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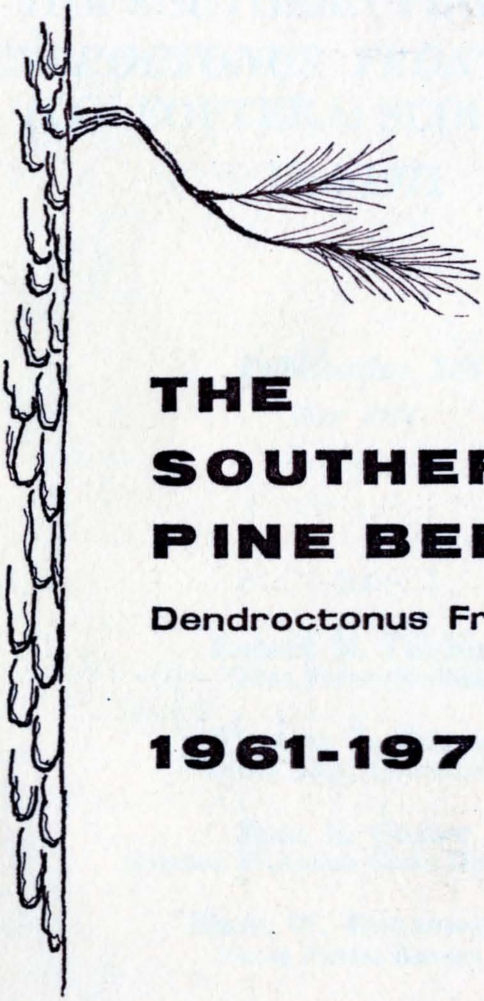

THE SOUTHERN PINE BEETLE

Dendroctonus Frontalis Zimm

1961-1971

Publication 108
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THE SOUTHERN PINE BEETLE
DENDROCTONUS FRONTALIS ZIMM.
(COLEOPTERA: SCOLYTIDAE)
1961-1971

Publication 108
May 1972

By

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INTRODUCTION

In the last decade, since the appearance of the comprehensive reviews of southern pine beetle (SPB), *Dendroctonus frontalis* Zimm. (Coleoptera:Scolytidae)*, literature by Thatcher (1960) and Dixon and Osgood (1961), much research progress on the insect has been realized. This review condenses reports of research on the insect published since 1961.

In most instances the papers reviewed herein have been published in referenced journals or are available as Ph.D. dissertations or M.S. theses.

SOUTHERN PINE BEETLE DEVELOPMENT

Southeast Texas has been a center of SPB activity since 1957 and considerable research effort has been directed to the area. Thatcher and Pickard (1967) investigated the seasonal development of the SPB in East Texas to determine the number of generations per year which the insect underwent. SPB were reared in a field insectary and completed seven and a partial eighth generations per year. A summer generation was completed in as few as 26 days while approximately 3½ months were required for a winter generation. Emergence of overwintering adults usually occurred during February and March (Thatcher 1967).

The intensity of attack, length of trunk infested, and subsequent development of SPB in East Texas, as measured by ratio of increase (ratio of increase $= \dfrac{\text{brood emergence/ft.}^2\text{ bark}}{2 \times \text{number of attacks/ft.}^2\text{ bark}}$), were demonstrated to vary seasonally (Thatcher and Pickard

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*We are indebted to W. H. Bennett, U. S. Forest Service, Alexandria, La. and R. C. Thatcher, U. S. Forest Service, Washington, D. C. for helpful suggestions in the preparation of this review.

1964). Average ratios were 2:1 or 3:1 for each generation from the late fall through early spring but dropped to less than 1:1 during June through September. Length of trunk infested was greatest during the cool season and least during the hot season. The number and size of new infestations increased most rapidly during April, May, and June then declined to a seasonal low in July and August. The intensification of artificial control measures in fall, winter, and early spring, when the insect has the highest potential for increase and the slowest rate of development was suggested.

Microenvironmental factors which influence the development of SPB under field and laboratory conditions have been studied. Phloem moisture content and temperature regimes necessary to produce vigorous SPB broods under field conditions were measured and later reproduced in environmental chambers controlled to approximate the measurements obtained in the field (Gaumer and Gara 1967). Optimum rearing conditions were found to range from 20° C to 22° C and 50% to 60% relative humidity. The phloem of brood logs dried at a rate which approached that of a naturally infested tree. A rapid decrease in phloem moisture content to levels below 200% (oven dry weight) for ca. 10 days was found to be essential for brood survival.

Bremer (1967) also investigated the role of different temperature regimes on the development of SPB. SPB introduced into pre-peeled log sections were reared in both constant and fluctuating temperature cabinets. The optimum temperature for beetle development was found to be near 24° C. Temperatures above 27° C and below 21° C and fluctuating temperatures (20° C - 30°C) were detrimental to brood production and to the survival of offspring.

SPB have been mass reared in pine bolts under laboratory conditions by Clark and Osgood (1964a, 1964b, 1966). Rearing containers consisted of trash cans supplied with supplemental air and mason jars for beetle collection. Artificially infested logs were placed inside the cans and emerging brood, which are positively phototaxic, collected in the mason jars.

Clark (1965a) reported a simple rearing technique for obtaining eggs or young larvae of the SPB. The technique involved the use of 14-inch bolts over which a chamber of heavy paper and polyethylene sheeting was constructed. Adult beetles were introduced into the chamber and 6 to 12 days later the chamber was removed and the bark shaved away to expose the SPB eggs and larvae. Cylindrical screen cages fitted with collecting funnels and trap jars were also used by Covington (1969) to rear five successive generations. The average brood production per attack was 25 beetles.

Clark (1965b) reported an artificial diet for the SPB and other bark beetles. The diet was prepared with either purified, finely ground cellulose or a homogenized inner bark base and contained various sugars, agar, mold inhibitor, and enriching ingredients. When prepared it was poured into petri dishes where it solidified. SPB eggs or early larvae were placed in slits cut in the surface of the diet and then gently covered over with a small piece of the substrate. As many as 24 eggs or larvae could be placed in a petri dish and about 20% of the eggs and larvae reached adulthood. No oviposition by adult female beetles on the diet was reported.

SOUTHERN PINE BEETLE PARASITES, PREDATORS, AND ASSOCIATES

The SPB has a large complement of insect parasites, predators, and associates. Bushing (1965) compiled a synoptic list of parasites in the family Scolytidae and reported 11 species of insects to be parasites of the SPB.

