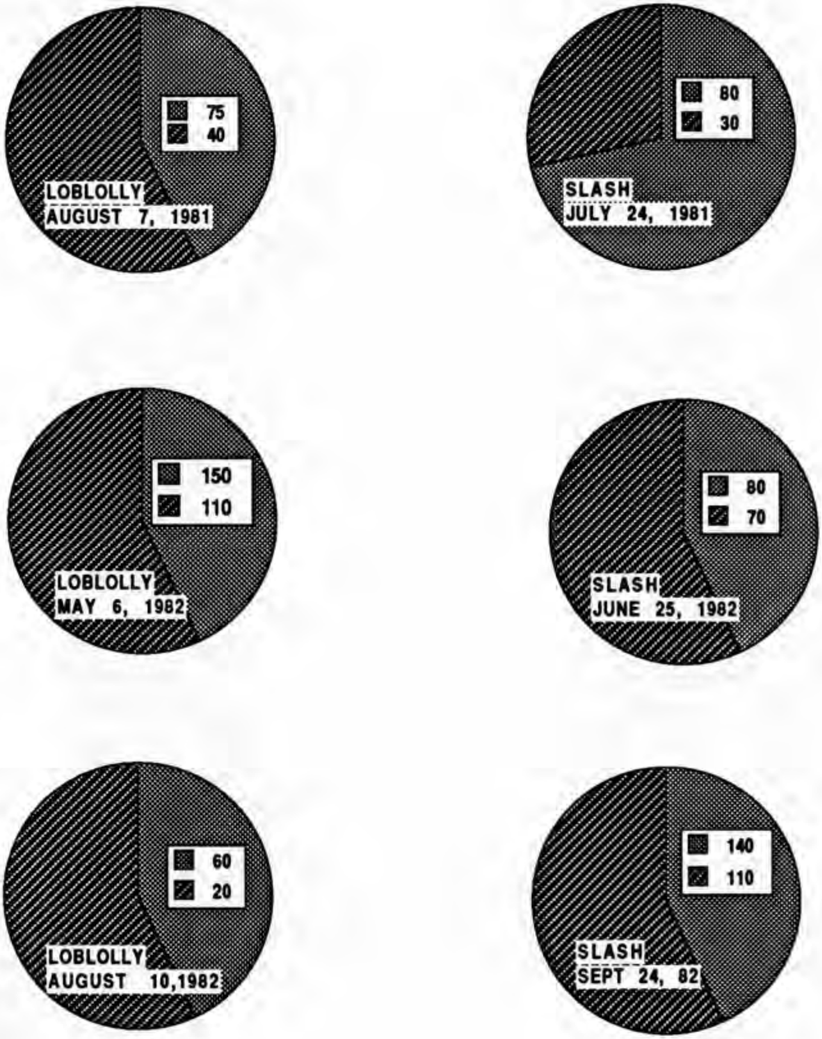

Fig. 2. Mean number of *Ips* spp. and beneficials emerging per 100 sq. cm. from loblolly and slash pine bolts in Louisiana; top number is *Ips* and lower number is beneficials.

TEXAS STUDIES

Medetera bistriata (Diptera: Dolichopodidae) made up 17.2 percent of the predator complex and 17.1 percent of the beneficials (Fig. 3). *Medetera bistriata* was found in relatively uniform populations throughout the season. Moser et al. (1971) and Dixon and Payne (1979) both found this fly a very abundant predator of *D. frontalis*. Moser et al. (1971) found *M. Bistriata* present year round. Riley and Goyer (1988) found *M. Bistriata* most abundant in June and August.

Medetera bistriata was found in significantly larger numbers in loblolly pine. It was found in constant numbers throughout the season in loblolly pine; however, in shortleaf pine they were found in very low numbers in May increasing to about the same numbers found in loblolly pine by August. *Medetera bistriata* also was found in significantly higher numbers in the top of the tree suggesting they are attracted to the section of tree with the highest population of bark beetles.

Scoloposcelis mississippensis, found in peak numbers in July through August and in October, made up 5.8 percent of the predator complex and 5.4 percent of the beneficial complex. Stein and Coster (1977) found *S. mississippensis* in peak populations in the fall whereas Riley and Goyer (1988) found it most abundant in May and June following peak numbers of bark beetles.

Scoloposcelis mississippensis was found in significantly larger numbers in shortleaf than in loblolly pine. In loblolly pine, it was found in peak numbers in July suggesting, as Riley and Goyer (1988) found, that it follows an abundance pattern similar to the *Ips* beetles. In the rest of the season it was found in very low numbers. *Scoloposcelis mississippensis* occurred sporadically in shortleaf pine but increased at the end of the season.

Lonchaea spp. and *Zabrachia polita* made up 5.6 percent and 4.0 percent of the predator complex (5.0 percent and 3.8 percent of the beneficial complex) respectively. They showed a seasonal abundance pattern with *Lonchaea* spp. most common from May to July and *Z. polita* most common in August through October. Moser et al. (1971) found *Lonchaea* spp. present from April to June and *Z. polita* abundant in May through August. Riley and Goyer (1988) found *Lonchaea* spp. the most abundant predator in her study, with peaks in June and again in September; she also found *Z. polita* most abundant in May through June and again in August through September. Her study did not show the relationship found by Bing (1985) between *Lonchaea* spp. and *Z. polita*.

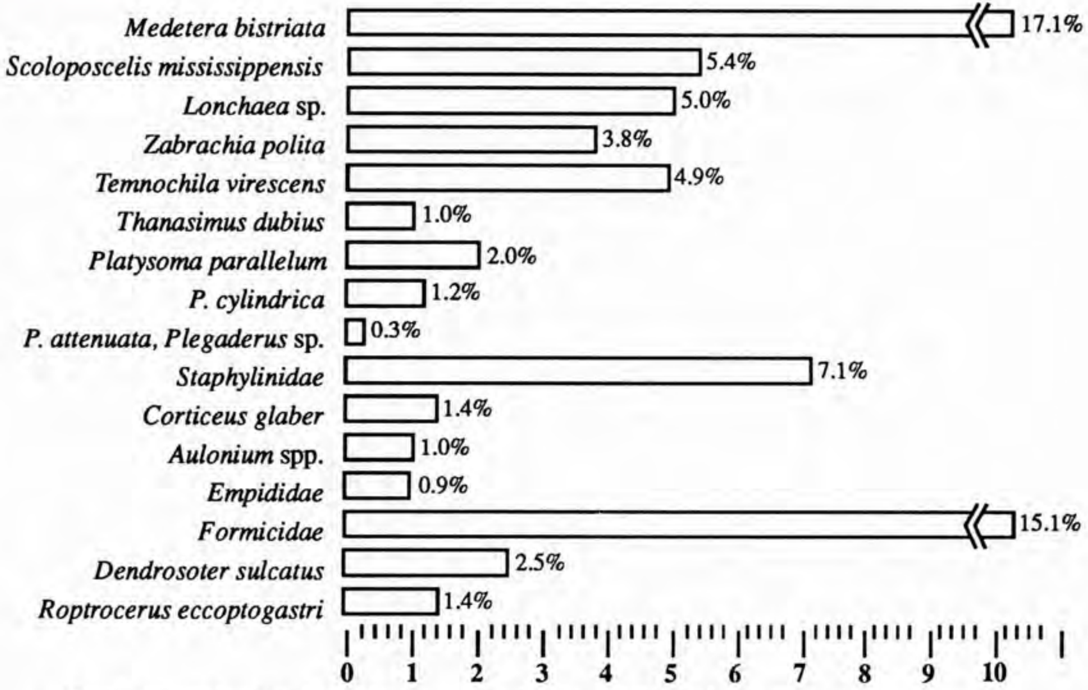

Fig. 3. Percent beneficial complex by species, lobolly and shortleaf pine, Texas.

Two beetles *Temnochila virescens* and *Thanasimus dubius* made up 5.2 percent and 1.1 percent of the predator complex (4.9 percent and 1.0 percent of the beneficial complex) respectively. Both species showed peak populations in July suggesting that they follow the same abundance pattern as the *Ips* beetles. Stein and Coster (1977) found *T. dubius* most abundant from February through May. Moser et al. (1971) found it present all year long except in January, and *T. virescens* present only in July. Riley and Goyer (1988) found *T. dubius* most numerous in September with a smaller peak in May through July. In our study *T. virescens* was found in larger numbers than *T. dubius* throughout the season. Billings and Cameron (1984) found that *T. virescens* was attracted almost exclusively to *Ips* attractants but showed little response to *D. frontalis* attractants. *Thanasimus dubius*, however, was attracted in significantly larger numbers to *D. frontalis* attractants than to *Ips* attractants. This preference of *T. virescens* for *Ips* beetles explains the higher numbers of *T. virescens* than *T. dubius*.

The histerid beetles made up 4.0 percent of the predator complex (3.7 percent of the beneficial complex). The histerids complex is made up of two major and two minor species. *Platysoma parallelum* and *P. cylindrica* made up 2.1 percent and 1.3 percent of the predator complex, (2.0 percent and 1.2 percent of the beneficial complex) respectively. The two minor species, *P. attenuata* and *Plegaderus* sp. made up 0.3 percent and 0.3 percent of the parasite complex. The two most abundant histerids both had peak populations in July; however, *P. cylindrica* also had a peak in May. Stein and Coster (1977) found *Platysoma* spp. most abundant in September. Riley and Goyer (1988) found maximum numbers of histerids in May and June following an abundance similar to the *Ips* beetle.

Five species of staphylinid beetles made up 7.5 percent of the predator complex (7.1 percent of the beneficial complex). The three species of *Placusa* made up 6.3 percent of the predator complex. The combined staphylinid species were found in peak numbers in July along with the *Ips* bark beetles. Moser et al. (1971) and Riley and Goyer (1988) found staphylinids occurring from May through October, with the majority of the species occurring in May and June and in September along with the bark beetle populations.

Corticeus glaber, making up 1.4 percent of the predator complex and 1.4 percent of the beneficials, was found in high numbers in May and July. This early season peak was also found by Smith and Goyer (1980), also found a peak in emergence during October and November. Moser et al (1971) found *C. glaber* present year round. Stein and Coster (1977) found peak numbers emerging from February to May. Riley and Goyer (1988) found *C. glaber* most abundant in May.

Two *Aulonium* species were collected with the most common species (*A. tuberculatum*) making up 1.0 percent of the predator complex (1.0 percent of the beneficial complex); the other species (*A. ferrugineus*) made up only 0.02 percent of the predator complex. The *Aulonium* spp. combined were found in two peaks throughout the summer, one in July and another in September. Moser et al. (1971) found them present year round. Riley and Goyer (1988) found them present in peak numbers in May.

An empidid fly species was found to make up 0.9 percent of the predator complex and 0.9 percent of the beneficial complex. The empidid species was most abundant in May and June and present at low levels the rest of the season. Moser et al. (1971) found them present only in July. No other seasonal information is available on empidids associated with bark beetles in the southeastern United States.

In Texas in 1983, *Sacium* sp. (Coleoptera: Orthoperidae) was the most abundant facultative predator making up 30 percent of the predator complex and 28.1 percent of the beneficial complex. *Sacium* sp. is carnivorous, occurring under decaying bark or rotting fungus-covered plant material (Moser et al. 1971, Arnet 1973, Dixon and Payne 1979). *Sacium* sp. populations increased from May through June, peaked in July and September, and declined sharply in October. The peak in July suggests that it follows an abundance pattern similar with *I. grandicollis*. Moser et al. (1971) found *Sacium* sp. most abundant in March and again in August through September.

Three species of ants (*Crematogaster* sp. and two unidentified species) made up 16.1 percent of the predators and 15.1 percent of the beneficials. These predators attack bark beetle adults and larvae on and under the bark surface (Dixon and Payne 1979).

Dendrosoter sulcatus (Hymenoptera: Braconidae) was the most abundant parasite making up 38.4 percent of the parasite complex and 2.5 percent of the beneficial complex. Dixon and Payne (1979) found it the third most abundant in their study. Bing (1985) found *D. sulcatus* most abundantly in May and June and again in September. Stein and Coster (1977) found in most abundantly in the spring and summer, and Moser et al. (1971) found both species present all year long. There were no significant differences in populations of *D. sulcatus* between the tree species. There was, however, significantly more *D. sulcatus* in the top of the trees probably due to a combination of thinner bark and higher beetle populations.

The second most numerous parasite, *Roptrocerus eccoptogastri*, comprised 22.3 percent of the parasite complex and 1.4 percent of the beneficials. Moser et al. (1971) and Dixon and Payne (1979) found it to be the most abundant parasite. Berisford and Franklin (1972) and Goyer and Finger (1980) both found *R. eccoptogastri* to be the major parasite in the parasite complex. *Roptrocerus eccoptogastri* was most abundant in Texas in May and found at low numbers throughout the rest of the season. Stein and Coster (1977) found it most abundant from March through May. Riley and Goyer (1988) found *R. eccoptogastri* most abundant in May .

Eleven minor parasites were found in association with *Ips* bark beetles. An encyrtid wasp made up 12.1 percent of the parasites (0.8 percent of the beneficials). Three braconid wasps, *Coeloides pissodis*, *Spathius pallidus*, and *Meteorus hypophloei* made up 2.3 percent, 0.9 percent, and 1.3 percent of the parasite complex (0.2 percent, 0.1 percent, and 0.1 percent of the beneficials), respectively. An Ichneumonid wasp made up 3.0 percent of the parasites (0.2 percent of the beneficials). Three pteromalid wasps (*Heydenis unica* and two species near *Dinotiscus*) made up 0.7 percent and 5.0 percent of the parasites (0.1 percent and 0.3 percent of the beneficials), respectively. A scelionis wasp (*Probaryconus* sp.) made up 5.4 percent of the parasite complex (0.4 percent of the beneficials). Two platygasterid wasps (*Platygaster* sp. and an unidentified species) made up 6.1 percent and 2.5 percent of the parasites (0.4 percent and 0.2 percent of the beneficials), respectively.

Cerambycids are thought to be either food competitors (Moser et al. 1971), or to kill bark beetles by their forging behavior (Miller 1984). Three cerambycids, *Monochamus titillator*, *M. carolinensis*, and *Neacanthocinus obsoletus*, were found to make up only about 1 percent of the total associate complex, however, they have the ability to destroy a large section of the phloem resource. Cerambycids increased significantly in August and September from a constant early season level. This increase may be due to the increased availability of phloem due to a drop in *Ips* numbers. Another reason for this increase may be that cerambycids function better in hotter weather than *Ips* beetles, thus enabling them to respond quicker and in larger numbers to a downed tree. Miller (1984) suspected that cerambycids did not arrive at a downed tree as quickly in cooler months as they did in late summer.

CONCLUSIONS

Overall, the temporal and numerical relationship between *Ips* spp. and their insect enemies indicated a density dependent relationship in felled pines in the Gulf coastal states of Louisiana and Texas. Some species of beneficials preferred different temperatures and ecological niches thus avoiding competition for *Ips* prey. Data indicated significant population reduction as a result of the combined feeding by the beneficial complex.

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SECTION ELEVEN

Impact of Arthropod Natural Enemies on *Dendroctonus frontalis* (Coleoptera: Scolytidae) Mortality and Their Potential Role in Infestation Growth

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ABSTRACT

Densities of southern pine beetle, *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae), attacks, eggs and late stage immatures were measured and related to southern pine beetle parasite and predator densities during three phases of area-wide southern pine beetle population levels: expanding (1975), epidemic (1976) and endemic (1978). Southern pine beetle attack densities were higher in 1976 and 1978 than in 1975. Egg density increased during the course of the infestation, while mean density of late stage immatures was significantly higher during the epidemic phase than in either the expanding or endemic years. During the course of the infestation both the numbers of natural enemies (parasites and predators) and the ratios of natural enemies to each of the southern pine beetle life stages increased significantly.

Using SPBMODEL, a model of southern pine beetle population dynamics, simulated growth for three southern pine beetle infestations during 1976 and 1978 showed a close correlation between observed and predicted

numbers of infested trees through time. When the model was modified and natural enemy-caused mortality was removed, predicted infestation growth was much more rapid and tree loss over a 90-day period was up to 40 times greater than when natural enemies were present. The potential role of southern pine beetle natural enemies in infestation development is also discussed.

