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Potential for Biological Control of Native North American *Dendroctonus* Beetles (Coleoptera: Scolytidae)[1]

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ABSTRACT Bark beetles of the genus *Dendroctonus* inflict serious damage in North American coniferous forests. Biological control, which has never been seriously attempted with bark beetles in the United States, should be reconsidered in light of results disclosed here. Impact of indigenous associates is discussed, as well as previous, unsuccessful attempts to introduce exotic enemies. Potential of insect enemies of allied pests is considered in light of Pimentel's theory of "new associations." Extraregional and exotic bark beetle predators from different forest ecosystems are shown to be able to detect aggregating pheromones (kairomones) of beetles related to their normal prey. Some guidelines for necessary experiments before new introductions are discussed, and two examples are reported. One involves a North American clerid, *Thanasimus undatulus* Say, a predator of the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, which responded to pheromones in cross-attraction field tests. The other involves the palearctic beetle, *Rhizophagus grandis* Gyllenhal, a specific predator of *D. micans* Kugelann. In laboratory bioassays, *R. grandis* was attracted to frass of three North American *Dendroctonus*. Because predators like *T. undatulus* and *R. grandis* may be able to locate infestations of other *Dendroctonus*, they are potential biological control agents. This research shows that trapping with aggregating pheromones in the habitat of related pests and field and laboratory olfactometric experiments are both useful in screening for potential insect biological control agents.

KEY WORDS *Dendroctonus*, predators, biological control, pheromones, allied insects

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COLLECTIVELY, bark beetles of the genus *Dendroctonus* Erichson are the most destructive natural biological agent in North and Central American coniferous forests. Most species breed in standing trees, and almost all species are capable of killing standing trees. The combined efforts of the aggressive bark beetles, *Dendroctonus brevicomis* LeConte, *Dendroctonus ponderosae* Hopkins, *Dendroctonus jeffreyi* Hopkins, *Dendroctonus rufipennis* (Kirby), *Dendroctonus murryanae* Hopkins, and *Dendroctonus pseudotsugae* Hopkins, in attacks on their preferred host trees result in the annual destruction of 8,258,800 m^3 of pine, spruce, larch, and fir (Wood 1982). In addition to the direct loss of timber, there is loss of wildlife habitat and use of the land for recreation, fishing, watershed, and range. Integrated forest pest management of pine bark beetles includes strategies that may reduce losses by identifying and preventing the ecological conditions that lead to outbreaks (Coulson & Stark 1982). However, these strategies are based on the assumption that all affected forests can be managed intensively. Once bark beetle outbreaks occur, remedial tactics consist of rapid salvage of as much killed timber as possible to reduce direct monetary losses and to remove sites for development of additional beetle broods. Chemical controls are effective, but impractical because of the cryptic nature of the pests, logistical and application difficulties in the forest, and the expense of application. Mechanical controls are labor-intensive and largely ineffective. No consideration is given to the destruction of beneficial organisms and the cost-effectiveness of the treatment. Remedial treatments applied in outbreak conditions consistently fail to suppress bark beetle populations (Klein 1978, Coulson & Stark 1982).

Limited research with mechanical exclusion devices shows evidence of the efficacy of insect natural enemies to regulate low-level populations of bark and engraver beetles (Linit & Stephen 1983, Riley 1983, Miller 1984a,b). There are no data on the impact of insect natural enemies during bark beetle epidemics (Mills 1983), and there are little quantitative data available on average population densities of bark beetles (Thatcher & Pickard 1964).

There is no logical reason why biological control has not been considered as a management strategy

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for *Dendroctonus* bark beetles (Coulson & Stark 1982). Possibly, biological control has not been intensively studied because bark beetles are native pests, and there has been no demonstrated natural control of these pests in North America. The few attempts to introduce exotic biological control agents at the turn of the century failed, possibly because of lack of knowledge of the importance of semiochemicals in bark beetle/host tree/insect enemy associations. Using southern pine beetle (SPB), *Dendroctonus frontalis* Zimmermann, as an example, the objective of this paper is to emphasize the need for, and to propose ways to attempt, biological control of the *Dendroctonus* bark beetles.

The Southern Pine Beetle: Current Management Strategies. The SPB is a sporadic pest in pine forests of the southern United States. Though the SPB may be an important factor in natural southern pine forest succession, intermittent SPB epidemics disrupt the stability of managed southern pine forest ecosystems, the economy of the area, and the industries that are based on the growth and production of southern pines. Direct and indirect losses result from periodic SPB outbreaks. The volume of killed trees is so great that trees either cannot be salvaged before they deteriorate, or they can only be salvaged for low-grade uses because of decay, stain, or insect damage. From 1960 to 1980, this insect killed 5,899,100 m^3 and 8.5 million cords of pine.[7] Only half the volume was salvaged. Losses from 1971 through 1982 were estimated at $334.5 million.[8] A recent estimate of annual damage is $53 million.[9] Much timber is left unsalvaged because it is inaccessible or because of the unfavorable economic consequences of excessive production. The land area that could be reforested is reduced and planning is disrupted because tree nurseries cannot replace even a portion of the SPB-killed timber. There is also a loss or alteration of wildlife habitat and recreational areas (Leuschner 1980). In spite of accelerated research, development, and application work on the problem by the USDA Forest Service since 1975, beetle populations are increasing (Billings 1984), and expectations are that similar losses will occur in the future.

SPB management has low priority during years in which the population of this native pest is at low levels. Current recommendations for management of SPB infestations are only a refinement of what they were in 1971 (Bennett & Ciesla 1971, Swain & Remion 1981, Thatcher et al. 1982), and they have no measurable impact on the general level of ecosystem-wide SPB populations. SPB populations were epidemic throughout the southern pine forest ecosystem from 1973 to 1975 (Price & Doggett 1978), and they were epidemic again in east Texas, Louisiana, Mississippi, and Alabama in 1985.

The SPB problem is ecosystem-wide. Existing pest-management strategies are applied to a fraction of the forest ecosystem and have no appreciable effect on the outcome of an area-wide attack. Current SPB infestation management tactics consist of cut-and-remove (salvage), cut-and-leave, or pile-and-burn methods in which the infested timber and a barrier zone of healthy trees are felled and either left on the ground or removed from the forest (Bennett & Ciesla 1971, Swain & Remion 1981, Thatcher et al. 1982). The cut-and-remove and pile-and-burn strategies result in increased mortality among beneficial insect populations that develop beneath the bark. However, these two strategies are used primarily to prevent the expansion and fusion of small beetle spots into extensive infestations. The native insect associate complex does not appear to regulate SPB populations during epidemic periods. Although the reasons for the start or the collapse of SPB outbreaks are not known, natural enemies may well be involved.