Franklin (1969a) verified, through observation and rearing experiments utilizing naturally and artificially infested SPB bolts, that six species of Hymenoptera were parasites of the SPB in Georgia. Nine additional species of Hymenoptera were implicated as parasites. A method for rearing and observing predators and hymenopterous parasites, which utilizes a gallon glass jar with a compressed air inlet to aid in maintaining suitable moisture content, has been described by Franklin (1967).

Two comprehensive lists of insects which are parasites, predators, or associates of the SPB have been published. Overgaard (1968) reared 42 families and 84 species of insects from naturally infested trees in Texas, Louisiana, and Mississippi. The trophic function of these species was provided where known. Of the 84 species seven were known predators and eight were known parasites of the SPB.

The relative abundance and within tree distribution of SPB associates collected in East Texas and Louisiana and reared in the laboratory was compiled by Moser et al. (1971) and Thatcher (1971). Forty families and 96 species and 25 families and 60 species were recovered in Texas and Louisiana respectively and the trophic function was also identified where known. Ten species were indicated to be predators of SPB and nine species were parasites.

The SPB parasites and predators identified from the studies of Bushing (1965), Franklin (1969a), Overgaard (1968), Williamson (1970, 1971), Moser et al. (1971), Thatcher (1971), and unpublished work by Camors and Payne from Southeast Texas are contained in Table 1 and Table 1a. From these studies, seven predators and 14 parasites have been assigned to the SPB.

Very little is known of the biology of the various SPB predators, with the exception of the clerid beetle, *Thanasimus dubius* (F.) (Coleoptera:Cleridae). Franklin and Green (1965) observed *T. dubius* predation of SPB on shortleaf pine, *Pinus echinata* Mill., in North Carolina. The intensity of predation was modified by bark condition of the host tree with thick bark trees being preferred. SPB attacks were less on trees with thick bark than on those with thin.

The biology and habits of *T. dubius* have been studied by Thatcher and Pickard (1966). Adult and larval feeding habits were studied along with the effect of predation on SPB attack and development in caged bolts. *Thanasimus dubius* adults in laboratory cages consumed an average of 2.2 adult SPB per day for the first 10 weeks, whereas during their development the larvae destroyed as many as 100 immature SPB. Details of the life cycle of *T. dubius* were also considered. Development under laboratory conditions was completed in 5 to 10 weeks.

McGraw and Farrier (1969) conducted an extensive study of the parasitic mites of the superfamily Parasitoidea (Acarina: Mesostigmata) associated with the SPB and other species of *Dendroctonus* as well as species of *Ips*. The report provides an excellent source for identification of the mites.

Moser and Roton (1971) investigated 96 species of mites associated with the SPB to determine which species might be of value in biological control.

Avian predation of the SPB has been observed for a number of years. Three species of woodpeckers have been identified as predators in the Gulf South: the pileated woodpecker (*Dryocopus peleatus* (L)), the downy woodpecker (*Dendrocopus pubescens* (L)), and the red-bellied woodpecker, (*Centurus carolinus* (L)).

The influence of woodpecker predation on broods of SPB has been suggested as a potential significant biological control.

Brood density in bark dislodged by woodpeckers has been compared by Overgaard (1970) with brood density in bark still remaining on trees. Samples were radiographed and interpreted according to procedures outlined by Fatzinger and Dixon (1965). Woodpeckers reduced brood density 24.4%, however, sufficient brood survived in dislodged bark to permit reinfestation.

The blue stain fungus, *Ceratocystis minor* (Hedgc. and Hunt), (Ascomycete) is usually associated with SPB and has been suggested to contribute both to the mortality of the trees and of the beetle. Franklin (1970) observed that parent beetles avoided stained areas but that oviposition did not appear to be affected. Barras (1970) found that beetle development was considerably better in laboratory prepared bolts which had not been inoculated with *C. minor* as compared to inoculated bolts. *Ceratocystis minor* inoculum causes rapid wilting of infected trees and may enhance beetle mass attack by curtailing production of oleoresins.

Several species of pathogenic bacteria and fungi have been isolated from SPB (Moore 1971). The most numerous bacteria species associated with dead beetles included *Pseudomonas aeruginosa* (Schroeter), *Bacillus thuringiensis* Berliner, and *Flavobacterium* spp. The important fungal species included *Fusarium solani* (Martius), *Beauveria bassisna* (Balsams), and *Aspergillus flavus* Link.

The impact of the fungal and bacterial pathogens on SPB in North Carolina was shown to be substantial and involved the destruction of nearly one third of the SPB brood examined. No single pathogen caused populations to fluctuate (Moore 1971).

A method suitable for isolating entomogenous fungi and bacteria from SPB was developed by Moore (1970a). Saprophytic fungal overgrowth was eliminated by surface sterilization which then allowed for the detection of internal and nonsporulating organisms.

Nematodes naturally associated with SPB have received little study. Only two species have been identified: *Mikoletzkya*

Table 1. — Parasites of the Southern Pine Beetle

I. HYMENOPTERA
  1. Braconidae
    a. *Cenocoelius nigrisoma* (Rohwer) b, c
    b. *Coeloides pissodes* (Ashmead) a, b, c, e, f
    c. *Dendrosoter sulcatus* Muesebeck a, b, c, d, e
    d. *Doryctes* sp. c, e, f
    e. *Spathius pallidus* Ashmead a, b, c, e, f
    f. *Ecphylus (Sactopus) schwatzii* (Ashmead) e
    g. *Spathius canadensis* Ashmead e
    h. *Vipio rugator* (Say) e
  2. Eurytomidae
    a. *Eurytoma tomici* Ashmead c
  3. Pteromalidae
    a. *Cecidostibia dendroctoni* Ashmead a, b, e, f
    b. *Heydenia unica* Cook and Davis a, b, d, e, f
  4. Torymidae
    a. *Roptrocerus eccoptogastri* (Ratzeburg) a, b, c
    b. *Roptrocerus zylophagorum* (Ratzeburg) a, b, e, f
    c. *Liodontomerus* sp. e

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a. Verified as SPB parasite by Franklin 1969.
b. Indicated as SPB parasite by Overgaard 1968.
c. Indicated as SPB parasite by Moser et al. 1971.
d. Verified as SPB parasite by Camors and Payne 1971.
e. Indicated as SPB parasite by Bushing 1965.
f. Indicated as SPB parasite by Thatcher 1971.

