SECONDARY ATTRACTION IN THE SCOLYTIDAE: AN ANNOTATED BIBLIOGRAPHY

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FOREST RESEARCH LABORATORY CANADIAN FORESTRY SERVICE VICTORIA, BRITISH COLUMBIA

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FOREWORD

Although the phenomenon of secondary attraction was recognized as early as 1930 in the family Scolytidae (Coleoptera), the subject received only occasional and limited attention until recently. During the past decade, however, many publications on various aspects of this complex subject have appeared. Research has progressed from the discovery of secondary attraction in many species to the isolation, identification and synthesis of insect-produced pheromones, and work of this nature is continuing. Knowledge of secondary attraction has now reached the point at which it may soon be applied on a practical basis to manipulate and control scolytid populations. At this time, therefore, we felt it would be useful to assemble, annotate and index the literature on the subject.

In this bibliography we follow the customary distinction between primary and secondary attraction. Primary attraction refers only to attraction emanating from host trees or logs. Secondary attraction includes additional attraction which follows initial attack of a new host by "pioneer" beetles. It usually results in the aggregation of a natural population and mass attack of the host. Secondary attraction may simply be an increase in

Associate Professor and Research Technician, respectively, Pestology Centre, Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia.

most often, however, it has proved to be a result of insect-produced, attractive compounds (pheromones) which may act alone or in combination with host volatiles. In many cases the precise nature of secondary attraction remains obscure or is subject to controversy. We have tried to identify such cases in the annotations.

Even though secondary attraction may not be the principal theme
of many of the publications listed, the annotations are primarily confined
to the contribution of each paper to this subject. We have not included
theses or descriptive brochures in the literature cited, since significant
discoveries included in such manuscripts are usually published elsewhere.

There are three indexes: author or co-author; taxonomic, including taxa that occur in the title or annotation, but not all other taxa mentioned in each manuscript; and subject, which, although quite selective, provides reference to most works that include significant contribution to the subject indexed.

The work was completed as part of a study on scolytid pheromones supported by Extra Mural Research Grant No. F58 from the Canada Department of Fisheries and Forestry. The review of the literature was concluded on March 31, 1971.

BIBLIOGRAPHY

1. Anderson, R. F. 1948. Host selection by the pine engraver. J. Econ. Ent. 41: 596-602.

In field tests with <u>Ips pini</u>, demonstrates that the activity of pioneer beetles in logs has a greater attractive effect than the host material itself, and presents data to show that this attraction is produced by the male beetles. Contends that the termination of attraction despite continued infestation argues against the role of yeasts in secondary attraction. Advances the theory that secondary attraction is important in aggressive species of <u>Dendroctonus</u> in attracting the large numbers of beetles necessary to overcome host resistance.

2. Anonymous. 1966. The seduction of bark beetles. Sci. Amer. 215: 64-65.

For general interest, reports the independent isolation and identification of the sex attractant produced by bark beetles in the genus <u>Ips</u> by 2 research groups: 1) G. B. Pitman and J. A. A. Renwick, of the Boyce Thompson Institute for Plant Research, and J. P. Vité, of the University of Göttingen (their isolation and identification later proved to be incomplete), and 2) R. M. Silverstein and J. O. Rodin, of the Stanford Research Institute. (D. L. Wood of the University of California was a co-worker with the latter group.) States that Silverstein's group has also synthesized the <u>Ips</u> pheromone.

 Atkins, M. D. 1966. Behavioural variation among scolytids in relation to their habitat. Can. Ent. 98: 285-288.

Discusses migration as an important part of adult behavior of most scolytids since the impermanence of their habitats necessitates its occurrence. Suggests that secondary attraction may have evolved in conjunction with the utilization of such habitats. Use of secondary attraction to increase the attractiveness of potential hosts would reduce losses of flying beetles during migration and host location.

4. Atkins, M. D. 1966. Laboratory studies on the behavior of the Douglas-fir beetle, <u>Dendroctonus pseudotsugae</u> Hopkins. Can. Ent. 98: 953-991.

As part of a comprehensive behavioral study, presents data indicating that <u>D. pseudotsugae</u> females exhibited more host-positive responses (i.e., boring activity) on logs infested with virgin females than on logs infested by mating pairs, and showed very few responses to uninfested logs. Males did not bore in, but searched the bark surface. When placed on logs containing virgin females, males either headed directly toward female galleries or found them by walking around them in circles of decreasing diameter, and then rapidly disappeared into the entrance hole.

5. Atkins, M. D. 1968. Scolytid pheromones - ready or not. Can. Ent. 100: 1115-1117.

Discusses some of the dangers and difficulties in use of scolytid pheromones such as: physiological and genetically controlled behavioral differences, host resistance, attraction of beneficial insects and poorly understood odor meteorology. Urges research on biology, behavior and genetics to balance that on pheromone identification and synthesis, in order to develop capacity for the "scientific use of scolytid pheromones."

6. Baker, J. E. and D. M. Norris. 1968. Further biological and chemical aspects of host selection by <u>Scolytus multistriatus</u>. Ann. Ent. Soc. Amer. 61: 1248-1255.

In discussion of this work on primary host attraction and selection, the authors reiterate an earlier contention that while pheromones in S. multistriatus may be present, proof of their existence is still lacking.

7. Bakke, A. 1967. Pheromon in the bark beetle, <u>Ips acuminatus</u> Gyll.

Z. angew. Ent. 59: 49-53.

Demonstrates in the field that males of this European species, while attacking logs, produce a pheromone which attracts both sexes equally.

8. Bakke, A. 1970. Evidence of a population aggregating pheromone in <u>Ips typographus</u> (Coleoptera: Scolytidae). Contrib. Boyce Thompson Inst. 24: 309-310.

Reports the results of field experiments in which fresh Norway spruce logs infested with 10 male <u>I</u>. <u>typographus</u> in greenhouse traps attracted approximately seven times as many beetles as uninfested control logs.

Apparently a codiscovery of a pheromone in <u>I</u>. <u>typographus</u> (See Nos. 114 and 115).

 Barr, B. A. 1969. Sound production in Scolytidae (Coleoptera) with emphasis on the genus <u>Ips</u>. Can. Ent. 101: 636-672.

A review of stridulation in the Scolytidae and an experimental investigation of its function in <u>Ips confusus</u>. Olfactory recognition of males
by females was indicated, since females entered and stridulated in
artificial entrance holes surrounded with attractive male frass. Suggests
that both pheromones and sound are important in species—specific communication.

10. Bedard, W. D. 1964. Variation in capacity of <u>Ips confusus</u> to reach attractive hosts, p. 137-142. <u>In</u> H. D. Gerhold, E. J. Schreiner, R. E. McDermott and J. A. Winieski (eds.), Breeding pest-resistant trees. Pergammon Press, Oxford.

An attempt to relate the variability of insects within a population to their destructive capacity as pests. Although some inhibition of <u>I</u>.

<u>confusus</u> response to male pheromone possibly occurred in the field,
beetles in laboratory bioassay vacillated between light— and pheromone—

positive responses when given the choice. Flight exercise, reduction in air pressure or brief feeding did not affect pheromone response, but injury such as unilateral antennectomy or higher concentration of attraction enhanced it. Reaches the conclusion that present knowledge of host-finding behavior is too limited to permit most test results to be a clear measure of host-finding capacity.

11. Bedard, W. D. 1965. The biology of <u>Tomicobia tibialis</u> (Hymenoptera:

Pteromalidae) parasitizing <u>Ips confusus</u> (Coleoptera: Scolytidae)

in California. Contrib. Boyce Thompson Inst. 23: 77-81.

As part of a comprehensive study on the biology of <u>T</u>. <u>tibialis</u>, reports that both sexes were attracted to the odor produced by male <u>I</u>. <u>confusus</u> boring in ponderosa pine, whereupon the female parasites oviposited into adult ips attracted to the same odor.

12. Bedard, W. D. and L. E. Browne. 1969. A delivery-trapping system for evaluating insect chemical attractants in nature. J. Econ. Ent. 62: 1202-1203.

For field bioassay of volatile attractants, describes a portable, continuous air-flow system consisting of an air pressure tank, aeration tube release system, and wire mesh cylinders coated with sticky material.

13. Bedard, W. D., R. M. Silverstein and D. L. Wood. 1970. Bark beetle pheromones. Science 167: 1638-1639.

A response to a published letter by Dr. G. B. Pitman (See No. 85).

Points out differences in methodology which make comparisons difficult.

Answers Pitman's specific comments on activation or accentuation of frontalin and activity of brevicomin. Presents data to show that brevicomin is an essential component of <u>D. brevicomis</u> pheromone (Pitman questioned this) and that myrcene is a far more effective synergist for brevicomin than 3-carene (which is not present in all <u>D. brevicomis</u> hosts), suggested by Pitman as the more likely synergist.

14. Bedard, W. D., P. E. Tilden, D. L. Wood, R. M. Silverstein, R. G. Brownlee, and J. O. Rodin. 1969. Western pine beetle: field response to its sex pheromone and a synergistic host terpene, myrcene. Science 164: 1284-1285.

In field tests, <u>Dendroctonus</u> <u>brevicomis</u> were attracted in decreasing numbers to: female infested bolts, myrcene with brevicomin, female frass extract, and <u>exo-brevicomin</u>. Myrcene alone was not attractive, but <u>exo-brevicomin</u> alone attracted the predator beetle <u>Temnochila</u> virescens chlorodia.

15. Bellas, T. E., R. G. Brownlee and R. M. Silverstein. 1969. Synthesis of brevicomin, principal sex attractant in the frass of the female western pine beetle. Tetrahedron 25: 5149-5153.

Describes in detail the reaction sequence and experimental synthesis of brevicomin through acid catalyzed hydrolysis and cyclization of the cis-epoxide.

16. Borden, J. H. 1967. Factors influencing the response of <u>Ips confusus</u> (Coleoptera: Scolytidae) to male attractant. Can. Ent. 99: 1164-1193.

In laboratory experiments, elucidates the effect of various factors on response of <u>I</u>. confusus to male attractant, including: decline in attractiveness of frass and insect response in fall and winter; reduced response after prior exposure of beetles to frass odor; the necessity of male maturity for attractant production; decline in attractiveness in direct relation to the number of mates the producing males have taken; decreased response in reproducing females, and inhibition of take-off flight in both sexes when in contact with or in the odor of attractive frass. Attempts to use laboratory data to construct and explain a probable sequence of events in nature.

17. Borden, J. H. and R. B. Bennett. 1969. A continuously recording flight mill for investigating the effect of volatile substances on the flight of tethered insects. J. Econ. Ent. 62: 782-785.

Describes the operation of a rotary flight mill with a photocell-ratemeter-paper chart recording system. Odor of female frass introduced into the path of flying male <u>Dendroctonus</u> pseudotsugae and <u>Trypodendron lineatum</u> caused abrupt cessation of flight.

18. Borden, J. H. and C. E. Slater. 1969. Sex pheromone of <u>Trypodendron</u>

<u>lineatum</u>: production in the female hindgut-Malpighian tubule
region. Ann. Ent. Soc. Amer. 62: 454-455.

Establishes that hindguts with Malpighian-tubules from virgin female

- T. lineatum, which had bored into host logs for 16 hours, were attractive at a concentration of two female equivalents to male beetles. Guts from mated females, otherwise given identical treatment, were not. Since females bored into but did not ingest wood stained with acid fuchsin, ingestion of host material is not considered a prerequisite to pheromone production.
- 19. Borden, J. H. and D. L. Wood. 1966. The antennal receptors and olfactory response of <u>Ips confusus</u> (Coleoptera: Scolytidae) to male sex attractant in the laboratory. Ann. Ent. Soc. Amer. 59: 253-261.

Describes 5 types of antennal sensilla including sensilla basiconica and sensilla trichodea, both of which are permeable to crystal violet dye.

Orientation after various surgical or coating treatments on the antennal clubs implicated sensilla trichodea as sex pheromone receptors. Orientation after unilateral antennectomy confirmed the hypothesis of klinotactic orientation.

20. Borden, J. H., R. G. Brownlee and R. M. Silverstein. 1968. Sex pheromone of <u>Trypodendron lineatum</u> (Coleoptera: Scolytidae): production, bio-assay, and partial isolation. Can. Ent. 100: 629-636.