INTRODUCTION

The southern pine beetle, *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae), is the most important bark beetle species affecting pine forests in the southern and southeastern United States. From 1982 to 1985 estimates of losses on national forests were approximately 92 million dollars (Kelley et al. 1986). Changes in forest conditions are believed to have contributed to the current epidemic levels of southern pine beetle populations. Total acreage of pine forests in the South has declined since the early 1950's; however, stands on the average are older and more densely stocked (Kelley et al. 1986), resulting in a generally more favorable resource for southern pine beetle colonization. The beetle does, however, also occur at damaging levels in young, small trees and in less highly stocked stands. Although the economic impact of this pest is substantial and research during the past 12 years has been extensive (for reviews see Thatcher et al. 1980, Branham and Thatcher 1985), understanding of southern pine beetle population dynamics remains insufficient to permit assessment of the factors responsible for initiation and cessation of southern pine beetle outbreaks.

The importance of naturally occurring biological control in the dynamics of southern pine beetle populations has long been a topic of speculation, but there are few real data available. Early researchers (e.g. Hopkins 1893, 1909) suggested that natural enemies were potentially important factors in control of southern pine beetle populations, but little was done to evaluate the extent of natural enemy-caused mortality until recently. Moore (1972), counting parasites and predators in bark samples, reported an average of 24% mortality that he believed was attributable to natural enemies, and Linit and Stephen (1983) in a more extensive study found that natural enemies contributed about 24 to 28% of the within-tree mortality suffered by developing southern pine beetle brood.

Berisford (1980) summarized and reviewed the available literature on biology and interactions of southern pine beetle natural enemies with their hosts. Subsequent to his review a number of researchers have examined aspects of *Thanasimus dubius* biology (Mizell and Nebeker 1981, 1982, Frazier et al. 1981, Mizell et al. 1984). Gargiullo and Berisford (1981) evaluated the effects of southern pine beetle density and bark thickness on eight hymenopterous parasites, and Kudon and Berisford (1980, 1981, 1985) investigated a number of facets of host selection and switching by parasites common to southern pine beetle and *Ips* species. Seasonal distribution, abundance, host density dependence and bark thickness were examined by Goyer and Finger (1980).

Our objectives are to report on within-tree densities of southern pine beetle natural enemies under three phases of area-wide infestation development (expanding, epidemic and endemic) and to relate this information to within-tree southern pine beetle densities during these same periods. We further speculate on the importance of natural enemies to the process of natural control of southern pine beetle populations based on our data and simulations with a mechanistic model of southern pine beetle population dynamics and infested spot growth.

METHODS

We have intensively sampled southern pine beetle populations in seven different years and four southern states since 1975. We discuss here data collected in southern Arkansas in three different years, 1975, 1976 and 1978. Five geographic locations, 14 separate infestations or "spots," and samples from 204 trees are included in the subset of data used in these analyses. All trees were climbed to locate the top of the southern pine beetle infestation and to determine the stage of beetle brood development within the tree. The infested bole length was divided into three sections (i.e. upper, middle and lower infested bole), and southern pine beetle population samples were collected from the middle portion of each of these sections. Generally two bark disc samples (1 dm^2 each) were taken for attack (Linit and Stephen 1978) and egg-dissection analyses, and two or more additional samples for radiographic analyses of late stage immatures and associates present in the bark. This study includes 1184 attack/egg samples and 1636 radiograph samples.

Samples that were dissected with the aid of a microscope were used to evaluate density of attacking adults, and all parent-adult galleries were cleaned and dissected to obtain estimates of total egg density and survival. The radiographs taken of bark discs containing late stage immatures were used to determine densities of southern pine beetle immatures, parasites, predators and other associated species.

Initially, all samples taken from one section of one tree were combined to represent the mean value of each variable present in that section. These data, summarized at the section level, were then used as the individual observations for all subsequent analyses. Each observation (N) is thus based on at least two (sq. dm) samples per height. Summary statistics and frequency distributions of the data were prepared using the Statistical Analysis System (SAS Institute Inc. 1985a), and examined to determine if frequency distributions of southern pine beetle and natural enemy densities approximated normality. Raw data as well as transformed data were analyzed using PROC UNIVARIATE (SAS Institute Inc. 1985a). Transformed data were distributed more symmetrically than the raw data, with the poorest fit to a normal distribution resulting from the 1976 data, which have very high numbers of observations. Means separations presented in Tables 2-4 were calculated on transformed data (square root transformation of count data, natural logarithm transformation of ratio data), using SAS General Linear Model procedure and Tukey's mean separation (HSD) tests (SAS Institute Inc. 1985b). Summary statistics (mean, standard error of the mean and median) presented in the text and tables are calculated from raw data.

Based on papers by Overgaard (1968), Moser et al. (1971) and Goyer et al. (1980), decisions were made on which species of natural enemies to include in an assessment of parasite and predator densities (Table 1). Some species included as natural enemies are perhaps facultative predators or parasites on southern pine beetle, but the techniques used to measure natural enemy densities in the samples are, as noted below, basically conservative in nature and probably underestimate densities.

We have developed a southern pine beetle population dynamics and infested spot growth model, SPBMODEL, which can be used to experimentally simulate southern pine beetle population growth and corresponding tree mortality (Stephen and Lih 1985). The model is a conceptual representation of the southern pine beetle life cycle. Temperature is the driving variable that regulates beetle development. SPBMODEL incorporates the effects of various components of within-tree southern pine beetle mortality, plus the influence of selected physical and biotic factors in the forest environment, on the process of tree colonization and beetle reproduction.

As beetles develop, mortality affects the beetles at particular stages of their life cycle. The parasite and predator counts on each sampling date for each sampled infestation in our data base represent numbers of natural enemies present during the late larval and pupal stages of the beetle. Natural enemy-caused mortality in a particular spot for each sampling date was calculated using the following assumptions. Each parasite kills one southern pine beetle larva, and each predator has already killed one larva and will kill one more. For at least two reasons these are conservative estimates of predation. First, some predators are undoubtedly overlooked in the examination of radiographs; and second, many predators, and possibly some parasites (Berisford et al. 1970), consume more than two prey in their lifetimes. Linear interpolation was used to determine natural enemy-caused mortality between sampling dates. Simulation runs were made for three infestations using the current model. To produce simulations that demonstrate the effects of eliminating natural enemies from the southern pine beetle life system, the mortality rates in SPBMODEL that affect larvae, pupae and brood adults were adjusted accordingly and the simulation runs repeated using the spot-specific adjusted mortality rates.

Table 1

Southern pine beetle parasites and predators included in natural enemy evaluations.

PARASITES
    Coeloides pissodis (Ashmead)
    Dendrosoter sulcatus Muesebeck
    Spathius pallidus Ashmead
    Heydenia unica Cook and Davis
    Roptrocerus xylophagorum (Ratzeburg)
    Dinotiscus dendroctoni (Ashmead)
    Eupelmus cyaniceps Ashmead
    Meteorus hypophloei Cushman
    Eurytoma tomici Ashmead
    Rhopalicus pulchripennis (Crawford)
PREDATORS
    Scoloposcelis mississippensis (Drake and Harris)
    Plegaderus pusillus LeConte, *P. transversus* Say
    Lyctocoris elongatus (Reuter)
    Leptacinus paurumpunctatus (Gyllenhal)
    Temnochila virescens (F.)
    Thanasimus dubius (F.)
    Corticeus glabor LeConte, *C. parallelus* Melsheimer
    Aulonium ferrugineum Zimm., *A. tuberculatum* LeConte
    Medetera bistriata Parent
    Lonchaea auranticornis McAlpine, *L. polita* Say
    Platysoma parallelum Say, *P. cylindrica* (Paykull), *P. attenuata* (LeConte)

RESULTS

In 1975 southern pine beetle attack and egg densities were low compared to subsequent years, averaging 3.7 attacks and 108 eggs/dm^2 (Table 2).

Table 2

Southern pine beetle (SPB) density/dm² of infested bark during expanding (1975), epidemic (1976) and endemic (1978) years in Arkansas.

SPB	Year	Mean	SE	Median	N
Attacks	1975	3.7 a	0.22	3.5	107
	1976	5.7 b	0.11	5.5	401
	1978	5.7 b	0.41	5.5	36
Eggs	1975	107.7 a	3.86	107.0	107
	1976	157.4 b	2.35	156.5	396
	1978	172.8 b	9.10	163.3	36
Late Stage Immatures	1975	35.1 a	1.63	35.0	107
	1976	43.2 b	1.16	40.0	356
	1978	31.9 a	1.52	29.5	95

Means followed by the same letter are not significantly different ($P = 0.10$); Tukey's studentized (HSD) test. Data were subjected to square root transformation for means separation.

The density of late stage immatures, however, was comparable to 1978 (ca. 35 and 32/dm², respectively (Table 2)). The mean values for all southern pine beetle density variables are very close to their medians. During 1975 the within-tree densities of parasites and predators, and thus the total natural enemy complex, were the lowest of any of the three years under consideration (Table 3). In addition, this was the only year when parasites outnumbered predators.

During 1976, southern pine beetle attack and egg densities (5.7 attacks and 157 eggs/dm²) were higher than the previous year (Table 2). The highest mean density of late stage immatures that was found, 43.2, occurred at this time. Parasites increased from a mean of 3.5 /dm² in 1975 to 5.4 in 1976 (Table 3), and this trend towards increasing numbers of natural enemies was seen even more with predators, the mean of which was 2.7 in 1975 and 6.6 in 1976. The total population of natural enemies during this outbreak year thus increased dramatically, from a mean of 6.2/dm² in 1975 to 12.0 in 1976. Although there was a significant increase in the ratio of natural enemies to attacks from 1975 to 1976 (2.3 to 2.5), and also a significant change in the ratio of natural enemies to eggs between these years (0.06 to 0.09), the numerical increases were nevertheless small (Table 4). A significant increase in the ratio of natural enemies to late

Table 3

Density of southern pine beetle (SPB) natural enemies (NE)/dm^2 of infested bark during expanding (1975), epidemic (1976) and endemic (1978) years in Arkansas.

Natural Enemy	Year	Mean	SE	Median	N
Parasites	1975	3.5 a	0.26	3.2	109
	1976	5.4 b	0.22	4.5	408
	1978	8.6 c	0.62	7.5	108
Predators	1975	2.7 a	0.19	2.3	109
	1976	6.6 b	0.20	5.8	408
	1978	9.7 c	0.58	8.4	108
Total Natural Enemies	1975	6.2 a	0.38	5.8	109
	1976	12.0 b	0.29	11.2	408
	1978	18.3 c	0.98	16.4	108

Means followed by the same letter are not significantly different ($P = 0.10$); Tukey's studentized (HSD) test. Data were subjected to square root transformation for means separation.

stage immatures also occurred. (It may be noted that simply dividing the mean or median values for natural enemies by those for southern pine beetle life stages (Tables 2 and 3) does not produce the same ratios as seen in Table 4. This is because these ratios were computed from the means for these variables at each sampling height on trees, and subsequently averaged.) Variation, expressed as standard error of the mean, was generally lowest in 1976 for most of the variables considered, which is probably a function of the much greater sample size in that year.

Average southern pine beetle attack density was virtually the same in 1978 as in 1976 (5.7 attacks/dm^2), but the mean number of eggs in 1978 (173/dm^2) was greater than in 1976 and dramatically greater than in 1975 (Table 2). Interestingly, the mean density value for late stage immatures in 1978 (31.9) was the lowest of any of the years sampled (Table 2). Parasite and predator densities were higher in 1978 than in any of the other years (Table 3), with a total natural enemy mean density of 18.3/dm^2, approximately three times the population observed in 1975. Median values confirmed this increase over time, although the medians for the natural enemy populations are slightly less than the means, suggesting a some

Table 4

Ratio of natural enemy density to southern pine beetle density during expanding (1975), epidemic (1976) and endemic (1978) years in Arkansas.

NE/SPB RATIO	Year	Mean	SE	Median	N
NE/Attacks	1975	2.30 a	0.21	1.58	106
	1976	2.50 b	0.09	2.05	401
	1978	5.00 c	0.77	3.93	12
NE/Eggs	1975	0.06 a	0.004	0.06	107
	1976	0.09 b	0.003	0.07	396
	1978	0.11 b	0.011	0.11	12
NE/Late stage immatures	1975	0.22 a	0.018	0.16	107
	1976	0.42 b	0.029	0.28	356
	1978	0.67 c	0.044	0.56	95

Means followed by the same letter are not significantly different (P = 0.10); Tukey's studentized (HSD) test. Data were subjected to natural log transformation for means separation.

what skewed distribution with some particularly high values. The ratios of natural enemies to southern pine beetle variables (Table 4) showed the highest values in 1978, with ratios of natural enemies to attacks and to eggs being approximately twice as great in 1978 as in 1975, and a ratio of natural enemies to late stage immatures that was three times greater in 1978 than in 1975.

Comparison of observed southern pine beetle infestation growth with simulated results are presented in Figs. 1-3. Plot 8 (Fig. 1) contained 22 infested southern pine beetle trees when it was first sampled on July 12, 1976. The infestation grew to 37 infested trees by about a month later, and contained about 120 infested trees 80 days after it was first sampled. As can be seen from Fig. 1, our model simulated the growth of this infestation very well. When the mortality attributed to natural enemies was removed and infestation growth again simulated, the results were not too different after one month of growth (about 35 infested by the original prediction and about 55 infested with natural enemies removed). By the end of three months, however, the size of the simulated spot without natural enemies was ca. 550 infested trees, compared to 165 infested trees with natural enemies present in the system.

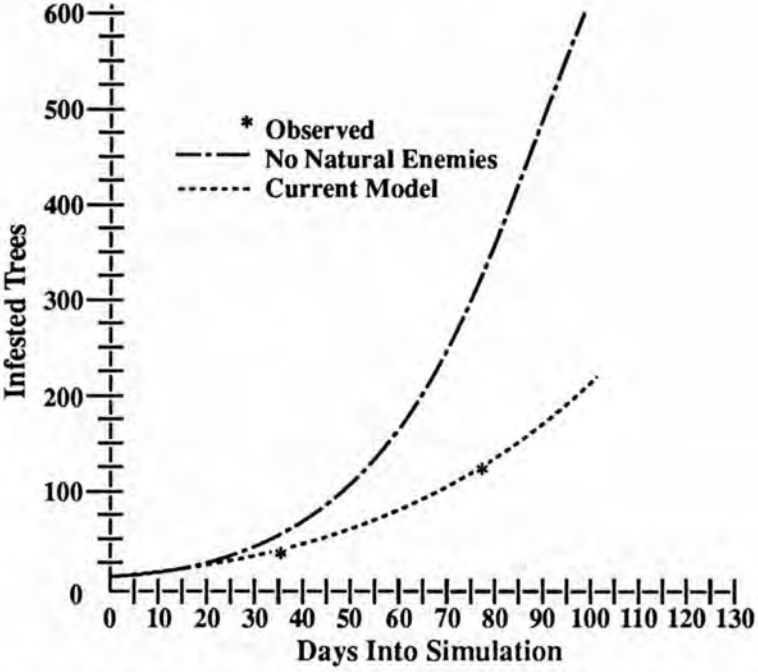

Fig. 1. Predicted and observed numbers of infested trees for Plot 8, Gum Flats, Arkansas, July 12, 1976.

Plot 7 (Fig. 2) was also sampled in 1976. It was a substantially larger spot when first visited on June 8, containing 215 infested trees. It grew to a maximum of 722 trees 70 days later, and then the infestation rate began to decline. Our simulation of spot growth was not as accurate as with Plot 8, and we underestimated the rate of infestation growth. When the impact of natural enemies was removed and the growth re-simulated, however, this spot grew even faster than Plot 8, and our predictions showed ca. 3800 infested trees by day 70.

In 1978, Plot 3 (Fig. 3) was first observed on June 15. At that time it contained 164 infested trees. The growth of the infestation was slow but reached ca. 300 trees a month after the first visit, and then numbers of infested trees declined to 206 by day 75. When natural enemies were removed, spot growth was not markedly affected during the first month; however, it did increase rapidly until ca. 2300 infested trees were predicted by the end of two months. This rapid growth became even more exponential, and our model predicted over 8000 infested trees by the end of month three.

