The Shothole Borer: An Ambrosia Beetle of Concern for Chestnut Orcharding in the Pacific Northwest

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ABSTRACT. The shothole borer of chestnuts, *Xyleborus dispar (Coleoptera: Scolytidae),* is a serious pest of young chestnut trees throughout the western Cascades and now may be the limiting factor in successful orchard establishment. It is increasingly more ubiquitous in forested areas where it evidently utilizes all broadleaf tree species in its range. Having an average of two generations per year, adult borers tunnel into host sapwood tissue for colonization. Mass attack on hosts contribute to the ultimate demise of seemingly healthy trees. A literature review was done to determine the extent of what is known about this beetle and to gain a better understanding of how to effectively prevent and/or control infestations in new or existing orchards.

The shothole borer,[1] *Xyleborus dispar* (F.) *(Coleoptera: Scolytidae),* is a European ambrosia beetle that most likely was introduced into the U.S. prior to 1816, (59) but was first officially reported by Peck in the Massachusetts Agricultural Journal in 1817 as *Anisandrus pryi* (Peck). It was found in the Northwest in Clarke County, Washington in 1901 and first reported as utilizing chestnut as a host species in the Northwest as early as 1912 (59). Shothole borer was reported in British Columbia in the early 1920's (28, 33) and was recorded in California as attacking a variety of deciduous trees in 1942 (31).

Shothole borer now has been found to be a pest throughout the northwestern states and western Canada (6). New chestnut plantings are extremely susceptible to attack by this beetle, representing a critical factor in successful orchard establishment. The purpose of this paper is to highlight important observations and conclusions made by previous researchers on ambrosia and bark beetles to gain a better understanding of how to effectively control infestations of *X. dispar* in new and existing chestnut orchards.

TAXONOMY

As insect pests, the bark and timber beetles, *Scolytidae*, have been studied extensively due to their significant economic destructive capabilities in both forest and agroecosystems. The original description of *X. dispar* was made in 1792 by Fabricius, who most likely gave it the species name based on the disparity between the two sexes. There have been four noteworthy attempts to classify the *Scolytidae* in North and Central America (4, 9, 54, 60). The most recent taxonomic monograph puts the shothole borer in the genus *Xyleborus* of the tribe Xyleborini and establishes genus synonymy with *Anisandrus, Anaeretusi* and possibly *Cyclorhipidion* (60).

DESCRIPTION

—Female. Length 2.8-3.7 mm, twice as long as wide; dark brown to black; elytra roughly 62.5% of total length, 1.3x longer than wide, striated longitudinally parallel, interstrial space shining, smooth.

—Male. Length 1.5-2.1 mm; dwarfed, thorax disk and elytra strongly convex; wingless.

—Egg. Length 1 mm x 0.06 mm diameter; oblong or oval and clear to white in color.

—Larvae. Length 5 mm x 1.45 mm at widest part; white, grublike, legless; slightly sclerotized heads with brown mouth parts; three instars (60).

—Pupae. Length 4 mm x 1.5 mm at widest part; white; males easily distinguishable by their small size relative to females. (16, 59).

BIOLOGY

The shothole borer, *X dispar,* is within an ecological group of the *Scolytidae* known as ambrosia beetles. These beetles are characterized by their utilization of the sapwood of physiologically stressed and recently dead trees for colonization and by the use of symbiotic fungi as their sole food source. *X. dispar* forms an ectosymbiotic relationship with the fungus *Ambrosiella hartigii* Batra (Fungi Imperfecti) that they transport into the host tree in specialized glands and cultivate on the tunnel walls of their galleries (3, 19, 48). When growing in the galleries of the host trees, the mycelial form of the fungus converts to a yeast-like derivative in response to borer excrements and continued cropping (3, 21, 27, 41). This yeast-like form of the fungus is what is known as ambrosia. Scolytid beetles are the primary invaders in dying plant material and thus function as vectors of the decay process in forest ecology. After the insect has moved on in search of a new host, the fungus remains and accelerates the break down and degradation of the host tree.