There is a need to develop biological control as a management strategy in the southern loblolly pine, *Pinus taeda* L., ecosystem. The SPB is largely inaccessible to treatment with insecticides or other direct control because the life cycle from egg to callow adult is spent beneath the bark of the host tree. Insecticides are not considered suitable for control of tree-killing beetles (Coulson & Stark 1982). Also, insecticides kill insect enemies of bark beetles (Dyer et al. 1975, Sweezey & Dahlsten 1983) and might prolong outbreaks. The necessity for treating large areas and the inability to locate and treat all infested trees make the use of insecticides impractical and prohibitively expensive. Insecticides could make a secondary pest a primary pest or result in environmental pollution. Without the establishment of economic thresholds, the decision to apply any control measure is intuitive rather than objective. The cultural approaches advocated and previously mentioned have limited effectiveness over ecosystem-wide infestations. Biological control should have been a primary choice in developing pest-management procedures for SPB (Stehr 1982), but at the time it was dismissed as inconsequential because the SPB pine beetle problem was considered to have a forest-management solution (Stevens 1981). The repeated recurrence of intermittent regional outbreaks of SPB, as recently as 1985 in east Texas and Louisiana, demonstrates an urgent need to reassess biological con-

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[7] General Management Review, Southern Region (R-8), Southeastern Forest Exp. Stn., Southern Stn., USDA For. Serv., 8–19 August 1983.

[8] Information compiled from yearly reports submitted by the committee on losses caused by forest insects to the Southern Forest Insect Work Conference. Courtesy of State and Private Forestry, Pineville, La.

[9] Integrated pest management in Southern forests: research priorities and opportunities. Report compiled by the South. Indust. For. Res. Counc. Natl. Assoc. Prof. Forestry Schools and Colleges, and USDA For. Serv., 21 June 1984, Athens, Ga.

trol. Biological control would provide the forest manager with an additional tactic for regulation of low-level SPB populations, and it may prevent development of large-scale outbreaks.

If successful, biological control would not disrupt the ecosystem and should become a part of an integrated approach to pest management (Dahlsten & Dreistadt 1984). Once the initial costs of research for suitable agents, importation, and evaluation are expended, no additional development costs would be required. Economical management of the pest may be achieved where chemical controls are impractical. Biological control agents adjust their population levels to those of the targeted pest population (Johansen 1971, Stehr 1982, van den Bosch et al. 1982). The pest population would fluctuate about a lower average density (Stehr 1982, van den Bosch et al. 1982) and damage would be reduced.

Biological Control of *Dendroctonus*. There are many lists of SPB insect associates, their sequence of arrival at and spatial distribution on attacked host trees, and indications of their relative abundance (Overgard 1968, Moser et al. 1971, Camors & Payne 1973, Stein & Coster 1977, Dixon & Payne 1979, Goyer & Finger 1980, Younan & Hain 1984). Biological control with insect enemies of allied pests has never been attempted vigorously in the United States with bark beetles. No major programs have been begun (Coulson & Stark 1982), but there have been at least three unsuccessful attempts to introduce exotic insect enemies from Europe for regulation of bark beetles in the United States (Clausen 1956, Dowden 1962, Coulson 1981). A. D. Hopkins received 6,098 *Thanasimus formicarius* (L.) (Coleoptera: Cleridae) from Germany between 1892 and 1894, and 2,200 were released in the forests of West Virginia against SPB. No field recoveries have ever been made (Clausen 1956, Dowden 1962). There are records of two shipments of *Rhizophagus grandis* Gyllenhal (Coleoptera: Rhizophagidae) from the USSR to the USDA Forest Service in Fort Collins, Colo., in 1976 and to the Pennsylvania Bureau of Forestry, Harrisburg, in 1977 (Coulson 1981), but they were not released (J. Schmid, J. Coulson, personal communication). A laboratory culture of 200 *T. formicarius* sent from the USSR was released against SPB in Mississippi in 1980, but no recoveries have been made (T. E. Nebeker, personal communication). Pschorn-Walcher (1977) considered the attempts made to use native insect enemies against an allied pest species to be merely superficial trials, and both he and Stevens (1981) recommended more experimentation before discarding the hypothesis. Some reasons for the previous failure of the few releases of bark beetle natural enemies are included in the following discussion.

In spite of past successes with pests of agricultural crops and in forestry, there is still a general lack of interest in biological control (D. L. Dahlsten, personal communication). No serious effort has been made to regulate North American bark beetle populations with other insects (Coulson & Stark 1982, Moeck & Safranyik 1984). In Europe and the USSR, the predator/prey association of *R. grandis* and *Dendroctonus micans* (Kugelann) is one in which the prey is effectively controlled by the predator under endemic conditions (Gregoire 1984). Intensive rearing efforts and releases of *R. grandis* have been undertaken in Soviet Georgia since 1967 (Tvaradze 1976), in Belgium and France since 1983 (Gregoire et al. 1985), and in Great Britain since 1983 (King & Evans 1984, Evans 1985). In this classical biological control situation the prey insect spreads faster than its predator. Where reassociated under endemic conditions, the pest population is brought into equilibrium with that of the predator.

The importance of insect enemies to scolytid population regulation (Dahlsten 1982) has not produced much interest in biological control (Coulson & Stark 1982). This lack of interest may be based on logistics problems associated with the vast areas involved, the expense of rearing natural enemies, the opinion that natural enemies are not an important component in bark beetle population dynamics, or the fact that bark beetles are native insects and no North American bark beetle population has been controlled by another insect (A. T. Drooz, personal communication). In the following paragraphs we review some of the literature on biological control that is relevant to *Dendroctonus*.

Pimentel (1963) and Hokkanen & Pimentel (1984) analyzed biological control programs for agricultural crops and concluded that, in more than a third of the successful efforts directed against either a native or introduced pest, the biological control agent came from a similar or a different habitat where it attacked a species or genus allied to that of the pest insect. Their analyses of biological control programs conclude that successful control is possible in 1 of 20 species releases in a classical biological control situation ("old association"), but in 1 of 6 species releases of insect enemies of allied pests ("new association") (D. Pimentel, personal communication). The inability of some native or exotic insect enemies to limit host numbers is attributed to the balance produced by their long-evolved association. Selection of potential "new association" natural enemies for biological control involves the choice of enemies of a close relative of the pest, ideally from the same genus, that feed on related hosts; obtaining natural enemies from a climatic region similar to that of the pest's habitat; and choosing natural enemies that have good searching ability, are highly host-specific, and have a high rate of increase compared with the pest.

Pimentel's (1963) suggestion that insect enemies of allied pest species can serve as biological control agents of native insect pests was criticized by

Pschorn-Walcher (1977) and Stevens (1981). They disputed the new-association theory, not the results. Neither disputed that 39% of the biological control successes were due to insect enemies of allied pests (Pimentel 1963). They questioned the theory that parasites long associated with a host would lose their ability to limit host numbers severely. Establishing successful extraregional or exotic biological control agents would be more difficult in the forest ecosystem with its stable and more diversified parasite complexes of forest pests than in a relatively unstable agroecosystem (Pschorn-Walcher 1977). Others believe that the relatively simple, but unstable, coniferous forest plant communities, with widely fluctuating insect populations, discourage practical biological control (Turnock et al. 1976).