Describes techniques for collection and preliminary isolation of <u>T. lineatum</u> pheromone, and bioassay in a modified arrestment olfactometer. Female frass was far more attractive than host sawdust. Frass extract and distillate were attractive in concentrations as low as 10⁻⁶ gram equivalents of raw frass. The ether eluate from silica-gel fractionation was highly attractive.

21. Borden, J. H., K. K. Nair and C. E. Slater. 1969. Synthetic juvenile hormone: induction of sex pheromone production in <u>Ips confusus</u>. Science 166: 1626-1627.

Reports that topical applications of greater than 25 μg of a juvenile hormone analog (10, 11-epoxyfarnesenic acid methyl ester) (EFA) in a 10% peanut oil solution induced male \underline{I} . confusus to produce sex pheromone. After 24 hours, guts from males treated with 100 μg of EFA were more attractive to female beetles than those from males allowed to produce pheromone naturally in ponderosa pine logs.

22. Borden, J. H., R. M. Silverstein and R. G. Brownlee. 1968. Sex pheromone of <u>Dendroctonus pseudotsugae</u> (Coleoptera: Scolytidae): production, bio-assay, and partial isolation. Can. Ent. 100: 597-603.

Describes collection, extraction, distillation and silica gel column fractionation of female <u>D</u>. <u>pseudotsugae</u> frass, and a bioassay in which beetles, walking toward a light source, may choose to orient into a baited airstream intersecting their path. Females produced attractive frass within 2 hours after entering host logs. Frass extract and distillate were attractive at approximately 10⁻⁴ and 10⁻³ gram equivalents, respectively. Some evidence of synergism appeared in attractive mixtures of silica gel column fractions.

23. Brown, W. L., Jr., T. E. Eisner and R. H. Whittaker. 1970. Allomones and kairomones: transspecific chemical messengers. BioScience 20: 21-22.

Discusses the significance of allomones and kairomones as two major classes of chemical messengers in addition to hormones and pheromones. Formally defines a kairomone as "a transspecific chemical messenger, the adaptive benefit of which falls on the recipient rather than on the emitter." As an example, cites the dual role of <u>Ips</u> pheromone which is secondarily employed as a kairomone by predator beetles.

24. Brownlee, R. G. and R. M. Silverstein. 1968. A micro-preparative gas chromatograph and modified carbon skeleton determinator. Anal. Chem. 40: 2077-2079.

For handling small chemical samples obtained from gas chromatography, describes various modifications built upon a modified Varian Aerograph 204, including: a capillary variable-ratio effluent splitter, a thermal gradient collector, a glass capillary-breaking device and a modified Beroza Carbon Skeleton Determinator, and refers to the use of these modifications in isolating and identifying brevicomin from Dendroctonus brevicomis female frass.

25. Caird, R. W. 1935. Physiology of pines infested with bark beetles. Bot. Gaz. 96: 709-733.

In a study of the physiology of pines infested by <u>Dendroctonus frontalis</u>, describes method of inducing attack by caging bark with emerging beetles around the base of uninfested trees. When the emergent beetles attacked the caged tree, field populations were attracted to it as well as neighboring trees.

26. Callaham, R. Z. and M. Shifrine. 1960. The yeasts associated with bark beetles. For. Sci. 6: 146-154.

As part of a review paper, includes a section on yeasts in relation to bark beetle attraction. Cites published and unpublished work which demonstrates that phloem inoculated with isolated yeasts or with unknown airborne organisms is attractive to bark beetles despite the fact that yeasts have only a weak capacity to ferment monosaccharides. However, the relationship of the yeast-produced attraction to secondary attraction of scolytids remains obscure and is not directly discussed. The work of H. L. Person is cited as the only demonstration of "attraction of a bark beetle to a phloem ferment produced by yeasts isolated from that bark beetle."

27. Castek, K. L., J. F. Barbour and J. A. Rudinsky. 1967. Isolation and purification of the attractant of the striped ambrosia beetle. J. Econ. Ent. 60: 658-660.

Describes the extraction of attractant from <u>Trypodendron lineatum</u> frass, and its isolation by gas-liquid chromatography. A mass spectrum of the attractive fraction was weak, but very similar to B-ocimene which, when tested in the field, was not attractive.

28. Chapman, J. A. 1962. Field studies on attack flight and log selection by the ambrosia beetle <u>Trypodendron lineatum</u> (Oliv.) (Coleoptera: Scolytidae). Can. Ent. 94: 74-92.

Principally on primary attraction. However, briefly discuses the possibility of secondary attraction in T. lineatum and questions the

the need for a mechanism that would induce simultaneous mass attack in a secondary insect which does not need to overcome host resistance.

29. Chapman, J. A. 1966. The effect of attack by the ambrosia beetle

Trypodendron lineatum (Olivier) on log attractiveness. Can. Ent.

98: 50-59.

Virgin female T. lineatum created a secondary attraction within two to three days after attacking logs. In field tests, both sexes were caught in glass barrier traps over "greenhouse" cages containing the logs. When males were allowed to mate with females shortly after their attack, the secondary attraction disappeared, but when males were allowed to join females which had been in logs over a month, there was no reduction in secondary attraction.

30. Chapman, J. A. 1967. Response behaviour of scolytid beetles and odour meteorology. Can. Ent. 99: 1132-1137.

With many examples from the literature, considers the response of scolytids to primary and secondary attractants in relation to the transport and dispersal of odors by air currents. Urges a greater understanding of the principles of micrometeorology in order to use attractant odors to manipulate scolytid populations more effectively.

31. Chapman, J. A. and E. D. A. Dyer. 1969. Cross attraction between the Douglas-fir beetle (<u>Dendroctonus pseudotsugae</u> Hopk.) and the spruce beetle (<u>D. obesus</u> (Mann.)). Bi-Mon. Res. Notes, Canada Dept. Fish. and For. 25: 31.

In field tests, <u>D. pseudotsugae</u> females introduced into either white spruce or Douglas-fir logs attracted both <u>D. pseudotsugae</u> and <u>D. obesus</u>, whereas <u>D. obesus</u> females in white spruce attracted both species, but would not bore into Douglas fir.

32. Chararas, C. 1966. Recherches sur l'attractivité chez les <u>Scolytidae</u>.

Étude sur l'attractivité sexuelle chez <u>Carphoborus minimus</u> Fabr.

Coléoptère <u>Scolytidae</u> typiquement polygame. C. R. Acad. Sci.

Paris 262D: 2492-2495.

Describes the results of experiments demonstrating that males of the polygamous <u>C</u>. <u>minimus</u> can produce an attraction for females within three days after attacking new host material, and that males can attract from 1 to 7 females. Cites tests with the other polygamous species, <u>Pityophthorus pityographus</u> and <u>Pityogenes chalcographus</u>, which indicate that the males of these species also are able to attract females.

33. Chararas, C. 1968. Recherches sur le comportment sexuel de <u>Pityokteines</u>

<u>spinidens</u> Reit. (Coléoptère <u>Scolytidae</u> polygame) et étude des

facteurs qui agissent sur le pouvour attractif du mâle a l'égard

de la femelle. C. R. Acad. Sci. Paris 266D: 1852-1855.

Reports that sex attraction commences when a mature male P. spinidens attacks a new host and constructs a nuptial chamber. The attraction is not produced by immature males until they have fed for 22 to 24 days, disappears rapidly in the absence of a viable male from a gallery, and in host specificity tests, was produced in four species of fir and one of spruce. Since males reared on media in the absence of host terpenes did not produce attraction, the author contends that attraction is

associated with terpene metabolism by the male beetles. Cites unpublished work which also demonstrates sex attraction in Ips sexdendatus, Phloeosinus armatus and Orthotomicus erosus.

34. Chararas, C. 1969. Recherches sur l'attractivité sexuelle de

Phloeosinus bicolor Brul., coléoptère Scolytidae parasite

spécifique des Cupressinae. C. R. Acad. Sci. Paris 268D: 10801083.

Reports experiments demonstrating that sexually mature male P. bicolor produce an attraction which induces mass attraction of the species. The attraction is associated with the male feces in which the terpene content is much lower than in host tissues. It is produced after successful construction of the nuptial chamber, is lost after 11 days or after copulation, and is species specific.

35. Coster, J. E. 1970. Production of aggregating pheromones in re-emerged parent females of the southern pine beetle. Ann. Ent. Soc. Amer. 63: 1186-1187.

Virgin female <u>Dendroctonus frontalis</u> were 4.5 times as attractive as reemerged females. Reemerged females contained frontalin and <u>trans</u>-verbenol in lesser quantities than in virgin females. Since a second mating is not required, a sex pheromone function seems superfluous, whereas an aggregating pheromone function is still of advantage in overcoming host tree resistance.

36. Coster, J. E. and R. I. Gara. 1968. Studies on the attack behavior of the southern pine beetle. II. Response to attractive host material. Contrib. Boyce Thompson Inst. 24: 69-75.

Olfactory stimuli appeared to dominate <u>Dendroctonus frontalis</u> behavior in flight, landing and gallery construction. Apparently, there are qualitative or quantitative differences in olfactory stimuli for landing and for entry of the host, as landing is not always followed by gallery construction.

37. Daterman, G. E., J. A. Rudinsky and W. P. Nagel. 1965. Flight patterns of bark and timber beetles associated with coniferous forests of western Oregon. Tech. Bull. Oregon State Univ. Agric. Exper. Sta. No. 87.

Summarizes the diurnal and seasonal flight patterns of scolytid beetles under various environmental conditions, and includes a brief report that the attractant produced by Trypodendron_lineatum attacking logs caused a striking increase in local flight activity.

38. Dyer, E. D. A. and D. W. Taylor. 1968. Attractiveness of logs containing female spruce beetles, <u>Dendroctonus obesus</u> (Coleoptera: Scolytidae).

Can. Ent. 100: 769-776.

In field tests, demonstrates that virgin female <u>D</u>. <u>obesus</u> boring in spruce logs produced a secondary attraction which attracted beetles (predominately males) from natural populations. Discusses the requirements for control with natural or synthesized secondary attractants in relation to the size of populations sampled in windfall areas.

39. Franke-Grossman, H. 1963. Some new aspects in forest entomology.

Ann. Rev. Ent. 8: 415-438.

As part of a comprehensive review, includes a lengthy discussion of recent work on host and secondary (sex) attraction in forest insects, including the Scolytidae. Cites the discovery that male <u>Ips</u> and female <u>Dendroctonus</u> create the secondary attraction. Therefore, an improbable sex specific association with yeasts would be required if they are to be involved in secondary attraction. Also cites an experiment in which yeast toxicants applied to attractive, infested logs did not result in attractant inhibition.

40. Franklin, R. T. 1970. Southern pine beetle population behavior. J. Georgia Ent. Soc. 5: 175-182.

In an isolated hardwood - shortleaf pine stand, baiting trees with infested bolts was effective in creating a single season <u>Dendroctonus</u> <u>frontalis</u> outbreak of 187 trees from a single infested tree, effectively converting the stand to a hardwood forest. Notes that emerging parent adults create a second period of pheromone production and mass attack and thereby increase the growth of an infestation. Suggests that while mid-summer attempts at direct control will fail because of the large number of beetles in flight, spring and early summer control can be effective by breaking emergence and pheromone production patterns.

41. Gara, R. I. 1963. Studies on the flight behavior of <u>Ips confusus</u>

(LeC.) (Coleoptera: Scolytidae) in response to attractive

material. Contrib. Boyce Thompson Inst. 22: 51-66.

Field observations of <u>I</u>. <u>confusus</u> flight from take-off to landing confirm that flight exercise is not a prerequisite to attractant response. Female and previously responding beetles were superior in their response to distant sources of attractants, but males and emerging beetles responded in equal numbers over short distances.

Maximum response distance was between 500 and 1000 meters. Results suggest that differences in response are due to environment (e.g. in diurnal variation) or to physiological condition of beetles and populations (e.g. differences in response ability between early and late emerging beetles) rather than to inherited ability.

42. Gara, R. I. 1966. What we have learned from new research on the southern pine beetle. Forest Farmer 25 (March): 6-7, & 18-19.