LIFE HISTORY

The life cycle of *X dispar* is described in several papers (7, 9, 16, 20, 29, 52, 59, 60). The one distinct feature that

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[1] Not to be confused with the bark beetle, *Scolytus rugulosus* (Muller) *(Coleoptera: Scolytidae)* of the same common name. Scolytus is in a separate tribe of the same subfamily. The important differences between bark beetles and ambrosia beetles is food source and the area of utilization within a host.

separates it from all the other bark and timber beetles is that it is the only species in the Scolytidae to exhibit a true diapause (60). Adult beetles overwinter within the sapwood tunnels they excavate in the limbs and trunks of infested trees. Males are flightless and spend their entire lives within the galleries or near tunnel entrances where mating occurs. Female emergence is timed with the beginning months of spring. Once the female has made contact with a suitable host, she crawls around on the trunk searching for a site to begin boring an entrance hole. This entrance hole is about the diameter of a pencil lead and in small trunks and branches is usually found at the base of leaf and bud nodes.

Immediately after tunneling into the xylem, fungal gardens are inoculated by the female and a small clutch of eggs is laid. Clutch size is reported as varying in number being between 1-10 eggs for the primary clutch and up to 45 eggs for subsequent clutches. Eggs typically are laid at the end of main or lateral galleries and take from two to three weeks to hatch (59). Larvae take about four weeks for full development and do not contribute to gallery excavation, but rather, move freely about while feeding upon the ambrosia. The pupal stage lasts another four weeks, making the total life cycle from egg to adult about 10-11 weeks (59). Tunnels are continually expanded by the parents as the brood size increases or until the moisture content of the host deteriorates. Host moisture must be available in the tunnels to be able to support the growth of the ambrosia. Adult females will leave the colony to find new hosts or will re-work an existing host.

Brood development is a temperature dependent function with development time being proportional to temperature. Brood development time from larvae to adult was accelerated by 52% when temperature was maintained at a constant 21 C (69.8 F) verses a constant 13 C (55.4 F) (2). Cool temperature appears to impede the growth of newly hatched larvae. Current flight period and patterns of flight also are influenced by the success of the beetle developmental period of the previous year. A warm previous season is conducive to the accelerated development of the brood and conceivably more fully developed adults would then be ready to emerge after the seasonal diapause the following spring (34). Typically there are two generations per year in Oregon (9).

Signs of early spring attack include wilting of newly emerged bud growth and frass tailings from borer excavations. Frass will usually be evident on infected limbs and alongside, or at the base of trunks. In late summer, galleries usually become considerably honeycombed throughout an infestation site to such an extent that trunks or branches become weakened and brittle, breaking easily when bent over, thereby exposing numerous larvae and adults.

HOST TREES

Host trees in association with *X dispar* include potentially all deciduous fruit and forest trees in its range (6, 59). Those that have been reported include: *Acer, Aesculus,* ***Alnus, Betula,*** *Castanea, Crataegus, Corylus, Cydonia, Fagus, Fraxinus, Juglans, Leriodendron, Males, Platanus, Populus, Prunus, Punica, Pyrus, Quercus, Salix, Vitis* (6, 9, 16, 17, 31, 60). In addition, *Xyleborus* sp. are reported throughout the world as pests of *Carya* (22), *Camillia* (8, 15, 37, 51), *Cocos* (32) and yam tubers (58).

The condition of the host tree is a major factor in susceptibility to attack. It has been consistently reported by several researchers (25, 30, 35, 43, 45, 46, 56) that ambrosia beetle attacks are limited primarily to hosts that are physiologically compromised due to some recent injury or stress. Under epidemic or outbreak proportions, these borers will attack perfectly healthy trees found in the vicinity of suitable hosts, if preferred host material is of limited availability.

HOST SELECTION AND FLIGHT RESPONSE

Olfaction is the dominant response factor in flight orientation to a suitable host (23, 24, 25). Field observations (10, 23, 34, 43) indicate that ambrosia beetles are stimulated to fly upwind and in the direction of the source in response to odor attractions. In the absence of olfactory stimulus, pioneering beetles are distributed uniformly throughout the stand (45). Beetles are guided to a chemical stimulus by a type of klinokinesis (47, 61), in which the attractant source is located by positive orientation to successive pulses from a volatile cloud within its atmospheric range.

There are two phases of olfactory guided dispersal: primary attraction (allocation) and secondary attraction (concentration) (24). Primary attraction involves the pioneering flight of adult beetles accurately pinpointing a specific target host within a given stand (7, 10, 11, 18, 46). The pioneer flight in *X. dispar* is done by the female since males lack the ability to fly. The chemical stimuli in this stage of olfactory guidance are volatile breakdown products of anaerobic host tissue metabolism (7, 26), the main component of which is ethanol (7, 36, 52). Single trees are selected in this early phase of attack based on their current physiological state, with host stress being positively correlated with the production of ethanol.