Recently, Goeden & Kok (1986) critiqued the conclusions of Hokkanen & Pimentel (1984) regarding use of insect enemies of weeds because their analysis was "biased toward cactaceous insects, and cacti are not representative of target weeds," and because several of their examples were inaccurate. Yet, in the Colombian Andes, Drooz et al. (1977) demonstrated a biological control success with a North American parasite against a forest pest from a different host genus in a different forest ecosystem. Carl (1982) concluded that although the use of natural enemies to control allied pests has not been a common practice, it is certainly worth trying. The conclusions of Hokkanen & Pimentel (1984) do not agree with actual field experience in biological control in agricultural crops and may not be generally applicable, but certainly this theory should be tested (W. H. Day, personal communication).

Mills (1983) reviewed the literature on the natural enemies of scolytids infesting conifer bark in Europe in relation to the biological control of *Dendroctonus* spp. in Canada. He suggested using aggregating pheromones to determine which of the early arriving predators may be useful as population management agents. The introduction of exotic insect enemies against native pests offers considerable potential if gaps in the native natural-enemy complex can be filled or if more effective species are discovered (Mills 1983). There is a remarkable taxonomic similarity among the bark beetle associate complexes in different forest ecosystems, but little research has been conducted on insect enemies of bark beetles (Dahlsten 1982). Insect predators of bark beetles have become adapted to use their prey as food for adults and for developing larvae. They use the host tree for mating, oviposition, and pupation. The host tree is the location from which dispersal flights are initiated to existing infestations or to start new infestations. Some predators are adapted to use beetle aggregation pheromones to locate beetles on host trees during the beetle attack period that is most suitable for their feeding, mating, and oviposition (Borden 1982, Payne et al. 1984). The development of the immature stages of these predators is synchronized with the availability of beetle larvae as food. The use by predatory or parasitic insects of the chemical communication system of the host insect provides an ideal tool for screening natural enemies that may be of use in the biological control of bark beetles.

The host plant is a possible complication when introducing entomophagous agents associated with European *Dendroctonus*. The scolytid *D. micans* attacks spruce, but the American species attack a number of hosts. The Douglas-fir beetle (DFB), *D. pseudotsugae*, attacks *Pseudotsuga* spp., *Larix occidentalis* Nutt., and *Tsuga heterophylla* (Raf.); the spruce beetle (SB), *D. rufipennis*, attacks *Picea* spp. within its range; and the SPB attacks only *Pinus* spp. (Wood 1963, 1982). DFB, SB, SPB, and at least three additional *Dendroctonus* species share pheromones or pheromone analogs (Borden 1982). As a result, pheromone-based search for SPB insect enemies should not necessarily be restricted to the range of a particular beetle host tree species. Enemies of related bark beetles that attack other host tree species may also be potential enemies of SPB. The exotic and extraregional insect natural enemies of the genus *Dendroctonus* are only a logical starting point.

The close association between the prey-locating behavior of bark beetle predators and the aggregation behavior of their prey is well illustrated by the coevolution of the prey-location kairomone system of *Thanasimus dubius* (F.) and the aggregation pheromone system of SPB (Payne et al. 1984). Evidence of similar prey-locating abilities, as shown by taxonomically, ecologically, and behaviorally similar bark beetle/predatory insect complexes (Berryman 1967, Dyer et al. 1975, Borden 1982, Dahlsten 1982, Payne et al. 1984), supports the use of pheromone cross-attraction surveys for selection of possible SPB insect enemies from the insect-associate complexes of allied *Dendroctonus* spp. (Mills 1983). SPB occurs in scattered infestations and is accessible to *T. dubius* only during the days SPB attacks the host tree (Coster et al. 1977). The predator uses kairomones to locate prey on the newly attacked host tree and may use the kairomone to locate mates (Payne et al. 1984). The capacity of a predator to respond to a variety of pheromones or pheromone components as kairomones provides it with the ability to find and use other beetle species as alternate prey on the same or a different host tree (Kohnle & Vité 1984). *T. dubius* is a facultative, preferential SPB predator, but it can perceive and react to pheromones of different bark beetle species as kairomones (Payne et al. 1984). This ability allows *T. dubius* to survive when its primary prey is scarce.

That potential biological control agents are present in extraregional or exotic locations can be dem-

Table 1. Technical description of bark beetle lures

Lure	Components	Relative proportions	Release rate[a]	Duration
MPB	Myrcene		20 mg/d	120 d
	trans-verbenol	Individual release vials	1 mg/d	
	exo-brevicomin		0.5 mg/d	
SB and SPB	Frontalin	0.67 g/release vial	10 mg/d	100 d
	α-pinene	0.33		
WPB	Frontalin	15 g/release vial	12 mg/d	100 d
	Myrcene	2.5	0.5 mg/d	
	exo-brevicomin			
I. typographus	2-methyl-3-butene-2-ol	15 in one release device	10 mg/d	?60 d
	cis-verbenol	0.70	1 mg/d	
	Ipsdienol	0.15	0.17 mg/d	

[a] Approximate release rate 1 day at 20°C.

onstrated in field cross-attraction trapping experiments and laboratory bioassays, such as those described here. Results of these surveys should show whether the primary stimuli for location of the beetle on the attacked host tree are chemically similar or similarly attractive in locations where insect enemies are collected and where they may be released (Borden 1982). Because aggregating pheromones are used in the survey, the insect enemies evaluated are the predators that arrive when the host tree is under attack by bark beetles (Coster et al. 1977, Borden 1982, Payne et al. 1984).

A series of careful tests should be conducted before any further attempt to introduce new associates. These tests should assess the capacity of the candidate insect enemies to locate the host or prey and to oviposit, grow, and develop normally with, and adapt to, the life cycle of the target species. We present here, as an example of such pilot studies, the results of two sets of experiments. The first of these is with *Thanasimus undatulus* Say (Coleoptera: Cleridae), a predator usually associated with the DFB. The second is with *R. grandis*, a specific predator of the palearctic species *D. micans*.

Materials and Methods

Trapping Experiments. In July and August 1984 pheromone cross-attraction studies were conducted in central Louisiana, Montana, and in Taiwan, Republic of China, 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 showed 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 SB/SPB, western pine beetle (WPB), *D. brevicomis;* mountain pine beetle (MPB), *D. ponderosae;* and *Ips typographus* (L.) (Table 1). 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, 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 were 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, were not normally distributed, and did not have homogeneous variance. Transformation procedures did not normalize the data. The six trap lines, each with five traps, were considered blocks. Significant differences ($\alpha = 0.05$) among ranks of catches in pheromone traps were analyzed with Duncan's (1955) multiple range test because the distribution of ranks is considered to be approximately normal (Conover 1980).

Laboratory Bioassays with *R. grandis*. During October 1984 one of the authors (J.C.M.) conferred with workers in Britain and Belgium who were using *R. grandis* in a program of classical biological control against the European spruce beetle, *D. micans*. The principal research that supported the European programs was conducted by J.C.G. and colleagues in Belgium on the biological control of *D. micans* by *R. grandis* in endemic populations and the development of mass-rearing techniques for *R. grandis* (Gregoire et al. 1985).