Describes the research program at the Southern Forest Research Institute created in 1962, primarily concerned with population dynamics and secondary attraction in <u>Dendroctonus frontalis</u>. Based on observations of natural and artificial infestations, concludes that infestations will enlarge and be self-sustaining as long as emergence of brood beetles synchronizes with the availability of attractants. Also describes attempts to manipulate populations which led to the discovery that infestations advance by a one-tree-at-a-time, switching mechanism, and eventually to the development of the "trap spot" control concept.

43. Gara, R. I. 1967. Studies on the attack behavior of the southern pine beetle. I. The spreading and collapse of outbreaks.

Contrib. Boyce Thompson Inst. 23: 349-354.

Demonstrates that the spreading or collapse of infestations depends upon the synchronization of beetle emergence and pheromone production within an area. Emerging beetles normally remained in the infestation area, providing continual sources of attractants. When pheromone sources were removed (by removing newly infested trees), emerging beetles dispersed and concentrated elsewhere. Concludes that outbreaks occur when beetle emergence coincides with the availability of attractants, causing the population to concentrate in a limited area.

Describes techniques of marking beetles with fluorescent powder, and a newly designed sleeve olfactometer.

44. Gara, R. I. 1967. A field olfactometer for studying the response of the southern pine beetle to attractants. J. Econ. Ent. 60: 1180-1181.

Describes an olfactometer consisting of a longitudinally hinged aluminum cylinder that fits around a tree, and a 490 ft³/min blower that forces attractive air out through holes in the cylinder. Responding beetles are caught on the cylinder in slanted troughs which terminate in collecting jars.

45. Gara, R. I. and J. E. Coster. 1968. Studies on the attack behavior of the southern pine beetle. III. Sequence of tree infestation within stands. Contrib. Boyce Thompson Inst. 24: 77-85.

Elucidates a "switching phenomenon" by which the center of <u>Dendroctonus</u> frontalis aggregation is shifted from one tree to another. Demonstrates that the nearest uninfested 8-ft experimental loblolly pine post to a center of attraction is the next attacked, and that this attack depends on the interaction between distance from (up to 15 ft), and level of attraction in the initial source. Moreover, natural infestations advanced by moving to the nearest uninfested tree.

46. Gara, R. I. and J. P. Vité. 1962. Studies on the flight patterns of bark beetles (Coleoptera: Scolytidae) in second growth ponderosa pine forests. Contrib. Boyce Thompson Inst. 21: 275-289.

Describes experiments using rotary nets and field olfactometers baited with freshly attacked pine logs which suggest that flight patterns of Dendroctonus brevicomis and Ips confusus consist of two phases, dispersal and concentration. Concludes that responses to olfactory stimuli are the dominating factor in concentration flights.

47. Gara, R. I., J. P. Vité, and H. H. Cramer. 1965. Manipulation of

Dendroctonus frontalis by use of a population aggregating pheromone.

Contrib. Boyce Thompson Inst. 23: 55-66.

Following initial host selection by <u>D</u>. <u>frontalis</u>, there are two phases of colonization: 1) progressively increasing attack focused by olfactory response toward or near to the initial portion of an infested tree, and

- 2) mass aggregation on various vertical objects near the original source of attraction. Manipulation of a defined field population was accomplished with attractive logs which concentrated beetles in preselected areas, or even sections of a single tree.
- 48. Goeden, R. D. and D. M. Norris, Jr. 1964. Attraction of Scolytus quadrispinosus (Coleoptera: Scolytidae) to Carya spp. for oviposition. Ann. Ent. Soc. Amer. 57: 141-146.

Primarily on flight patterns and attraction of <u>S</u>. <u>quadrispinosus</u> to <u>Carya</u> spp. Presents data which indicate that a beetle-associated component elicited a much greater response of beetles in the field than attraction of the host tree alone.

49. Goeden, R. D. and D. M. Norris, Jr. 1965. Some biological and ecological aspects of ovipositional attack in <u>Carya</u> spp. by <u>Scolytus quadrispinosus</u> (Coleoptera: Scolytidae). Ann. Ent. Soc. Amer. 58: 771-777.

After ovipositional attack by S. quadrispinosus ceased, great numbers of beetles were trapped in the vicinity of an infested tree. Concludes that this is a response to a beetle-associated attractant of an unknown source, and discusses its significance in group attack, and when unsuccessful on surrounding trees, its importance in their predisposition for later attack.

50. Graham, K. 1967. Fungal-insect mutualism in trees and timber. Ann. Rev. Ent. 12: 105-126.

A review on all aspects of fungal-insect mutualism. In a brief section, contends that the role of yeasts in secondary attraction of scolytids is questionable.

51. Hertel, G. D., F. P. Hain, and R. F. Anderson. 1969. Response of

Ips grandicollis (Coleoptera: Scolytidae) to the attractant

produced by attacking male beetles. Can. Ent. 101: 1084-1091.

Artificially infested logs attracted only 2.4% of 9417 released I. grandicollis in the field. Additional experiments demonstrated: a decrease in number of beetles attracted per male as the number of male attacks increased, a maximum response 360 ft from a high-density breeding area possibly indicating the need for a dispersal flight, a decrease in attraction after 4 days, and a peak response in late afternoon to early evening.

52. Hierholzer, O. 1950. Ein Beitrag zur Frage der Orientierung von <u>Ips</u> curvidens Germ. Z. Tierpsychologie 7: 588-620.

A comprehensive and intensive study on the orientation behavior of this European ips. Includes a section on close-range orientation of females to males in the bark. In laboratory experiments, females of the appropriate age released on bark disks containing males in nuptial chambers, joined males in far higher numbers than would be expected by chance alone. Contact with male frass was the stimulus to search for and enter male galleries, and the rapid antennal movements when contact was made suggest an olfactory stimulation. In spite of the apparent

olfactory orientation at close range, there was no evidence to indicate olfactory orientation from a distance.

53. Hughes, P. R. and G. B. Pitman. 1970. A method for observing and recording the flight behavior of tethered bark beetles in response to chemical messengers. Contrib. Boyce Thompson Inst. 24: 329-336.

Describes a laboratory flight bioassay in which flying tethered beetles in the center of four converging airstreams can rotate 360° in a horizontal plane in response to odors presented in the airstreams. Turning, wingbeat frequency and thrust were automatically recorded. Male and female Dendroctonus brevicomis were attracted to mixtures of frontalin or brevicomin with 3-carene. Females (males not tested) were repelled by verbenone and were mostly indifferent to 3-carene alone. Suggests that this bioassay will be useful in monitoring chemical isolation of pheromones, in elucidating discrepancies between laboratory and field behavior, and in facilitating dosage-response studies.

54. Jacobson, M. 1965. Insect sex attractants. Interscience Publishers,
New York.

In a comprehensive book on sex attraction in the class Insecta, includes a chapter on "assembling scents" primarily devoted to a review of secondary attraction studies in the scolytid genera <u>Dendroctonus</u>, <u>Ips</u> and <u>Trypodendron</u>. Also refers to scolytids in other sections, e.g. on pheromone isolation and their use in surveys.

55. Jacobson, M. 1966. Chemical insect attractants and repellents. Ann. Rev. Ent. 11: 403-422.

In a general review, includes a section on "assembling scents", produced by one sex but attracting both sexes, and as of the review date, found only in scolytids. Refers to the presence of these substances in the genera <u>Dendroctonus</u>, <u>Ips</u> and <u>Trypodendron</u> and discusses the production site, nature of response, and termination of production after mating.

56. Jantz, O. K. and J. A. Rudinsky. 1965. Laboratory and field methods for assaying olfactory responses of the Douglas-fir beetle,

Dendroctonus pseudotsugae Hopkins. Can. Ent. 97: 935-941.

Laboratory tests revealed that female beetles boring in both host and nonhost species produced a volatile substance that both attracts and arrests adult beetles. Male arrestment provided a reliable method for laboratory bioassay of volatile substances. In the field, logs with mated females failed to attract flying beetles, but in the laboratory, arrestment continued for some time after mating occurred.

57. Jantz, O. K. and J. A. Rudinsky. 1966. Studies of the olfactory
behavior of the Douglas-fir beetle, <u>Dendroctonus pseudotsugae</u>
Hopkins. Tech. Bull. Oregon State Univ. Agric. Exper. Sta. No. 94.

Reports the behavioral responses exhibited by Douglas-fir beetles to various attractant sources in the field and laboratory. Demonstrates: pheromone production by females in host and nonhost logs, arrestment of beetles walking over attractant sources, an abrupt decrease in beetles attracted by recently mated females, and attraction of reemerged females.

58. Kangas, E., H. Oksanen and V. Perttunen. 1970. Responses of

<u>Blastophagus piniperda</u> L. (Col., Scolytidae) to trans-verbenol,
cis-verbenol, and verbenone, known to be population pheromones
of some American bark beetles. Ann. Ent. Fenn. 36: 75-83.

In laboratory choice chamber tests, demonstrates that <u>B. piniperda</u> is attracted to <u>trans-verbenol</u>, a naturally attractive pine phloem fraction (Pe 42), or a mixture of the two. In various mixtures, verbenone and <u>cis-verbenol</u> neutralized attraction or caused repellency.

59. Kangas, E., V. Perttunen, H. Oksanen and M. Rinne. 1967. Laboratory
experiments on the olfactory orientation of <u>Blastophagus piniperda</u>
L. (Coleoptera, Scolytidae) to substances isolated from pine rind.
Acta. Ent. Fenn. 22: 1-87.

Principally a study of primary orientation. However, notes that the odor of adult, swarming females did not attract either sex in a laboratory choice chamber, and contends that the field behavior of <u>B. piniperda</u> does not suggest pheromone orientation.

60. Kinzer, G. W., A. F. Fentiman, Jun., T. F. Page, Jun., R. L. Foltz, J. P. Vite and G. B. Pitman. 1969. Bark beetle attractants: identification, synthesis and field bioassay of a new compound isolated from Dendroctonus. Nature (Lond.) 221: 477-478.

Reports the isolation and identification of 1,5-dimethyl-6,8-dioxabicyclo (3.2.1) octane (suggested to be "the principal pheromone responsible for mass aggregation" of <u>Dendroctonus frontalis</u>) from the hindguts of 6500 male <u>D. brevicomis</u>. Spectral data of the synthetic and isolated compounds

were identical. One gram of the pure synthetic compound attracted only three beetles in three, 10-min field tests, but when combined with <u>Pinus</u> taeda eleoresin, it attracted 32 beetles in the same period, comparable to the combination of 2500 crushed <u>D. frontalis</u> with eleoresin which attracted 13 and 34 beetles in two separate tests. Addition of <u>trans</u>verbenel to the mixture of the synthetic compound plus eleoresin did not enhance attraction. Proposes the trivial name "frontalin" for the compound.

61. Kliefoth, R. A., J. P. Vité, and G. B. Pitman. 1964. A laboratory technique for testing bark beetle attractants. Contrib. Boyce Thompson Inst. 22: 283-290.

A laboratory device is described for assaying the attractant and arrestant potential of different substances simultaneously. A perforated arena surface allows beetles to find and crawl into holes from which pheromone emanates. Light, temperature, humidity and fresh air flow are controlled in an enclosed test box. In trial tests, <u>Ips ponderosae</u> and Ips confusus each preferred their own attractant.

62. Lanier, G. N. 1970. Sex pheromones: abolition of specificity in hybrid bark beetles. Science 169: 71-72.

In field and laboratory, examines 1) the production of, and 2) response to pheromones produced by $\underline{\text{Ips amiskwiensis}}$, $\underline{\text{I. borealis}}$ and $\underline{\text{I. pilifrons}}$ and $\underline{\text{F}}_1$ and backcross hybrids of $\underline{\text{I. amiskwiensis}}$ with either of the other two species. Hybrids were intermediate to the parent species in both characteristics. Suggests that hybrid pheromones and pheromone receptors are mixtures of those in the parent species.

63. Lanier, G. N. 1970. Biosystematics of the genus <u>Tps</u> (Coleoptera: Scolytidae) in North America. Hopping's Group III. Can. Ent. 102: 1404-1423.