An important factor in a host's resistance to the primary phase of infection in conifers is oleoresin exudation pressure, (OEP), which can be directly related to water stress (45). Low epithelial cell turgor pressure in resin duct lining results in decreased sap flow in response to a disturbance. If a beetle encounters heavy resin flow in a pioneer tunnel, it will be mechanically flooded out and/or chemically repelled, rendering the borer attack unsuccessful (40, 45, 55). In the coastal Pacific Northwest there is typically no critical soil moisture deficiency that negatively affects the OEP during the early season flight of ambrosia beetles (45). This is not necessarily true of the summer flight.

Should a primary attack be successful, species specific attractant pheromones then will be produced by the pioneering female (7, 12, 40, 45, 47). This initiates the concentration phase of olfactory-guided flight. Attractant pheromones have been isolated from the alimentary system (39, 56) and frass of pioneering female beetles (47). The intensity of secondary attractant is dependent on the concentration of the pioneering beetle's host infestation (47) and/or entirely on the condition of the host (7, 56). A synergistic influence, possibly associated with ethanol, has been suggested as the factor responsible for increasing the activity of this insect-produced attractant pheromone (7). Host logs not undergoing active anaerobic metabolism, experimentally baited with pioneer beetles, produced no attraction (7).

The secondary attractant pheromone is a far stronger olfactory guide relative to primary attractants. It stimulates female beetles to converge en masse upon a host and begin colonization, following a primary attack. Some species of ambrosia beetles will mass aggregate on vertical objects near established sources of attraction without any apparent regard for the suitability of the object as host material (45). This suggests that visual orientation aids olfactory guidance (20). It has been shown in field studies with ambrosia beetles that response to secondary attraction can occur within four hours (43). There are distinct seasonal and diurnal response patterns to secondary attractants and these patterns are influenced by temperature, light and wind speed (7, 18 ,47, 48).

FLIGHT CAPACITY

Differences in the capacity of flight response to attractant stimuli between individuals and populations within a brood have been shown to be based on the physiological condition of the beetles rather than inherited ability (23). A very thorough study (49) on the effects of temperature upon the various activities of the Douglas-fir beetle, *Dendroctonus pseudotsugae* H. emphasizes temperature as the most important of several environmental factors that influence a given beetle activity. It has been shown that ambient temperature determines mode of action once the threshold temperature for that action has been reached.

Absolute limits of activity were laboratory tested (49) and found to be between 0-1 C (32-33.8 F), where there is a reaction to contact or light; and 49 C (120.2 F), when thermal death occurs. Heat injury resulted in temperatures over 38-39 C (100.4-102.2 F). At temperatures over 10 C (50 F) beetles exhibited relatively high boring ability. An increase in temperature elicited increased boring activity correspondingly. At higher ambient temperatures beetles are able to bore through thicker bark in relatively shorter time periods.

Activity response showed a 6-hr lag when plotted against daily temperatures due to the insulative effect of the host. Thus, boring activity was greatest in late evening to midnight, with the least activity occurring in the mornings. Flight activity occurred between a threshold of 10 C (50 F); to the maximum reported flight temperature of 32 C (89.6 F) depending on the species, its population density and the availability of sources of attraction (24, 34, 43, 48). Ambrosia beetles will fly at cooler temperatures in the presence of sunlight (48). Spring peak flights occurred at mid-day with flight ceasing one hour before sunset (47). No flight occurred in *Ttypodendron lineatum (Oliv.)* at night, at temperatures above 29.7 C (86 F) or at heights above 2 m when wind velocities exceed 3 mph (47). Directed flight from low light to high light intensities was noted and implications for flight from shaded forests to clearcut areas were mentioned (48).

Relative humidity increased heat tolerance and survivability in test beetles (49). Since relative humidity is effectively 100% inside beetle galleries, only temperatures above 43 C (109 F) are considered injurious. Surface temperatures on logs exposed to solar radiation for an afternoon commonly reach this temperature. This may explain a preference in beetles for attack concentrations on the cooler surface areas of hosts, such as underneath a branch node or on the shaded side of a branch or trunk.