R. grandis is a small beetle, 4–6 mm long, that is a specific predator of *D. micans* throughout its range, except in newly colonized areas. The adults locate their prey's brood chambers by olfactory cues with great efficiency (>80% of the brood chambers are colonized in Belgium) and at any stage of the bark beetle's development. Eggs are laid in the brood chambers, and both adults and larvae feed on all developmental stages, including young, callow adults. The predator's fertility in the laboratory averages 60–100 eggs, and each predator larva requires the equivalent of one fully grown prey larva for its complete development.

Tests were designed to determine if this predator should be considered for introduction into the United States against *Dendroctonus* spp. We report here the first step in this testing process. In the laboratory, we compared the orientation of *R. grandis* towards frass samples from three North American species: SPB; the black turpentine beetle (BTB), *Dendroctonus terebrans* (Olivier); SB; and the usual prey species, *D. micans*. Frozen frass of SPB and BTB was sent from Louisiana to Belgium for bioassay with *D. micans*. Also, frass of SB was sent from Alaska. The frass to be tested was stored at −18°C upon arrival at the Brussels laboratory.

The bioassay was designed to determine the predators' response to a gradient of odor in still air. Tests were run in glass petri dishes (9 cm diameter) with moist filter paper on the bottom (Fig. 1). The test arena was divided into two symmetrical halves, each containing a circular area (1 cm diameter). Frass from the species to be tested was deposited in a capsule (1 cm diameter), and a control area (1 cm diameter) was drawn on the opposite half of the paper disk. The petri dish was then covered with a piece of gauze (Tergal), which was held tightly in place with a rubber band. To avoid modification of insect behavior due to physical contact (arrestant effect) and to prevent beetles from moving particles of frass to other locations of the test arena, the insects were deposited on, and separated from the frass by, the gauze screen. There were four replicates of each test, and 12 naive males or females were used for each replicate. The insects were held at 5°C following emergence as adults and were exposed to room temperature for ca. 4 h before the test. The *R. grandis* were then placed on the gauze in the middle of the arena and maintained there a few seconds within a glass capsule. The glass capsule was removed, and the petri-dish arena was covered with a glass plate. The space between the gauze and the plate allowed the insects to move freely, but sufficient contact was maintained to satisfy their thigmotactic needs and to prevent them from walking on the glass plate instead of the gauze. The gauze between the dish and the cover allowed a certain amount of gas exchange, enough to prevent saturation of the atmosphere by the volatiles, as demonstrated during the experiments by the insects' reactions to the odor gradients. Every 2 min during the 10-min test period, the insects present on the different parts of the test area (A–D) were counted. The tests were conducted under red, inactinic light.

The statistical methods used for analysis of data were paired *t* tests for comparing the number of *R. grandis* found at the frass (A) and the control (D) (Fig. 1) after 10 min in each series of four replicates; and a two-way analysis of variance (ANOVA) for an overall comparison of the means in A from all experiments after 10 min. The data, being proportions, were transformed using the arcsine transformation, $y = 2(\text{arcsine}\sqrt{x/n})$, where x is the number of *R. grandis* remaining on A and $n = 12$, the total number of beetles in each replicate.

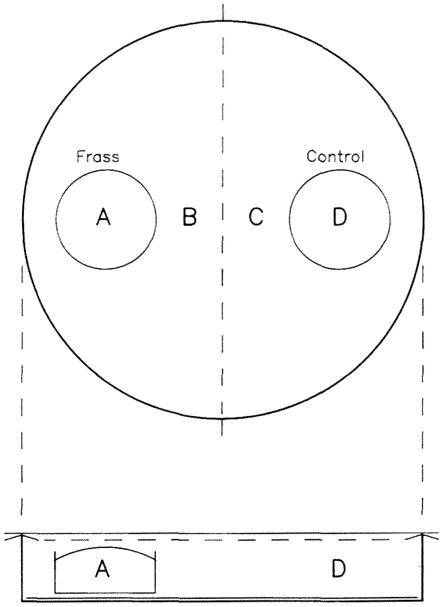


Fig. 1. Odor-gradient test chamber: A, frass test area (1.0 cm diameter); D, control area (1.0 cm diameter).

Results and Discussion

Trapping Experiments. During the SPB, WPB, MPB, and *Ips* pheromone surveys in Montana, 29 insect species or insect groups were collected. Of the 29 species, four insects showed significant differences among the ranked traps and significant differences among the rank means that indicated attraction to aggregation-pheromone lures (Table 2). Catches of MPB in MPB traps and catches of *Ips* (*confusus* LeConte?) with *Ips typographus* pheromone were ranked significantly higher than the ranked catches in the remaining traps. There was no significant difference in ranked catch of *T. undatulus* from SPB- and WPB-baited traps, but these ranked significantly higher than the ranks of the MPB- and *Ips*-baited traps, and unbaited check traps. Ranked catches in MPB, *Ips*, and check traps were not significantly different. Ranked capture of *Enoclerus sphegeus* was highest in *I. typographus*-baited traps, significantly less in MPB-baited traps, and significantly less than both in the SPB-, WPB-baited, and unbaited traps.

In four of six weekly collections made from 5 July to 10 August (Fig. 2) average *T. undatulus* catch was highest in SPB- or WPB-baited traps.

Table 2. Duncan's multiple range test of significant differences among ranked means for catches in pheromone traps

Insect							
MPB		*I. (confusus?)*		SPB		*E. sphegeus*	
Rank mean	Pheromone in trap	Rank mean	Pheromone in trap	Rank mean	Pheromone in trap	Rank mean	Pheromone in trap
5.0a	MPB	5.0a	*Ips*	4.5a	WPB	4.9a	*Ips*
2.8b	*Ips*	2.7b	SPB	4.5a	SPB	3.8b	MPB
2.8b	Check	2.5b	MPB	2.7b	*Ips*	2.1c	SPB
2.4b	SPB	2.5b	Check	2.3b	MPB	2.1c	WPB
2.1b	WPB	2.3b	WPB	1.0c	Check	2.1c	Check

Means within a column followed by the same letter are not significantly different ($P < 0.05$).

In 3 of 4 wk in July when large captures were possible, more *T. undatulus* were collected in the SPB–baited than in WPB–baited traps. Relatively few *T. undatulus* were captured in any of the MPB– or *Ips*-baited traps. Only seven *T. undatulus* were collected from unbaited check traps in 6 wk, and few were captured in any of the August collections. In the 5 and 21 July collections, *T. undatulus* was consistently attracted in higher numbers to traps baited with SPB and WPB than to *Ips* or MPB aggregating pheromone (Fig. 2). There was only 1 wk between 5 and 21 July in which more *T. undatulus* were collected from the WPB– than from the SPB–baited trap. Few *T. undatulus* were captured in any traps during the two August collection periods.

In five of six weekly collections between 12 July and 10 August, the SPB traps also captured the DFB (Fig. 3). Although not resulting in significant differences in ranked catches, 199 DFB were captured in SPB and WPB traps, 20 were collected from MPB and *Ips* traps, and 16 were taken from the check traps. We conclude that this is a coevolved predator/prey system because the flight periods of *T. undatulus* and the Douglas-fir beetle are similar, few or no other bark beetles were recovered from SPB traps, and large numbers of *T. undatulus* were captured in other traps baited with DFB pheromone.