Table 1a.— Predators of the Southern Pine Beetle

I. COLEOPTERA
  1. Cleridae
    a. *Thanasimus dubius* (F.) b, c, d, g
  2. Histeridae
    a. *Cylistix cylindrica* (Paykull) e, g
  3. Ostomidae
    a. *Tenebroides collaris* (Strum) b, c, g
    b. *Temnochila virescens* (F.) b, c, d, g
II. DIPTERA
  1. Dolichopodidae
    a. *Medetera bistriata* Parent f, g
III. HEMIPTERA
  1. Aradidae
    a. *Aradus cinnamomeus* Panzer b
  2. Anthocoridae
    a. *Lyctocoris elongatus* Reuter b, g
    b. *Scoloposcelis mississippensis* Drake and Harris b, d

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b. Indicated as SPB predator by Overgaard (1968)
c. Indicated as SPB predator by Moser et al. (1971)
d. Verified as SPB predator by Camors and Payne (1971)
e. Indicated as predator by Williamson (1970)
f. Indicated as predator by Williamson (1971)
g. Indicated as predator by Thatcher (1971)

bandelier (Massey) (Massey 1966) and *Aphelenchulus barberus* Massey (Massey 1957).

Of the SPB associates identified, few have been treated in detail. The flight and attack pattern of the ambrosia beetle, *Platypus flavicornis* (F.) (Coleoptera:Platypodidae) in relation to SPB infestations was studied by Coster (1969). *Platypus flavicornis* attacked the lower stems of pine trees which had been mass attacked previously by the SPB. The ambrosia beetles began to arrive from 4 to 6 days after mass attack by SPB and continued to land on the trees for ca. 10 days. Orientation was believed to be associated with host produced odors.

SOUTHERN PINE BEETLE HOST AND SITE FACTORS

Since the earliest investigations of SPB, it has been clear that adverse environmental factors and variations in host condition are related to fluctuations in beetle populations. Bennett

(1968) points out that in addition to the changes by natural disturbances, man-induced factors such as logging practices and incomplete silvicultural procedures may contribute to a high incidence of SPB.

Hardin County, in Southeast Texas, has been the center from which many SPB outbreaks in Texas originate. Soil and stand conditions in this area were examined to attempt to relate these factors to past incidence of SPB outbreak (Lorio 1968). Approximately 56% of the county was characterized by imperfectly or poorly drained soils and was largely forested with pine-hardwood mixtures. During any one year, 75% or more of the SPB spots reported occurred over poorly or imperfectly drained soils. The basal area of the sites investigated varied from about 75 to 250 ft.^{2} and estimates of the site index ranged between 61 and 110 feet at 50 years. Increment cores indicated that radial growth had decreased in stands with more than 125 ft.^{2} basal area. The data presented support the supposition that SPB infestations are related to poorly drained and over-stocked sites.

Oleoresin exudation pressure (OEP) has been identified as an indicator of the internal water balance of a tree (Vite′ 1961). Although not as yet demonstrated, OEP has been suspected to influence the susceptibility of southern pines to attack (Lorio and Hodges 1968b). Several methods for measuring OEP for limited time periods have been developed and refined for bark beetle studies using either Bourdon gauges (Vite′ 1961, Anderson 1964) or manometers (Hodges and Lorio 1968). Methods for continuous recording have also been developed (Dodge and Miller 1968, Helseth and Brown 1970).

Oleoresin exudation flow (OEF) has also been proposed as a measure of tree resistance to bark beetles (Wilson 1968, Mason 1969, Walrod 1970). However, Hodges and Lorio (1971) established that OEF was poorly correlated with the relative water content (RWC) of needles and the water potential of twigs.

The effects of induced moisture stress on OEP and the RWC of the inner bark of loblolly pine, *P. taeda* L. and the susceptibility of stressed trees to SPB attack were investigated by Lorio and Hodges (1968a). Diurnal patterns of OEP were related to change in soil and atmospheric moisture. RWC of inner bark reflected soil moisture conditions and diameter growth response. SPB attack was most severe on trees which had been continuously flooded and had suffered the greatest reduction in OEP and RWC.

In further studies with OEP and bark beetle susceptibility, Lorio and Hodges (1968b) compared OEP in pines on flat sites to that in pines growing on the low mounds typically found in the Gulf Coast Plains. During drought, OEP was more reduced on the poorly drained flat sites than in pines growing on the mounds. The response was attributed to deficient pine root systems on flat sites which, in turn, were thought to be the result of mortality caused by certain rootlet pathogens. In addition Lorio and Hodges (1971) found that the soil water regime and tree growth responses on flat sites indicated an unstable growth site that probably affected tree rooting and, in time, tree susceptibility to SPB attack.

In addition to the effects on OEP, soil moisture condition brings about certain chemical changes of the inner bark of pines that may be related to beetle development (Hodges and Lorio 1969). Loblolly pines, subjected to drought, showed a marked increase in reducing sugars, nonreducing sugars, and total carbohydrates; and approximately an equivalent decrease in starch. Continuous flooding of trees resulted in the same basic pattern except that the increase in sugars occurred later, after severe stress had been established (Hodges and Lorio 1969). Increases in beetle populations were suggested to be related to chemical changes in inner-bark tissue which favorably influence beetle nutrition.

Alterations of carbohydrate and amino acid content brought on by SPB and its associated fungi during colonization of host trees have been shown (Hodges et al. 1968a, 1968b, Barras and Hodges 1969). In uninfested trees, concentrations of the free amino acids were greater 8 m. above the ground than at the 1 m. level. The reverse situation was true for protein bound amino acids (Hodges et al. 1968a). These changes in chemical composition were suggested to be related to the preference of bark beetles for certain parts of a tree.

When loblolly pines were inoculated with SPB and its associated fungi, a marked decrease in total free amino acids occurred in the inner bark (Hodges et al. 1968b). Concurrently, protein-bound amino acids increased. SPB-fungi infection had no qualitative effect on amino acid composition. Total nitrogen content in the infected materials was increased. While the source of such nitrogen was unknown, there appeared to be a relationship between SPB and its normal fungal associates that favored development of the beetles.

In a similar study Barras and Hodges (1969) investigated the influence of SPB and associated microorganisms on the carbohydrate content of the inner bark of loblolly pine. Glucose, fructose, and sucrose were detected in inner bark treated with the SPB-microorganism complex (*C. minor* and the unidentified mycangial fungus) and the two fungi separately and together. The treatments drastically lowered the reducing-sugar level. Starch content remained unchanged in all treatments.