As part of a taxonomic work, demonstrates that female $\underline{\text{Ips integer}}$ and $\underline{\text{I. plastographus plastographus}}$ responded to their respective males in field tests, but laboratory-reared F_1 $\underline{\text{integer-plastographus}}$ hybrid males were intermediately attractive to both species.

64. Lejeune, R. R., L. H. McMullen and M. D. Atkins. 1961. The influence of logging on Douglas-fir beetle populations. For. Chron. 37: 308-314.

Primarily an economic consideration of the effects of logging. However, in a resume of life history and habits, notes that early attacking <u>Dendroctonus pseudotsugae</u> produce a strong secondary attraction that induces the mass attack necessary to kill living trees.

65. Lyon, R. L. and P. J. Shea. 1967. Chemosterilants to control bark beetles...tepa shows promise in preliminary test. U. S. For. Serv. Res. Note PSW - 139.

Shows that tepa is 97% effective in reducing <u>I</u>. <u>confusus</u> egg hatch, and proposes using the male sex pheromone jointly with chemosterilants.

66. Mason, R. R. 1965. Populations of ips engraver beetles following summer thinning in a loblolly pine plantation. Hiwassee Land Co., Calhoun, Tennessee For. Res. Note No. 14.

Demonstrates that experimental summer thinnings were mass attacked by

ips in response to attraction emitted by the first attacking beetles. The mass flight of $\underline{\text{Ips}}$ grandicollis was at least twice as long (up to 70 days) as that of $\underline{\text{I}}$. $\underline{\text{avulsus}}$.

67. Mason, R. R. 1969. Behavior of <u>Ips</u> populations after summer thinning in a loblolly pine plantation. For. Sci. 15: 390-398.

Essentially a more extensive and intensive report on a study already described (See No. 66). Demonstrates an abrupt rise in numbers of <u>Ips avulsus</u> in flight near fresh pine thinning slash within 3 to 5 days after felling, and contends that this concentration flight is a clear indication of the response of field populations to secondary attraction.

68. Mason, R. R. 1970. Comparison of flight aggregation in two species of southern <u>Ips</u> (Coleoptera: Scolytidae). Can. Ent. 102: 1036-1041.

Flight aggregation experiments and calculation of aggregation indexes demonstrate that <u>Ips avulsus</u> shows a higher degree of flight aggregation than <u>I. grandicollis</u>. Suggests that degree of aggregation in flight is an effective index of aggressiveness since <u>I. avulsus</u> concentrates to sources of secondary attraction sometimes to the point of swarming, and can kill healthy timber, while <u>I. grandicollis</u> has an attack flight of longer duration, shows an inability to concentrate a large number of attacks, and kills only weak or damaged trees.

69. McCambridge, W. F. 1967. Nature of induced attacks by the Black Hills beetle, <u>Dendroctonus ponderosae</u> (Coleoptera: Scolytidae). Ann. Ent. Soc. Amer. 60: 920-928.

Attack patterns of <u>D</u>. <u>ponderosae</u> were studied, using trees baited with infested bolts or with induced attack in a small area by caged beetles. Effective attraction was produced, using equal numbers of both sexes. Observations were noted as to which trees were attacked first, at what density and height, and at which time of day the greatest number of attacks occurred.

70. McMullen, L. H. and M. D. Atkins. 1962. On the flight and host selection of the Douglas-fir beetle, <u>Dendroctonus pseudotsugae</u> Hopk.

(Coleoptera: Scolytidae). Can. Ent. 94: 1309-1325.

Part of a comprehensive study on flight and host selection. Presents the first convincing data demonstrating that initial attack by virgin female <u>D</u>. <u>pseudotsugae</u> created a strong attraction for other beetles, particularly males, that the presence of the male in the gallery reduces attractiveness, and that host and beetle-produced factors act as a complex in mass attraction.

71. McNew, G. L. 1967. Boyce Thompson Institute for Plant Research, Inc. Science 158: 1489-1492.

An overall review of research at the Boyce Thompson Institute, including the Forest Entomology Program which is mainly concerned with bark beetle attractants. Describes three research laboratories and cites accomplishments with pheromones of <u>Dendroctonus</u> and <u>Ips</u> spp.

72. McNew, G. L. 1970. The Boyce Thompson Institute program in forest entomology that led to the discovery of pheromones in bark beetles. Contrib. Boyce Thompson Inst. 24: 251-262.

Reviews work at the Boyce Thompson Institute (BTI) field laboratories on host tree physiology, and on host selection and pheromones of scolytids. Notes initial progress on <u>Ips confusus</u> pheromones and abandonment of the work by BTI when the pheromone identity was elucidated by other workers. Describes in detail the identification of <u>trans</u>-verbenol and frontalin from <u>Dendroctonus</u> species, and the use of pheromones in manipulation and control programs. In reviewing the work done by BTI, creates the impression that only one research group was engaged in a concentrated effort to elucidate scolytid pheromones when, in fact, there were at least two, each working on the same problems and each contributing significantly to progress in this essential area of research.

73. Meyer, H. J. and D. M. Norris. 1967. Behavioral responses by <u>Scolytus</u>

<u>multistriatus</u> (Coleoptera: Scolytidae) to host- (<u>Ulmus</u>) and

beetle-associated chemotactic stimuli. Ann. Ent. Soc. Amer. 60:
642-647.

Presents data to show that secondary attraction in <u>S</u>. <u>multistriatus</u> has its origin in the tree tissues and not in the beetle <u>per se</u> making the gallery. Proposes that a similar phenomenon may occur in other species, and questions the validity of the term "pheromone" in such cases.

74. Miller, J. M. and F. P. Keen. 1960. Biology and control of the western pine beetle. U. S. Dept. Agric. Misc. Publ. No. 800.

In a summary of the first 50 years of research on <u>Dendroctonus brevicomis</u>, briefly refers (p. 52) to an unpublished report by J. E. Patterson in which newly emerged beetles were confined in a cage enclosing the lower eight feet of the bole of a living tree. Shortly after the caged beetles attacked, natural populations were attracted from at least a 1/4-mile distance and attacked the tree. Also reports similar experiments by H. L. Person (p. 41) in which attack was induced in a series of trees.

75. Morgan, F. D. 1967. <u>Ips grandicollis</u> in South Australia. Aust. For. 31: 136-155.

As part of a study on <u>I. grandicollis</u> introduced into Australia from North America, reports that females were strongly attracted to male frass in the laboratory, suggests that the males produce this attractant, and associates the attraction with the concentration of beetles on attacked hosts.

76. Nijholt, W. W. 1970. The effect of mating and the presence of the male ambrosia beetle, <u>Trypodendron lineatum</u>, on "secondary" attraction. Can. Ent. 102: 894-897.

In field tests with infested logs in "greenhouse" cages, demonstrates that both virgin and mated females produced secondary attraction. In both instances, introduction of males greatly reduced the attraction. Concludes that reduced attraction is associated with the males' presence rather than the reproductive experience of the female, and hypothesizes that the males mask the female pheromone.

77. Nijholt, W. W. and J. A. Chapman. 1968. A flight trap for collecting living insects. Can. Ent. 100: 1151-1153.

Describes a glass barrier trap modified with a darkened cylinder with one end allowing entry of light. Trapped insects crawl toward the light and are recovered alive. Demonstrates use of the trap in assessing secondary attraction produced by Trypodendron_Lineatum.

78. Oksanen, H., V. Perttunen and E. Kangas. 1970. Studies on the chemical factors involved in the olfactory orientation of <u>Blastophagus</u>

<u>piniperda</u> (Coleoptera: Scolytidae). Contrib. Boyce Thompson Inst.

24: 299-304.

Primarily a discussion of the chemistry of terpenoid compounds in relation to their attractiveness to <u>B. piniperda</u>. Reports laboratory tests in which extracts of swarming females were only slightly attractive to males, thus indicating the lack of a pheromone in swarming females, but not ruling out the possibility that feeding females produce pheromones.

79. Payne, T. L. 1970. Electrophysiological investigations on response to pheromones in bark beetles. Contrib. Boyce Thompson Inst. 24: 275-282.

Reports the recording of electroantennograms (EAG's) from the antennae of two <u>Dendroctonus</u> species, using tungsten electrodes and an airflow system of 1,000 ml/min. In agreement with behavioral responsiveness, antennae were not pheromone specific on a response - no response basis, but male <u>D. frontalis</u> antennae were more responsive to frontalin than

female antennae, female <u>D</u>. <u>brevicomis</u> antennae were more responsive to frontalin than male antennae, and male <u>D</u>. <u>brevicomis</u> antennae were more responsive to brevicomin than female antennae. There was no significant difference in EAG amplitude in either species to «-pinene or 3-carene, but the author suggests terpene specificity may occur in a second order of neural transmission.

80. Payne, T. L. 1971. Bark beetle olfaction. I. Electroantennogram responses of the southern pine beetle (Coleoptera: Scolytidae) to its aggregation pheromone frontalin. Ann. Ent. Soc. Amer. 64: 266-268.

Presents the first electroantennograms recorded from scolytids and demonstrates that both sexes of <u>Dendroctonus frontalis</u> respond equally to as little as 1 µg of frontalin per 10 µl of 70% ethanol in an airstream delivered at a rate of 1000 ml per minute.

81. Person, H. L. 1930. Theory in explanation of the selection of certain trees by the western pine beetle. J. Forestry 29: 696-699.

Proposes the theory that secondary attraction in <u>Dendroctonus brevicomis</u> is created by attractive fermentation products from a yeast introduced into the inner bark by first attacking beetles.

82. Perttunen, V., H. Oksanen and E. Kangas. 1970. Aspects of the external and internal factors affecting the olfactory orientation of Blastophagus piniperda (Coleoptera: Scolytidae). Contrib. Boyce Thompson Inst. 24: 293-297.

Reviews recent work, mostly on primary attraction in B. piniperda, including the results of laboratory bests in which trans-verbenol, host pine phloem fraction Pe 42, or a mixture of the two were attractive. Also reports that in field tests, female-infested logs were no more attractive than uninfested logs, thus failing to prove the existence of a female-produced aggregating pheromone.

83. Pitman, G. B. 1966. Studies on the pheromone of <u>Ips confusus</u> (LeConte).

III. The influence of host material on pheromone production.

Contrib. Boyce Thompson Inst. 23: 146-158.

In two separate tests, pulped phloem supplemented with glucose favored pheromone production more than other carbohydrates. Phloem tissue with a comparatively high concentration of nonelectrolytes was a more favorable medium for pheromone production. Infested phloem with low sugar concentrations (natural or induced) did not support production of high potency pheromones. Phloem from the upper crown was the most favorable dietary substrate for pheromone production.

84. Pitman, G. B. 1969. Bark beetle manipulation with natural and synthetic attractants. pp. 56-58. <u>In Insect-plant interactions</u>, National Academy of Sciences, Washington, D. C.

From a work conference held in March, 1968. Surveys results of research on pheromone chemistry, host-insect interactions in pheromone synthesis, and use of synthetic attractants in the field. Reports identification of trans-verbence as the "major attractive component" of Dendroctonus frontalis, Dendroctonus frontalis, Dendroctonus frontalis, Dendroctonus frontalis, Dendroctonus frontalis, and, tentative, Dendroctonus frontalis, and, tentative, Dendroctonus frontalis and Dendroctonus frontalis and Dendroctonus frontalis and Dendroctonus frontalis and Dendroctonus frontalis frontal

85. Pitman, G. B. 1969. Pheromone response in pine bark beetles: influence of host volatiles. Science 166: 905-906.

Points out the role of host volatiles interacting with aggregating pheromones in <u>Dendroctonus</u> spp. Reports indifferent attraction in the field from pure brevicomin, said to be attractive by other workers, principally W. D. Bedard (see No. 14), and that it is synergized by 3-carene (rather than myrcene, as reported by Bedard's group). Notes that brevicomin attracts mostly <u>D</u>. <u>brevicomis</u> males while frontalin attracts females.

86. Pitman, G. B. and J. P. Vité. 1963. Studies on the pheromone of <u>Ips</u>

<u>confusus</u> (LeC.). I. Secondary sexual dimorphism in the hindgut
epithelium. Contrib. Boyce Thompson Inst. 22: 221-226.