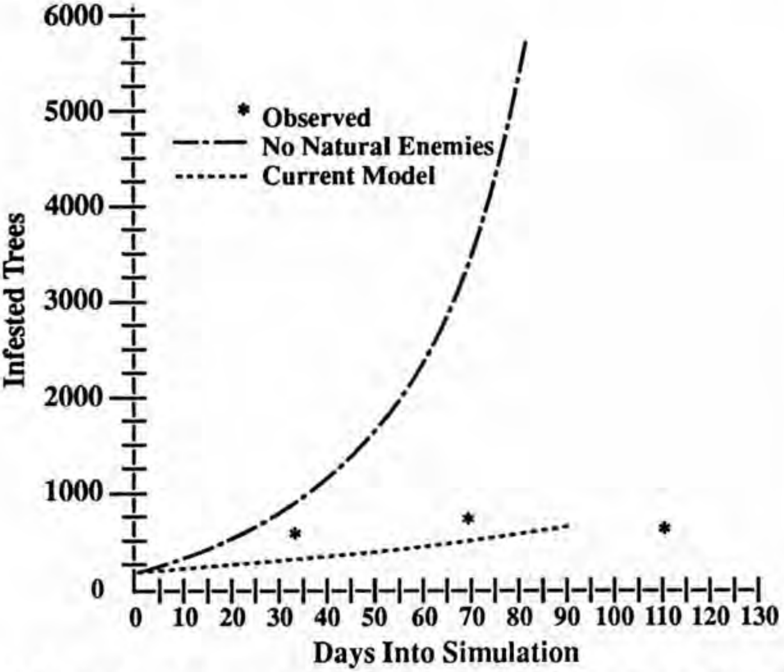

Fig. 2. Predicted and observed numbers of infested trees for Plot 7, Gum Flats, Arkansas, June 8, 1976.

DISCUSSION

Arkansas is on the northern fringe of the southern pine beetle range and does not have as long or as extensive a history of outbreaks as neighboring states to the south. First detection of southern pine beetle in Arkansas (Arkansas Forestry Commission data) was in 1969 when a few small infestations (spots) were detected in one southern county bordering Louisiana. Activity remained low for several years, but by 1974 approximately 400-500 spots were detected across the southern region of the state (Fig. 4). Infestation levels increased exponentially, with the maximum outbreak levels occurring in 1977, at which time nearly 3600 spots were detected. Unfortunately, we were not able to obtain population samples in 1977. The following year a dramatic population decline occurred (not only in Arkansas, but also in the neighboring states of Texas and Louisiana), and infestation levels were tremendously reduced with only about 240 spots being detected in the entire state.

In 1975, when southern pine beetle populations were just beginning to rapidly expand, average survival of eggs to late stage immatures was high. Using data from Table 2, it can be seen that approximately 33% of eggs survived to late stage immatures (i.e. pupae and callow adults). Although the specific factors responsible could not be determined, this high survival correlates well with low densities of parasites and predators observed in that year (Table 3). The ratios of total natural enemies to eggs and late stage immatures were significantly lower during that period than in either of the two subsequent years (Table 4).

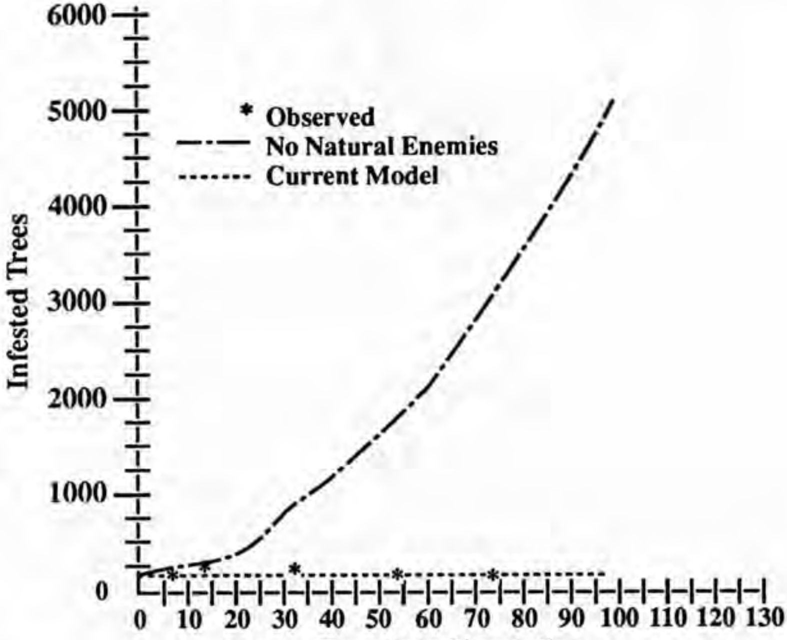

Fig. 3. Predicted and observed numbers of infested trees for Plot 3, Gurdon, Arkansas, June 15, 1978.

Southern pine beetle area-wide populations were at extremely high levels in 1976. During this period average survival from eggs to late stage immatures was ca. 28%, a somewhat lesser value than observed in 1975; however, given the much higher initial egg density in 1976, the resulting mean density of late stage immatures was significantly greater than detected in 1975.

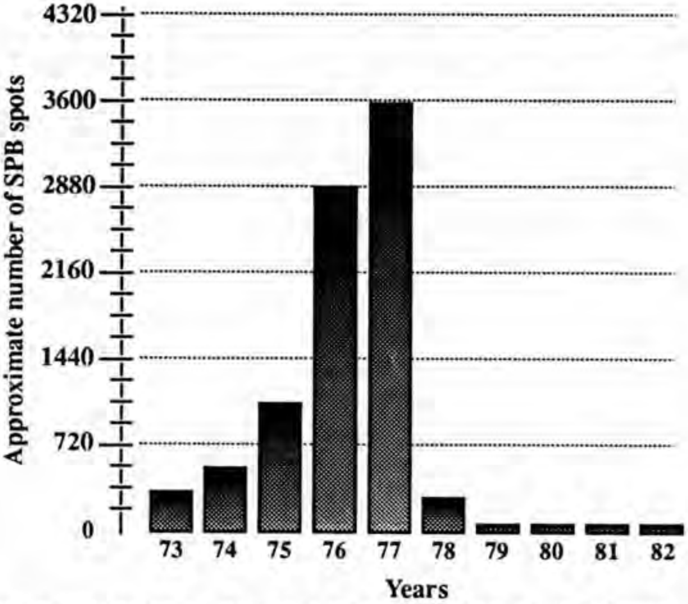

Fig. 4. Numbers of southern pine beetle infestations observed in Arkansas between 1973 and 1982.

Area-wide populations continued to increase in 1977 but then declined to almost nonexistent levels in 1978. One large infestation was sampled intensively during that endemic year. Survival from eggs to late stage immatures was much lower than had been found in previous years (only 18%), so despite the higher egg density, the density of late stage immatures was significantly less than during the epidemic phase of 1976. Indeed, density of late stage immatures was at the lowest level of any of the three years observed, while egg density was at its peak. This dramatizes the decline in realization of biotic potential by the beetle during this endemic population phase. Coincident with this reduced survival of southern pine beetle immatures was a startling increase in the within-tree density of natural enemies. During 1978, sample densities of natural enemies averaged 18.3/dm^2 which was a significant increase over 1976, and approximately three times greater than in 1975, a year in which the outbreak was still expanding.

Examination of ratios of natural enemy density to the southern pine beetle variables (attacks, eggs and late stage immatures) shows a general increase in the proportion of natural enemies over the different phases of infestation for each of the southern pine beetle variables considered (Table 4). The greatest change in ratio is found by comparing natural enemy density to density of late stage southern pine beetle immatures. It is also interesting to note that the greatest change in the ratio generally appears to be from epidemic to endemic phases of infestation (i.e. 1976-1978). We could speculate that natural enemies are exhibiting a delayed density dependent response to increase in southern pine beetle density, and at the time when the bark beetle populations crash the natural enemy/southern pine beetle ratios are the most favorable. Although there is no evidence that natural enemies were responsible for the observed population crash in 1978, if the natural enemy ratio remained favorable for several years, then this certainly could have been an important element in keeping populations of southern pine beetle at endemic levels, as has been observed in Arkansas.

The simulations of infestation growth (Figs. 1-3) are representative of the ability of the model to accurately predict short-term infestation growth (Nettleton et al. 1985, Stephen and Lih 1985). Generally, predictions are fairly close to observed values. A limited number of spots were sampled for spot growth data during epidemic population years, and most of these spots were used in originally establishing model parameters. Model refinements using data from other years and geographic areas have increased accuracy of predictions during all phases of area-wide population levels. The model averaged 16.7% error in its prediction of numbers of dead trees over the 92-day, post-initialization prediction period for 70 infested spots representing all three area-wide population levels. Our ability to accurately portray the role of natural enemies in southern pine beetle population dynamics is less certain. A much greater level of understanding of natural enemy biology, host selection, behavior, response to host density, dispersal, and relation with *Ips* species (e.g. Kudon and Berisford 1980, 1985) is needed before we can be confident in a natural enemy subcomponent of our southern pine beetle model.

We can speculate, however, that the dramatic increases in spot growth that result from eliminating the mortality that we attribute to natural enemies are at least what would be seen given the improbable situation that they were totally eliminated from the southern pine beetle ecosystem. A more likely scenario would be one in which natural enemy effectiveness would, at some level, be impaired through the action of specific control methods for southern pine beetle that also cause direct mortality to natural enemies (e.g. pesticides, or pheromone traps that are attractive to specific natural enemies), or that interfere with natural enemy searching or dispersal behavior (e.g. felling of trees for salvage or cut-leave, or pheromones used for disruption).

Natural enemies have seldom been identified as important factors in regulating *Dendroctonus* populations. We suggest that there are several unique aspects to southern pine beetle biology that may enhance the potential impact of natural enemies on this species in comparison to other *Dendroctonus* species. Developmental times for generations produced in the warmer parts of the South may be about one month in duration, resulting in as many as seven to nine generations per year (Payne 1980). A large proportion of the attacking adult population re-emerges (Cooper and Stephen 1978, Coulson et al. 1978) shortly after oviposition is completed, and these adults, in concert with emerging brood, produce a continual allocation of beetles (Coulson 1979) to attack and produce pheromones in adjacent trees. The continual presence of a pheromone source results in infestations forming as "spots" that serve to concentrate both southern pine beetle and its natural enemies. Within an active spot there is a completely overlapping series of southern pine beetle generations that exist simultaneously in all stages of development. The potential for natural enemies to respond to their hosts through both a functional and numerical response may thus be greatly enhanced in comparison to other *Dendroctonus* species that have only one or two discrete generations per year.

CONCLUSIONS

Densities of southern pine beetle attacks, eggs and late stage immatures were measured and related to southern pine beetle parasite and predator densities during three different years (1975, 1976 and 1978), representing distinct phases of a southern pine beetle area-wide infestation (expanding, epidemic and endemic, respectively). Density of southern pine beetle attacks increased from 3.7/dm^2 in 1975 to 5.7 in both 1976 and 1978. Egg density increased during each of the three years of the study from ca. 108/dm^2 in 1975 to 173/dm^2 in 1978. Mean density of late stage immatures was 35.1 in 1975, increased to 43.2 in 1976, and then declined to 31.9 in 1978. During these same years numbers of natural enemies (both parasites and predators) grew steadily, with a mean total density of natural enemies in 1975 of 6.2/dm^2, increasing to 12.0 in 1976, and reaching a maximum of 18.3 in 1978. The ratios of natural enemies to each of the southern pine beetle life stages measured also increased through the course of the infestation.

Simulations of infested spot growth during 1976 and 1978 showed a close correlation between observed and predicted numbers of infested trees. When the simulation model was modified to include spot-specific mortality and density data, and the mortality attributed to natural enemies was removed, the predicted spot growth was much more rapid. Over a 90-day period the number of infested trees was up to 50 times greater when natural enemies were not present. It was concluded that southern pine beetle natural enemy populations exhibited a delayed density dependent response to increasing southern pine beetle population density, and although natural enemies may not have been responsible for the observed area-wide southern pine beetle decline, they may have been important in keeping them at endemic levels for the next several years.

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Inoculative Release of An Exotic Predator for the Biological Control of the Black Turpentine Beetle

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ABSTRACT

An inoculative release of the Eurasian predatorial beetle, *Rhizophagus grandis*, was made for control of the black turpentine beetle, *Dendroctonus terebrans* Olivier, a prominent native pest of southern pines. If this central Louisiana release proves successful, and rearing programs are perfected, further releases should expand the geographical range of *R. grandis*. Because the larval frass of other species of *Dendroctonus* is highly attractive to *R. grandis*, this exotic predator may also attack the brood of some or all of the South's *Dendroctonus* species, including that of the southern pine beetle, *Dendroctonus frontalis* .

BACKGROUND

The black turpentine beetle (BTB), *Dendroctonus terebrans* Olivier, is a native pest of pines in southern United States. It is particularly injurious in Georgia and Florida where gum naval stores operations are an important industry (Smith and Lee 1967). During turpentine operations, slash pine (*Pinus elliottii* Engelmann) and longleaf pine (*Pinus palustris* Miller) are commonly attacked and killed by the beetle. Additionally, the BTB quickly attacks trees damaged during logging operations and trees located near construction sites in urban areas. Apparently normal healthy trees may also be attacked, although BTB damage usually involves less than 10% of a stand during a single season. One "epidemic," however, in the 1950's, reportedly affected more than 25% of a single healthy stand (Smith and Lee 1967).

Although not as aggressive or wide spread as the southern pine beetle (SPB), *Dendroctonus frontalis* Zimmermann, the BTB shows a preference for weakened trees, such as those damaged by fire, tapped for naval stores, or injured during logging operations. The BTB ranks third as overall damage agent among 10 major forest pests in the 13 southern states. However, according to USDA Forest Service and university researchers working in Florida and Georgia where the turpentine industry is important, BTB ranks as the most destructive pest.

Current Control Strategies

A number of control strategies are currently used to reduce bark beetle population numbers and/or to manage outbreaks. These strategies can be categorized as 1) spot control by salvage, 2) chemical treatment, and 3) preventive management of susceptible stands by silvicultural methods. Of the first two categories, rapid salvage is the preferred alternative (Swain and Remion 1981). Except for urban areas, chemical control is not widely practiced because it is not cost effective and because of environmental concerns.

Currently, preventive control by silvicultural treatment is the best overall strategy in combating outbreaks. Research over the past decade has provided successful silvicultural prevention methods that are now widely accepted (Belanger 1980, Lorio 1980). Unfortunately, economic constraints sometimes preclude use of prevention methods by many landowners in the southern United States.

Applied biological control of bark beetles is still an ignored and underdeveloped technique. Of the many organisms and allied beetle species associated with *Dendroctonus*, only native insects, mites, nematodes, and fungi have received much attention (Berisford 1980). Recent studies have been oriented toward determining specific roles and impacts of native associates so that computer models can be developed to forecast population trends. Studies have been designed to implement control strategies that can capitalize on population suppression by native natural enemies (Kinn 1984, Moser and Dell 1980). Other studies are searching for exotic or extraregional natural enemies (Moser 1981, Moser and Bogenschutz 1984, Moser et al. 1978). Although the native natural enemies may have a considerable impact on beetle populations, they still do not always control epidemic levels of the *Dendroctonus* bark beetles. It is possible then that the best hope in this area lies with the release of exotic natural enemies. One exotic insect predator, *Rhizophagus grandis* Gyllenhal (Coleoptera: Rhizophagidae), appears to have potential as a control agent (Miller et al. 1987).

The Biological Control Approach

Rhizophagus grandis is a specific predator, attacking only the spruce bark beetle, *Dendroctonus micans* (Kugelann). The distribution of both host and predator now extends westerly from eastern Siberia to France and England, south to Turkey, and to the northern tip of Norway (Bevan and King 1983). *D. micans* is the only species of *Dendroctonus* within this vast area. In the recent past, *D. micans* has expanded westerly from its Siberian origin. As the beetle invaded Europe during the past 100 years, population explosions coincided with this advance (Carle 1975). Apparently these outbreaks occurred when *D. micans* temporarily "outran" its predator, *R. grandis;* but once the predator–prey balance was achieved, *D. micans* again became endemic (J-C. Grégoire, personal communication). Presently, large-scale programs are under way to introduce the predator in spruce stands in parts of England, France, Russia, and Turkey where the scolytid is still epidemic (Grégoire et al. 1985). Efforts are especially intense in England, where *D. micans* was first discovered in 1982 (Bevan and King 1983). In 1984, 30,000 *R. grandis* adults were produced in large breeding units for distribution in England's outbreak areas of *D. micans* (Evans 1985). In 1985, 29,000 were reared in Belgium (J-C. Grégoire, personal communication).