Lightning strikes also induce drastic physical and chemical changes in pines. Lightning strikes on loblolly pines have been found to reduce OEP, oleoresin flow, and RWC of inner-bark tissue and result in a decrease in sucrose and an increase in reducing sugar content of inner bark (Hodges and Pickard 1971). Such changes generally favor success of SPB attack and subsequent brood development. Lightning struck pines have long been observed to serve as centers for new infestations, particularly during the hotter summer months when SPB activity is reduced in the Western Gulf Region.

The fact that lightning struck trees are rapidly colonized by bark beetles suggests that some sort of attractant is released as a result of the severe damage or electrical discharge, or as a result of subsequent chemical changes in the tree following the early establishment and development of microorganisms in the wounds. However, in studies of the attractiveness to SPB of yeasts, fungi, and bacteria normally found in lightning struck trees, no evidence of attraction could be found (Howe et al. 1971). It was concluded that the weakened trees were found by the beetles through chance and then successfully overcome.

The condition of the host tree has, thus, been found to influence brood development and survival through several means. Generally, host factors favorable to SPB exhibit their effects by either pre-disposing the tree to attack by the adult beetles or providing inner-bark conditions favorable for brood development. In addition, the host may influence the release of attractants by attacking beetles.

Vite´ and Crozier (1968) noted that host material subjected to desiccation lost its attractiveness rapidly. Since loss of attractiveness coincided with the beginning of extensive feeding, and since extensive feeding was prohibited in hosts where the oleoresin flow was sustained, it was concluded that condition of the host, principally its water balance, had a strong influence on the production and release of attractants.

Coster (1970a) tested the response of field populations of SPB to infested host materials of three different moisture contents. The drier host logs became attractive rapidly and then declined while the hosts with the highest moisture content became attractive more slowly and then retained a high level of attractiveness for a longer period of time. Gas-liquid chromatography confirmed the field results showing that the principle insect-produced component of the SPB pheromone, frontalin, was depleted most rapidly when the beetles began their attack in hosts with the lower inner bark moisture content. High moisture levels reduced the rate of depletion of attractant substances from the beetles, presumably by providing a longer period of oleoresin flow that prevented the insects from beginning to feed extensively.

SOUTHERN PINE BEETLE OLFACTORY BEHAVIOR

Since the initial observations by Anderson (1948) on the manner in which *Ips pini* (Say) selects and attacks host trees, remarkable research progress on bark beetle aggregation and host selection have occurred.

The first field experiments on the response of the SPB to attractants were conducted by Vitе́ et al. (1964) in southeast Texas. Southern pine beetles were attracted in large numbers by volatile materials emanating from log sections infected with SPB. Response to the attractive log sections was most pronounced in the forenoon and throughout the afternoon and was strongly influenced by weather conditions. Greatest attraction occurred on clear days.

Subsequently it was found that field populations of SPB could be manipulated by attaching freshly attacked log sections to pre-selected trees or by exhausting air from a box containing a large number of freshly attacked log sections (Gara et al. 1965). Male and female SPB responded in approximately equal numbers. In the same study, canvas sleeve olfactometers, mechanized aerial sweep nets, and trough-type olfactometers were used to study attack behavior and colonization. Colonization occurred in two phases: an initial phase, focused by olfactory response toward a tree and to the portion of the tree originally attacked, and an eruptive phase in which mass aggregation occurred on vertical objects near established sources of attraction. SPB were successfully induced to attack pre-selected trees and the possibility of utilizing the attractant principle in biological control procedures was suggested (Gara et al. 1965).

To aid in studying the olfactory behavior of SPB a field olfactometer was designed which enabled collection of responding beetles in jars. The olfactometer eliminated the necessity of removing individual beetles from traps (Gara 1967b).

The spread and collapse of SPB outbreaks was shown by Gara (1967a) to be closely related to the production of attractants. Emerging SPB attacked newly infested or adjacent trees near their brood trees. Infestations were shown to enlarge as long as emergence synchronized with the availability of the attractive principle. When sources of attraction were unavailable in the vicinity of the outbreak, the beetles dispersed and concentrated elsewhere, in some cases up to a mile or more from the original infestation.

The flight, landing, and gallery construction activities of the SPB, as influenced by attractive host materials, have been investigated by Coster (1967) and Coster and Gara (1968). Flying SPB were found in greater concentration near sources of attraction. Landing appeared to be induced by olfactory stimuli and was related to the intensity of the stimuli. Under epidemic conditions the area of attraction was greater and beetles were induced to land as far away as 30 feet from the center of attraction. Under endemic conditions landings were confined to much shorter distances (ca. 5 ft.). Within the endemic area, boring activity was limited to the immediate area of the attractant source, whereas under epidemic conditions SPB attack was less selective. Wind velocity greater than 4.5 mph curtailed SPB flight activity.

Within a particular SPB infestation the sequence of attack was shown not only to be influenced by concentration of attractant, but also by the presence of uninfested stems near the center of attraction. Such trees received the majority of initial attacks when populations were high (Gara and Coster 1968). Wide spacing 20 to 25 feet was considered sufficient to curtail expansion of individual infestations.

Boring frass and crushed SPB were found to be attractive to SPB in laboratory tests conducted by Tsao and Yu (1967). Frass produced by female beetles was more attractive to males than females; conversely the frass of male beetles was more attractive to females than males. An n-hexane extract of females was strongly attractive to males and slightly repellent to the females. The attractiveness of extracts of virgin females to males was greater than for mated females.

Vite′ and Renwick (1968) tested solvent extracts of SPB for attractiveness in the field and confirmed the hindgut area to be the source of highest concentration of the attractant. SPB were capable of releasing the population aggregating pheromone(s) immediately after emergence. The chemical messengers responsible for aggregation of SPB were reported to be insect-produced, and therefore correctly termed pheromones. Solvent extracts of crushed beetles and resin together were highly attractive to flying SPB.

Emergent, unfed female SPB contain the largest amounts of pheromone compounds, but the quantity of the chemicals declined as feeding progressed (Coster and Vite′ 1972). In the same studies, mating did not cause immediate loss of either field attractiveness or hindgut pheromone content. In fact, logs containing mated beetles were more attractive during the first 48 hours of attack than were logs containing virgin females alone.