Histological differences noted in the epithelium of the ileum of male <u>I. confusus</u> were consistent with previous olfactory tests implicating the hindgut and fecal matter of mature male beetles as the source of the species specific pheromone.

87. Pitman, G. B. and J. P. Vité. 1969. Aggregation behavior of <u>Dendroctonus</u>

<u>ponderosae</u> (Coleoptera: Scolytidae) in response to chemical

messengers. Can. Ent. 101: 143-149.

Suggests that <u>trans</u>—verbenol represents the aggregating pheromone in <u>D. ponderosae</u> since it was attractive when tested with oleoresin in the field. Crushed emergent female <u>D. brevicomis</u> and <u>D. frontalis</u>, both of which contain large amounts of <u>trans</u>—verbenol, were also attractive.

Although hindgut extracts from feeding <u>D</u>. <u>ponderosae</u> females were attractive to walking beetles in the laboratory, <u>trans</u>-verbenol was not. Responding beetles had a distinct preference for traps with a horizontal "log" configuration.

88. Pitman, G. B. and J. P. Vité. 1970. Field response of <u>Dendroctonus</u>

<u>pseudotsugae</u> (Coleoptera: Scolytidae) to synthetic frontalin.

Ann. Ent. Soc. Amer. 63: 661-664.

GLC analysis revealed the presence of frontalin in the guts of fed and unfed <u>D. pseudotsugae</u> females, but not males. In the field, frontalin in combination with one of five monoterpenes was most attractive when released with camphene. Trees baited with frontalin plus alphapinene were attacked by beetles. Proposes that <u>D. pseudotsugae</u> and <u>D. brevicomis</u> share the same pheromone, frontalin, but maintain species specificity through utilization of different synergistic host terpenes.

89. Pitman, G. B., R. A. Kliefoth and J. P. Vité. 1965. Studies on the pheromone of <u>Ips confusus</u> (LeConte). II. Further observations on the site of production. Contrib. Boyce Thompson Inst. 23: 13-18.

Describes a technique for bioassay of minute amounts of materials.

Confirms hindguts as the source of pheromone and also implicates

Malpighian tubules in pheromone production. Female beetles were

indifferent to clear air and expressed phloem sap, repelled by mono
terpenes and raw oleoresin, but attracted to as little as one male

fecal pellet.

90. Pitman, G. B., J. A. A. Renwick, and J. P. Vité. 1966. Studies on the pheromone of <u>Ips confusus</u> (LeConte). IV. Isolation of the attractive substance by gas-liquid chromatography. Contrib. Boyce Thompson Inst. 23: 243-250.

A major nonhost volatile was detected with gas-liquid chromatography in the hindguts and Malpighian tubules of male (but not female) I. confusus within two hours after feeding commenced. Highest amounts were obtained after four days of feeding, but after 14 days (even though the authors report that it was "nearly undetectable") the quantity of the volatile component was seven times greater than after two hours. Hypothesizes that this volatile, which was attractive to walking beetles, is the population aggregating pheromone of I. confusus.

91. Pitman, G. B., J. P. Vité and J. A. A. Renwick. 1966. Variation in olfactory behavior of <u>Ips confusus</u> (LeC.)(Coleoptera: Scolytidae) between laboratory and field bioassays. Naturwiss. 53: 46-47.

Variations in olfactory behavior to the same stimuli between flying beetles in the field and walking beetles in laboratory bioassays lead the authors to question the practice of using laboratory observations to appraise field behavior.

92. Pitman, G. B., J. P. Vité, G. W. Kinzer and A. F. Fentiman, Jun. 1968.

Bark beetle attractants: <u>trans-verbenol isolated from Dendroctonus</u>.

Nature (Lond.) 218: 168-169.

Describes the isolation of <u>trans-</u>verbenol from hindguts of female

D. ponderosae, its synthesis from alpha pinene, and its attractiveness

in field tests after being dissolved in petroleum ether (1 mg/ml) and sprayed on female-infested logs.

93. Pitman, G. B., J. P. Vité, G. W. Kinzer and A. F. Fentiman, Jr. 1969. Specificity of population-aggregating pheromones in <u>Dendroctonus</u>. J. Ins. Physiol. 15: 363-366.

Reviews evidence that <u>Dendroctonus</u> population-aggregating pheromones are not specific to sex or species and, therefore, proposes that orientation specificity is largely maintained by the specificity of olfactory receptor systems.

94. Reece, C. A., J. O. Rodin, R. G. Brownlee, W. G. Duncan and R. M.

Silverstein. 1968. Synthesis of the principal components of
the sex attractant from male <u>Ips confusus</u> frass: 2-methyl-6methylene-7-octen-4-ol, 2-methyl-6-methylene-2, 7-octadien-4-ol,
and (+)-cis-verbenol. Tetrahedron 24: 4249-4256.

Reports the detailed methodology used in synthesis of the three pheromone compounds of \underline{I} . $\underline{confusus}$, and subsequent verification of synthesis by spectrometric comparison of synthetic and isolated compounds.

95. Renwick, J. A. A. 1967. Identification of two oxygenated terpenes from the bark beetles <u>Dendroctonus frontalis</u> and <u>Dendroctonus brevicomis</u>. Contrib. Boyce Thompson Inst. 23: 355-360.

Gas chromatography and infrared, ultraviolet, NMR and mass spectrophotometry were used to study volatile materials from approximately 20,000 hindguts from each sex of emerged <u>D. frontalis</u> and <u>D. brevicomis</u>. Males of both species produce verbenone as the major component, and females of both species produce <u>trans</u>-verbenol.

96. Renwick, J. A. A. 1970. Chemical aspects of bark beetle aggregation.

Contrib. Boyce Thompson Inst. 24: 337=341.

Describes and compares various procedures used in isolation and identification of bark beetle pheromones. Discusses the relative specificity of pheromone compounds in relation to their relatively unspecific terpene synergists, and the need for resolution of the mechanisms by which scolytids perceive and respond to such olfactory stimulants.

97. Renwick, J. A. A. and J. P. Vité. 1968. Isolation of the population aggregating pheromone of the southern pine beetle. Contrib.

Boyce Thompson Inst. 24: 65-68.

Flying <u>Dendroctonus frontalis</u> in the field were found to be attracted to crushed, emergent <u>D. frontalis</u> females, <u>D. brevicomis</u> males and <u>D. pseudotsugae</u> females. All were found by gas chromatographic analysis and mass spectrometry to have a common hindgut compound with a molecular weight of 142.

98. Renwick, J. A. A. and J. P. Vité. 1969. Bark beetle attractants:

mechanism of colonization by <u>Dendroctonus frontalis</u>. Nature (Lond.)

224: 1222-1223.

Proposes a mechanism whereby verbenone produced by aggregating males first reduces the response of further males and then, in high concentrations, inhibits the response of both sexes, thereby terminating the mass attack. Renwick, J. A. A. and J. P. Vité. 1970. Systems of chemical communication in <u>Dendroctonus</u>. Contrib. Boyce Thompson Inst. 24: 283-292.

Discusses the interaction of host tree volatiles and pheromones produced by both sexes of <u>Dendroctonus</u> species. Proposes that induction and termination of mass attack are controlled by sequential release of various compounds in <u>D. ponderosae</u>, <u>D. brevicomis</u> and <u>D. frontalis</u>.

100. Renwick, J. A. A., G. B. Pitman and J. P. Vité. 1966. Detection of a volatile compound in hindguts of male <u>Ips confusus</u> (LeConte) (Coleoptera: Scolytidae). Naturwiss. 53: 83-84.

Gas chromatography indicated a major component present in the hindguts of males feeding in fresh phloem. The compound was attractive to walking beetles, suggesting that it is the aggregating pheromone of <u>I. confusus</u>.

101. Rice, R. E. 1968. Observations on host selection by <u>Tomicobia tibialis</u>
Ashmead (Hymenoptera: Pteromalidae). Contrib. Boyce Thompson
Inst. 24: 53-56.

In the field, <u>T. tibialis</u> was attracted to host material infested with male <u>Ips</u> spp., and did not respond to <u>Dendroctonus</u>-infested material. Suggests that attraction to <u>Ips</u> aggregating pheromones is the first response in a three-step host selection sequence.

102. Rice, R. E. 1969. Response of some predators and parasites of Ips
Confusus (LeC.) (Coleoptera: Scolytidae) to olfactory attractants.

Contrib. Boyce Thompson Inst. 24: 189-194.

Two beetle predators, Enoclerus lecontei and Temnochila virescens chlorodia, and a hymenopteran parasite, Tomicobia tibialis, were investigated for their response to host associated odors and I. confusus aggregating pheromone. The parasite responded only to materials associated with I. confusus males. The two predators were more attracted to host tree terpenes than to the pheromone.

103. Roe, A. L. and G. D. Amman. 1970. The mountain pine beetle in lodgepole pine forests. USDA Forest Service Res. Pap. INT-71.

As part of a comprehensive review, briefly discusses the possibility of using pheromones in <u>Dendroctonus ponderosae</u> control. Stresses lack of practical field demonstrations to date.

104. Rudinsky, J. A. 1962. Ecology of Scolytidae. Ann. Rev. Ent. 7: 327-348.

A comprehensive review, which includes a section on host finding.

Discusses various theories of primary and secondary attraction, including the pioneering work by R. F. Anderson, J. P. Vité and D. L. Wood, which disclosed that in the genus <u>Ips</u>, secondary attraction is produced by the first attacking beetles.

105. Rudinsky, J. A. 1963. Response of <u>Dendroctonus pseudotsugae</u> Hopkins to volatile attractants. Contrib. Boyce Thompson Inst. 22: 23-38.

The substance responsible for mass attraction of Douglas-fir beetles was found to be produced by sexually mature, unmated females. Describes field and laboratory bioassays and examines diurnal and seasonal response characteristics and the influence of temperature, wind and light. Successful concentration of the material in the laboratory suggests its possible use in control and prevention of outbreaks.

106. Rudinsky, J. A. 1966. Host selection and invasion by the Douglas-fir beetle, <u>Dendroctonus pseudotsugae</u> Hopkins, in coastal Douglas-fir forests. Can. Ent. 98: 98-111.

Presents convincing data for two major phases of attraction in the selection and colonization of Douglas fir by <u>D</u>. <u>pseudotsugae</u>: "host" or "primary attraction" by the emission of volatile terpenes from freshly cut, wounded and/or windthrow trees (response ratio 19: 23), and "mass attraction" created by unmated females soon after successful invasion of the tree (response ratio 29: 13).

107. Rudinsky, J. A. 1966. Observations on olfactory behavior of scolytid beetles (Coleoptera: Scolytidae) associated with Douglas-fir forests. Z. angew. Ent. 58: 356-361.

Discusses scolytid host selection and secondary attraction. Reports that after responding to primary attractants, virgin female <u>Dendroctonus</u> pseudotsugae, feeding on host phloem, produce an attractive substance

which induces mass attraction of males and females. <u>Trypodendron</u>

<u>lineatum</u> females, however, mate on the outside of the tree, and

(contrary to earlier results, see No. 113) mated females produce

attractants over a long period of time while boring into host logs.

108. Rudinsky, J. A. 1968. Pheromone-mask by the female <u>Dendroctonus</u>

<u>pseudotsugae</u> Hopk., an attraction regulator. Pan-Pac. Ent.

44: 248-250.

In field tests, demonstrates that the secondary attraction of <u>D. pseudotsugae</u> is masked to both sexes when normal males stridulate outside or enter the female gallery, or males with the elytral declivity excised (so they can not stridulate) enter the female gallery. Since the masking occurs immediately after introduction of the males, resumes within 10 minutes after males are removed, and does not occur when females are killed, the female must mask her own attractant in response to a male stimulus. Primary attraction to host stimuli was not masked, ensuring optimal host utilization. The mask prevents the aggregation of unneeded males and excessive attack density, while still permitting the mass invasion of a tree.

109. Rudinsky, J. A. 1969. Masking of the aggregating pheromone in Dendroctonus pseudotsugae Hopk. Science 166: 884-885.

Similar to an earlier report (See No. 108). Provides detailed methods and extensive quantitative data to support the existence of a pheromone mask produced by <u>D</u>. <u>pseudotsugae</u> females in response to stridulation of males or their presence in the female gallery.