It is important to note that there are two distinct seasonal flights in the Pacific Northwest: an early spring flight and an August summer flight. The summer flight coincides with decreased soil moisture when hosts are potentially more drought stressed (45). Summer flight ability is enhanced by temperatures between 25-32 C (77-89.6 F) (49). There are two daily summer peaks: one before and one after noon (47). These peaks can be determined by monitoring local microclimatic data.

Flight distances of bark beetles were reported up to 500-1000m (1500-3000 ft) (23). Flight mill lab tests showed that beetles were physiologically capable of flight for up to 11.27 km (7 mi) in 4 h. This can amount to 24-32 km (15-20 mi) per day for several days in still air with healthy Douglas-fir beetles, *D. pseudotsugae.* This implies the virtual impossibility of controlling population outbreaks by silvicultural methods (1). Relative velocity was recorded to be 115 in/min (4.29 mph) in *D. pseudotsugae* (49).

DISCUSSION

Castanea spp. seem to be a preferred host of *X dispar* in the Pacific Northwest. Apparently healthy chestnut trees showing no obvious signs of stress often are attacked. Upon more thorough examination, it often can be shown that some of these trees may actually be under stress due to one or several factors including: transplant shock, winter freeze or sunburn, high water table, poor soil, mechanical injury, graft incompatibility or some other disease or insect infestation. The vascular system of *Castanea* is ring porous, characterized by large diameter vessels that seal themselves off in response to injury. This walling off of portions of the vascular system can result in cambial dieback due to a girdling effect. This phenomenon may render thin-barked trunks and limbs in chestnut relatively more susceptible to injury than other hosts under similar environmental influences. As chestnut bark thickens and becomes more woody, increased resistance to borer attack may occur.

Positive correlations have been made between epidemic outbreaks and periods of rainfall deficiency, catastrophic winds, snows, floods and fires (13, 30, 53). Differences in length of dispersal (primary fight phase) and the distance beetles will fly to an attractant source have been reported during normal and epidemic population conditions (24). Under normal conditions, pioneer beetles will fly long periods over long distances in search of a suitable host. Under epidemic outbreaks, beetle populations explode into the surrounding hosts in the immediate vicinity without regard for their suitability as compatible hosts. In mass aggregation like this, beetle populations can overcome even healthy trees.

The Pacific Northwest has been experiencing reduced rainfall and increased snowpack deficiencies since 1986. In addition, timber clearcutting has reached record levels over this same time period. The combined effect has had significant impacts on the overall health of host ecosystems. Such a cycle would encourage population levels of *X dispar* due to decreased host resistance to borer attacks and may contribute to some of the problems currently experienced with young chestnut orchard establishment.

CONCLUSION

Based on this review of literature, some control methods are offered as suggestions for combating the shothole borer in potential and existing chestnut orchard blocks. Prevention is by far the best control, but may be impractical, given the limits of control on natural climatic cycles and the proximity of uncontrollable attractant sources to an already established orchard. When possible, considerations for the location of a potential chestnut orchard should take into account both the health and relative proximity of potential beetle attractant sources adjacent to a proposed orchard site. Avoid planting near unhealthy forests or abandoned orchards and recent clearcuts. Orientation of the orchard should be with respect to prevailing winds and sources of primary and secondary attractant volatiles.

Cultural practices should begin with the monitoring of orchards for determination of seasonal flight periods and time of day at which peak flight occurs on a given site. An understanding of borer reproduction cycles will enhance the ability to predict beetle activity and can contribute to some of the controlling factors affecting potential host stress. One of the most important potential controllable factors available to the orchardist for influencing host resistance to borer attack may be to increase cell turgor pressure. High plant cell turgor pressure can be obtained by maintaining adequate soil moisture in the orchard during peak flight periods. Another controllable factor is the limiting of point source primary attractants within the orchard. Noncompatible graft unions, nutritionally or otherwise stressed trees and bark damage caused by winter freezing or sun scalding, can initiate cambial fermentation and often become some of the most common point sources of primary attractants in chestnut orchards. Judicious thinning of these and all other nonvigorous and unhealthy growth in the orchard should be done and, along with any prunings, burned.