Within the palearctic spruce forests, *R. grandis* is found in association only with *D. micans*, there being no records of its having attacked other scolytids. But perhaps this is because no other *Dendroctonus* species may be available to it within the predator's natural range in Eurasia. *R. grandis* has a high searching efficiency and is found in more than 80% of *D. micans* galleries (Grégoire et al. 1985). *R. grandis* is able to detect both larval and adult allomones of *D. micans* (Tondeur and Grégoire 1979), but *R. grandis* females will not oviposit unless larval frass of *D. micans* is present (Grégoire et al. 1984). The key allomones attracting *R. grandis* to *D. micans* galleries appear to be *exo*-brevicomin, which may be produced by *D. micans* adults, and (-)-verbenone, produced by *D. micans* larvae (Tømmerås et al. 1985).

Grégoire et al. (1981) suggested that other *Dendroctonus* species with gregarious larvae, such as BTB, might also be attractive to *R. grandis*. In a series of bioassays performed in February, 1985, J-C. Grégoire demonstrated that larval frass of three native North American species of *Dendroctonus (D. terebrans, D. frontalis,* and *D. rufipennis* (Kirby), the spruce beetle) were highly attractive to both males and females of *R. grandis*. The most surprising find was that the frass of *D. frontalis* (whose larvae are not gregarious) was also highly attractive (Miller et al. 1987). This suggests that if *R. grandis* was introduced into the United States and successfully established as a predator on *D. terebrans*, then the predator might also impact the SPB. *D. terebrans*, however, remains the primary target because it has an ecology similar to that of *D. micans*. Both BTB and *D. micans* have a long life cycle and gregarious larvae, facilitating prey exploitation by *R. grandis*.

Fig. 1. Male *Rhizophagus grandis* in gallery of *Ips grandicollis* inside phloem sandwich (USDA Forest Service photo).

It should be mentioned at this point that in 1933 and 1934 about 800 specimens of an unidentified *Rhizophagus* from England were released in Quebec, Canada, against the spruce beetle in an outbreak area, but the introduced beetles failed to become established. Turnock et al. (1976) classified this release as a futile colonization attempt, doomed by inadequate selection of natural enemies and by poor handling and release techniques. This species could not have been *R. grandis* because it was not introduced

troduced into Britain until 1982. Moreover, other known species of *Rhizophagus* are much less species specific and their predatory qualities are questionable (J-C. Grégoire, personal communication). Specimens of *R. grandis* were sent to the United States on three occasions (1976-78) for laboratory tests against North American *Dendroctonus* species, but none were released (Coulson 1981). The Canadian Forestry Service at Victoria B. C. has imported individuals to control *Dendroctonus ponderosae* Hopkins (H. A. Moeck, personal communication).

Fig. 2. Young BTB larvae feeding gregariously in phloem sandwich. Below are an adult and two larvae of *Rhizophagus grandis* (USDA Forest Service photo).

This biological control agent, if successfully established, should spread throughout the host's range, effecting widespread control that is cost effective. Theoretically, *R. grandis* should also attack broods of the more aggressive SPB, because the predator adults are highly attracted to larval frass of the scolytid (Miller et al. 1987). Indeed, *R. grandis* adults entered SPB galleries through holes made by them, and consumed the larvae in phloem sandwiches. These sandwiches (Moser and Roton, unpublished) had been previously attacked by SPB in the field. However, *R. grandis* egg laying was not observed. The same phenomenon was observed in another sandwich field-attacked by *Ips grandicollis* (Fig. 1).

Rearing Procedures

Attempts will be made to determine the best way to rear the predators in order to build up populations for release in central Louisiana. Experience in Europe has shown that large numbers of *R. grandis* for release in the field can be artificially reared on brood of *D. micans* (Fig. 1) in spruce bolts, and by a semiartificial breeding method (Grégoire et al. 1986). This latter rearing method was first developed in Russia (Kobakhidze et al. 1968) and is currently being used in England. In 1985, the British Forestry Commission reared adults of *R. grandis* in spruce billets at a cost of about $2.50 per beetle, counting materials and labor (H. F. Evans, personal communication). For that project, a constant temperature of 20 degrees C., 65-75% R. H., and an artificial lighting regime of 18 hours/day were maintained in rearing rooms (Evans 1985).

Fig. 3. Phloem sandwich with mature BTB larvae, some of which are constructing pupal cells. Young larvae were introduced at right. They feed gregariously at first; later the older larvae disperse (USDA Forest Service photo).

In 1986 and 1987, three shipments totaling 300 hundred pairs of *R. grandis*, reared by J-C. Grégoire in Belgium, were shipped to the Alexandria Forestry Center in Louisiana to test methods of rearing the predator on BTB and SPB. Although preliminary tests showed that the predator could be reared on BTB, using both the bolt and the semiartificial methods, the latter method was chosen because using bolts was too labor intensive. Our immediate objective was to obtain eggs of *R. grandis* so that they could be surface-sterilized in White's solution (Barras 1972), thus reducing the chances of microorganisms being introduced from Europe. *R. grandis* readily laid eggs in phloem sandwiches (Fig. 2) inoculated with about 20 BTB larvae, and one male and two females of *R. grandis* (only one pair was needed, but the extra female doubled the egg production). Young BTB larvae fed gregariously (Fig. 3) similar to those of *D. micans*, but older larvae became solitary (Fig. 2). Individual females laid as many as 133 eggs per sandwich. After 5 to 8 days the sandwiches were opened, and the easily visible eggs (Fig. 4) were collected.

After surface sterilization, the eggs were placed in polystyrene boxes where the resulting larvae were reared on the alternate food sources described by Grégoire et al. (1986). This method conserved BTB larvae that were sometimes scarce and were needed as oviposition stimuli for *R. grandis*. Although the *R. grandis* larvae would readily feed gregariously on BTB larvae inside the sandwiches (Fig. 5), the predator larvae (as well as adults, Fig. 6) could be conveniently fed a variety of foods including frozen dipterous maggots and even commercial cat food. Prepupae were placed in moist sand to pupate, after the technique described by Grégoire et al. (1986).

Fig. 4. Portion of phloem sandwich with eggs of *Rhizophagus grandis* (arrows) in BTB frass (USDA Forest Service photo).

Fig. 5. Young and mature larvae of *Rhizophagus grandis* feeding gregariously on larva of BTB in artificial rearing chamber (USDA Forest Service photos).

Fig. 6. Adult of *Rhizophagus grandis* feeding on pellet of commercial dry cat food. At left (arrow) is remains of BTB larva consumed previously by the predator.

Whereas *Beauveria bassiana* (Balsamo) Vuillemin caused major rearing losses to *D. micans* and *R. grandis* brood in Europe, another pathogen [probably *Metarhizium anisopliae* (Metschinikoff) Sorokin] soon caused 100% losses to both host and predator larvae in the first Alexandria Forestry Center rearing containers. The disease was controlled in later rearings by using 0.5 g each of sorbic acid and methyl paraben, mixed with 400 g of the bark dust medium used to fill the polystyrene boxes.

Field Release Techniques

In England single pairs of *R. grandis* are placed in small plastic cups each having about 50 ml capacity. A small amount of moist sand is added. The cups are then taken into the field where the contents, including the predators, are carefully poured out at the bases of trees that have been attacked by *D. micans* (King and Evans 1985). In France, about 50 predators are placed at the base of each single infested tree, and the predators quickly vanish, running into the bark or taking flight (Grégoire et al. 1985). Both release methods take advantage of the extraordinary searching abilities of *R. grandis*.

The minimum number needed for an inoculative release is unknown, but it is probably less than the 2,350 individuals released per area in France (Grégoire et al. 1985). This is the lowest number listed in published reports for areas in which individuals were recovered the next year. However, H. F. Evans (personal communication), in England, recovered a number of *R. grandis* larvae 6 months later after releases of only 10 and 25 individuals respectively. Adults, larvae, and prepupae have been found overwintering (Grégoire, personal communication). Beirne (1975) has shown that of species (none of which were *Rhizophagus*) released for biological control in Canada, 60% of those averaging more than 800 individuals per release became colonized, but of those averaging less than 800 per release, only 15% became colonized. Hence, although it appears possible to establish *R. grandis* by using small numbers, a large release may greatly increase chances of success.

In Europe, when populations of *R. grandis* are established, they tend to "stay put" and not move rapidly into new distant areas. For this reason, a number of inoculative releases would have to be made throughout the southern United States to quickly establish the predator throughout the range of BTB.

Although the BTB is ubiquitous in pine forests of central Louisiana, high populations often occur in stumps after logging operations. Emerging adults may also attack nearby trees. It is at the interface of one of these areas and the surrounding forest that would be the ideal habitat to release the large numbers of *R. grandis* adults. As of April 1, 1988, there were about 150 pairs of adults being held in the refrigerator for release in the field. On April 7, the first 20 pairs were released in four localities of Grant Parish, Louisiana on two trees and 6 stumps similar to the method by King and Evans in England.

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SECTION THIRTEEN

Cross-Attraction Surveys for Insect Enemies of Southern Pine Beetle

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ABSTRACT

Bark beetles remain in the forefront of pests damaging North American coniferous forests. Analysis of recent epidemics indicate that until about 1970, pest management practices at best only slowed the impact of tree mortality. Within the past 8 to 10 years, integrated pest management has been implemented to prevent, reduce or minimize tree mortality from major bark beetles. However, it appears that one facet of forest pest management, biological control for bark beetles, was almost entirely ignored. This cooperative pilot study indicates the potential of extraregional bark beetle predators from different forest ecosystems as biological control agents because they are able to detect aggregating pheromones (kairomones) of beetles related to their normal prey. Predators such as *Thanasimus undatulus* respond to pheromones of *Dendroctonus frontalis* and *D. brevicomis* in cross-attraction field tests in Montana. Because *T. undatulus* will respond to pheromones of other *Dendroctonus*, it might be a potential biological

control agent. Trapping with aggregation pheromones in habitats of related pests is useful for screening for potential predators for the North American *Dendroctonus* spp.

INTRODUCTION

Pine forests and woodlands occupy about one-third of the total land area of the world. In the United States, 33 percent of the total land area is classified as forestland. Of this, approximately 18 percent encompasses the major pine forest type (USDA Forest Service 1981). Pine forests provide timber for lumber, paper and other derived products, habitat for wildlife, forage area for livestock, watershed cover, and settings for outdoor recreation and aesthetic enjoyment. As demand for these products and uses increased, maintaining this renewable resource challenged managers. The aim is to regenerate, to grow, and to maintain forests as pest-proof as possible (Waters et al. 1985).

Of the destructive agents laying claim to the pine forests, bark beetles remain in the forefront. They impact merchantable volume, watershed, wildlife habitat, range resources, recreational and aesthetic values, wilderness areas, and subsequent fuel buildup increases the risk of wildfire (Loomis et al. 1985).

Management strategy development for protection and maintenance of this valuable resource has challenged pest managers during the past 50 years. Almost every imaginable technique aimed at killing bark beetles has been tried. Burning, peeling, solar radiation, burying and submerging in water, removal of infested logs from the forest, trap trees, bait traps, flame throwers, detonating cord, and chemical insecticides have all been aimed at killing beetles in trees (Waters et al. 1985). In recent years, more environmentally acceptable methods such as uses of the fungus *Beauveria bassiana*, insect growth regulators, cut and leave, cut-and-topping infested host trees, and 5 behavior-modifying chemicals such as pheromones, and pine oil, a by-product of sulfate wood pulping have been investigated the past 20 years (Waters et al. 1985).

Various control methods have been tested and retested since the 1950's. Miller and Keen (1960) concluded that direct control aimed at killing beetle populations has only limited effect in reducing tree mortality. Billings (1980) concluded that "direct control options for southern pine beetle (SPB) currently available to the land manager remain few and relatively unchanged from previous years." Tactics such as spraying bark-penetrating fumigants and injecting systemic pesticides, fell-and-burn, flame throwers, cut-and-leave, tree monkey, and salvage removal have been recommended for management of many pine bark beetles in localized areas during the past 15-20 years (McGregor and Cole 1985, Swain and Remion 1981, Thatcher et al. 1982, Whitney et al. 1978). Many managers have concluded that remedial treatments applied to outbreaks have consistently failed to suppress bark beetle populations (Klein 1978, Coulson and Stark 1982). However, some successful control efforts have been reported (Whitney et al. 1978).

More recently, forest pest managers began to realize that in order to reduce losses, it was necessary to change the stand conditions which promoted the outbreak. This placed emphasis on investigating stand and environmental factors contributing to and prolonging beetle epidemics, and then through a process of implementing a combination of pest management techniques with those of forest management, total impact on all resource values could be reduced (McGregor and Cole 1985, Thatcher et al. 1982, Waters et al. 1985).

Even though many new and exciting techniques have been developed, tested, and retested, and are still in use on many beetle infested forests, very little attention has been given to the use of natural enemies as one additional tool for bark beetle management. Coulson and Stark (1982) stated that there is no logical reason why biological control has not been considered as a management strategy for *Dendroctonus* bark beetles. There are little data on the impact of insect natural enemies during bark beetle epidemics (Mills 1983). Cole (1974, 1975, 1981) and Schmitz (1985) found that various factors including temperature, drying of the phloem, between and within brood competition, parasites and predators, and woodpeckers were the most effective natural agents in reducing bark beetle populations. Since managers are not able to manipulate temperatures which kill beetles directly and affect drying of the phloem and they have a small chance of importing woodpeckers, it appears plausible that manipulation of parasites and predators may be a viable option for beetle management, particularly during endemics. Limited research with mechanical exclusion devices shows evidence of efficacy of insect natural enemies to regulate low-level bark and engraver beetle populations (Miller et al. 1987).

In recent years, the identification, synthetic production, and implementation of semiochemicals for bark beetles have made the available options for importation and manipulation of predators more feasible. Semiochemicals (message-bearing chemicals) have been successfully used to bait trees (Borden 1982), monitoring (Borden 1984), mass-trapping (Bedard and Wood 1974, Bakke 1983), and interruption of bark beetle populations (Wood and Bedard 1977, Richerson et al. 1980, Tilden et al. 1981, McGregor et al. 1984). Semiochemicals can be divided into: 1) pheromones, intraspecific chemical messengers; 2) allomones, interspecific chemical messengers of benefit to the emitter; and 3) interspecific chemical messengers of benefit to the perceiver (Borden 1984). Some predators are adapted to utilize beetle aggregation pheromones to locate beetles on host trees during the beetle attack period that is most suitable to their feeding, mating, and oviposition (Borden 1982).

Why biological control has not been considered as a management strategy for *Dendroctonus* bark beetles might be attributed to 1) lack of interest in use of predators for native pests; 2) that no North American bark beetle has been controlled by another insect; 3) the opinion that natural enemies are not an important component in bark beetle population dynamics; 4) the expense of rearing bark beetle natural enemies; 5) the lack of interest in use of biologicals due to the rapid expansion of epidemics; 6) the few attempts to introduce exotic biological control agents have failed; and 7) because of a lack of knowledge in the use of semiochemicals in bark beetle/insect enemy associations (Coulson and Stark 1982, Miller et al. 1987).

Current management recommendations are only a refinement of what they were in 1971, and have no measurable effect on the SPB populations over the total epidemic area (Miller et al. 1987). Semiochemicals provide a means for attracting, trapping, and manipulating predators that may be effective biological control agents of the SPB, particularly for endemic populations. The capacity of a predator to respond to a variety of pheromones or pheromone components, i.e. kairomones, provides it with the ability to find and utilize other hosts as alternate food on the same or a different host tree (Kohnle and Vité 1984).

The objective of this paper is to show how semiochemicals were used to cross-attract predators which possibly might be used to attempt biological control against the southern pine beetle.

That potential biological control agents are present in extraregional or exotic locations can be demonstrated in field cross-attraction trapping studies as was done in cooperation with scientists at the Southern Forest Experiment Station. Because aggregating pheromones were used to survey, the insect enemies evaluated were predators that arrive when the host tree is under mass attack by bark beetles (Borden 1982, Coster et al. 1977, Payne et al. 1984). Presented here are results of a portion of a pilot study in which *Thanasimus undatulus* (Coleoptera: Cleridae), a predator usually associated with the Douglas-fir beetle, was attracted to pheromones of the southern pine and western pine beetles.

METHODS

In July and August 1984, pheromone cross-attraction studies were conducted in central Louisiana, Montana, and in Taiwan, ROC, to determine the response of insect natural enemies to commercially available aggregating pheromones of North American bark beetles. The same studies were conducted later in northern California and in the People's Republic of China. Only the results of the completed Montana tests show an obvious predator response, and they are described here.