Early investigations of SPB pheromone behavior were concerned primarily with the production of attractants by virgin beetles and the effects of the chemicals on the behavior of flying beetle populations. Parent adults of SPB are known to emerge from their initial host and attack a second time, producing a second brood. Franklin (1969a) pointed out the two-fold significance of this phenomenon: (1) one group of parent beetles could produce at least two offspring generations and (2) the aggregating pheromone was produced at two intervals, rather than one, in the life cycle of the beetle. Over-lapping emergence from different trees occurred.

Coster (1970a) compared the attractiveness and pheromone content of re-emerged females with that of virgin female SPB. Gas-liquid chromatography was used to detect two components of the pheromone, frontalin and *trans-verbenol,* in SPB hindguts. Virgin females attracted about 4.5 times as many beetles from natural populations as did the re-emerged females. Virgin female SPB contained 4.1 times as much frontalin and 1.9 times as much *trans*-verbenol as the re-emerged beetles.

COMPOUNDS IMPLICATED IN SOUTHERN PINE BEETLE ATTRACTION

Several compounds have been identified and associated with SPB attraction. Verbenone, *trans* -verbenol, frontalin, and α-pinene all have been demonstrated to play a significant role in SPB aggregation.

Renwick (1967) identified the two volatile oxygenated terpenes, *trans*-verbenol and verbenone, from the hindguts of SPB and western pine beetle (*D. brevicomis* Lec.) (WPB), through gas chromatographic, infrared, and nuclear magnetic resonance spectroscopy analysis. Verbenone was associated with the males of both species and *trans*-verbenol with the females.

A population aggregating pheromone was isolated by Renwick and Vite′ (1968) from the hindgut of SPB females. Using mass spectral data it was confirmed that the same compound occurred both in WPB males and Douglas-fir beetle (*D. pseudotsugae* Hopk.) (DFB) females. Since the compound occurred in much greater amounts in WPB, subsequent identification was performed using this source. The compound, 1,5-dimethyl-6,8-dioxabicyclo (3.2.1) octane, was identified and synthesized by Kinzer et al. (1969) from diethyl ether extracts of approximately 6,500 hindguts of WPB males. The trivial name "frontalin" was assigned to the compound.

The three volatile compounds mentioned thus far (*trans*-verbenol, verbenone, and frontalin) along with two additional compounds *cis*-verbenol, and brevicomin, exo-7-ethyl-5-methyl-6,8-dioxabicyclo (3.2.1) octane, (an aggregation pheromone of the western pine beetle) were all reported to be associated with male and/or female SPB in the following manner (Pitman et al. 1969):

	Compound				
	***Cis*-verbenol**	***trans*-verbenol**	**verbenone**	**brevicomin**	**frontalin**
Male, emergent	**0**	**m**	**M***	**m**	**0**
Female, emergent	**m**	**M***	**m**	**0**	**m***

M = A major component, m = a minor component, 0 = trace or absent
*** = Verified by mass spectrometry.**

The five compounds listed by Pitman et al. (1969) were also reported to occur in various combinations and proportions in three other *Dendroctonus* species and aggregation was hypothesized to be maintained by specificity of olfactory receptor systems.

More recent studies have, however, failed to confirm the presence of brevicomin in SPB (Vite′ and Renwick 1971). *Endo*-brevicomin, the isomer of brevicomin, was detected in some male SPB in sub-nanogram quantities.

Renwick and Vite′ (1969) investigated resin volatiles from SPB host pine trees in southeast Texas (loblolly pine; shortleaf pine; longleaf pine, *P. palustris* Mill., and slash pine, *P. elliottii* Engelm.), and found α-pinene to be the major terpene component. The attractiveness of frontalin was substantially enhanced by the addition of α-pinene over the addition of any other host-tree terpene.

Many of the discoveries relating to isolation of SPB attractants were accomplished using a technique termed "differential diagnosis" (Vite′ and Renwick 1970). Comparative gas chromatographic analysis and field bioassays were combined to detect compounds which were active in SPB attraction.

A review of the research leading to the isolation, identification, and synthesis of SPB attractants is given by McNew (1970), while Wood and Silverstein (1970) and Silverstein (1970) have provided critiques of the same research.

ROLE OF SPB ATTRACTANT COMPOUNDS

The first compounds isolated and identified from SPB were *trans*-verbenol in females and verbenone in males (Renwick 1967). Since *trans*-verbenol was present in large amounts in female hindguts, its possible implication as a component and/or precursor of the pheromone was investigated. Early field tests indicated that neither verbenone nor *trans*-verbenol *per se* was attractive to flying SPB (Pitman et al. 1968, Vite′ and Crozier 1968). The addition of synthetic *trans*-verbenol to naturally infested billets did, however, increase their attractiveness to field populations (Pitman et al. 1968).

Since frontalin appeared to be equally attractive when bioassayed with either oleoresin or *trans*-verbenol (Kinzer et al.

1969, Renwick and Vite′ 1969), it was deduced that *trans*-verbenol acted as a supplement to host terpenes in beetle attraction. During colonization of trees with low OEP, *trans*-verbenol was thought to substitute for α-pinene in providing the highly attractive mixture necessary for attracting large numbers of beetles (Renwick and Vite′ 1969, 1970). No role for *cis*-verbenol has been reported for SPB.

Verbenone, released predominantly by males, affects flying populations in two manners (Renwick and Vite′ 1969). At low concentrations, the sex ratio of responding beetles is altered through a decreased response of males. At higher concentrations, verbenone inhibits the response of both sexes. The compound is, thus, important in regulating attack density on host trees.

Verbenone also appears to affect certain predators of SPB (Vite′ and Williamson 1970, Williamson 1971).

Frontalin is the major insect-produced component of the aggregating pheromone (Kinzer et al. 1969). The synthetic material is relatively unattractive when presented alone but the addition of either α-pinene or *trans*-verbenol greatly increases its effectiveness (Renwick and Vite′ 1969). Male SPB predominate in the response to this frontalin-α-pinene or frontalin-*trans*-verbenol mixture by a ratio of about 3:1. Several analogs of frontalin were found to be unattractive to SPB, except for 5,7-dimethyl-6,8-dioxabicyclo (3.2.1) octane (Renwick 1970b). Its attractiveness was only slight.

Frontalin, as a component of the aggregating pheromone, appears to be used by certain SPB predators to locate their prey. Both *T. dubius* and *M. bistriata* respond to pheromone sources (Vite′ and Williamson 1970, Williamson 1971).