Suggestions for future research include the development of resistant cultivars (8, 42), the use of ethanol-based (26, 36, 38) and/or pheromone confusion traps (25, 39, 43, 44, 56), the introduction of predator control organisms (14) and the development of biological pesticides (5, 50, 57). Research also needs to be done to determine proper trap placement for effective control. A concern with the use of attractant-chemical traps for control of *X dispar* is the possibility of inducing epidemic proportion responses within the orchard.

LITERATURE CITED

1. Atkins, M. D. 1961. A study of the flight of the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins *(Coleoptera:* Scolydidae). 3. Flight capacity. Can. Ent. 93:467-474.
2. Atkins, M.D. 1967. The effect of rearing temperature on the size and fat content of the Douglas-fir beetle. Can. Ent. 99:181-187.
3. Batra, L.R. 1967. Ambrosia fungi: A taxonomic revision and nutritional studies of some species. Mycologia 59:976-1017.
4. Blandford, W.F.H. 1895-1907. Family Scolytidae in Biologia Centrali-Americana, 4:81-298.(From Bright, 1968).
5. Bridges, J. R. and Norris, D.M. 1977. Inhibition of reproduction of *Xyleborus ferrugineus* by ascorbic acid and related chemicals. J. Ins. Physio. 23:497-501.
6. Bright, D.E., Jr. 1968. Review of the tribe Xyleborini in America north of Mexico *(Coleoptera:* Scolytidae). Can. Ent. 100:1289-1323.
7. Cade, S.C. 1970. The host selecton behavior of *Gnathotrichus sulcatus* Leconte *(Coleoptera:* Scolytidae). Unpublished Ph.D. thesis, College of Forest Resources, University of Washington, 112 pp.
8. Calmiado, D. 1972. Differences in susceptibility of tea clones in Ceylon to the shothole borer beetle, *Xyleborus fomicatus* (Eich.) *(Coleoptera:* Scolytidae). Z. Agnew. Ent. 68:300-307.
9. Chamberlin, WJ. 1939. The Bark and Timber Beetles of North America. Ore. State Coop. Assoc., Corvallis, Ore. 470 pp.
10. Chapman, J.A. 1962. Field studies on attack flight and log selection by the ambrosia beetle *Trypodendron lineatum (Oliv.) (Coleoptera:* Scolytidae). Can. Ent. 94:74-92.
11. Chapman, J.A. 1963. Field selection of different log odors by scolytid beetles. Can. Ent. 95:673-676.
12. Chapman, J.A. 1966. The effect of attack by the ambrosia beetle *Trypodendron lineatum* (Oliv.) on log attractiveness. Can. Ent. 98: 50-59.
13. Craighead, F.C. 1925. Bark-beetle epidemics and rainfall deficiency. J. Econ. Ent. 18:577-586.
14. Danthanarayana, W. 1968. Outbreaks of caterpillar pests as limiting factors in controlling shothole borer *Xyleborus fomicatus* (Eich.) *(Coleoptera:* Scolytidae) of tea in Ceylon. In International Congress of Entomology, 13th, Moscow. Trudy 2:319-320.
15. Danthanarayana, W.1973. Host plant-pest relationships of the shothole borer of tea, *Xyleborus fomicatus (Coleoptera:* Scolytidae). Ent. Exp. Appl. 16:305-312.
16. Doane, R.W., Van Dyke, E.C., Chamberlin, WJ. and Burke, H.E. 1936. Forest Insects. McGraw-Hill Book Co., Inc. New York, N.Y. and London, England. 137 pp.
17. Essig, E.O. 1926. Pages 510-521 in: Insects of Western North America. MacMillian Press, New York, N.Y.
18. Francia, F.C. and Graham, K. 1967. Aspects orientation behavior in the ambrosia beetle *Trypodendron lineatum* (Olivier). Can. J. Zoo. 45:985-1002.
19. Francke-Grosmann, H. 1967. Ectosymbiosis in Wood Inhabiting Insects. Pages 141-205 in: Symbiosis, Vol. II. S.M. Henry, ed. Academic Press, New York, N.Y.
20. French, J.RJ. 1972. Biological interrelationships between the ambrosia beetle *Xyleborus dispar* and its symbiotic fungus *Ambrosiella hartigii.* Unpublished Ph.D. Thesis, Dept. of Ent., Oregon State University, Corvallis, Ore. 139 pp.
21. French, J.RJ. and Roeper, R.A. 1972. *In vitro* culture of the ambrosia beetle *Xyleborus dispar (Coleoptera:* Scolytidae) with its symbiotic *fungus,Ambrosiella hartigii.* Ent. Soc. Amer. Ann. 65:719-721.