Lindgren eight-funnel traps (Phero-Tech, Vancouver, B.C., Canada) were baited with the commercially available aggregating pheromones of southern pine beetle (SPB) *D. frontalis;* western pine beetle (WPB), *D. brevicomis* LeConte; mountain pine beetle (MPB), *D. ponderosae* Hopkins, and *Ips typographus* (L.) (Table 1). Three replicates of a trap line consisting of baited Lindgren funnel traps and an unbaited control trap were set out in a randomized block design at two locations 48 km apart in the Flathead National Forest, Montana. Collections were placed in 70% ethanol. Tests were conducted during the period of adult dispersal and host-tree colonization for MPB. Each insect collected was identified, and the number of each species was counted. The data for each insect for the six weekly collections was pooled for each trap to detect any obvious indications of kairomonal response to the aggregation pheromone lures. Analysis of the pooled data was conducted with the Friedman's ranking test (Conover 1980) because the collection data for each insect contained a large number of zero counts, exhibited a non-normal distribution, and a non-homogeneous variance. Transformation procedures did not normalize the data. The six trap lines, each with five traps, were considered blocks. Significant differences (a=0.05) among pheromone capture trap ranks were analyzed with the Duncan's multiple range test because the distribution of ranks is considered to be approximately normal (Conover 1980).

RESULTS

During SPB, WPB, MPB, and *Ips* pheromone surveys in Montana, 29 insect species or insect groups were collected. Of the 29 species, four insects show significant difference among the ranked traps and significant differences among the rank means that indicated attraction to aggregation pheromone lures (Table 2). MPB trap capture of MPB and *Ips typographus* pheromone catches of *I. pini* (Say) were ranked significantly higher than the ranked capture of the remaining traps. There was no significant

Table 1

Technical description of bark beetle lures.

Lure	Component	Relative proportion	Release rate[1]	Duration
MPB	Myrcene		20 mg/day	120 days
(*D. ponderosae*)		*trans*-Verbenol		
		Individual	1 mg/day	
	exo-Brevicomin	release vials	0.5 mg/day	
SB	Frontalin	0.67 g	10 mg/day	100 days
(*D. rufipennis*)	α-Pinene	0.33 per		
and **SPB**		release		
(*D. frontalis*)		vial		
WPB	Frontalin	15 g	12 mg/day	100 days
(*D. brevicomis*)	Myrcene	2.5 per	0.5 mg/day	
	exo-Brevicomin	release		
		vial		
I. typographus	2-Methyl-3-	15 in	10 mg/day	? 60 days
	butene-2-olcis-	one		
	Verbenol	0.70 release	1 mg/day	
	Ipsdienol	0.15 device	0.17 mg/day	

[1] Approximate release rate at 20°C.

difference in ranked trap catch of *T. undatulus* from SPB- and WPB-baited traps, but these ranked significantly higher than the ranks of MPB-, *Ips*-baited, and unbaited-check traps. Rank capture among MPB, *Ips*, and check traps was not significantly different. Ranked trap capture of *Enoclerus sphegeus* was highest in *I. typographus* pheromone-baited traps, significantly less in MPB baited traps, and significantly less than both the SPB, WPB, and unbaited-check traps.

In four of six weekly collections made from 5 July - 10 August (Fig. 1), average *T. undatulus* capture was highest in SPB- or WPB-baited traps. In the 5 and 21 July collections, *T. undatulus* was consistently attracted in higher numbers to SPB and WPB than to *Ips* or MPB aggregating pheromone-baited traps (Fig. 1). There was only one week between 5 and 21 July in which more *T. undatulus* were collected from the WPB-baited funnel traps than from the SPB-baited trap. Few *T. undatulus* were captured in any traps during the two August collection periods.

Table 2

Duncan's multiple range test of significant differences among ranked means for pheromone trap collection. Montana 1984.[a]

Insect

MPB		*I. (confusus?)*		SPB		*E. sphegeus*	
Rank Mean	Trap Pheromone	Rank Mean	Trap Pheromone	Rank Mean	Trap Pheromone	Rank Mean	Trap Pheromone
5.0a	MPB	5.0a	*Ips*	4.5a	WPB	4.9a	*Ips*
2.8b	*Ips*	2.7b	SPB	4.5a	SPB	3.8a	MPB
2.8b	Chk	2.5b	MPB	2.7b	*Ips*	2.1c	SPB
2.4b	SPB	2.5b	Chk	2.3b	MPB	2.1c	WPB
2.1b	WPB	2.3b	WPB	1.0c	Chk	2.1c	Chk

[a] Column means followed by different letters are significantly different (a = 0.05). MPB, mountain pine beetle; Ips typographus; SPB, southern pine beetle; WPB, western pine beetle; Chk, check.

In five of six weekly collections between 12 July through 10 August, SPB pheromone-baited funnel traps also captured DFB (Fig. 2). Although not resulting in significant differences in ranked trap capture, 199 DFB were caught in SPB and WPB traps, 20 were collected from MPB and *Ips* baited traps, and 16 from check traps. We conclude that this is a co-evolved predator/prey system because the flight periods of *T. undatulus* and the Douglas-fir beetle are similar, and few or no other bark beetles were collected from SPB pheromone-baited traps. Also, large numbers of *T. undatulus* were captured in other traps baited with DFB pheromone (Miller et al. 1986).

Because of its responsiveness to SPB and WPB pheromones, *T. undatulus* may be a potential biological control agent of these scolytids. This conclusion is supported by the results of Chatelain and Schenk (1984), who found that *T. undatulus* was attracted in large numbers to sticky traps on MPB-attacked trees baited with frontalin or *exo*-brevicomin. Augmenting populations of *T. undatulus* on these MPB brood trees by baiting with frontalin increased the incidence of *T. undatulus* larvae threefold and the mortality of emerging MPB adults by 7.1%

DISCUSSION

Pheromone trapping of *T. undatulus* represents only a first screening for potential biological control agents. Commercial pheromones, although

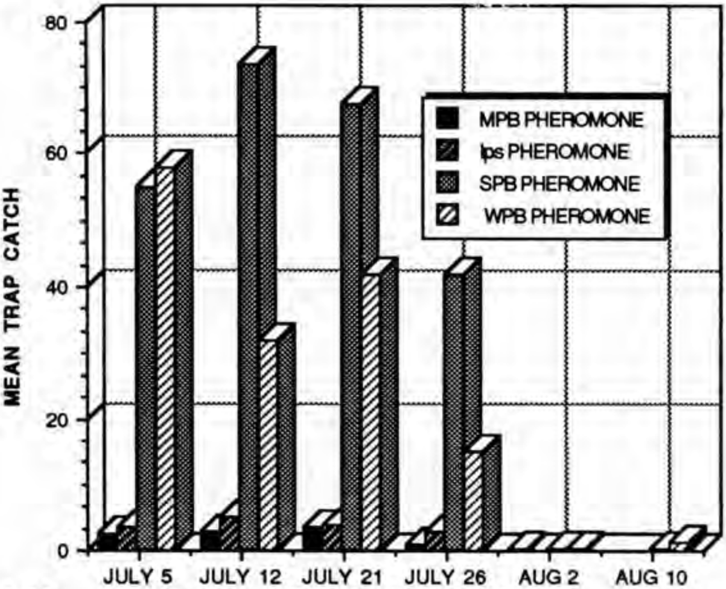

Fig. 1. Mean weekly capture of *T. undatulus* adults in replicated pheromone-baited Lindgren traps on the Flathead National Forest, Montana, 5 July - 10 August 1984. Each bar represents the average catch from three randomly placed traps.

sufficient for attracting the target bark beetles, might not provide all the necessary cues for attracting all the insect associates. However, the selectivity of the attractant could be beneficial in attracting a manageable number of candidate insect enemies. In addition, we are not sure how closely the development of insects like *T. undatulus* will be synchronized to the development of their new prey species. *T. undatulus* probably will not complete its development within the < 30-day summer life cycle of SPB, but it may develop during the winter when the SPB life cycle is 60-90 days. *T. undatulus* may have an obligatory winter diapause and complete development only after a certain number of low-temperature hours or days. Also, we must consider the extent to which current silvicultural practices in use against SPB would allow successful establishment of a population of *T. undatulus*.

This pheromone survey provides evidence that insect enemies of SPB, DFB, and WPB should be able to locate any of these related insect as prey. The response to the prey's odor is a necessary prerequisite for a bark beetle biological control agent, but this characteristic alone may not be sufficient. The actual success in each case would depend upon the specific variables in the biology and ecology of each potential target pest, such as generation

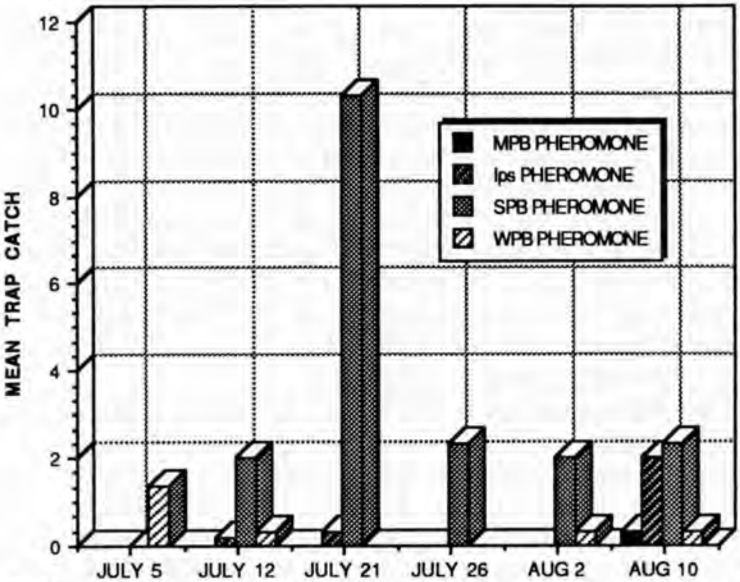

Fig. 2. Mean weekly capture of DFB, *D. pseudotsugae*, in replicated pheromone-baited Lindgren traps in the Flathead National Forest, Montana, 5 July - 10 August 1984. Each bar represents the average catch from three randomly placed traps.

time, larval behavior, and synchronization of life cycles. Another question to be considered is that of the compatibilities of the ecologies of predator and prey. As detailed for *T. undatulus*, the length of the life cycle may have to be synchronized (Miller et al. 1987).

Another determination that should be made is would *T. undatulus* compete with the insect enemies already in place. Even though a predator responds to pheromones does not mean that it would exist in a habitat, or that it would not disrupt some natural controls in existence for a native pest species.

We feel the results justify expansion of the search for bark beetle biological control agents beyond the limits of bark beetle/host tree associations. The results show cross-attraction of extraregional predators to SPB aggregating pheromones and the location of insects that are potential biological control agents of *Dendroctonus* spp. Survey results contribute to the development and the possible use of a kairomone-based methodology to simplify the preliminary evaluation of host/prey preferences of insect biological control agents. It demonstrates a practical application for the results of insect pheromone studies and pheromone-based behavioral studies (Miller et al. 1987).

Until now, biological control of bark beetles was not considered feasible in the United States, mainly because there was not a clear case of spontaneously occurring biological control or any large and successful program involving the use of natural enemies. The required prerequisite for introducing associates of allied species is that they should be able to locate their new target. This ability is suggested by the results involving *T. undatulus* cross-attraction to pheromones of allied North American *Dendroctonus*. Pheromone screenings for *T. undatulus* and possibly other predacious species appear to be suitable as potential biological control agents. If effective, they could be used either singly or integrated with other forest management strategies against North American *Dendroctonus*, for which alternative management tactics are needed.

This study demonstrates the presence of extraregional predatory insects having biological and behavior characteristics that provide them with the potential to be biological control agents for the SPB and possibly other native North American *Dendroctonus* bark beetles. We propose that biological control should be included in the integrated management strategies against North American bark beetles, provided that an appropriate methodology can be developed and followed. The lack of knowledge of the importance of natural controls in prevention of epidemics, insufficient knowledge of the importance of the time of release and the presence of proper semiochemicals signals warrants additional pheromone surveys. Results of this field survey provide evidence that predatory species possess some of the necessary ecological and behavioral characteristics to be considered as potential biological control agents.

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SECTION FOURTEEN

Responses of Insect Associates of Allied Species to *Dendroctonus* and *Ips* (Coleoptera: Scolytidae) Aggregation Pheromones: A Search for Biological Control Agents

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ABSTRACT

Replicates of Lindgren 8-funnel traps baited with commercially prepared pheromones of *Dendroctonus frontalis* Zimmermann, *D. brevicomis* LeConte, *D. ponderosae* Hopkins, and *Ips typographus*, and an unbaited check were used in 1984 or 1985 in the United States, Belgium, the People's Republic of China (PRC), and the Republic of China (Taiwan), and in 1986 in Mexico and Israel to detect potential insect biological control agents of southern pine beetle from populations of allied *Dendroctonus*. Kairomonal cross-responsiveness to pheromones of *Dendroctonus* and *Ips* was shown for numerous scolytids and associated insects. *Thanasimus undatulus* Say (Cleridae) from Montana and a *Rhizophagus* sp. (Rhizophagidae) from California were attracted in greater numbers than other insect associates to the frontalin-containing aggregation pheromones of the southern pine beetle and western pine beetle. Surveys in the PRC showed the attraction of *Dendroctonus armandi* to southern pine beetle pheromone, and attraction of *Pityogenes* sp. and *Dryocoetes hectographus* to western pine beetle pheromone. The PRC results suggest that additional surveys could capture insect enemies of importance as potential biological control agents. Brief surveys in the fall of 1985 in Belgium collected *Thanasimus formicarius*, the clerid predator of *I. typographus*, in mountain pine beetle pheromone-baited traps; *Rhizophagus* grandis, an effective predator of *Dendroctonus micans*, was only attracted to *D. micans* frass volatiles. Additional surveys in Mexico detected associated insect enemies of *D. mexicanus*, and the southern pine beetle was detected in Israel. While demonstrating successful results, these surveys revealed some problems associated with conducting cooperative pheromone searches for extraregional and exotic biological control agents.

INTRODUCTION

Biological control of bark beetles has received little attention because the impact of insect enemies on bark beetles is not well known; data on insect enemies are only gathered incidental to studies on beetle population dynamics or studies that evaluate the effect of behavioral chemicals. Biological control by inoculation of exotic predators or parasitoids has been attempted without knowledge of the existence and significance of kairomones and pheromones to the location of the host tree, prey, or mating (Clausen 1956, Dowden 1962, Coulson 1981).

Dendroctonus beetles are native pests without an original habitat source for exotic insect enemies (Stevens 1981). One possible solution to problems associated with the biological control of native pests like the southern pine beetle, *Dendroctonus frontalis* Zimmermann (SPB), is the augmentation of the existing insect enemy complex through the importation and inoculative release of insect predators and parasitoids found associated with other closely related bark beetle species. The use of insect enemies of allied pest species (Pimentel 1963, Hokkanen and Pimentel 1984, Moeck and Safranyik 1984, Miller et al. 1987) is a potential control methodology. An evaluation of European insect enemies of related *Dendroctonus* and *Ips* with aggregation pheromones of potential prey is advocated by Mills (1983) to search for egg predators for release in Canada.

Each species of *Dendroctonus* has a unique complex of natural enemies (Miller and Keen 1960, Dahlsten 1970, Deyrup 1976, Stephen and Dahlsten 1976, Whitmore 1983). Apparently, the most promising of these insect enemies are predatory beetles in the families Cleridae, Trogositidae (Ostomidae), and Histeridae. They are associated with the western pine beetle, *D. brevicomis* LeConte (WPB) (Dahlsten 1970), the mountain pine beetle, *D. ponderosae* Hopkins (MPB) (Moeck and Safranyik 1984), the spruce beetle, *D. rufipennis* (Kirby) (SB) (Whitmore 1983), and the SPB (Moser et al. 1971).

The most important biological question with regard to importation of predatory or parasitic insects is whether the imported insect can locate the intended host. Host tree odors (Ball 1970, Ball and Dahlsten 1973) and bark beetle pheromones (Vité and Williamson 1970, Williamson 1971, Bakke and Kvamme 1978) are the most important cues an insect predator or parasitoid can use to locate a host bark beetle.