Significance of ranked catch is not dependent upon the magnitude of differences among means. It involves the consistency with which the traps baited with the same lure catch the most numbers of a specific insect, and use of Friedman's test is dictated by the collection of nonparametric data. Pooled data for collections of DFB show trends that suggest an attraction to SPB and WPB pheromones. However, DFB capture was most frequent and consistent in only one of the two locations in which surveys were conducted, and only three of the six catches were highly ranked. The low, but not significant, F probability for Friedman's test ($P > F = 0.1774$) suggests that the use of additional trap lines or better placement of trap lines in areas of DFB flight would show that the DFB is attracted to SPB and WPB pheromones. In the case of the predator, *E. lecontei*, capture in a single MPB–baited trap was relatively high, whereas catch in the other five MPB–baited traps was low. This resulted in no significant difference in ranked capture of *E. lecontei* in MPB–baited traps, even though inspection of the pooled data suggested attraction.

Because of its responsiveness to SPB and WPB pheromones, *T. undatulus* is a potential biological control agent for these scolytids. This conclusion is supported by the results of Chatelain & Schenk (1984), who found that *T. undatulus* was attracted in large numbers to sticky traps on MPB–attacked trees baited with frontalin or brevicomin. Augmenting populations of *T. undatulus* on these MPB brood trees by baiting with frontalin increased the incidence of *T. undatulus* larvae 3-fold and the mortality of emerging MPB adults by 7.1% (Chatelain & Schenk 1984).

Laboratory Bioassays with *R. grandis*. The mean number of *R. grandis* (±SEM) counted in the various parts of the test arena every 2 min after starting the experiments are presented in Fig. 4–7. The results of the *R. grandis* bioassays of *D. micans*, SPB, BTB, and SB frass (Fig. 4–7) should be read using Fig. 1 as reference. For example, Fig. 6 and 7 are read using male *R. grandis* response to BTB frass: at 10 min six males were at the frass (Fig. 6, A), one male was at the control area (Fig. 6, D), eight males were on the frass side of the chamber (Fig. 7, A + B), and three males were in the control side of the chamber (C) but not in the control circle, calculated by subtracting values in (A + B) + D from 12.

Both sexes of *R. grandis* are attracted to frass of the four tested *Dendroctonus* species. At 4 min into the bioassay, 6–8 of the *R. grandis* males were in the frass area (Fig. 6, A), and 8–11 were on the frass side of the petri dish (Fig. 7, A + B). These values did not change throughout the 10-min bioassay period. One *R. grandis* male went to the control circle (D) and remained there throughout the testing period (Fig. 7).

Tests of *R. grandis* female response show an attraction similar to that of the males to all the *Dendroctonus* frass (Fig. 4 and 5). From 4 min

Fig. 2

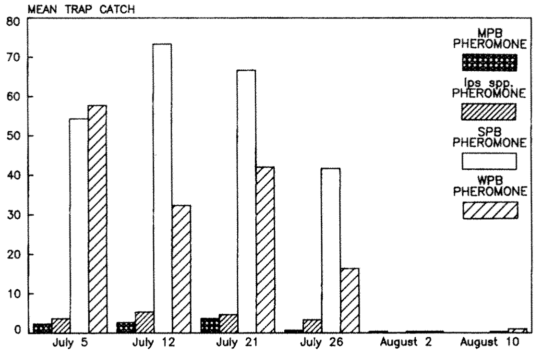


Fig. 3

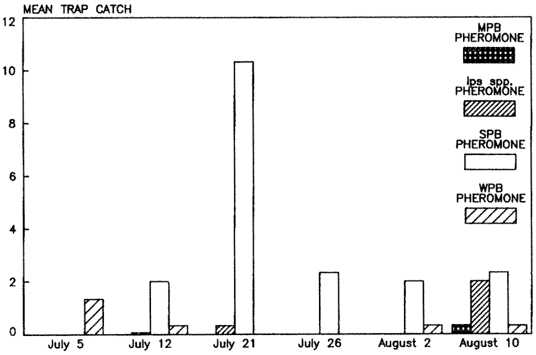
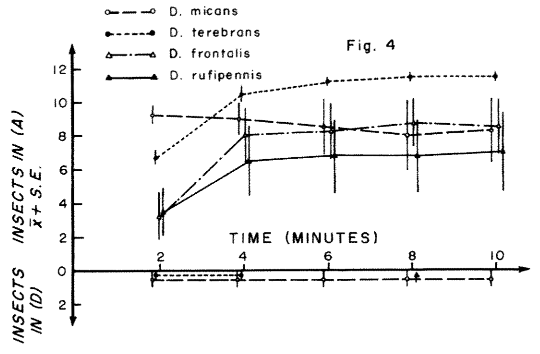


Fig. 2. Mean weekly catch of *T. undatulus* adults in replicated pheromone-baited Lindgren traps on the Flathead National Forest, Montana, 5 July–10 August 1984. Each bar represents the average catch from three randomly placed traps.

Fig. 3. Mean weekly catch of DFB 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.



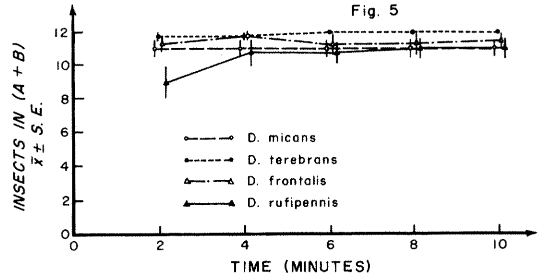


Fig. 4 and 5. Response of 12 female *R. grandis* to the frass of various *Dendroctonus* spp. (mean of four replicates). (4) A is the 1.0-cm frass test area; D is the 1.0-cm control area. (5) A + B is the frass test area of the 9.0-cm still-air odor-gradient chamber.

through the end of the bioassay period, 6–10 *R. grandis* females were at the frass (Fig. 4, A), and 10–12 were on the frass side of the test chamber (Fig. 4, A + B). One female was found in the control circle (D) during the 10-min *D. micans* bioassay; for 4 min, one female was in D during the BTB bioassay, and one female was in D at 8 min during the SPB frass bioassay (Fig. 4).

Except for bioassays of BTB frass with male *R. grandis* and of SB frass with female *R. grandis*, the number of insects on the test area was significantly higher than on the control area (Table 3). Direct observation during the tests showed that female *R. grandis* did respond to the SB frass, but they were either too mobile or too ready to aggregate with other females in the exact vicinity of the odor source, or they remained on the other side of the petri dish. The very high numbers of female *R. grandis* present on the frass side of the test chamber (Fig. 5, A + B) confirm these observations. The lack of response of male *R. grandis* to BTB frass may have resulted from the number of insects in the control area (Fig. 6, D). It is not known why a single female *R. grandis* remained in the control area during the *D. micans* frass bioassay (Fig. 4, D).