110. Rudinsky, J. A. 1969. Studies on timber beetles. p. 64-65. <u>In</u> Insect-plant interactions, National Academy of Sciences, Washington, D. C.

From a work conference held in March, 1968. Stresses that response to primary and secondary attractants appears to be related to the physiological state of adult beetles, host condition, and environmental factors. Reports the presence of secondary attraction in <u>Pseudohylesinus nebulosus</u>, <u>Scolytus unispinosus</u> and (apparently) in <u>Gnathotrichus spp.</u>
Mentions chemical studies in progress on the pheromones of <u>Dendroctonus pseudotsugae</u> and <u>Trypodendron lineatum</u>.

111. Rudinsky, J. A. 1970. Sequence of Douglas-fir beetle attraction and its ecological significance. Contrib. Boyce Thompson Inst. 24: 311-314.

Reviews the behavioral sequence and interacting olfactory and auditory stimuli involved in primary and secondary attraction in <u>Dendroctonus</u> <u>pseudotsugae</u>. Emphasizes the pheromone mask, produced by the female in response to stridulation by the male, and its role in: conserving the male population by inhibiting further response to a female with a mate, signalling the cessation of mass attack, thus avoiding over-crowding. Its effect is limited to a small area around a gallery entrance, allowing flying beetles to respond to host volatiles, and enabling nearby unmated females to attract males.

112. Rudinsky, J. A. and G. E. Daterman. 1964. Response of the ambrosia beetle <u>Trypodendron lineatum</u> (Oliv.) to a female-produced pheromone. Z. angew. Ent. 54: 300-303.

Demonstrates that the factor inducing mass attraction of \underline{T} . <u>lineatum</u> is a species specific, sex depending pheromone produced in the boring made by females shortly after entering the xylem of a suitable host. An ethanol extract of the borings was attractive to released beetles in the field.

113. Rudinsky, J. A. and G. E. Daterman. 1964. Field studies on flight patterns and olfactory responses of ambrosia beetles in Douglas-fir forests of western Oregon. Can. Ent. 96: 1339-1352.

In field tests, demonstrates that a species-specific sex pheromone produced by sexually mature, unmated females boring in host xylem tissue is responsible for mass attraction of <u>Trypodendron lineatum</u>.

<u>Gnathotrichus</u> spp. responded conclusively only to the borings produced by female <u>Dendroctonus</u> pseudotsugae.

114. Rudinsky, J. A., V. Novák and P. Švihra. 1971. Pheromone and terpene attraction in the bark beetle <u>Ips typographus</u> L. Experientia 27: 161-162.

In field tests, demonstrates that <u>I</u>. <u>typographus</u> were more attracted to logs infested with male beetles than to uninfested logs, logs infested with females or pairs, or 1% solutions of four monoterpenes individually in ethanol. Three species of insect predators were attracted to both male-infested logs and the terpene solutions.

Apparently a codiscovery of a pheromone in <u>I</u>. <u>typographus</u> (see No. 8).

115. Rudinsky, J. A., V. Novák and P. Švihra. 1971. Attraction of the bark beetle <u>Ips typographus</u> L. to terpenes and a male-produced pheromone. Z. angew. Ent. 67: 179-188.

Similar to results reported elsewhere (see No. 114), but provides more detailed methods and numerical data. Reports the discovery of a male-produced aggregating pheromone to which natural populations responded in flight with a peak response near mid-day. If females were allowed to join males in infested logs, the sex ratio of the responding population shifted from 1 male: 1.16 females to 1: 1.94. Two species of predaceous beetles, Thanasimus formicarius (Cleridae) and Epuraea pygmaea (Nitidulidae), and one species of predaceous fly, Medetera signaticornis (Dolichopodidae), were attracted to both 1% ethanol solution of four monoterpenes and to male-infested logs.

Apparently a codiscovery of a pheromone in I. typographus (see No. 8).

116. Schneider, I. and J. A. Rudinsky. 1969. The site of pheromone production in <u>Trypodendron lineatum</u> (Coleoptera: Scolytidae): bioassay and histological studies of the hindgut. Can. Ent. 101: 1181-1186.

Based on evidence gained through laboratory bioassays, morphological observations and histological studies, proposes the hypothesis that:

"A pheromone acting as (an) aggregation attractant is produced by a layer of secretory cells at the posterior ileum and anterior rectum of female T. lineatum in the presence of digested bark and wood particles, and under the influence of a substance or a process activating or activated by the maturation of the fertilized egg."

117. Schönherr, J. 1966. Probleme der Borkenkäfer-Pheromon-Forschung in Amerika. Allg. Forstzeitschrift 21: 520-522.

A review of work on scolytid secondary attraction, primarily in North America. Discusses the interaction of host and beetle-produced odors and of visual stimuli in host selection, the production and detection of secondary attraction, and notes the occurrence of daily and seasonal response patterns. Considers practical application of pheromones in population manipulation, possibly in combination with contact insecticides or sterilization methods, but stresses the need for development of synthetic pheromones and, in Europe, the probable dependence on naturally-produced attractants for many years to come.

118. Schönherr, J. 1970. Evidence of an aggregating pheromone in the ash-bark beetle, <u>Leperisinus fraxini</u> (Coleoptera: Scolytidae).
Contrib. Boyce Thompson Inst. 24: 305-307.

In preliminary field tests, demonstrates that <u>Leperisinus</u>—infested bolts were more attractive than uninfested logs. In subsequent tests with male—infested logs, proves that male beetles are the source of mass attraction, despite the fact that females initiate the attack in nature. Responding beetles were of the same sex ratio as the flying population and showed a unimodal response peak in late afternoon.

119. Seybert, J. P. and R. I. Gara. 1970. Notes on flight and host-selection behavior of the pine engraver, <u>Ips pini</u> (Coleoptera: Scolytidae). Ann. Ent. Soc. Amer. 63: 947-950.

Determines the behavior of I. pini from the beginning of flight to the

point of host selection, as related to temperature, pheromones (logs baited with males), and host orientation. Insects released in high temperature and low wind velocity flew higher than at low temperatures and, therefore, may fly above low level attractant traps. In the absence of attractants, beetles tended to fly downwind.

120. Shorey, H. H. and L. K. Gaston. 1967. Pheromones, p. 241-265. In W. W. Kilgore and R. L. Doutt (eds.), Pest control. Biological, physical, and selected chemical methods. Academic Press, New York.

In a general review of the biology and potential use of insect pheromones, includes a section entitled "Aggregation Pheromones" concerned solely with scolytids. Cites the discovery of pheromones produced by the initially attacking sex in seven species, reviews the behavioral aspects of pheromone biology using Ips confusus as an example, and contends that species specificity has not been adequately proved.

121. Silverstein, R. M. 1969. Terpenes and insect behavior. p. 73-75.
<u>In</u> Insect-plant interactions, National Academy of Sciences,
Washington, D. C.

From a work conference held in March, 1968. Points out that terpenes are ubiquitous in nature and refers to the importance of terpene alcohols in the attractant pheromones of at least three scolytid species. Reports successful isolation, identification and synthesis of pheromones of <u>Ips confusus</u> and <u>Dendroctonus brevicomis</u> and successful field tests with I. confusus pheromones.

122. Silverstein, R. M. 1970. Methodology for isolation and identification of insect pheromones — examples from Coleoptera, p. 285-299. In D. L. Wood, R. M. Silverstein and M. Nakajima (eds.), Control of insect behavior by natural products.

Academic Press, New York.

From a symposium held in January, 1968. For three beetles, including the scolytids <u>Ips confusus</u> and <u>Dendroctonus brevicomis</u>, describes the isolation and identification of sex pheromone compounds. Provides detailed analysis of chemical and spectrometric identification techniques supported by numerous structural formulae and sample spectra.

123. Silverstein, R. M. 1970. Attractant pheromones of Coleoptera. p.

21-40. In M. Beroza (ed.), Chemicals controlling insect behavior.

Academic Press, New York.

From a symposium held in April, 1969. Review of work on identification of attractant pheromones in eight species in four families of Coleoptera, including four scolytids: <u>Ips confusus</u>, <u>Dendroctonus brevicomis</u>, <u>D. ponderosae</u> and <u>D. frontalis</u>. Includes historical summaries, general methodology for isolation and identification, and synthetic pathways for all known pheromone compounds. Provides a critique of differences in philosophy and methodology found in different research groups which have led to "occasionally intemperate polemics."

124. Silverstein, R. M. and J. O. Rodin. 1965. Spectrometric identification of organic compounds on a milligram scale. The use of complementary information. Microchem. J. 9: 301-308.

Discusses the problems and methodology involved in identification of milligram and microgram quantities of organic compounds as opposed to conventional chemical methods. Illustrates micromethodology, using infrared, mass, ultra-violet and NMR spectra to identify two compounds isolated from the attractive frass of male Ips confusus.

125. Silverstein, R. M., J. O. Rodin and D. L. Wood. 1966. Sex attractants in frass produced by male <u>Ips</u> confusus in pondersoa pine. Science 154: 509-510.

Reports the isolation, identification and synthesis of three terpene alcohols from the frass of <u>I. confusus</u>. The compounds are: I)

(-)-2-methyl-6-methylene-7-octen-4-ol, II) (+)-<u>cis</u>-verbenol, and

III) (+)-2-methyl-6-methylene-2,7-octadien-4-ol. Although neither compound was active alone, a combination of the synthesized compound I with either of the other two mimicked the attraction of the isolated compounds or male frass. This is the first report of synergism of sex pheromone compounds in any insect.

126. Silverstein, R. M., J. O. Rodin and D. L. Wood. 1967. Methodology for isolation and identification of insect pheromones with reference to studies on California five-spined ips. J. Econ. Ent. 60: 944-949.

Using <u>Ips</u> <u>confusus</u> as an example, describes the methodology involved in isolating and identifying insect pheromones. Deals mainly with isolation and spectrometric techniques of identification.

127. Silverstein, R. M., J. O. Rodin, D. L. Wood and L. E. Browne. 1966. Identification of two new terpene alcohols from frass produced by <u>Ips confusus</u> in ponderosa pine. Tetrahedron 22: 1929-1936.

Two new terpene alcohols were isolated from frass produced by <u>I</u>.

<u>confusus</u> males feeding in ponderosa pine. They are: (-)-2-methyl6-methylene-7-octen-4-ol and <u>trans-2-methyl-6-methylene-3,7-octadien-</u>
2-ol. They serve as internal markers in the isolation of the sex
pheromone. (The former compound was later shown to be one of three
principal sex pheromone components for <u>I</u>. <u>confusus</u> and to be involved
in the pheromone of <u>I</u>. <u>latidens</u> as well).

128. Silverstein, R. M., R. G. Brownlee, T. E. Bellas, D. L. Wood, and L. E. Browne. 1968. Brevicomin: principal sex attractant in the frass of the female western pine beetle. Science 159: 889-890.

Reports the isolation, identification and synthesis of exo-7-ethyl-5-methyl-6,8-dioxabicyclo(3.2.1)octane, the principal component of the sex attractant produced by female <u>Dendroctonus brevicomis</u>. Proposes the trivial name, brevicomin. In the laboratory, as little as 1 jug of brevicomin was attractive to male beetles. In addition, other fractions were synergistic with brevicomin.

129. Smith, R. H. 1966. Forcing attacks of western pine beetles to test resistance of pines. U. S. For. Serv. Res. Note PSW - 119.

As one method of inducing attacks on selected trees to test their resistance to <u>Dendroctonus brevicomis</u>, reports that four to six artificially infested bolts hung at a height of 15 feet attracted field populations which first attacked the baited tree near the bolts, subsequently attacked up and down the bole, and within a few days also attacked nearby, unbaited trees.

130. Stark, R. W. 1968. Substances attractives chez les Scolytides.
Bull. Soc. Ent. Suisse 41: 245-252.

Discusses the subject of scolytid pheromones, and provides a chronological list of publications on <u>Ips confusus</u> pheromones through 1967. Special attention is placed on host tree interaction with pheromones, methodology involved in isolation, identification and synthesis of pheromones, problems in pheromone terminology, site of pheromone production, and conflicting viewpoints on the role of isolated compounds as pheromones in the genus <u>Dendroctonus</u>.