Bark beetles and their insect associates exhibit broad kairomonal responses (Vité and Williamson 1970, Vité et al. 1974, Lanier et al. 1972, Lanier and Wood 1975). This was demonstrated for North and Central American populations of the SPB (Vité et al. 1974). Chapman and Dyer (1969) may have coined the term "cross-attraction" in reference to the reciprocal, pheromonal attraction of the Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins) (DFB) to spruce (*Picea glauca* (Moench) Voss) and the SB to Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Lanier and Wood (1975) used the term "cross-responsiveness" to describe the response of *Ips* to their own pheromones and those of related species, and they confirmed cross-responsiveness in the field among five *Ips* species. Both *Ips typographus* and *Dendroctonus micans* have olfactory receptor cells that can detect compounds characteristic of the reciprocal genus (Tømmerås et al. 1984). *Thanasimus dubius* (F.) responds to the SPB aggregation pheromone [(-) frontalin] for prey location and possibly mate location, yet they can perceive and respond to *Ips* bark beetle pheromones and feed on these beetles as alternate prey (Payne et al. 1984). *Thanasimus*

Table 1

Variation in host trees and methodology in 1984-86 pheromone cross-attraction surveys.

Location {Host/ Forest type}	Trap placement detail
Montana 1984	
Flathead National Forest {*Pinus contorta* var. latifolia Engel.} {*P. ponderosa* Lawson} {*Pseudotsuga menziesii* (Mirb.) Franco}	2 sets of 3 trap lines in two locations 48 km apart during *Dendroctonus ponderosae* flight period, July 5-Aug 10.
Louisiana 1984	
Catahoula Ranger District Kisatchie National Forest {*Pinus taeda* L.} {*P. echinata* Miller}	Traps 161 m apart, 6.1 m from road, June 26-Oct 2 collection period, trap lines on east-west roads 1 mile apart.
California 1984-85	
Blodgett Research Forest Eldorado County {*P. ponderosa* Lawson} {*P. lambertiana* Doug.} {*Abies concolor* (Gord. & Glend.)}	Sites 1.6 km apart, traps 100+ m apart in young regeneration clearcuts & 100+ m from clearcut edge, Sept & Oct 84, June-Aug 85.
Alaska 1985	
Bonanza Creek Expt. Forest 40 km west of Fairbanks {*Picea glauca* (Moench)} {age 100-150 yrs}	16 funnel Lindgren traps with seudenol added as 6th treatment (Dyer & Hall 1980, Werner & Holsten 1984), many *D. pseudotsugae* and *Ips.*
Republic of China (Taiwan) 1984-85	
{*Pinus taiwanensis* Hayata} {age 50-80 yrs}	Traps 10 m apart, collected every 3-4 weeks live or in rainwater, Sept 84-July 85, undisturbed recreational site.
People's Republic of China	
Shaanxi Province Hanxi Forestry Bureau 1984-1986 {*Pinus armandii* Franch.} {*P. tabulaeformis* Carr.} {*Populus davidiana*} {*Betula utilis* var. sinensis} {*Picea asperata*}	South slope of Qiling Mountains, 4 traps of each pheromone in two test areas, timber depot, alt. 600 m & mixed forest, alt. 1970 m.
Belgium 1985	
Forêt domanialé de l'àigoual Airé-de-Coté, Lozèré {*Picea excelsa* } {age 89 yrs} {(Grégoire & Pasteels 1985)}	Traps 20 m apart in each line, replaced WPB lure with fresh *D. micans* larval frass daily, 17 Sept-9 Nov.
Mexico 1986	
Amecameca, Mexico, D.F. Temetzontla, Tlaxcala {*Pinus leiophylla* Schiede & Deppe}	Traps 100 m apart & 10 m or more from road endemic *D. mexicanus*, 14 April-17 June.

formicarius (L.) can detect and indentify many bark beetle species including, *I. typographus*, *D. micans*, and *D.ponderosae* (Dyer et al. 1975, Hansen 1983, Tømmerås 1985). Frontalure has been used to attempt MPB suppression with *Thanasimus undatulus* Say in Montana (Chatelain and Schenk 1984). The pine weevil, *Hylobius abietis* L., responds positively to its own frass and pheromones isolated from frass of bark beetles that feed on the same host plants (Mustaparta 1974). Lanier et al. (1972) showed differences in pheromone production and reception by *Ips* spp. and differences in reception by the predator *Enoclerus lecontei* (Wolcott) and the parasitoid *Tomicobia tibialis* Ashmead.

The study reported here tested the ability of insect enemies of bark beetles in various habitats to respond to aggregation pheromones of SPB, other *Dendroctonus* spp., and *I. typographus*. We describe the results of pheromone surveys in North America, Europe, and Asia for potential insect enemies of the SPB and other North American *Dendroctonus* spp.

MATERIALS AND METHODS

In July and August 1984, pheromone cross attraction studies were conducted in central Louisiana, Montana, northern California, and the Republic of China (ROC) (Taiwan) to determine the response of insect natural enemies to commercially available, synthetic aggregation pheromones of North American bark beetles and an *Ips* species. Similar studies were conducted in 1985 in Alaska, Belgium, and the People's Republic of China (PRC), and surveys in Israel and Mexico were added in 1986. Differences in individual surveys are summarized in Table 1.

The general methodology as used in Montana in 1984 consisted of 8-funnel Lindgren traps baited with aggregation pheromones of SPB, WPB, MPB, and *I. typographus* (Table 2). Three replicates of a trap line made up of four pheromone traps and an unbaited control trap were set out in a randomized block design at two locations 48 km apart in the Flathead National Forest. Collections in some surveys were made into a 50:50 mix of ethylene glycol and water, in some surveys 70% ethanol and water was substituted, and in one survey captures were live (Table 1). Tests were conducted during the period of adult dispersal and host-tree colonization for MPB in Montana and for other scolytids in other locations. In 1985, seudenol was added as a sixth treatment in Alaska, and WPB pheromone was replaced with larval frass of *D. micans* in Belgium (Table 1). The counts of each insect were pooled for each trap for the entire collection period to show any obvious indications of pheromonal or kairomonal attraction to the aggregation pheromone lures. Data were analyzed with Friedman's

Table 2

Technical description of bark beetle lures.

Lure	Component	Relative proportion		Release rate[1]	Duration
MPB	Myrcene			20 mg/day	120 days
(*D. ponderosae*)	*trans*-Verbenol				
		Individual		1 mg/day	
	exo-Brevicomin	release vials		0.5 mg/day	
SB	Frontalin	0.67	g	10 mg/day	100 days
(*D. rufipennis*)	α-Pinene	0.33	per		
and **SPB**			release		
(*D. frontalis*)			vial		
WPB	Frontalin	15	g	12 mg/day	100 days
(*D. brevicomis*)	Myrcene	2.5	per	0.5 mg/day	
	exo-Brevicomin		release		
			vial		
I. typographus	2-Methyl-3-	15	in	10 mg/day	? 60 days
	butene-2-olcis-		one		
	Verbenol	0.70	release	1 mg/day	
	Ipsdienol	0.15	device	0.17 mg/day	

[1] Approximate release rate at 20°C.

ranking (FR) test (Conover 1980) because there were many zero counts, a non-normal distribution, and non-homogeneous variance, which could not be adjusted with statistical transformations. Although six trap lines were used in Montana, three were used in most other locations. Each trap line was considered a block. For significant F values, the FR test was followed by Duncan's (1955) multiple range (DMR) test on the means of the rankings. The distribution of ranks is considered to be approximately normal (Conover 1980).

RESULTS AND DISCUSSION

Attraction of *Dendroctonus* and *Ips* bark beetles to their respective aggregation pheromones was expected. Because the fauna in some of the survey locations were not known and synthetic aggregation pheromones had not previously been used in these areas, it was not possible to speculate on the native bark beetles or associated insects that might be attracted.

Response to the artificially produced pheromones that are used may not be exactly the same, or as intense as response to naturally produced compounds, because of the absence of minor components or the absence of host-tree-contributed compounds during beetle attack. These surveys were conducted without the use of the additional steam-distilled turpentine volatiles, which increase catch 50- to 100-fold (Billings 1985).

In some cases, no firm conclusions can be drawn from the data because some species counts were low or too variable from identically baited traps at different locations. Replication of trap lines was implemented to test for differences in means of the number of captured insects with analysis of variance. Inspection of the pooled data for obvious differences in magnitude of catch was the first step in analysis. The FR test was used because the data exhibited many zero counts, were abnormally distributed, and had a non-homogeneous variance. However, significance in the FR test with the small number of replicates requires some consistency in the level of catch in the traps using the same lures. One of the limitations with rankings is that they do not show the magnitude of the differences among trap catches. When one of the three rankings is low, possibly because of placement of competing lures, the FR test may not indicate a difference in the ranks. However, the DMR test conducted on the means of the ranks is significant at 0.05 or less, indicating differences among ranks. For this reason, some insect catches are included for which the FR test shows an F prob. > 0.05, but there are obvious numerical differences among treatment response variables that indicate attraction trends. Counts for some species were essentially nonexistent. No analysis was possible or even needed in such cases. Bark beetles and associated insect species that showed significant differences in captures across the pheromone treatments are presented in Table 3.

With some qualifications, at each location in Louisiana, Montana, Alaska, and California, *Ips* spp. were attracted to both *I. typographus* and MPB pheromones.

In Montana in 1984, the survey detected 24 species or insect groups. Inspection of the pooled data for the four lures and the unbaited control showed pheromonal attraction by the scolytid beetles *D. ponderosae*, *D. pseudotsugae*, and *Ips confusus*, and kairomonal attraction by the clerids *Thanasimus undatulus*, *Enoclerus sphegeus* (F.), and *E. lecontei* (Table 3). *T. undatulus* and *E. sphegeus* are apparently capable of responding kairomonally to more than a single pheromone, which suggests the ability to use more than one prey species. *T. undatulus* was attracted to both SPB and WPB lures. It has been fed and partially reared in vivo on SPB in loblolly pine bolts and in vitro on SPB larvae. A release, but no recapture,

Table 3

Results of pheromone cross-attraction surveys, 1984-86.[1]

Location	Pheromone			
	D. ponderosae	*D. frontalis*	*D. brevicomis*	*Ips typographus*
Louisiana				
	•*D. frontalis*	*D. frontalis*		•*Temnochila virescens*
	•*Ips avulsus*	•*Cossonus corticola*		*Ips calligraphus*
	•*Ips calligraphus*	•*Ips avulsus*		*Ips avulsus*
				•*Platysoma parallelum*
Montana				
	D. ponderosae	•*Thanasimus undatulus*	*D. brevicomis*	*Ips confusus*
	•*Enoclerus lecontei*	•*D. pseudotsugae*	•*T. undatulus*	•*Enoclerus sphegeus*
	Enoclerus sphegeus			•*D. pseudotsugae*
Alaska				
	D. ponderosae		*D. brevicomis*	•***Ips borealis***
			•*Ips perturbatus*	•***I. perturbatus***
		•*Polygraphus rufipennis*	•*P. rufipennis*	
California				
	•*Pityopthorus* sp.	•*Rhizophagus* sp.	*D. brevicomis*	*Ips latidens*
		•*Pityophthorus* sp.	•*Rhizophagus* sp.	•*Enoclerus lecontei*
			•*Pityophthorus* sp.	
Republic of China (Taiwan)				
				•*Coptoclerus* sp.
People's Republic of China				
		D. armandi	*Pityogenes* sp.	*Ips nitidus*
			Dryocoetes hectographus	*Ips typographus*
Belgium				
	•*Thanasimus formicarius*			*Ips typographus*
				•*T. formicarius*
Israel				
		D. frontalis		
Mexico				
		•*D. mexicanus*	•*D. mexicanus*	
		•*Thanasimus* sp.		
		•*Hymenoptera*	•*Hymenoptera*	

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[1] Within a location • species were strongly attracted or cross-attracted to aggregation pheromones as shown by Freidman's ranking test and DMR test on the means of the ranks. Other species listed were attracted to their native aggregation pheromone or cross-attracted in magnitudes showing strong attractive trends, but not by the statistical procedures given. Within a location a small number of these and other species may have been captured in other traps, but such capture is not considered pertinent.

of 345 individuals was made on the Kisatchie National Forest, Louisiana, in 1985 (unpublished research). The DFB was attracted to SPB and WPB lures. This result and other data suggest that DFB is the principal attractive prey for *T. undatulus*. Although *E. sphegeus* responded to both *I. typographus* and MPB lures, *E. leconei* was captured only in MPB-baited traps. This suggests that, like *T. undatulus*, *E. sphegeus* has a broad kairomonal response, and it may be a potential biological control agent for *I. typographus*.

In Louisiana in 1984, the four pheromone treatments and unbaited control trap captured 22 species or groups of SPB-associated insects. The sums of pooled data for each treatment showed a pheromonal or kairomonal response from *Ips calligraphus* (Germar), *I. avulsus* (Eichhoff), *T. dubius*, *Temnochila virescens* (F.), *Cossonus corticola* Say, and *Platysoma parallelum* Say (Table 3). *I. avulsus* and *I. calligraphus* were attracted to *I. typographus* and MPB lures. The clerid predator *T. dubius* was attracted to both SPB and WPB pheromones. *T.virescens* was attracted only to *I. typographus* lures and *C. corticola* to only SPB lures. The response of *T. virescens* to *I. typographus* lure suggests this insect as a possible predator of *I. typographus*. Though the response by *T. dubius* was numerically greater to SPB-baited traps, variability of catch in one of the sets of traps prevented the mean ranked trap catch from being determined significant. The small catch of *D. frontalis* in the SPB-baited pheromone traps suggests that the trap lines were not placed close enough to active SPB infestations or that the amount of pheromone released may not have been sufficient to compete with natural pheromone sources.

In Alaska in 1985, 19 species or species groups were identified in the 13 June – 6 August survey. Of these, pooled data from *Ips perturbatus*, *I. borealis*, *D. rufipennis* (Kirby), *Polygraphus rufipennis*, *Trypodendron lineatum*, and possibly *Nicrophorus* sp. showed trends that suggested attraction to the aggregation pheromone lures. Only *I. perturbatus*, *I. borealis*, and *P. rufipennis* showed significant differences among ranked trap catch means, and only *P. rufipennis* showed discrete separations between ranked catches in WPB- and SPB-baited traps and the other four treatments (SB pheromone was added in the Alaska tests) (Table 3). There was no obvious response of insect enemies to pheromone lures. *I. perturbatus* responded to WPB, *I. typographus*, and seudenol lures, and *I. borealis* responded to *I. typographus* and seudenol. Previous research in Alaska indicated that seudenol attracts more adult beetles than frontalin when traps are located away from white spruce trees (Werner and Holsten 1984).

In 1984 in California, all *E. lecontei* were caught in the *I. typographus* traps. This was unexpected, considering the large numbers of its native host, *D. brevicomis*, caught in its respective pheromone trap. Only three T.

virescens chlorodia (Mannerheim) were caught during this study; apparently they were attracted to no particular bark beetle pheromone. WPB, *Pityophthorus* sp., and *Enoclerus* sp. showed significant differences among means of the ranks for trap catches. Significant numbers of WPB were consistently captured in WPB-baited traps, and *Enoclerus* sp. were attracted to *Ips*-baited traps significantly and more consistently than to other baited traps. *Pityophthorus* sp. showed numerical trends of attraction to SPB, MPB, and WPB traps. In 1985, only WPB, *Ips* latidens, and *E. lecontei* produced statistically significant or near significant differences among the means of ranked traps for pooled capture data. All the *E. lecontei* were caught in the *Ips*-baited traps. *E. lecontei* is attracted to *I. paraconfusus* pheromones (Byers and Wood 1980). It is interesting that *E. lecontei* was not attracted to either WPB or MPB pheromones, because the predator is a common associate of these scolytids in California (Dahlsten and Stephen 1974, Dahlsten 1970). In Montana, *E. lecontei* was collected in MPB-baited traps, but not in *I. typographus*-baited traps. This suggests that the kairomonal response of predators co-evolves with the composition of their native prey species complex (Payne et al. 1984), making these insect enemies of allied pests suitable candidates for screening as extraregional biological control agents. *Rhizophagus* spp. were the only predators that were more abundant in the SPB-baited pheromone traps, and many were trapped in the WPB-baited traps. There may be an attraction to the common frontalin component of the two synthetic attractants.