The larval parasite *Heydenia unica* (Cook and Davis) (Hymenoptera:Pteromalidae) was attracted in significant numbers to olfactometers baited with frontalin, *trans*-verbenol, verbenone, and α-pinene. The latter alone attracted twice as many *H. unica* as any of the pheromones and four times as many *H. unica* as the control (Camors and Payne 1971).

Synthetic *endo*-brevicomin, detected in male SPB, is a strong inhibitor of SPB to synthetic pheromone sources (Vité and Renwick 1971). It has been suggested that *endo*-brevicomin may serve to prevent overcrowding of populations in host trees.

Using synthetic chemicals Renwick and Vité (1969) and Renwick (1970a) duplicated the host selection and attack process of SPB. Attack mechanisms for SPB, WPB, and DFB were proposed by Renwick and Vité (1969, 1970). The attack mechanism for SPB was given as follows: "Females beginning the attack release frontalin and *trans*-verbenol as they land on the bark. Initial boring causes the exudation of resin and release of α-pinene. The resulting potent attractant combination causes the aggregation of large numbers of beetles, with males predominating by about 3 to 1. In epidemic conditions many females land on adjacent trees, which become the next focal point of attraction. The aggregating males in turn release verbenone, which first reduces the response of males and eventually reaches a level that inhibits further response of both sexes. The inhibition by high verbenone concentrations is accompanied by the cessation of resin exudation, and frontalin is no longer produced by the successfully feeding females."

Borden and Stokkink (1971) have provided an annotated bibliography of publications dealing with secondary attraction in the family Scolytidae.

SOUTHERN PINE BEETLE OLFACTORY PERCEPTION

The mutual occurrence of the various host and insect-produced attractants of *Dendroctonus* spp. has inspired research into the mechanisms of olfactory perception.

Electrophysiological techniques have been developed by Payne (1970, 1971) to measure SPB response to attractants. Electroantennograms (EAG'S), which are a measure of the change in voltage potential which occurs along the antenna in response to an olfactory stimulus, were recorded from the antennae of male and female SPB in response to host and insect-produced attractants (Payne 1970, 1971).

Both male and female SPB responded, at the antennal level, with increased intensity to increased concentrations of frontalin. Similar results were found for SPB response to the host tree terpenes α-pinene and 3-carene and to the aggregation pheromone of the WPB, brevicomin. Antennal olfactory response to frontalin and brevicomin were similar. Behaviorally, however, brevicomin has been found to inhibit attraction of SPB to frontalin (Vite' and Renwick 1971). It is interesting to note that although the SPB has not been found to produce brevicomin, it does possess antennal olfactory receptors responsive to the pheromone. It is apparent that olfactory perception by the SPB of pheromones produced by other bark beetle species is not specific on a response-no response basis at the antennal level. Specificity of response to pheromones of closely related species most likely occurs in the second order of neural transmission. Antennal olfactory perception of pheromones in the SPB appears to be no more specific than is pheromone production in the genus *Dendroctonus* (Payne 1970).

SOUTHERN PINE BEETLE SUPPRESSION

Many insecticidal "control" procedures for SPB have evolved and subsequently been abandoned. Early efforts centered on introducing poisons into living attacked trees. Later, chemicals, mainly kerosene and ortho-dichlorobenzene, were applied to infested trees in attempts to control the insect.

Benzene hexachloride (BHC) (Hexachlorocyclohexane), application to infested trees was the standard control procedure in the South from the early 1950's until late in the 1960's. The standard formulation of BHC in SPB control was 0.5% gamma isomer in diesel oil. Bennett and Pickard (1966) reported that a 1.0% gamma isomer BHC in water emulsion was as effective as the standard oil solution in summer control. In winter the emulsion was less effective. Estimated effectiveness of control for the summer, using either the oil or the emulsion treatment, was indicated to be 97%. In winter, the control was estimated to be 81% for the emulsion and 97% for the oil of formulation.

The standard application procedure formerly used to control SPB involved felling and bucking infested trees and spraying the infested materials completely with BHC. Logs were rolled over in order to achieve complete chemical coverage of the bark. Anderson (1967) investigated the efficiency of BHC application to infested logs which were not rolled over to achieve full coverage with insecticide and concluded that only approximately 40% of the brood were destroyed when the modified technique was used.

The use of fast-acting herbicides containing cacodylic acid (dimethyl arsenic acid) injected into trees recently infested by bark beetles has been suggested as a potential control measure.

Ollieu (1969) compared several alternative methods of southern pine beetle control. The efficiency, based on brood reduction, of cacodylic acid-injected trees was compared to that of several modifications of cutting and topping, cutting and leaving, and control trees. The cacodylic acid treatment of freshly attacked trees resulted in 97% reduction of brood as compared to control trees. Treatment was less successful in reducing brood survival if trees had been attacked 3 to 4 days before treatment. The "cut and top" and "cut and leave" procedures resulted in lower brood survival than control trees.

Williamson (1970) studied the movement of cacodylic acid in loblolly pine and the effect of the chemical on SPB and concluded that development of the beetle was maintained below levels of increase in treated trees. Presumably the moisture content of the trees injected with cacodylic acid was maintained at a level adverse to the development of SPB. Procedures for injecting cacodylic acid were also studied by Williamson (1970). The most efficient method involved introducing the chemical via a squeeze bottle into circumferential ax frills approximately 4 feet from the base of the tree.

One of the primary objections to using insecticide treatment for control of the SPB has been that beneficial insects (parasites and predators) were sacrificed along with the pest species. Williamson (1970) reported that beneficial insects were unaffected in trees treated with cacodylic acid. In the same study Williamson (1970) found that BHC effectively destroyed larvae and adults of beneficial insects as they moved on and within the tree bark in search of SPB.

R. G. Crozier (unpublished report in Williamson 1970) demonstrated statistically the inadequacy of BHC in SPB management for East Texas. SPB populations were shown to increase, as evidenced by the increased number of reported infestation spots, with both efficiency of control (i.e., removal of infested trees by salvage) and increased use of BHC.

The potential use of host- and insect-produced attractants in the manipulation of bark beetle populations to permit management of the pest has been recognized for a number of years. Vite′ and Pitman (1967) defined the aim of manipulation as the "use of stereotyped olfactory response in which the insects react to plant- and insect-produced attractants for concentrating, dispersing or otherwise misdirecting field populations to their detriment."