131. Stark, R. W. 1968. L'Entomologie forestière à l'Université de Californie, Berkeley, USA. J. For. Suisse 119: 689-697.

Reviews forest entomological studies at the University of California, Berkeley, including work on scolytid pheromones. Describes the isolation, identification and synthesis of pure pheromone compounds from <a href="https://example.com/linearing-com/linea

132. Tsao, C. H. and C. Yu. 1967. Sex pheromones of the southern pine beetle, <u>Dendroctonus frontalis</u> Zimm., (Coleoptera: Scolytidae). J. Georgia Ent. Soc. 2: 13-20.

Describes sensitive laboratory bioassay methods using capillary tubes containing frass or frass extract or glass rods dipped in extract. Demonstrates that: female frass was more attractive to males than females, male frass was more attractive to females than males, and that when insects were extracted in n-hexane, female extract strongly attracted males but slightly repelled females, and male extract was slightly repellant to both sexes.

133. Vité, J. P. 1965. Die Wirkung pflanzen- und insekteneigener Lockstoffe auf <u>Pityophthorus</u> und <u>Pityogenes</u> (Coleoptera: Scolytidae). Naturwiss. 52: 267.

Demonstrates that male <u>Pityophthorus confertus</u> and <u>annectens</u>, and <u>Pityogenes carinulatus</u> boring in their respective hosts in field olfactometers, attracted large numbers of beetles of the same species from natural populations. Responding beetles showed a distinct daily response rhythm.

134. Vité, J. P. 1965. Ist die vorbeugende Begiftung von Fangbäumen zweckmässig? Allg. Forstzeitschrift 20: 438-439.

An examination of the trap tree concept and the role of secondary attraction in its application. Contends that insecticide treatment of trap logs prevents establishment of pioneer beetles and hence, the production of secondary attraction, thereby limiting success of Kyloterus lineatus (Trypodendron lineatum), Pityogenes chalcographus and Ips typographus are far more strongly attracted to freshly attacked host material in field olfactometers than to unattacked logs or those sprayed with host terpenes, and claims that I.

typographus will attack fresh host material when it is baited with infested bark. Calls for reexamination of the trap tree method in light of recent elucidation of the phenomenon of secondary attraction.

135. Vité, J. P. 1965. Über die Anwendbarkeit insekteneigener Lockstoffe im Forstschutz. Forst Holzwirt. 20: 98-102.

A review of lepidopteran sex pheromones and scolytid population aggregating pheromones, particularly in the genera <u>Dendroctonus</u> and <u>Ips</u>. Cites the apparent absence of pheromones in some <u>Dendroctonus</u> spp., the lack of their detection in <u>Scolytus</u>, the method and site of pheromone production, interaction with host tree volatiles, and the influence of environmental factors and distance on response to pheromones. Notes problems in and cost of procuring pure pheromones but, on the basis of North American research, suggests that pheromones could be used to manipulate natural populations, e.g. in combination with chemosterilants or in inducing attack on unsuitable brood material.

136. Vité, J. P. 1967. Sex attractants in frass from bark beetles. Science 156: 105.

Questions the terminology "sex attractant" designated by Silverstein and co-workers for three compounds isolated from the frass of male Ips confusus and the conclusion, based on laboratory bioassay, that they are responsible for the mass attack phenomenon. Advocates the

use of field, rather than laboratory bioassays, and isolation of compounds from pure fecal matter or hindguts rather than frass.

137. Vité, J. P. 1968. Timber industry attacks bark beetle problem through basic research. Texas Industry 36(September): 14-16.

Discusses the pheromone research program of the Boyce Thompson Institute, primarily on the southern pine beetle. Notes that the major component in female <u>Dendroctonus frontalis</u> is <u>trans-verbenol</u>, whereas verbenone is found in males. Another compound named frontalin was found in <u>D. frontalis</u> females in extremely minute amounts. However, it was found in large quantities in male <u>D. brevicomis</u>, and in female <u>D. pseudotsugae</u>. A mixture of <u>trans-verbenol</u> and frontalin was highly attractive to <u>D. frontalis</u> and <u>D. brevicomis</u>, suggesting that an effective control method may result from these experiments.

138. Vité, J. P. 1970. Erste Anwendung synthetischer Populationslockstoffe in der Borkenkäferbekämpfung. Allg. Forstzeitschrift 25: 615-616.

A review of research at the Boyce Thompson Institute of Plant Research which has led to the discovery of frontalin as a principal population aggregating pheromone in <u>Dendroctonus frontalis</u>, <u>D. brevicomis</u> and <u>D. pseudotsugae</u>, and <u>trans</u>—verbenol in <u>D. ponderosae</u>. Emphasizes the necessity for pheromones to act in combination with host tree volatiles to ensure successful mass attack, and discusses the practical application of these materials in manipulating bark beetle populations.

139. Vité, J. P. 1970. Pest management systems using synthetic pheromones.

Contrib. Boyce Thompson Inst. 24: 343-350.

Reviews the use of pheromones and host terpenes to attract <u>Dendroctonus</u> species. Contends that baiting trees is a simpler and less costly method than using pheromones in conjunction with traps. Illustrates this contention with a description of the "ground-check control" method in which a ground survey crew detects a <u>D. frontalis</u> infestation, baits nearby trees with "frontalure" (frontalin plus <-pinene), and injects them with cacodylic acid which will kill the developing brood but not insect predators. Baiting trees with pheromones was also effective with <u>D. brevicomis</u>, <u>D. pseudotsugae</u> and <u>D. ponderosae</u>.

140. Vité, J. P. and R. G. Crozier. 1968. Studies on the attack behavior of the southern pine beetle. IV. Influence of host condition on the aggregation pattern. Contrib. Boyce Thompson Inst. 24: 87-93.

Contends that host condition has a strong influence on the aggregation behavior of Dendroctonus frontalis, since stumps and large log sections were far superior targets for mass aggregation than small infested trees and log sections. As host material dried out, or as feeding commenced, attraction was lost. Gas chromatography revealed that during the course of feeding, sex-specific volatiles in the gut, particularly trans-verbenol, were depleted.

141. Vité, J. P. and R. I. Gara. 1961. A field method for observation on olfactory responses of bark beetles (Scolytidae) to volatile materials. Contrib. Boyce Thompson Inst. 21: 175-182.

Describes different methods of field testing scolytid produced attractants, including funnel traps, rotary nets and window traps. Rotary nets were the most effective as they could be used with or (as a check) without attractants.

142. Vité, J. P. and R. I. Gara. 1962. Volatile attractants from ponderosa pine attacked by bark beetles (Coleoptera: Scolytidae). Contrib. Boyce Thompson Inst. 21: 251-273.

Describes a new field olfactometer and extensive field experiments which demonstrated that the species specific, attractive materials which induce mass attack of ponderosa pine are produced by male <u>Ips</u> and female <u>Dendroctonus</u>, both of which must bore in suitable breeding material. There is no evidence for the involvement of yeasts. There is an apparently temperature-dependent bimodal diurnal response, and released <u>Ips</u> <u>confusus</u> responded to attractant within two to 50 minutes over distances between 10 to 600 meters.

143. Vité, J. P. and G. B. Pitman. 1967. Concepts in research on bark beetle attraction and manipulation. Proc. XIV Intern. Union Forest. Res. Organ. Munich, Sec. 24: 683-701.

An extensive review of scolytid secondary attraction and population aggregation. Categorizes aggregating attractants as follows: 1) odors emanating from the host, 2) attacking beetles increase the release and/or production of a host stimulus, e.g. by stimulating

resin flow or by frass removal, and 3) insect-produced volatiles (pheromones). Concludes that the greatest potential for population manipulation is in aggressive species such as <u>Dendroctonus brevicomis</u>, <u>D. frontalis</u> and <u>D. ponderosae</u>, which use aggregation pheromones to concentrate their population in a short time.

144. Vité, J. P. and G. B. Pitman. 1968. Bark beetle aggregation: effects of feeding on the release of pheromones in <u>Dendroctonus</u> and <u>Ips</u>.

Nature (Lond.) 218: 169-170.

Extensive feeding by females of <u>Dendroctonus</u> spp. in new host material soon inhibits release of attractants. In contrast, feeding by males of <u>Ips</u> spp. triggers and sustains attractant production. Biological and evolutionary implications of these differences are discussed.

145. Vité, J. P. and G. B. Pitman. 1969. Insect and host odors in the aggregation of the western pine beetle. Can. Ent. 101: 113-117.

When offered with freshly tapped ponderosa pine oleoresin, crushed emergent female <u>Dendroctonus brevicomis</u> or synthetic brevicomin attracted both sexes of the western pine beetle in flight. The sex ratio of responding insects could be controlled, more males responding to sources high in pheromone content, and more females responding to sources low in pheromone content.

146. Vité, J. P. and G. B. Pitman. 1969. Aggregation behavior of <u>Dendroctonus</u>

<u>brevicomis</u> in response to synthetic pheromones. J. Ins. Physiol.

15: 1617-1622.

In field tests, milligram quantities of synthetic frontalin (1,5-methyl-

6,8-dioxabicyclo(3.2.1)octane) in combination with brevicomin and oleoresin attracted more beetles than either oleoresin plus brevicomin or frontalin. Frontalin predominately attracted females, and brevicomin, males. Suggests that in a mass attack, females first release frontalin, which attracts more females, and then (after feeding commences) brevicomin, which attracts males. A simple capillary type release system is described.

147. Vité, J. P. and G. B. Pitman. 1970. Management of western pine beetle populations: use of chemical messengers. J. Econ. Ent. 63: 1132-1135.

In field tests, volatiles were deployed from hollow plastic vial caps secured to mailing tubes covered with Stikem Special. Frontalin alone was more attractive than either brevicomin or the terpene 3-carene, each of which attracted approximately equal numbers of beetles. Frontalin attracted beetles in a sex ratio (males: females) of 1:1.4 and brevicomin attracted beetles in a sex ratio of 1:0.3. Trees baited with frontalin mixed with 3-carene were attacked at far higher densities than trees baited with brevicomin and 3-carene. Concludes that frontalin is apparently the principal aggregating pheromone in Dendroctonus brevicomis.

148. Vité, J. P. and J. A. A. Renwick. 1968. Insect and host factors in the aggregation of the southern pine beetle. Contrib. Boyce
Thompson Inst. 24: 61-63.

Presents data to show that the chemical messengers responsible for <u>Dendroctonus frontalis</u> aggregation are produced in the female hindgut prior to attack on a new host. Therefore, they are correctly termed pheromones, and can be released prior to feeding, immediately upon arrival at a new host.

149. Vité, J. P. and J. A. A. Renwick. 1970. Differential diagnosis and isolation of population attractants. Contrib. Boyce Thompson Inst. 24: 323-328.

Describes the differential diagnosis of scolytid pheromones by gas chromatographic analysis of hindgut volatiles of the attractive sex before, during and after the time of maximum attraction. Comparison with the nonattractive sex and with other species determines the distribution of candidate compounds, and active materials are monitored by field bioassay. Argues for the superiority of differential diagnosis over conventional isolation techniques which require the use of organic solvents, large amounts of crude starting material and a chemical instead of "biological" cleanup.

150. Vite, J. P. and D. L. Williamson. 1970. <u>Thanasimus dubius</u>: prey perception. J. Ins. Physiol. 16: 233-239.

In field experiments, <u>T. dubius</u> responded with similar daily response rhythms as its prey to synthetic frontalin alone or in combination with oleoresin or <u>trans</u>-verbenol in an approximately equal sex ratio. Addition of verbenone resulted in approximately half the female response. On tree-trunk simulating olfactometers, the clerids caught and fed on responding prey insects (<u>Dendroctonus frontalis</u>), and engaged in mating. Discusses the significance of this highly synchronized chemical messenger system by which prey adults and males are intercepted prior to the cryptic phase, and notes that apparently similar systems occur with other scolytid species.

151. Vité, J. P. and D. L. Wood. 1961. A study on the applicability of the measurement of cleoresin exudation pressure in determining susceptibility of second growth ponderosa pine to bark beetle infestation. Contrib. Boyce Thompson Inst. 21: 67-78.