The majority of the scolytids were caught during the first two weeks of trapping, indicating that trapping was initiated sometime during the end of the early summer peak of scolytid flight. This result was not anticipated because studies have shown WPB and MPB flight at the Blodgett Forest to occur near the end of June and the beginning of July (Stephen and Dahlsten 1976). Although predators were caught over a more prolonged period than the scolytids, the majority were caught during the first two weeks of trapping. Previous studies have found the peak flight of predators to be closely associated with, but following, that of WPB and MPB (Stephen and Dahlsten 1976). It is likely that trapping included a greater proportion of the primary predator flight than that of the scolytids. The *Rhizophagus* flight contrasted with the flight of the primary predators and scolytids because it was more prolonged and increased later in the trapping season.

Inconclusive surveys were conducted in Taiwan, ROC, in 1984 and 1985. Although a few scolytids were captured in the pheromone traps, there were no captures of *Dendroctonus armandi* Tsai et Li, primary scolytids, or insect enemies associated with bark beetles. Though the host tree for D. *armandi*, *Pinus armandi*i Franch., is supposed to occur on

Taiwan (Critchfield and Little 1966), the traps were apparently placed in a *P. taiwanensis* (*taiwaniana* sic.) Hayata forest. Surveys were conducted intermittently and not when *D. armandi* flights might have been expected. In 1986 and 1987 the location of the surveys was moved, and an unknown clerid was collected in large numbers from the *I. typographus* pheromone traps (unpublished research). The clerid has not yet been identified, but it could be a potential biological control agent for *I. typographus* in Europe.

Only summarized pooled data from the *Dendroctonus* aggregation pheromone surveys of 1985 are available from Shaanxi Province in the PRC (Table 3). D. *armandi* responded to SPB lures. *Pityogenes* sp. and *Dryocoetes hectographus* were attracted to WPB lures. *Ips nitidus*, *I. typographus*, and *Scolytoplatypus* sp. were caught in *I. typographus*-baited traps. Our experience has been that when primary bark beetles are responsive to a pheromone, the earliest arriving insect predators are usually kairomonally attracted by the same pheromone (Miller et al. 1987). Future surveys should capture these predators. The local cooperator considered the results of *D. armandi* capture inconclusive when comparing the numbers of *I. typographus* captured in the *I. typographus*-baited traps. However, the numerically greater *Ips* response is pheromonal, while the *D. armandi* response is kairomonal.

From September through November 1985 in Belgium, no insects were collected in the SPB pheromone-baited traps, *T. formicarius* was collected from both MPB- and *I. typographus*-baited traps, and *Rhizophagus grandis* was collected from only the traps baited with *D. micans* frass. The control traps captured a few *R. grandis* (Grégoire and Pasteels 1985). Although limited by cool temperatures, the catches of *T. formicarius* in MPB- and *Ips*-baited traps and *R. grandis* in traps baited with larval frass of *D. micans* are consistent with results of laboratory tests (Miller et al. 1987) and other published studies (Kohnle and Vité 1984, Tømmerås 1985). In our laboratory, *R. grandis* has been reared on black turpentine beetles, *Dendroctonus terebrans* (Olivier), in loblolly pine logs and in vitro on SPB, and is considered suitable as a biological control agent for the black turpentine beetle (Moser and Branham 1987). Kohnle and Vité (1984) describe *T. formicarius* as having a flexible response to insect- and host-produced volatiles such that its "generalist" response is a means of taking advantage of more prey species as a food source for both adults and larvae. Moeck and Safranyik (1984) and Mills (1983) suggest use of *T. formicarius* as a possible biological control agent for MPB.

In 1985 in Amecameca, Mexico, 30 species groups were captured in pheromone trap surveys. Of these, only *Dendroctonus mexicanus* showed significant, consistent attraction to the SPB aggregation pheromone (Table 3). The distribution of *Cossonus* spp., colydiids, and the clerid *Enoclerus* in traps suggested attraction to SPB and WPB pheromones, but the numbers caught were too small for any firm conclusions to be drawn. In Tementzontla, the rank of SPB-baited traps for *Thanasimus* spp. capture was significantly greater than any of the other traps. The rank of traps baited with SPB and WPB pheromones was the same, and was significantly greater than the rank means of traps with other lures for the Hymenoptera group. This is notable because large numbers of different species of Hymenoptera have not been collected from the other pheromone-based surveys. Most Hymenoptera arrive following mass attack by *Dendroctonus* on the host tree, when the life cycle stages of their hosts are abundant (Camors and Payne 1973, Stephen and Dahlsten 1976, Edson 1978, Dixon and Payne 1979, Younan and Hain 1984). *D. mexicanus* responded to both WPB and SPB pheromone-baited traps more consistently, and higher numbers were caught. Statistically, however, trap ranks for WPB, SPB, and the unbaited check were not significantly different. Numerically, most *D. mexicanus* were captured in the WPB-baited traps, fewer (in order) in the SPB, check, *Ips* , and MPB traps.

No significant cross-responsiveness to *Dendroctonus* was noted in surveys in Israel. However, small numbers of D. *frontalis*, the southern pine beetle, were collected in SPB-baited traps at two separate locations (Mendel and Argaman 1986). This unexpected result suggests establishment of this primary forest pest in an unexploited habitat. There are serious economic implications for pine and spruce forests around the Mediterranean Sea.

CONCLUSIONS

The surveys described here show cross-responsiveness (attraction) of some *Dendroctonus* predators to pheromones of allied pest species, and they provide supporting data for cross-responsiveness of *Ips* spp. to *I. typographus* aggregation pheromone. The results of these surveys suggest that insect enemies of allied *Dendroctonus* may be reciprocal sources for biocontrol agents for native North and Central American *Dendroctonus* Biological control with extraregional or exotic insect enemies of allied pests that exhibit a more flexible response to attractive volatiles produced by their insect prey (Kohnle and Vité 1984) may be used against native *Dendroctonus* bark beetles.

This research demonstrates the utility of cross-attraction surveys for detection of potential insect enemies of allied species. The surveys identified a number of extraregional and exotic predators, and some parasitoid groups, that show a kairomonal response to *Dendroctonus* pheromones that could allow them to locate sources of allied prey in other than their native habitat (Table 3). *T. undatulus* is a possible biological control agent for SPB in the Southeastern United States and WPB in California, for *Dendroctonus* species in Mexico that use a frontalin-based aggregation pheromone, and possibly for D. *armandi* in the PRC. *T. formicarius* is a potential agent for MPB. *Rhizophagus* sp. from California is a possible biological control agent for SPB, and *R. grandis* from Europe for black turpentine beetle and other species, like *Dendroctonus valens* LeConte and D. *Rhizophagus* Thos. and Bright, that have a common brood chamber and larvae with gregarious feeding habits. *E. lecontei*, *E. sphegeus*, and *T. virescens* from the United States, and the unidentified clerid from Taiwan, ROC, are possible biological control agents for *I. typographus* in Europe and Asia. The co-evolution of differences in kairomonal receptivity to bark beetle aggregation pheromones among different predator populations could explain why significant numbers of the clerid predator *E. lecontei* were captured in MPB-baited traps in Montana and only in *I. typographus*-baited traps in California. For the same reason, the DFB predator *T. undatulus* from Montana may be a possible extraregional imported biological control agent for WPB in California. Clerids and Hymenoptera from Mexico may be sources for biological control agents for SPB and WPB. The survey results demonstrate the ability of cross-attraction surveys to detect introduction of an exotic pest species (SPB) in Israel. The sometimes fragmentary results show the difficulties associated with conducting cooperative surveys for extraregional and exotic insect enemies of allied species.

Variation in information obtainable from the surveys depended on the ability of cooperators to construct a standardized survey and follow the supplied instructions. In the ROC, surveys were conducted for two years without producing evidence of *D. armandi* or insect associates. The return of data has been intermittent and in a pooled format that does not allow analysis. Also, live collection of specimens was used because the collaborator had no experience with collection into preservatives, and the intervals between recoveries could have allowed specimens to feed on each other or escape. A 1986 report indicates the movement of traps to another location and the collection of large numbers of clerids, so the problem may have been improper trap placement or no beetles at the location. Communication with the PRC has also been intermittent, and results have been supplied as pooled data. However, the PRC cooperator is familiar with the biology, ecology, and behavior of *D. armandi* . He placed traps in the *Pinus armandii* and *P. tabulaeformis* host-tree habitat and captured *D. armandi* in SPB-baited traps along with *Pityogenes* sp. and *Dryocoetes hectographis* in WPB-baited traps. Unfortunately, in these and other foreign locations, surveys have been conducted for brief periods that may have missed the flight period of the local *Dendroctonus* sp. or other primary scolytid, resulting in little consistent data on insect enemies.

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SECTION FIFTEEN

An Administrative Perspective on North American Bark Beetles and Biological Control Opportunities

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Bark beetles are an expensive problem for forest management. Answers are elusive and the demand for solutions is becoming more urgent. Devoting a full day to discussions about bark beetle biological control reflects on their importance and the need for relief.

In the United States, five species of *Dendroctonus*, four in the West and one in the Southwest, demand our attention. These five species occur exclusively in coniferous forests. Their impact on forest management and productivity is substantial. The prognosis for the future is that losses will increase.

Of the approximately 480 million acres of commercial forests in the United States, forests covering 203 million acres are predominantly coniferous. The five bark beetles mentioned above are potentially serious pests of the conifer forests growing on over 153 million acres. In other words, over 75 percent of the total commercial coniferous forest land in this country could be impacted by these destructive insects.

The southern pine beetle, *Dendroctonus frontalis* Zimm., is the most serious of the five major bark beetles. The 50 million acres of loblolly/shortleaf pine *(Pinus taeda/P. echinata)* forests in the South where this pest occurs represent the largest coniferous forest type in the United States. The forest economy of the United States is becoming focused in the South. With the ability to produce four to seven generations per year, this bark beetle can quickly exploit conditions favoring population irruptions and cause catastrophic economic losses.

The mountain pine beetle, *Dendroctonus ponderosae* Hopkins, is properly recognized as a serious pest of western coniferous forests. The ponderosa and lodgepole pine *(P. ponderosae/P. contorta)* types attacked by this insect occupy over 39 million acres. These forests are important to the local timber economies, watershed management strategies, and dispersed and developed outdoor recreation enterprises of many communities in the Rocky Mountains. An associated problem is the increased fire hazard created by the extensive areas of beetle-killed trees.

The western pine beetle, *Dendroctonus brevicomis* LeConte, is another pest of ponderosa pine. Although at low levels now, the western pine beetle has been responsible for extensive tree mortality throughout California, Oregon, and Washington. The two to four generations per year produced by this beetle also give it the capability to quickly exploit conditions favorable to population buildups.

The spruce beetle, *Dendroctonus rufipennis* Kirby, occurs throughout the range of spruce in North America. The principal targets in the United States are 13 million acres of Sitka spruce in Alaska (Picea) and the Engelmann spruce *(P. engelmannii)* component of the 20 million acres of spruce-fir forests in the western mountains. Because of the higher elevations and cooler climates in which spruce grows, the spruce beetle may take from one to three years to complete a single generation. Normally present in downed or stress-weakened trees, outbreaks of this insect have been responsible for extensive spruce mortality.

The Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, is the dominant bark beetle throughout the 31 million-acre range of Douglas-fir, *Pseudotsuga menziesii.* In the Pacific coastal region, sporadic outbreaks are very destructive but usually of short duration. Outbreaks in the Rocky Mountains are of longer duration. A dramatic increase in Douglas-fir beetle activity is anticipated in areas currently being defoliated by the western spruce budworm. Thus far, however, only isolated pockets of Douglas-fir beetle infestations have been observed.

Another important North American bark beetle is the Mexican bark beetle, *Dendroctonus mexicanus.* This pest attacks many of the 30 to 40 species of pine found in Mexico. The principal hosts are Chihauhau, Montezuma, Ocote, Caribbean, and pseudostrobus pines. The Mexican bark beetle has an average of three generations per year and behaviorally resembles the southern pine beetle in many aspects.

Common to all bark beetles is their role in removing the old and making way for the new. Each species of bark beetle responds to a unique set of local conditions. To forest managers, a bark beetle outbreak is normally a symptom of a forest under stress. Forests that are insect- and disease-weakened, storm-damaged, drought-stressed, or biologically mature are highly susceptible to bark beetle outbreaks.

For managed forests, bark beetles frequently become a problem when the biological timetable gets ahead of the management timetable. Forest managers risk bark beetle outbreaks when they try to store mature trees on the stump until roads are constructed or timber sales scheduled. Areas reserved from timber harvesting are particularly susceptible to bark beetle attack. The recent increase in the number and size of wilderness and study area reservations is setting the stage for dramatic bark beetle outbreaks. The prospect of bark beetles within the reserves spilling over onto adjacent multiple-use lands is a major concern. Without doubt, bark beetles are and will continue to be serious problems for managers of coniferous forests. The extensive acreages of pine, spruce, and Douglas-fir guarantee it.

USDA Forest records indicate the magnitude of recent bark beetle outbreaks (Table 1). The two most damaging bark beetles from 1979 through 1985 were the mountain and southern pine beetles. During this period, an average of 15 million acres of pine forests were infested per year. These two bark beetles were responsible for killing trees containing over 2.1 billion cubic feet of sawtimber and pulpwood. At an average price of roughly $90 per thousand cubic feet, that material would be worth more than $190 million.

Table 1

Area infested and timber volume killed by the mountain pine beetle and the southern pine beetle from 1979 to 1985.

Year	Acres Infested (million)	Volume Killed (million cubic feet)
1979	19.4	474
1980	16.8	746
1981	5.6	212
1982	11.5	261
1983	15.0	281
1984	17.3	22*
1985	19.2	125*

*Volume data for mountain pine beetle unavailable.

From 1979 to 1985, Federal agencies spent $26.4 million and State agencies spent $10.7 million to control bark beetle outbreaks (Table 2). This $37.1 million resulted in the salvage of over 714 million cubic feet of beetle-killed trees. Since the value of beetle-killed trees is less than for green trees, at an estimated average value of $25 per thousand cubic feet, the $37.1 million expenditure was partially offset by a return of $17.9 million (Table 3). The value of the green trees protected as a result of salvage actions substantially exceeded the amount expended.

The Forest Service is the Federal agency responsible by law for forest pest management on lands of all ownerships. The Forest Pest Management staff within the Forest Service provides technical and financial assistance to the National Forests, other Federal agencies, and the State forestry agencies for high priority suppression activities. In the fiscal year that just ended, the Forest Service received project proposals for bark beetle suppression totalling over $9.4 million. The agency provided $6.2 million, or approximately 66 percent of the amount requested. Thus far this fiscal year, bark beetle suppression project funding requests from State and Federal forest land management agencies exceed $4.3 million. More than half of that amount was requested for southern pine beetle control.

Table 2

State and Federal expenditures for all bark beetle control from 1979 to 1985 ($million).

	Fed.	State and Private Lands	
Year	Lands	Fed. Exp.	State Exp.
1979	1.1	1.0	1.2
1980	1.9	1.9	2.5
1981	1.9	1.3	1.8
1982	1.9	0.2	1.0
1983	2.2	0.8	1.2
1984	3.7	0.6	1.1
1985	6.7	1.2	1.9

Given the amounts expended for control and the value of the trees killed annually, one might expect bark beetle prevention to have a high priority. Unfortunately, that is not the case. In too many instances, only when the forest manager is confronted with an outbreak emergency do thoughts of bark beetle management occur. It is easy to justify spending pest suppression funds when a bark beetle crisis is inescapable; it takes more vision to justify spending silviculture and timber sale preparation funds to create a forest that can withstand bark beetle attacks 15 or 50 years away.

From the past specialist's perspective, the best prospects for dealing successfully with the bark beetle problem are associated with vegetation management strategies that produce healthy and vigorous trees of low susceptibility to bark beetle attack. Unfortunately, as more forest land is withdrawn from multiple use into reserves, as falling demand for forest products dampen investment incentives for timber management, and as government support programs for forestry disappear, the prospect that vegetation management will reach its potential as a pest management tool is also diminished.

The practical aspect of forest management involves meeting current needs for forest resources while maintaining and enhancing sufficient resources for the future. Multiple-use management, timber sale administration, road construction, reforestation, environmental protection, and fire prevention all compete with forest pest management for the resource manager's attention. Similarly, bark beetle biological control strategies and tactics must also be compatible with these competing activities.

Table 3

Total expenditures for all bark beetle control and the volume salvaged from all ownerships between 1979 and 1985.