Based on a knowledge of SPB behavior, the availability of synthetic frontalin and α-pinene (formulated together and called "frontalure"), and information concerning the mode of action and effect of cacodylic acid on SPB, a pest management technique was proposed (Vite′ et al. 1970 from Williamson 1970) and utilized on a trial basis by the Texas Forest Service and cooperating landowners in East Texas during 1970. In general, the technique, termed "ground check control," involved baiting cacodylic acid treated trees with frontalure.

The rationale behind the use of the ground check control procedure along with details of application of the system have been reviewed by Vite′ (1970, 1971).

The standard mixture of frontalure used during the 1970 trial application of the system was 1 part frontalin to 2 parts α-pinene. Frontalure was deployed in plastic vial caps attached to selected trees by spring tacks. The average release rate of frontalure from the caps was approximately 1 mg. hour at 22° C for about 40 days.

Two approaches have been utilized in the manipulation of *Dendroctonus* species with attractants (Vite′ 1970): (1) induction of aggregation on host trees and (2) traps. The induction of aggregation on host trees has been accomplished in two ways: (a) "point application," in which host trees were baited in the area of naturally occurring bark beetle outbreaks or the baiting of trees marked for harvest, and (b) "area application," in which host trees were baited at certain intervals regardless of the actual occurrence of active brood trees. Several methods and types of trapping devices have also been utilized (Vite′ 1970).

Salvaging timber infested with SPB has become a widely used method of curtailing the activity of SPB. If salvage is carried out shortly after trees are attacked by SPB, the timber is still merchantable and suitable for the manufacture of certain wood products. Kucera (1969) reviewed some of the advantages and disadvantages of salvage logging and suggested the importance of combining salvage with chemical control procedures. Part of the expense of chemical control could be deferred through sale of timber.

Barron (1971) studied wood substance loss and changes in moisture content of trees killed by SPB. Specific gravity reduction after six months varied from 5% to 16%. Moisture content declined 29% to 52% within the first month after attack, but then quickly tapered off. Based on the study, the following recommendations were suggested for consideration in using salvaged timber: (1) encourage early utilization of beetle-killed trees, (2) relate wood property reported in the study to limits for appropriate usage, (3) make weight adjustments for weight-scaling beetle-killed trees, (4) chemically treat high-value logs when rapid utilization is not possible, (5) leave trees standing until time for shipment to the mill to reduce deterioration, and (6) conduct an exhaustive study to determine guides for field identification of time since death of beetle-killed trees.

Biological control agents have been suggested as suitable population deterrents for SPB. The influence of the DD-136 strain of the nematode *Neoaplectana carpocapsae* Weiser (Steinernematidae) on SPB was evaluated by Moore (1970a). The nematodes were concentrated in 0.1% formalin plus a wetting agent and sprayed onto SPB infested bolts. Forty-four percent of the brood and adult SPB were killed as a result of the activity of the nematodes.

SOUTHERN PINE BEETLE SURVEY AND DETECTION

The occurrence of SPB over large geographic and often remote areas has necessitated the development of suitable aerial survey and detection methods.

Three systems have been utilized and have certain advantages and disadvantages both of which are determined largely by the intended use of the survey information collected.

The first method of aerial detection, "sketch-mapping," was developed by Heller et al. (1955). In this method aerial observers plot SPB infestation spots on existing aerial photographs or maps. The marked photographs are used by crews on the ground for locating the infestation spots. Survey flight lines are determined, again, based on the purpose for which the survey is being conducted.

Aldrich et al. (1958) investigated the observational limits for aerial sketch-mapping of SPB damage in the Southern Appalachian mountains and concluded that strip width should be restricted to ½ mile when small SPB spots were to be detected. Best observational results were obtained from an altitude of 1000 feet and at speeds not greater than 100 miles per hour. Discolored foliage of infested pine trees could be observed for distances of 2 miles at altitudes of 3000 to 5000 feet over level terrain (Heller et al. 1955). Aldrich et al. (1958) have indicated that aerial sketch-mapping tends to be inaccurate because observers overlook infestation spots, a failing which results in an underestimation of insect activity.

The second method of survey, "operation recorder survey," was developed by Ketcham (1964) and is reported to be more accurate than sketch mapping. The observer is restricted to viewing a 5-chainwide strip at a flying altitude of 500 feet. Information from operation recorder surveys can be subjected to statistical analysis which provides estimates of the number of infestation spots and number of actively infested trees per 1000 acres with 90% confidence limits (Ketcham 1964).

The most notable disadvantage to the operation recorder method is that it can be used only in areas of level terrain, because differences in ground elevation vary the width of the sample strip viewed by the aerial observers (Ciesla et al. 1967).

The third method of survey, "aerial photographic survey," was described by Ciesla et al. (1967). Fifty-acre plots were superimposed on color aerial photographs taken at a scale of 1:3960. The plot size of 50 acres was selected because it could be easily placed on a 9 x 9-inch aerial photograph at the 1:3960 (16 inches = 1 mile) scale. Heller et al. (1959) had demonstrated the scale to be highly effective for detecting trees killed by SPB.

Ektachrome infrared Aero film has been shown to be superior to standard color film for photographic surveys. Color film has also been shown (Heller et al. 1959) to be more suitable than panchromatic black-and-white film.

The information obtained from aerial photographic surveys and subsequent ground surveys is suitable for providing estimates of the number of spots and number of trees actively infested by SPB per 1000 acres of host type with 90% confidence limits (Ciesla et al. 1967).

The methods used by the U. S. Forest Service in surveying, detecting, and evaluating SPB have been reported in detail. Procedures utilized in aerial photography, radiographic sampling of

SPB brood density, and interpretation of the significance of the survey data are considered (Anonymous report 1970, 1970a).

Aerial detection of SPB is based upon the ability of an observer or camera to distinguish between attacked and unattacked trees, which is possible with pines only when foliage coloration has faded. The degree to which the foliage of an attacked tree has faded has little relationship with the stage of development of SPB. The season of the year influences the rapidity of coloration change and also the predominant life stage within the tree (Doggett 1971).

The potential use of synthetic attractants as a survey instrument was investigated by Nash (1970). SPB and parasites and predators of SPB responded to mixtures of frontalin and α-pinene deployed in plastic vial caps and positioned on sticky mailing tubes.