The results of the paired *t* tests comparing the mean numbers of *R. grandis* counted on the test area (A) and the control area (D) after 10 min in each series of four replicated tests are given in Table 3. Significantly more *R. grandis* of both sexes were found in the test area than in the control area in bioassays of attraction to *D. micans* frass and SPB frass. Significantly greater numbers of female *R. grandis* were found in the test area than in the control area when the test area held BTB frass, and significantly more male *R. grandis* were found in the test area than in the control area when the test area held SB frass. There were no significant differences between number of female *R. grandis* found in the test and control areas in bioassays of SB frass or between numbers of male *R. grandis* in test and control areas during bioassays of BTB frass.

The two-way analysis of variance (Table 4) showed no differences among *R. grandis* count means for attraction to the frass of the four tested *Dendroctonus* spp. Over the whole series of tests, no differences in response were seen for male and

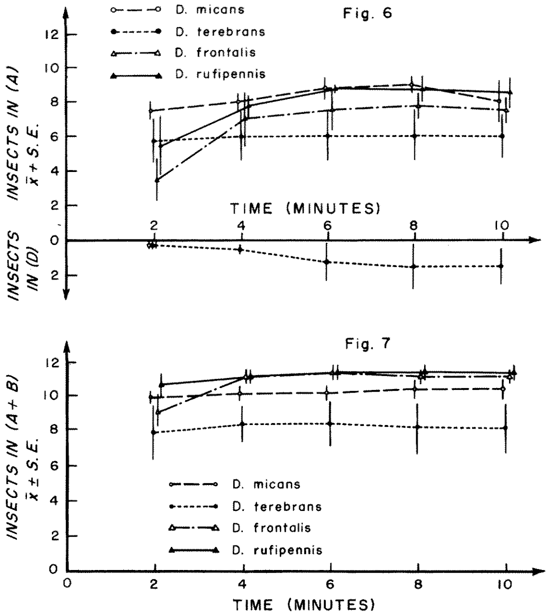


Fig. 6 and 7. Response of 12 male *R. grandis* to the frass of various *Dendroctonus* spp. (mean of four replicates). (6) A is the 1.0-cm frass test area; D is the 1.0-cm control area. (7) A + B is the frass test area of the 9.0-cm still-air odor-gradient chamber.

female *R. grandis*; there was variation in the response depending upon the sex of the predator. This produced a highly significant *F* value for the interaction ($P < 0.001$) (Table 4). The significant sex-×-frass interaction (Table 4) may have been due to the degree of response by female (Fig. 4 and 5) and male (Fig. 6 and 7) *R. grandis* to frass of BTB at the end of 10 min. Though both sexes of *R. grandis* were attracted to frass of all *Dendroctonus* spp., more female *R. grandis* were attracted to BTB frass than to the frass of the other *Dendroctonus* spp. (Fig. 4 and 5). Conversely, for male *R. grandis,* BTB frass was the least attractive of any of the four *Dendroctonus* spp. (Fig. 6 and 7).

These results show a general response of *R. grandis* to the frass volatile chemicals of the North American *Dendroctonus* species. Orientation at short range in response to an odor gradient is different from long-range orientation to an odor source linked to odor-triggered anemotaxis. Another point worth considering is the experimental method used. In testing insects in groups of 12 we assumed, based on preliminary tests, that there would be minimal interference among the beetles. This interference may not have been negligible and could have led to the reduced response by the female *R. grandis* for SB frass and of the male *R. grandis* for BTB frass. An obvious next step would be to conduct similar screen tests with individual beetles, or to conduct experiments in a wind tunnel to test long-range orientation. Although kept frozen, some frass samples could have been old when tested, and their origins were not always similar. The frass samples used were larval frass (*D. micans* and BTB), one adult frass (SPB), and one of unknown origin (SB). In spite of these differences, our results show that the odor of the frass of North American *Dendroctonus* spp. elicits a strong attraction in *R. grandis* similar to that elicited by the odor of the frass of its native prey, *D. micans* (Fig. 4–7). The response to the SB frass was not unexpected because this species attacks all species of *Picea* within its range (Wood 1963, 1982). The intensity of this response makes *R. grandis* attractive as a potential biological control agent for SB. The significant response of both sexes of *R. grandis* to SPB and BTB frass also shows it to be a potential biological control agent for both these pests.

Table 3. Results of paired *t* tests comparing the mean numbers of *R. grandis* on test (A) and control (D) areas shown in Fig. 1

Origin of frass	Male	Female
D. micans	$t_{obs} = 5.66$*	$t_{obs} = 3.56$*
D. terebrans	$t_{obs} = 2.18$NS	$t_{obs} = 39.84$*
D. frontalis	$t_{obs} = 8.66$*	$t_{obs} = 4.60$*
D. rufipennis	$t_{obs} = 7.24$*	$t_{obs} = 2.65$NS

*, $P < 0.05$; NS, not significant.

These results are interesting because the bark beetle's respective host trees apparently did not influence the response of *R. grandis* during the tests. SPB and BTB both attack *Pinus* within their range, but SB and *D. micans* attack mainly *Picea.* The latter, however, was recorded epidemic on pine on at least one occasion (Voolma 1980). *R. grandis* has also been found on scotch pine, *P. sylvestris* L., in brood chambers of *D. micans* (Palm 1948). This suggests that the host tree does not play an exclusive part in the orientation mechanisms of *R. grandis.* In addition, the commercial pheromone for SPB and SB is the same. However, it is not unusual to have two related insects from separate geographic areas using the same pheromone for intraspecific communication.

Trapping of *T. undatulus* with pheromones

Table 4. Comparison of the attraction of male and female *R. grandis* to the frass of various *Dendroctonus* species: two-way ANOVA

Sources of variation	df	SS	MS	*F*
Origin of frass	3	798.25	266.08	0.19NS
Sex of predators	1	2,390.00	2,390.00	1.75NS
Interaction	3	36,019.69	12,006.56	8.77***
Residual variation	24	32,838.56	1,368.27	

***, $P < 0.001$; NS, not significant.

represents only a first screening for potential biological control agents. Commercial pheromones, although 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. Pheromones might be a poor substitute for the actual frass of the bark beetles, which contains many more compounds. More efficient screening could be performed using frass or frass extracts instead of commercial pheromones. In addition, we are not sure how closely the development of insects like *T. undatulus* will be synchronized with the development of their new prey species. *T. undatulus* may not complete its development within the <30-d summer life cycle of SPB, but it may develop during the winter when the SPB life cycle is 60–90 d. *T. undatulus* may have an obligatory winter diapause and complete development only under 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*. *T. undatulus* may be more suitable as a biological control agent for WPB because of the similarities in the biology and behavior of WPB and DFB and the similarity of the climatic conditions in their habitats.

These studies provide evidence that insect enemies of SB, SPB, BTB, and *D. micans* should be able to locate any of these related insects 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 time, larval behavior, and synchronization of life cycles. Possibly, *R. grandis*, a predator of gregarious larvae of *D. micans*, would fail with solitary SPB larvae and meet only mild success with partly gregarious SB larvae. Laboratory tests of *R. grandis* are only a first step; they must be followed by thorough field experiments. Trapping experiments using SPB frass extracts are planned for Europe in 1986. Another question to be considered is that of the compatibility of predator and prey ecology. As detailed for *T. undatulus*, the life cycle may have to be synchronized. *R. grandis*, as a predator of the gregarious larvae of *D. micans*, seems very likely to be successful against *D. terebrans*, which also has gregarious larvae and a long life cycle on a living host tree.