Year	Expenditures ($million)	Volume Salvaged* (million cubic feet)
1979	3.3	63
1980	6.3	226
1981	5.0	13
1982	3.1	7
1983	4.2	238
1984	5.4	24
1985	9.8	143

*These values under-report the volume actually salvaged since most timber sales also included harvest removal of beetle-killed conifers.

The pest manager's responsibility is to make sure that bark beetle biological controls are practical, cost efficient, and effective. Since it is unlikely that a silver bullet technique will be discovered or designed to control native bark beetles, we must be more realistic in our expectations. However, our research can be both imaginative and innovative. Bark beetle biological control legitimately merits a share of the research resources available.

Among the more desirable characteristics biological control techniques should have are: (1) effectiveness during periods of low bark beetle population levels to help extend the interval between outbreaks; (2) reasonable establishment and maintenance costs to encourage implementation; (3) compatibility with ongoing forest resource management activities to facilitate acceptance; (4) ease of manipulation to permit prompt responses to incipient outbreak situations; and (5) applicability in small stands to provide individual landowners with a way of protecting their trees. This list also reflects, from a user's perspective, the order in which research priorities should be established.

Regrettably, biological control strategies for bark beetles seem to have limited chances for success. A possible and promising exception to this discouraging prospect are strategies using semiochemicals. Using attractants to manipulate bark beetles into trees that can then be cut and removed from the forest before outbreaks gain momentum has been very successful. Mass trapping strategies and confusion strategies are also being examined. European foresters believe that mass trappings buy time to manage forests to a less susceptible condition by preventing outbreaks of *Ips*. However, the Canadian and U. S. experiences so far have been that mass trapping for mountain pine beetle is not effective. On the other hand, MCH (methylcyclohexanone) has been used successfully to prevent Douglas-fir beetle outbreaks. Although not much has been done on the southern pine beetle, recent work looks promising.

Compounding the problem, U. S. resource managers may be reluctant to accept strategies that employ semiochemicals because of high costs. In addition, the U. S. Environmental Protection Agency has ruled that pheromones, when used in trapout strategies, are in fact pesticides and thus require full registration. The cost of researching and registering these products will be a further impediment to their use.

What can be done when research funds are limited, answers are elusive, and the number of research scientists is shrinking? It is obvious that coordination of our efforts is essential. It is apparent that we can not afford the luxury of everybody doing their own thing. Focusing on specific problems, concentrating resources on those problems, stratifying problem-solving responsibilities, and accelerating the timetable are all appropriate. Business as usual will not get the job accomplished. We must be creative in attracting the political and administrative attention required to ensure that resources for biological control do not disappear as other issues gain favor. Ample opportunities will exist to test the hypotheses and strategies discussed at this symposium. Producing useful answers will help guarantee continued support.

SECTION SIXTEEN

An Overview of Biological Control Research in the Forest Service

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INTRODUCTION

Although the title of this Symposium mentions only biological control of bark beetles, I was asked to report on the total research effort on biological control in the Forest Service's Insect and Disease Research program. Let me first define biological control as I will be using it. Some use a broad definition of biological control that includes the use of (1) cultural practices, such as silvicultural prescriptions to enhance the survival and effectiveness of natural enemies; (2) plant species resistant to the pest organism; (3) sterile males or genetic manipulation of the host; and (4) disrupt normal behavior or development. The Forest Insect and Disease Research program (FIDR for short) includes a substantial commitment to all of these areas of research. I will be using biological control here as the science that deals with the role of natural enemies (e.g., parasites, predators, insect pathogens, microbial organisms antagonistic to plant pathogens) in the regulation of their hosts. In a more applied sense, I will be discussing biological control as one of many management tactics used to keep insect populations within economically acceptable bounds.

The importance of biological control to the protection and conservation of natural resources is irrefutable. Biological control, along with plant resistance, forms the core around which effective integrated pest management (IPM) programs are developed. The biological control component of such programs is economical, provides sustained effectiveness, and is environmentally safe. Often pesticide usage cannot be reduced without a parallel increase in the efficiency of natural control agents.

OVERVIEW

Funds allocated for the entire research program in FIDR in FY 1986 was $21,093,000, subsequently reduced by about 4.3% in conformance with the Deficit Control Act. The proportion devoted to biological control research was 12.7% or $2,680,000 and 17.8 scientist years.

Most of these resources were for research on insect pests (75%); the remainder for research on tree diseases and wood decay (17%) and weed control (8%). Research on insect pests is about evenly divided between parasites and predators as a group (39%) and microbials such as viruses and bacteria (36%). Eighteen Research Work Units (RWU) conduct this research in eight Forest Experiment Stations across the country. The largest single concentration of biological control research is carried on at the Northeastern Forest Experiment Station at the Center for Biological Control of Eastern Forest Insect and Disease Pests, Hamden, Connecticut. Emphasis is on the gypsy moth; studies include parasites, predators (vertebrate and invertebrate) and microbials. By far the majority of biological control research in FIDR is aimed at control of defoliators. Only one unit currently conducts research on biological control of bark beetles (Pineville, Louisiana). Two units do most of the research on developing microbials as pesticide sprays (Hamden and Corvallis, Oregon).

Most research on diseases deals with the use of organisms antagonistic to plant pathogens, and this mostly in the western states. One unit conducts research on control of weeds (Honolulu, Hawaii).

The following summarizes the major areas of biological control research in FIDR. I will emphasize the FIDR work units that account for most of the research instead of trying to cover all of them.

Parasites and Predators for Insect Control

Several work units are engaged in research on parasites. Three account for most of it. At the Center for Biological Control at Hamden, research on parasites for gypsy moth has been underway for many years. A number of exotic species have been intensively studied. Current emphasis at the Center is on understanding the role of parasites in regulating low level gypsy moth populations, which can lead to integrated management strategies that enhance parasite effectiveness. The research is designed to obtain the knowledge and technology needed to determine the parasites' impact on gypsy moth in low density host populations which are now well documented. It is now also known that simple percentage parasitism figures significantly underestimate the contribution of parasites to generational mortality. Methods to calculate total generational mortality based on a sample of the percentage parasitism have been developed.

Research on predators at Hamden continues to focus on the role of predation in low level gypsy moth populations. Specifically the objective is to determine the interactive variables that determine the rate of predation so that forest management practices are compatible with the maximum effect of the predator, or can be modified to enhance predator effectiveness. Variables being studied are site characteristics, alternative food abundance, predator foraging behavior, etc.

Recent results show that (1) predator diversity and abundance are important factors in determining stand susceptibility to defoliation by gypsy moth; and (2) shrub density and protective cover have a major effect on small mammal foraging behavior and subsequent gypsy moth survival.

At the Forest Service Laboratory in Orono, Maine, numerous methods of enhancing effects of natural enemies of the spruce budworm are being evaluated. Particularly promising are methods of increasing predator populations through silvicultural and forest management practices. The aim is to develop management strategies that support and enhance natural enemies of the budworm and help prevent or minimize the effects of epidemics. Results so far have shown definite changes in species diversity and abundance of invertebrate predators such as ants and spiders by type of cutting practice. In studies of bird predation, it is clear that bird impact is strongly related to budworm populations. Birds consumed fully 87% of the budworms in stands supporting low-level populations, but only 2% in high-level populations. This unit is also investigating the use of the egg parasite *Trichogramma minutum* in aerial releases.

At LaGrande, Oregon, research on introduced larch casebearer, *Coleophora laricella*, parasites is winding down. The parasites *Agathis pumila* and *Chrysocharis laricinella* have been established and have increased their populations while damaging casebearer populations have decreased to low levels. Life-table and before-and-after evaluations are being used to assess the role of introduced parasites in this shift. Evidence from eight generations of study now indicate that the parasites are the key factor in reduced casebearer populations.

Other research at LaGrande is underway to develop management guidelines that will enhance the role of natural enemies as regulators of major forest defoliating insects such as western spruce budworm and Douglas-fir tussock moth. Insectivorous birds, foliage foraging ants, and forest-inhabiting spiders have been identified as dominant biotic regulators of both of these important defoliators.

Research on natural enemies of bark beetles is currently active only at Pineville, Louisiana. Attempts are underway to look for exotic predators either in the United States or in foreign countries that prey on related bark beetles with the intent of introducing and releasing them for control of the native southern pine beetle. You have already heard about the surveys by collaborating scientists in other countries using southern pine beetle pheromone to search for foreign natural enemies that can respond to it and about the promising predators so far under study, so I will not repeat that here. The approach being taken, i.e., attempting to control a native pest with exotic natural enemies, is not often researched but there is good evidence that this approach may yield results. It will be a challenging task worth watching in view of the above and since practical biological controls for bark beetles have been an elusive goal for research in the past.

Microbials for Insect Control

Two work units are primarily responsible for research on insect pathogens. In the West, most of this research is done at Corvallis, Oregon. Currently emphasis is on laboratory and field testing of available microbials against western coniferous defoliators. In the near future, this work will include testing new strains of *Bacillus thuringiensis* (B.t.) that become available from commercial sources, including those developed by species crosses or genetic engineering.

This unit was responsible for developing the nuclear polyhedrosis virus of the Douglas-fir tussock moth as a microbial insecticide, registered under the name TM Biocontrol-1, the first microbial registered in the United States for a forest insect pest. The virus is being mass-produced on the tussock moth host and stockpiled for use in future outbreaks. A significant recent development is the successful transfer of the virus through serial passage to a substitute host, the cabbage looper. The adapted virus maintains high virulence for the Douglas-fir tussock moth. Use of a surrogate host like the cabbage looper promises to significantly simplify and accelerate the mass production process. This unit has also done considerable research on improving the formulation of the virus with additions of ultraviolet absorbers to reduce inactivation by sunlight.

The Center for Biological Control at Hamden carries the major responsibility for research on insect pathogens in the East. Research is conducted either directly or through funding of cooperators on many aspects of microbial epizootiology, mode of action, interaction of microbials with parasites, and the practical aspects of developing microbial insecticides.

cides. Current research places emphasis on laboratory bioessays and field studies of (1) new strains of B.t., including those genetically engineered by industry; (2) new adjuvants for extending field persistence and efficacy of the gypsy moth polyhedrosis virus; and (3) efficacy of microsporidia (*Nosema* and *Pleistophora*) isolated from gypsy moth populations in Europe.

This unit was responsible for developing the background information that led to the registration of the gypsy moth virus under the name Gypchek. It represents only the second microbial registered for a forest insect pest in the United States. Research in this unit also led to the registration of a virus for the European pine sawfly under the name Neochek-S. A class A quarantine facility has been developed at the Center so that foreign beneficial organisms can be introduced directly for study. A virus processing facility is now completed that is capable of producing enough Gypchek for both research and pilot scale studies. The potency and quality of the product is superior to that produced in the past. A new strain of B.t., called NRD-12, was isolated, bioessayed, and field tested against the gypsy moth and spruce budworm. It is more virulent than the standard commercial strain, HD-1. NRD-12 is now being commercially produced and formulated by Sandoz, Inc. Scientists at the Center have contributed in a major way to the evaluation and application of new B.t. formulations and in the development of guidelines for their use. These activities have contributed to the acceptance of B.t. as a suppression tactic against both the spruce budworm and gypsy moth.

In the area of virus epizootiology, advances are being made in our understanding of the mode of action of Gypchek. It is now established that Gypchek can be a latent virus, being transmitted transovarially from generation to generation.

A new work unit has been established at Delaware, Ohio, to exploit biotechnology in search of solutions to microbial control with emphasis on the gypsy moth. Attempts will be made to manipulate the gypsy moth virus genetically to enhance its effectiveness. This unit will also research diagnostic methodology for use in studies of epizootiology and will study the processes that determine host specificity and define the pathogenic mechanism of insect baculoviruses.

Biological Control of Tree Disease

Biological control of tree diseases is based primarily on the use of organisms antagonistic or pathogenic to plant pathogens. The major effort in this area is on use of antagonistic microfungi commonly found in the forest environment to control laminated root rot (*Phellinus weirii*) and Armillaria root rot (*Armillaria obscura*). This work is centered at the Pacific Northwest Forest and Range Experiment Station in Corvallis, Oregon. Several species of *Trichoderma* isolated from roots of stumps infested with laminated root rot will kill the root pathogen in culture. Numbers of these organisms in stumps and roots can be increased by the use of low levels of several common fumigants to which the antagonistic organisms are resistant.

Filtrates of *Trichoderma* can also inhibit rhizomorph production of Armillaria in culture. Inhibition is attributed to diffusible antibiotics produced by *Trichoderma*. The evidence suggests that several isolates or even species of *Trichoderma* could be used in a single inoculation for control since they do not antagonize one another.

The work unit in St. Paul, Minnesota, North Central Forest Experiment Station, is evaluating the effectiveness of two fungal antagonists (*Penicillium oxalicum* and *Trichoderma viride)* as biological control agents for diseases in forest tree nurseries caused by soilborne pathogens. As with the research at Corvallis, the fungal agents were shown not to antagonize each other, and better control of damping off was observed when both antagonists were inoculated into the soil at the same time.

Research is underway at the Delaware, Ohio, laboratory, Northeastern Forest Experiment Station, on ways to utilize a strain of the antibiotic-producing bacterium (*Bacillus subtilis*) for control of the fungal pathogen of the Dutch elm disease, *Ceratocystis ulmi*. Research is in progress to purify and characterize the antibiotics, which have been shown to protect elm seedlings from infection by the Dutch elm disease pathogen in limited laboratory studies. Similar studies are also being done at Stoneville, Mississippi, on the oak wilt disease using antibiotics produced by a species of *Pseudomonas*. Although somewhat futuristic, there is the possibility of cloning the genes in the bacteria responsible for antibiotic production, inserting them in the oak or elm genome, and growing trees that produce their own antibiotic.

One unit at the Forest Products Laboratory at Madison, Wisconsin, is studying fungal antagonists as potential biological agents against wood decay fungi. This research is in its early phases. Several organisms so far tested have actively depressed growth in some decay organisms.

Biological Control of Weeds

Only one work unit performs research on biological control of weeds. This unit is located in Honolulu, Hawaii, Pacific Southwest Forest and Range Experiment Station. The research is done in collaboration with the National Park Service and the state of Hawaii and involves four phases: (1) foreign exploration to obtain candidate control insects; (2) evaluation of the biotic agents against the noxious weed and against non-target plants to clarify host range and therefore feasibility for introducing and releasing; (3) mass-rear and release the promising biological control agents; and (4) monitor results for successful and effective introduction. The weeds presently being studied includes banana poka, fireweed, blackberry, and gorse. The research is presently at phase two.

CLOSE

We have experienced a significant loss of qualified scientists in biological control in the last few years due to retirements. Their prominence would most certainly qualify them for entry in a reference book on Who's Who in Biological Control Research; able and respected scientists such as Frank Lewis, Mauro Martignoni, and Arnold Drooz. With flat or decreasing budgets over the last few years, we have been unable to replace them. Our programs in biological control are bound to suffer accordingly. The USDA and the Forest Service have a commitment to Integrated Pest Management, or perhaps better, Integrated Resource Management. The key role of biological control in effective pest management obligates us to continue a strong research effort in this area for practical management tools within the limits of our resources.

INDEX

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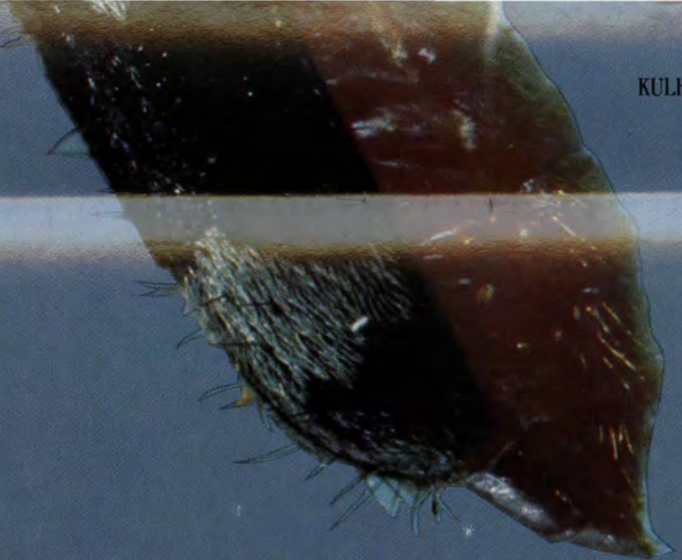
Potential for Biological Control of Dendroctonus and Ips Bark Beetles



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