TAXONOMIC ASPECTS

Recent taxonomic studies on SPB have been directed toward the elucidation and significance of morphological structures which are suitable for use in distinguishing the sex of SPB. The prominence of frontal tubercles depth of frontal groove, presence or absence of a transverse ridge on the anterior portion of the pronotum, differences in the seventh tergite, and stridulating mechanism have all been indicated as useful means of separating the sexes of SPB. Osgood and Clark (1963) conducted a study to determine the accuracy of these characters in making sexual determinations. The frontal tubercles were found to be more numerous and the frontal groove much deeper on males than females. The males also lacked the transverse ridge on the pronotum which was characteristic of females. Use of these characters provided 100% accuracy in determining the sex of SPB. In the same study the sex ratio of SPB adults was found to be 1 to 1.

The transverse ridge across the anterior area of the pronotum, which was characteristic of the females, was shown by

Barras (1966) to be a mycangium or fungus respiratory organ. The ridge was most easily observed in callow adults, which lack other distinct features commonly used as secondary sex characters. Happ et al. (1971) further investigated the fine structure and function of the mycangium.

Schofer and Lanier (1970) have associated a protruding lobe between the eighth sternite and ninth tergite of females of the mountain pine beetle *D. ponderosae* (Hopk.) and have indicated that the character may be of value in sexing pupae of all *Dendroctonus* spp.

A taxonomic revision of all *Dendroctonus* placed *D. frontalis* in synonymy with *D. arizonicus* Hopk. and *D. mexicanus* Hopk. (Wood 1963).

ECONOMICS

The SPB is generally considered the most economically important insect pest of Southern forests. Outbreaks of SPB have been reported in the southern United States since 1882.

Table 2. Statistics on the Southeast Texas Southern Pine Beetle Epidemic, 1958-1969

Calendar Year	TFS Expenditures	Landowner Expenditures	Gross Area Affected (Acres)	Number Infested Spots
1958	3,259	$ 15,114	60,000	55
1959	2,762	23,399	100,000	108
1960	6,213	103,565	200,000	437
1961	8,400	178,174	600,000	943
1962	21,615	469,806	4,500,000	2500
1963	21,095	94,059	2,000,000	1639
1964	11,870	34,687	2,900,000	534
1965	40,153	140,371	3,000,000	1685
1966	97,222	194,343	4,000,000	1925
1967	98,751	400,000	4,500,000	3221
1968	178,638	483,000	6,000,000	2993
1969	98,814	73,560	6,292,000	2365

Table 3. Volume of Pine Timber Killed by the Southern Pine Beetle in Southeast Texas since 1958

Year	Sawlogs (M bd. ft.) *	Pulpwood (Cords) *	Total (M cu. ft.) *
1958	500	0	84
1959	2,500	2,500	598
1960	8,000	8,000	1,912
1961	17,887	24,000	4,715
1962	93,043	111,110	23,538
1963	4,084	1,920	820
1964	2,501	1,420	520
1965	3,797	7,743	1,192
1966	6,256	6,930	1,544
1967	7,194	8,566	1,818
1968	17,644	22,037	4,533
1969	7,341	7,478	1,760
Grand Total	170,747	201,704	43,034

*Conversion factors: 167 cu. ft./M bd. ft. and 72 cu. ft./cord

East Texas has sustained the most consistent series of infestations with eight different outbreaks having been reported. The latest and most severe epidemic began in 1958 and is still continuing in 1971. The original area of infestation, in the latest outbreak, was confined to a 60,000-acre tract in southeast Texas, in 1958, and has subsequently spread to include 6.2 million acres.

Damage caused by SPB has had a marked effect on the economy of East Texas. In the interlude between 1958 and 1969 individual landowners and the Texas Forest Service have expended $2,798,870 in attempting to manage the insect (Table 2).

The volume of pine timber killed in Texas by SPB is contained in Table 3. A conservative estimate of 170,747 M bd. ft. of sawlogs and 201,704 cords of pulpwood or a grand total of 43,034 M cu. ft. valued at over 5.5 million dollars were destroyed by SPB.

The intensity of occurrence of SPB in East Texas from 1966-1971, based upon aerial detection of multiple-tree infestations, has been recorded by the Texas Forest Service (Figure 1).

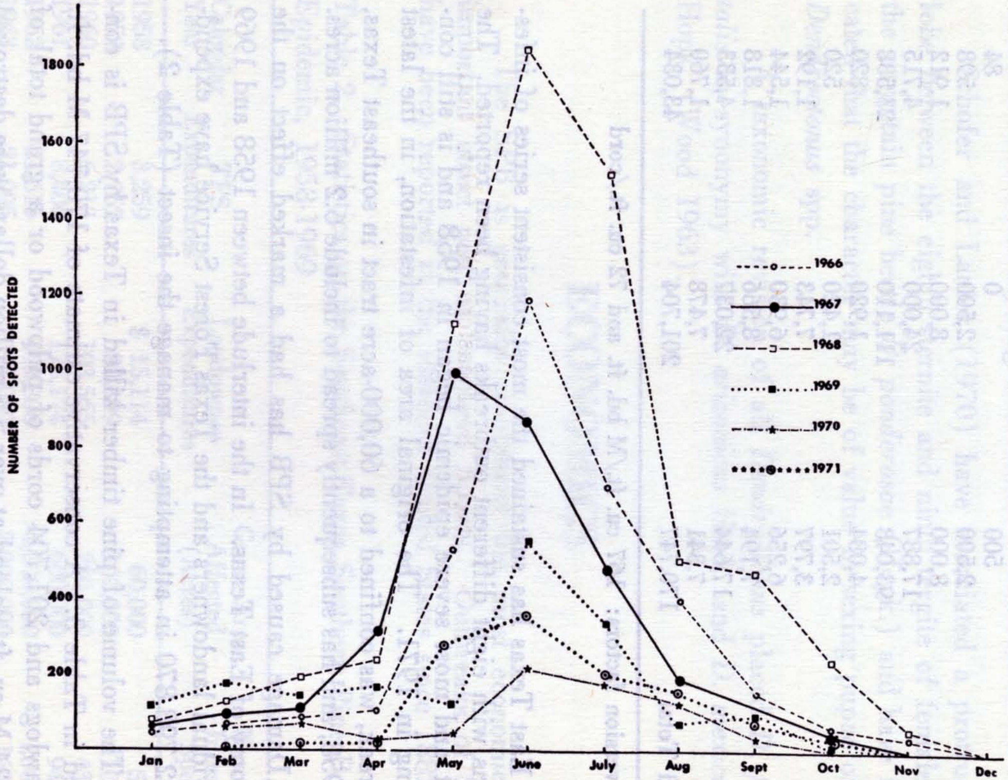

Figure 1. Newly detected southern pine beetle spots by month for 1966-1971.

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