We have shown that some *Dendroctonus* predators respond to bark beetle aggregation pheromones or frass volatile chemicals of potential new prey species. The determination that has to be made is what would happen in competition by these species with the insect enemies that are already there. Just because a predator responds to pheromones does not mean that it could live in a given habitat, or that it would disrupt the controls in existence for a native pest species.

We now believe that the attempt by Hopkins to use *T. formicarius* for control of SPB (Clausen 1956, Dowden 1962) and the attempt by Nebeker failed because *T. formicarius* kairomones are not the same as the SPB aggregating pheromone (Kohnle & Vité 1984). *T. formicarius* was probably not able to locate any SPB–attacked trees. Its response in the field to kairomonal synthetic compounds (Kohnle & Vité 1984) suggests that this clerid may be attracted to WPB or MPB.

The results of our experiments suggest that the predators tested can be used in a study to verify the contentions of Pimentel (1963), Carl (1982), Hokkanen & Pimentel (1984), and the work of Drooz et al. (1977) that show that insect enemies of allied species have potential as biological control agents. These 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, the attraction of exotic predators to frass volatiles of SPB, BTB, and SB, and the location of insects that are potential biological control agents of *Dendroctonus* spp. This research contributes to the development and the possible use of kairomone-based methods 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 research and pheromone-based behavioral research.

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. In Europe, however, the case of *D. micans* suggests that biological control is generally applicable to bark beetles. The main 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 of two series of experiments presented here: one involving *T. undatulus* cross-attraction to pheromones of allied North American *Dendroctonus*, and the other involving *R. grandis* attraction to frass of North American *Dendroctonus*. Introducing associates of allied species has been discussed as a promising way to achieve biological control (Pimentel 1963, Carl 1982, Hokkanen & Pimentel 1984) and has proved at least once to be efficient (Drooz et al. 1977). *T. undatulus*, *R. grandis*, and other species to be discovered through aggregation-pheromone screenings 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.

Conclusions. These studies demonstrate the presence of extraregional and exotic predatory insects having biological and behavioral characteristics that provide them with the potential to be biological control agents for the SPB and other native North American *Dendroctonus* bark beetles. In addition, we suggest that the lack of success of previous attempts at biological control was due to the lack of knowledge of prey-pheromone, predator-kairomone specificity where the exotic predator *T. formicarius* was released, and that this insect may be a potential predator of bark beetles in a different habitat. Continuing biological investigations of pest and natural enemy species are necessary so that we can make use of the extraregional and exotic insect agents available to us.

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. These studies provide evidence that at least two predatory species possess some of the necessary ecological and behavioral characteristics to be considered as potential biological control agents. The bulk of the work remains ahead. Only a methodical approach to the problem of new introductions will prove successful, and it is imperative that such an approach be taken in the near future.

References Cited

Bennett, W. H. & W. M. Ciesla. 1971. Southern pine beetle. U.S. Dep. Agric. For. Serv., For. Pest Leafl. 49.

Berryman, A. A. 1967. Estimation of *Dendroctonus brevicomis* (Coleoptera: Scolytidae) mortality caused by insect predators. Can. Entomol. 99: 1009–1014.

Billings, R. 1984. Forest pests in East Texas: past approaches, future challenges, pp. 1–5. *In* Proceedings, 10th Anniversary East Texas Forest Entomology Seminar, Kurth Lake, Tex.

Borden, J. H. 1982. Aggregation pheromones, pp. 74–139. *In* J. B. Mitton & K. B. Sturgeon [eds.], Bark beetles in North American conifers. Univ. of Texas, Austin.

Camors, F. B., Jr., & T. L. Payne. 1973. Sequence of arrival of entomophagous insects to trees infested with the southern pine beetle. Environ. Entomol. 2: 267–270.

Carl, K. P. 1982. Biological control of native pests by introduced natural enemies. Biocont. News Info. 3: 191–200.

Chatelain, M. P. & J. A. Schenk. 1984. Evaluation of frontalin and exo-brevicomin as kairomones to control mountain pine beetle (Coleoptera: Scolytidae) in lodgepole pine. Environ. Entomol. 13: 1666–1674.

Clausen, C. P. 1956. Biological control of insect pests in the continental United States. U.S. Dep. Agric. Tech. Bull. 1139.

Conover, W. J. 1980. Practical nonparametric statistics, 2nd ed. Wiley, New York.

Coster, J. E., T. L. Payne, E. R. Hart & L. J. Edson. 1977. Aggregation of the southern pine beetle in response to attractive host trees. Environ. Entomol. 6: 725–731.

Coulson, J. R. 1981. The Soviet–American environmental agreement and exchange of beneficial organisms, 1972–1979, pp. 1–11. *In* Proceedings, Joint American–Soviet Conference on Use of Beneficial Organisms in the Control of Crop Pests, College Park, Md.

Coulson, R. N. & R. W. Stark. 1982. Integrated management of bark beetles, pp. 315–349. *In* J. B. Mitton & K. B. Sturgeon [eds.], Bark beetles in North American conifers. Univ. of Texas, Austin.

Dahlsten, D. L. 1982. Relationships between bark beetles and their natural enemies, pp. 140–182. *In* J. B. Mitton & K. B. Sturgeon [eds.], Bark beetles in North American conifers. Univ. of Texas, Austin.

Dahlsten, D. L. & S. H. Dreistadt. 1984. Forest insect pest management. Bull. Entomol. Soc. Am. 30: 19–21.

Dixon, W. N. & T. L. Payne. 1979. Sequence of arrival and spatial distribution of entomophagous and associate insects on southern pine beetle-infested trees. Tex. Agric. Exp. Stn. Bull. MP-1432.

Dowden, P. B. 1962. Parasites and predators of forest insects liberated in the United States through 1960. U.S. Dep. Agric. Handb. 226.

Drooz, A. T., A. E. Bustillo, G. F. Fedde & V. H. Fedde. 1977. North American egg parasite successfully controls a different host genus in South America. Science 197: 390–391.

Duncan, D. B. 1955. Multiple range and multiple *F* tests. Biometrics 11: 1–41.

Dyer, E. D. A., P. M. Hall & L. Safranyik. 1975. Numbers of *Dendroctonus rufipennis* (Kirby) and *Thanasimus undatulus* Say at pheromone-baited poisoned and unpoisoned trees. J. Entomol. Soc. B.C. 72: 20–22.

Evans, H. F. 1985. Great spruce bark beetle, *Dendroctonus micans:* an exotic pest new to Britain. Antenna 9: 117–121.

Goeden, R. D. & L. T. Kok. 1986. Comments on a proposed "new" approach for selecting agents for the biological control of weeds. Can. Entomol. 118: 51–58.