22. Gagne, IA. and Kearby, W.H. 1979. Life history, development and insect-host relationships of *Xyleborus celsus (Coleoptera:* Scolytidae) in Missouri pest of black hickory, *Carya texana*. Can. Ent. 111:295-304.
23. Gara, R.I. 1963. Studies on the flight behavior of *Ips confuses* (Lec.) *(Coleoptera:* Scolytidae) in response to attractive material. Contrib. Boyce Thompson Inst. 22:51-66.
24. Gara, R. I. and Vite, J.P. 1962. Studies on the flight patterns of bark beetles *(Coleoptera:* Scolytidae) in second growth ponderosa pine forests. Contrib. Boyce Thompson Inst. 21:275-290.
25. Gara, R.I., Vite, J.P. and Cramer, H.H. 1965. Manipulations of *Dendroctonus frontalis* by use of a population aggregating pheromone. Contrib. Boyce Thompson Inst. 23:55-66.
26. Graham, K. 1968. Anaerobic induction of primary chemical attractancy for ambrosia beetles. Can. J. Zoo. 46:905-908.
27. Happ, G.M., Happ, C.M. and French, J.RJ. 1976. Ultrastructure of the mesonotal mycangium of an ambrosia beetle, *Xyleborus dispar* (F) *(Coleoptera:* Scolytidae). Int. J. Insect. Morpol. Embryol. 5:381-391.
28. Hopping, R. 1922. Coniferous hosts of 1pidae of Pacific Coast and Rocky Mountain region. Can. Ent. 54:128-134.
29. Jack, I.D. 1964. Observations on the biology of the shothole borer and the ambrosia beetle in tree fruit orchards in the Okanagan valley of British Columbia, 1963-64. Unpublished report by the Ent. Branch of the British Columbia Dept. of Ag. 30 pp.
30. Johnson, N.E. and Belluschi, P.G. 1969. Host-finding behavior of the Douglas-fir beetle. J. For. 67:290-295.
31. Linsley, E.G. and MacLeod, G.F. 1942. Ambrosia beetles attacking deciduous fruit trees in California. J. Econ. Ent. 35:601.
32. Maramorosch, K., Martorell, L.F., Bird, J. and Melendez, P.L. 1972. *Platypus rugulosus* (Platypodidae) and *Xyleborus ferrugineus* (Scolytidae) and certain diseases of coconut palms in Puerto Rico. N.Y. Ent. Soc. J. 80:238-240.
33. Mathers, W.G. 1940. The shothole borer, *Anisandrus pyri* (Peck), in British Columbia *(Coleoptera:* Scolytidae). Can. Ent. 72:189-190.
34. McMullen, L.H. and Atkins, M.D. 1962. On the flight and host selection of the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopk. *(Coleoptera:* Scolytidae). Can Ent. 94:1309-1325.
35. Miller, J.M. and Keen, F.P. 1960. Biology and control of the western pine beetle, USDA Misc. Publ. 800.381 pp.
36. Moeck, H.A. 1970. Ethanol as the primary attractant for the ambrosia beetle *Trypodendron lineatum (Coleoptera:* Scolytidae). Can. Ent. 102:985-995.
37. Muraleedharan, N. and Kandasamy, C. 1981. A new host record for the shothole borer *Xyleborus fomicatus* of tea. South India. Assoc. for Adv. Ent. 6:127.
38. Phillips, T.W., Wilkening, Ai., Atkinson, T.H., Nation, J.L , Wilkinson R.C. and Foltz, J.L. 1988. Synergism of turpentine and ethanol as attractants for certain pine-infesting beetles *(Coleoptera).* Ent. Soc. of Am. 17:456-462.
39. Pitman, G.B., Vite, J.P., Kinzer, G.W. and Fentiman, A.F., Jr. 1969. Specificity of population aggregating pheromones *in Dendroctonus.* J. Insect Physiol. 15:363-366.
40. Renwick, J.A.A. and Vite, J.P. 1970. Systems of chemical communication *in Dendroctonus.* Contrib. Boyce Thompson Inst. 24: 283-292.
41. Roeper, R.A. and French, J.J.R. 1981. Growth of the ambrosia *fungus Ambrosiella hartigii* on various nitrogen sources in association with the beetle *Xyleborus dispar.* Mycologia 73:202-204.