As part of a study on the characteristics of potential host trees, demonstrates that initial attack by <u>Dendroctonus</u> spp. was similar in trees with low or high (greater than four atmospheres) oleoresin exudation pressure (o.e.p.), but that mass attack occurred at a much higher rate in trees with lower o.e.p. Suggests that in trees with lower o.e.p., the beetles could survive and initiate a mass attraction.

152. Vité, J. P., R. I. Gara and R. A. Kliefoth. 1963. Collection and bioassay of a volatile fraction attractive to <u>Ips confusus</u> (LeC.) (Coleoptera: Scolytidae). Contrib. Boyce Thompson Inst. 22: 39-50.

Reports that only mature male <u>I. confusus</u> produce the substance which causes species—specific mass attraction. It originates in the hindgut, but only in the presence of food material. Describes two field olfactometers, and a release and recapture field bioassay, and argues for the superiority of field over laboratory bioassays.

153. Vité, J. P., R. I. Gara and H. D. von Scheller. 1964. Field observations on the response to attractants of bark beetles infesting southern pines. Contrib. Boyce Thompson Inst. 22: 461-470.

Dendroctonus frontalis, <u>Ips</u> avulsus, <u>I. grandicollis</u> and <u>I. calligraphus</u> were attracted in large numbers to southern pine logs infested by their own species. In the absence of such material, all species were

cross attracted to other logs. In addition, <u>D. frontalis</u> was strongly attracted to petroleum ether extract of <u>D. brevicomis</u> attractant.

Other scolytids, woodborers and predaceous beetles were attracted to both host and beetle-associated stimuli. Characteristic flight and response patterns revealed a lesser morning peak, a depression in midday, and a peak response flight in late afternoon and evening.

154. Wasserman, H. H. and E. H. Barber. 1969. Carbonyl epoxide rearrangements. Synthesis of brevicomin and related (3.2.1) bicyclic systems. J. Amer. Chem. Soc. 91: 3674-3675.

Describes the application of thermal rearrangement of **5**, **€** - epoxy ketones to the synthesis of brevicomin. When <u>cis</u>-6,7-epoxyhonan-2-one was heated to 210° in a base-washed sealed tube, a 95% conversion took place to yield 90% <u>exo</u>-brevicomin and 10% of its <u>endo</u> isomer. The synthetic brevicomin was identical to an authentic sample of brevicomin and was active when bioassayed by Dr. R. M. Silverstein.

155. Wilkinson, R. C. 1964. Attraction and development of <u>Ips</u> bark beetle populations in artificially infested pine bolts exposed on firetowers and turntables in Florida. Florida Ent. 47: 57-64.

Demonstrates that adult <u>Ips</u> spp. were not strongly attracted to uninfested logs placed up to 91 ft above ground, but that both sexes of <u>I. grandicollis</u> and <u>I. calligraphus</u> readily sought out and colonized similarly treated logs in which males of the same species had been introduced.

156. Wilkinson, R. C., W. T. McClelland, R. M. Murillo and E. O. Ostmark. 1967. Stridulation and behavior in two southeastern <u>Ips</u> bark beetles (Coleoptera: Scolytidae). Florida Ent. 50: 185-195.

As part of an extensive study on morphology of stridulating organs and stridulation in relation to reproductive behavior and gallery construction, demonstrates that contact with attractive male frass induced females to find the entrance to the nuptial chamber and begin stridulation.

157. Williamson, D. L. 1971. Management to reduce pine beetle infestations.

Forest Farmer 30 (January): 6-7, & 18.

Proposes a pest management system for <u>Dendroctonus frontalis</u> involving: survey for damage, baiting uninfested pines near attacked trees with frontalure (1 part frontalin and 2 parts <-pinene), injection of cacodylic acid into all trees over 6 inches diameter at breast height (including baited trees) within 15 to 25 feet of the infested trees, and follow up with salvage logging, survey and, when necessary, repetition of the procedure. Unlike chemical control procedures currently in use, the proposed system concentrates the pest in known areas and enhances predation by the clerid beetle Thanasimus dubius.

158. Wood, D. L. 1962. The attraction created by males of a bark beetle <u>Ips confusus</u> (LeConte) attacking ponderosa pine. Pan-Pac. Ent. 68: 141-145.

Demonstrates secondary attraction in <u>Ips</u> confusus by using bark-wood samples infested with males tested in a multiple-choice, laboratory

olfactometer. A positive response was elicited in 80% of all females and 50% of all males. Boring dust from outer bark was not attractive. Crushed males removed after feeding were attractive, although newly emerged males were not.

159. Wood, D. L. 1962. Experiments on the interrelationship between oleoresin exudation pressure in <u>Pinus ponderosa</u> and attack by <u>Ips confusus</u> (LeC.) (Coleoptera: Scolytidae). Can. Ent. 94: 473-477.

In field experiments on the role of oleoresin exudation pressure on the resistance of host trees to <u>I. confusus</u> attack, demonstrates that successful establishment (and not initial attack) of pioneer males is a necessary prerequisite to production of secondary attraction.

160. Wood, D. L. 1963. Studies on host selection by <u>Ips confusus</u> (LeConte) (Coleoptera: Scolytidae) with special reference to Hopkin's host selection principle. Univ. Calif. Publ. Ent. 27: 241-282.

As part of a study on host selection, demonstrates conclusively that ponderosa pine logs or ground phloem disks infested with male <u>I. confusus</u> were highly attractive to females, which are almost invariably attracted to galleries containing males. Female-infested material was no more attractive than uninfested material.

161. Wood, D. L. 1969. Bark beetle pheromones. p. 88-89. <u>In</u> Insectplant interactions, National Academy of Sciences, Washington, D. C.

From a work conference held in March, 1968. A summary report on work at the University of California, Berkeley, including: isolation,

identification and synthesis of scolytid pheromones, manipulation of populations with pheromones, and specificity of pheromones in the genus Ips.

162. Wood, D. L. 1970. Pheromones of bark beetles, p. 301-316. <u>In</u>
D. L. Wood, R. M. Silverstein and M. Nakajima (eds.), Control
of insect behavior by natural products. Academic Press, New York.

From a symposium held in January, 1968. Documents the existence of secondary attraction in scolytids, and reviews biological aspects of pheromone production and response, principally in <u>Ips confusus</u>. Reports field studies in which <u>I. confusus</u> and some of its beetle predators were attracted to synthetic pheromones. Also presents results of hitherto unpublished work (done in collaboration with G. N. Lanier) which demonstrates cross attraction between species in various taxonomic groups within the genus <u>Ips</u>.

163. Wood, D. L. and R. W. Bushing. 1963. The olfactory response of <u>Ips</u>

<u>confusus</u> (LeConte)(Coleoptera: Scolytidae) to the secondary

attraction in the laboratory. Can. Ent. 95: 1066-1078.

Shows that olfactory response to <u>I. confusus</u> secondary attraction can be bicassayed with a highly sensitive, arena-type, multiple-choice, laboratory olfactometer. Males exhibit an "area" orientation near the attractive material, whereas females have a characteristic "point" or "straight-line" klinotactic response. Attractant is produced within four to six hours after males enter host material and food has passed through the gut. As the season progressed, female response declined from a maximum level in late May and June. Discusses relationship of secondary attraction to attack patterns in nature.

164. Wood, D. L. and R. M. Silverstein. 1970. Bark beetle pheromones.

Nature (Lond.) 225: 557-558.

An analysis of scolytid pheromone work by the Boyce Thompson Institute and the Battelle Memorial Institute. Critically examines: the interaction or lack of it between <u>Dendroctonus frontalis</u> and its host tree in secondary attraction, procedures in isolating from <u>D. brevicomis</u> males a pheromone named frontalin and reported to be the principal pheromone of <u>D. frontalis</u> females, methodology of field testing, and doubtful association of <u>trans-verbenol</u> with <u>D. frontalis</u> pheromone.

165. Wood, D. L. and R. W. Stark. 1966. The effects of gamma radiation on the biology and behavior of adult <u>Ips confusus</u> (LeConte)

(Coleoptera: Scolytidae). Can. Ent. 98: 1-10.

As part of a study on gamma radiation, shows that irradiation had no significant effect on production of or response to sex pheromone, and suggests that mass trapping with sex attractants could be utilized in place of mass rearing to provide large numbers of beetles for sterilization by irradiation.

166. Wood, D. L. and J. P. Vité. 1961. Studies on the host selection behavior of <u>Ips confusus</u> (LeConte) (Coleoptera: Scolytidae) attacking <u>Pinus ponderosa</u>. Contrib. Boyce Thompson Inst. 21: 79-95.

Characteristically, a few successful initial attacks by <u>I</u>. <u>confusus</u> are followed by a much larger mass attack. Host selection behavior was studied by baiting felled trees with newly infested bark. Mass attack was intimately associated with the presence of live, mature

males in initial galleries. Suggests that Person's theory that secondary attraction arises from yeast fermentation in host phloem is refuted by the fact that male, but not female, attack elicits mass attraction.

167. Wood, D. L., R. M. Silverstein and M. Nakajima. 1969. Pest control. Science 164: 203-210.

A preliminary review of a symposium on "Control of Insect Behavior by Natural Products" (later published in a book of the same title (See Nos. 122 and 162)), including reports of chemical and behavioral studies on scolytid pheromones.

168. Wood, D. L., L. E. Browne, R. M. Silverstein and J. O. Rodin. 1966.
Sex pheromones of bark beetles - I. Mass production, bio-assay, source, and isolation of the sex pheromone of <u>Ips confusus</u> (LeC.).
J. Ins. Physiol. 12: 523-536.

Describes a refined bioassay for <u>I. confusus</u> sex pheromone and the methods of production, extraction and isolation of the pheromone by various chromatographic techniques. Reports experiments which prove decisively that the pheromone is present in male fecal pellets and that it is also produced in nonhosts. Discusses bioassay techniques, pheromone source and isolation procedures.

169. Wood, D. L., R. W. Stark, R. M. Silverstein and J. O. Rodin. 1967.
Unique synergistic effects produced by the principal sex attractant compounds of <u>Ips confusus</u> (LeConte) (Coleoptera: Scolytidae).
Nature (Lond.) 215: 206.

In field bioassays, three sex attractant compounds, I) (-)-2methyl-6-methylene-7-octen-4-ol, II) (+)-cis-verbenol, and
III) (+)-2-methyl-6-methylene-2,7-octadien-4-ol, were tested
individually and in all possible combinations. The combination
of compounds I, II and III was most attractive to I. confusus,
I and III together marginally attractive, and none of the other
combinations attractive. Ips latidens was marginally attracted
to I alone and highly attracted to a combination of I and II. The
I. latidens response was verified in the laboratory and the addition
of compound III shown to eliminate the response.

170. Wood, D. L., L. E. Browne, W. D. Bedard, P. E. Tilden, R. M.

Silverstein and J. O. Rodin. 1968. Response of <u>Ips confusus</u>

to synthetic sex pheromones in nature. Science 159: 1373-1374.

Reports the first demonstration of a flight response to synthetic compounds delivered in the field in an air stream. Predators of

<u>I. confusus</u>, <u>Enoclerus lecontei</u> and <u>Temnochila virescens chlorodia</u> were also attracted.

171. Yu, C. and C. H. Tsao. 1967. Gallery construction and sexual behavior in the southern pine beetle, <u>Dendroctonus frontalis</u> Zimm. (Coleoptera: Scolytidae). J. Georgia Ent. Soc. 2: 95-98.

As part of a study on gallery construction and sexual behavior, proposes that an individual <u>D</u>. <u>frontalis</u> introduced into an established gallery can detect the sex of the resident beetle without seeing or contacting it, presumably by perceiving beetle-produced odors.

172. Zenther-Møller, O. and J. A. Rudinsky. 1967. Studies on the site of sex pheromone production in <u>Dendroctonus pseudotsugae</u>

(Coleoptera: Scolytidae). Ann. Ent. Soc. Amer. 60: 575-582.

With laboratory tests in an arrestment olfactometer, demonstrates that male <u>D. pseudotsugae</u> were arrested by the ethanol extract of the posterior part of the hindgut of pheromone producing females, or if two drops of phloem extract were added, by the anterior hindgut or Malphighian tubules. An increase in length of Malpighian tubules in pheromone-producing females further supports their suggested role in pheromone production.

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