Goyer, R. A. & C. K. Finger. 1980. Relative abundance and seasonal distribution of the major hymenopterous parasites of the southern pine beetle, *Dendroctonus frontalis* Zimmermann, on loblolly pine. Environ. Entomol. 9: 97–100.

Gregoire, J-C. 1984. *Dendroctonus micans* in Belgium: the stiuation today, pp. 48–62. *In* Proceedings, European Economic Community Seminar on the Biological Control of Bark Beetles (*Dendroctonus micans*), Brussels.

Gregoire, J-C., J. Merlin, J. M. Pasteels, R. Jaffuel, G. Vouland & D. Schvester. 1985. Biocontrol of *Dendroctonus micans* by *Rhizophagus grandis* in the Massif Central (France); a first appraisal of the mass-rearing and release methods. Z. Angew. Entomol. 99: 182–190.

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

Johansen, C. 1971. Principles of insect control, pp. 171–190. *In* R. E. Pfadt [ed.], Fundamentals of applied entomology. Macmillan, New York.

King, C. J. & H. F. Evans. 1984. The rearing and release of *R. grandis* against *D. micans* in the United Kingdom, pp. 87–97. *In* Proceedings, European Economic Community Seminar on the Biological Control of Bark Beetles (*Dendroctonus micans*), Brussels.

Klein, W. H. 1978. Strategies and tactics for reducing losses in lodgepole pine to the mountain pine beetle by chemical and mechanical means, pp. 148–158. *In* A. A. Berryman, G. D. Amman, R. W. Stark & D. L. Kibbee [eds.], Theory and practice of mountain pine beetle management in lodgepole pine forests—a symposium. Univ. of Idaho, Moscow.

Kohnle, U. & J. P. Vité. 1984. Bark beetle predators: strategies in the olfactory perception of prey species by clerid and trogositid beetles. Z. Angew. Entomol. 98: 504–508.

Leuschner, W. A. 1980. Impacts of the southern pine beetle. U.S. Dep. Agric. For. Serv. Tech. Bull. 1631: 137–152.

Linit, M. J. & F. M. Stephen. 1983. Parasite and predator component of within-tree southern pine beetle (Coleoptera: Scolytidae) mortality. Can. Entomol. 115: 679–688.

Miller, M. C. 1984a. Effect of exclusion of insect associates of *Ips calligraphus* (Germ.) (Coleoptera: Scolytidae) brood emergence. Z. Angew. Entomol. 97: 289–304.

1984b. Mortality contribution of insect natural enemies to successive generations of *Ips calligraphus* (Germar) (Coleoptera: Scolytidae) in loblolly pine. Z. Angew. Entomol. 98: 495–500.

Mills, N. J. 1983. The natural enemies of scolytids infesting conifer bark in relation to the biological control of *Dendroctonus* spp. in Canada. Biocont. News Info. 4: 305–328.

Moeck, H. A. & L. Safranyik. 1984. Assessment of predator and parasitoid control of bark beetles. Can. For. Serv. Info. Rep. BC-X-248.

Moser, J. C., R. C. Thatcher & L. S. Pickard. 1971. Relative abundance of southern pine beetle associates in East Texas. Ann. Entomol. Soc. Am. 64: 72–77.

Overgaard, N. A. 1968. Insects associated with the southern pine beetle in Texas, Louisiana, and Mississippi. J. Econ. Entomol. 61: 1197–1201.

Palm, T. 1948. Ett angrepp av *Dendroctonus micans* Kugel. pa tall (Col.: Scolytidae). Entomol. Tidskr. 69: 212–214.

Payne, T. L., J. C. Dickens & J. V. Richerson. 1984. Insect predator–prey coevolution via enantiomeric specificity in a kairomone–pheromone system. J. Chem. Ecol. 10: 487–492.

Pimentel, D. 1963. Introducing parasites and predators to control native pests. Can. Entomol. 95: 785–792.

Price, T. S. & C. Doggett [eds.]. 1978. A history of southern pine beetle outbreaks in the southeastern United States. Georgia Forestry Commission, Macon.

Pschorn-Walcher, H. 1977. Biological control of forest insects. Annu. Rev. Entomol. 22: 1–22.

Riley, M. A. 1983. Insect enemies of *Ips calligraphus* (Germar) on felled loblolly (*Pinus taeda* L.) and slash (*P. elliottii* Englemann) pines in Louisiana. M.S. thesis, Louisiana State Univ., Baton Rouge.

Stehr, F. W. 1982. Parasitoids and predators in pest management, pp. 135–173. *In* R. L. Metcalf & W. H. Luckmann [eds.], Introduction to insect pest management. Wiley, New York.

Stein, C. R. & J. E. Coster. 1977. Distribution of some predators and parasites of the southern pine beetle in two species of pine. Environ. Entomol. 6: 689–694.

Stevens, R. E. 1981. Natural enemies of bark beetles in the United States: potential for biological control, pp. 59–62. *In* Proceedings, Joint American–Soviet Conference on Use of Beneficial Organisms in the Control of Crop Pests, College Park, Md.

Swain, K. M., Sr., & M. C. Remion. 1981. Direct control methods for the southern pine beetle. U.S. Dep. Agric. Agric. Handb. 575.

Sweezey, S. L. & D. L. Dahlsten. 1983. Effects of remedial application of lindane on emergence of natural enemies of the western pine beetle, *Dendroctonus brevicomis* (Coleoptera: Scolytidae). Environ. Entomol. 12: 210–214.

Thatcher, R. C. & L. S. Pickard. 1964. Seasonal variations in activity of the southern pine beetle in East Texas. J. Econ. Entomol. 57: 840–842.

Thatcher, R. C., G. N. Mason, G. D. Hertel & J. L. Searcy. 1982. Detecting and controlling the southern pine beetle. South. J. Appl. For. 6: 153–159.

Turnock, W. T., K. L. Taylor, D. Schroder & D. L. Dahlsten. 1976. Biological control of pests of coniferous forests, pp. 289–311. *In* C. B. Huffaker & P. S. Messenger [eds.], Theory and practice of biological control. Academic, New York.

Tvaradze, M. S. 1976. On the acclimatization of *Rhizophagus grandis* for control of *Dendroctonus micans*. Sb. Nauch. Rab. Izuch. B. E. Luboeda Gruzii, Tbilisi 2: 76–90 (in Russian).

van den Bosch, R., P. S. Messenger & A. P. Guitierrez. 1982. An introduction to biological control. Plenum, New York.

Voolma, K. 1980. The distribution and ecology of the European spruce beetle *Dendroctonus micans* Kug. (Coleoptera, Scolytidae) in Estonia. Metsanduslikud Uurim. 16: 44–51.

Wood, S. L. 1963. A revision of the bark beetle genus *Dendroctonus* Erichson (Coleoptera: Scolytidae). Brigham Young Univ., Provo, Utah.

1982. The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. Great Basin Nat. Mem. 6.

Younan, E. G. & F. P. Hain. 1984. Sequence of arrival of insects associated with severed pines during a collapsing southern pine beetle epidemic. N.C. Agric. Res. Serv. Tech. Bull. 277.

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