42. Ranasinghe, M.A.S.K. and Wickremesinghe, R.L. 1988. Use of acetates to induce host resistance to *Xyleborus fomicatus (Coleoptera:* Scolytidae) attacking tea. Pages 251-256 in: Proceedings Br. Conf. Pests Dis. London. British Crop Protection Council. Vol. 1.
43. Rudinsky, J.A. 1963. Response of *Dendroctonus pseudotsugae* Hopkins to volatile attractants. Contrib. Boyce Thompson Inst. 22:22-38.
44. Rudinsky, J.A. 1966. Scolytid beetles associated with Douglas-fir Responses to terpenes. Science 152:218-219.
45. Rudinsky, J.A. 1966. Host selection and invasion by the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, in coastal Douglas-fir forests. Can. Ent. 98:98-111.
46. Rudinsky, J.A. 1970. Sequence of Douglas-fir beetle attraction and its ecological significance. Contrib. Boyce Thompson Inst. 24:311-314.
47. Rudinsky, IA. and Daterman, G.E. 1964. Field studies on flight patterns and olfactory responses of ambrosia beetles in Douglas-fir forests of western Oregon. Can. Ent. 96:1339-1352.
48. Rudinsky, J.A. and Schneider, I. 1969. Effects of light intensity upon the flight pattern of two *Gnathotrichus (Coleoptera:* Scolytidae) species. Can. Ent. 101:1248-1255.
49. Rudinsky, J.A. and Vite, J.P. 1956. Effects of temperature upon the activity and behavior of the Douglas-fir beetle. For. Sci. 2:258-267.
50. Sivapalan, **P** and Shivanandarajah, V. 1977. Inhibitory effects of extracts from seeds and roots of tea, seeds of *Sapindus emarginatus,* azasterols and nonsteroidal amines on the development of *Xyleborus fomicatus in vitro.* Ent. Exp. Appl. 22:274-279.
51. Sivapalan, P. 1969. Control of the shothole borer of tea *Xyleborus fomicatus* (Eich.): final report on research conducted under grant authorized by U.S. Public Law 400. Tea Research Institute of Sri Lanka, 64 pp.
52. Souto, DJ. 1974. Studies on the initial host selection behavior of Scolytids associated with a second growth Douglas-fir forest. Unpublished Masters thesis, College of Forest Resources, University of Washington, 82 pp.
53. St. George, R.A. 1929. Weather, a factor in outbreaks of the hickory bark beetle. J. Econ. Ent. 22:573-580.
54. Swaine, J.M. 1918. Canadian bark beetles. Dom. Can. Dep. Agric., Ent. Brch, Tech. Bull. No. 14 (2).
55. Vite, J.P. and Wood, D.L. 1961. A study on the applicability of the measurement of oleoresin exudation pressure in determining susceptibility of second growth ponderosa pine to bark beetle infestation. Contrib. Boyce Thompson Inst. 21:67-78.
56. Vite, J.P. and Pitman, G.B. 1968. Bark beetles aggregation: Effects of feeding on the release of pheromones in *Dendroctonus* and *Ips.* Nature (London) 218:169-170.
57. Wickremasinghe, R.L. and Thirugnanasuntheram, K. 1980. Biochemical approach to the control of *Xyleborus fomicatus (Coleoptera:* Scolytidae). Plant Soil. The Hague 55:9-15.
58. Williams, J.O. 1988. Occurence of *Xyleborus ferugineus* (Fabr.) *(Coleoptera:* Scolytidae) on yam tubers in Nigeria. Insect Sci. Appl. 9:41-42.
59. Wilson, H.F. 1913. The shothole borer of the Northwest; or the pear blight beetle of the East. *(Xyleborus dispar* Fabricus). Pages 97-107 in: Biennial Crop Pest and Horticultural Report, 1911-1912. Ore. Agr. College Exp. Sta., Corvallis, Ore.
60. Wood, S.L. 1982. The Bark and Ambrosia Beetles of North America, A Taxonomic Monograph. Great Basin Naturalist Mem. #6, Brigham Young University, Provo, Utah.
61. Wright, R.H. 1958. The olfactory guidance of flying insects. Can. Ent. 90:81-8139.