AN ABSTRACT OF THE THESIS OF

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Title Certain Biotic Factors Influencing the Invasion and Survival of the Douglas-Fir Beetle *Dendroctonus Pseudotsugae* Hopkins (Coleoptera:Scolytidae), in Fallen Trees

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Factors considered were phloem moisture, sour-phloem (which may be furthered by the presence of ample phloem moisture), oleoresin of the host, and the presence of unmated female beetles in suitable host material.

Levels of phloem moisture present in variously prepared logs in the field ranged from about 100 to upwards of 250 percent of dry weight. Observation of such host material during the main season of beetle flight supported the conclusion that the Douglas-fir beetle attack volume was not related to moisture level. Experimentation with short logs which had either been soaked or not soaked verified this conclusion; at the same time it was demonstrated that *Gnathotrichus sp.*, *Dryocetes autographus* (Ratzeburg), and *Hylastes nigrinus* (Mannerheim) were attracted to the logs which had been made wetter.

Within the range observed in the field, moisture level did not influence brood success. The case where moisture implements an

air-tight seal, its effectiveness being indicated by sour-phloem development, is an exception.

Sour-phloem is a decay condition which develops under anerobic circumstances. Moisture is viewed as an accessory to its formation in that it implements an air-tight seal of intact bark. At the time of attack only incipient sour-phloem was present in various of the pieces of host material in this study and in this stage of development did not influence attack by the Douglas-fir beetle. Sour-phloem, however, was associated with restricted brood development, more likely as an indicator of low oxygen levels rather than as a detrimental habitat factor in itself.

Minimal oleoresin exudation pressures (1 to 17 pounds per square inch) were measured in fallen Douglas-firs which, observed through the attack season and later analyzed, were seen to have an appreciable number of incidences where oleoresin was judged to have interfered with beetle entry. Similarly, brood size and success was determined to have been limited by oleoresin.

The introduction of unmated female beetles was seen to so strongly prompt other females to attack a log that it not only affords an explanation of how beetles are attracted en masse but also explains why there can be beetle indifference to otherwise suitable host material which happens to lack prior entered females. Male beetles are also attracted by the unmated females. Beetle response is to odor; air blown over a properly treated and hidden log attracted beetles.

The intensity of mass attack relates to the intensity of the earliest attack. The species demonstrates a gregarious habit which, it is argued, would facilitate mating, shatter the tree's defensive oleoresin exudation, enable mass tunneling of the inner bark so that adequate ventilation would be afforded the brood, and serve to insure that it will place economic demand on the population of its host.

The strong displacement effect of logs having female beetles warrants strong consideration when studies are made seeking to identify attractive factors that belong to the host *per se*. When forced entry of females was made into irregular host material, it received subsequent attack.

Intensity of attack, as judged from the experiment of one season, is independent of host felling dates when the range of these is less than a year.

Air temperature observation in connection with the studies provided insight with regard to the predicability of attack in suitable host material as spring warming continued.

CERTAIN BIOTIC FACTORS INFLUENCING THE INVASION AND SURVIVAL OF THE DOUGLAS-FIR BEETLE *DENDROCTONUS PSEUDOTSUGAE* HOPKINS (COLEOPTERA:SCOLYTIDAE), IN FALLEN TREES

by

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INTRODUCTION

The Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, like all members of its genus, spends the greater part of its life cycle in the phloem region of its host tree. Usually, this is Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco. Food demands of the beetle population are minimal; it is the vulnerability of the zone in which galleries are cut and feeding occurs which emphasizes destructiveness of the species. Furthermore, and perhaps more important, the beetles transmit blue-stain fungi, including *Ceratocystis pseudotsugae* Rhumbold, which, in penetrating the xylem, may be theorized as causing an interruption of sap transport (34, p. 886; 38, p. 2). Also, because the beetle's protected niche isolates it from applied controls common elsewhere in entomology, its destructiveness is intensified.

Recently fallen, fire-scorched, and damaged trees are predictably attacked; large quantities of such material are identified with population increases of the beetle (10, p. 1, 2; 38, p. 1; 77, p. 4; 93, p. 1; 105, p. 12; 144, p. 4). Often it is a segment of an enlarged beetle population that enters physiologically sound trees and causes their death (10, p. 2). The greater the mass of beetles on a host tree, the more likely that the latter's resistance will be overwhelmed. Conversely, given a fixed number of beetles, it would be seen that some trees in a more vigorous physiological condition could withstand and recover from the attack. Furniss (43, p. 5) has estimated that 30 percent of standing Rocky Mountain Douglas-fir trees survive beetle entry. Such survival for scolytids generally is related to oleoresin interference with beetle activity (51, p. 69; 58, p. 21; 99, p. 179-182; 101, p. 139-140; 116, p. 340; among others). However, Bedard (10, p. 4) has cited excessive moisture beneath the bark as a host factor causing failure of Douglas-fir beetle attack.

Various studies have attempted to identify tree characteristics correlated with Douglas-fir resistance to its beetle.

Walters (143) measured the growth rate of trees against a number of externally visible factors so that four classes of presumed different vigor could be established. A later study disclosed "... that the older, slower growing trees are most susceptible. Specifically, trees of over 150 years of age with a ten-year diametral growth of less than 11 millimeters are most likely to be infested" (145, p. 327).

Mathers (91, p. 3) earlier had compared beetle-killed trees with uninfested ones and concluded, "... no obvious reason was found for one tree and not others in the same vicinity to be attacked."

He did think, however, that tree vigor, as indicated by the number of growth rings in the outer half inch of increment borings, did correlate with attack. Injured trees were noted to be preferentially attacked.

McCowan and Rudinsky (93, p. 13) also compared attacked and unattacked trees and measured a slightly lower increment per year for the preceding 24 years in the former, as compared with the latter.

A regional pattern to the beetle success - tree susceptibility relationship is described by Bedard (10, p. 2). As compared with the situation in the Pacific Coast region, west of the Cascade Mountains, he states that, "In the more arid Rocky Mountain portion of its range, the Douglas-fir beetle is much more aggressive." In the coastal region, the beetle usually, but not always, appears to depend on some contributing cause which provokes an outbreak. In the Rockies, many of the outbreaks apparently develop in uninjuried timber and sweep over large areas (10, p. 1, 2).

A pattern of Douglas-fir beetle attack which is characteristic both in the interior and on the coast is its concentration in one locality and in groups of trees in a forest (58, p. 21). Furniss (43, p. 3), for the Rocky Mountain population, noted such attack and cited this as advantageous in control operations.

A paper by Evenden and Wright (38, p. 3) includes an aerial photograph of Douglas-fir timber clearly showing the beetle-caused

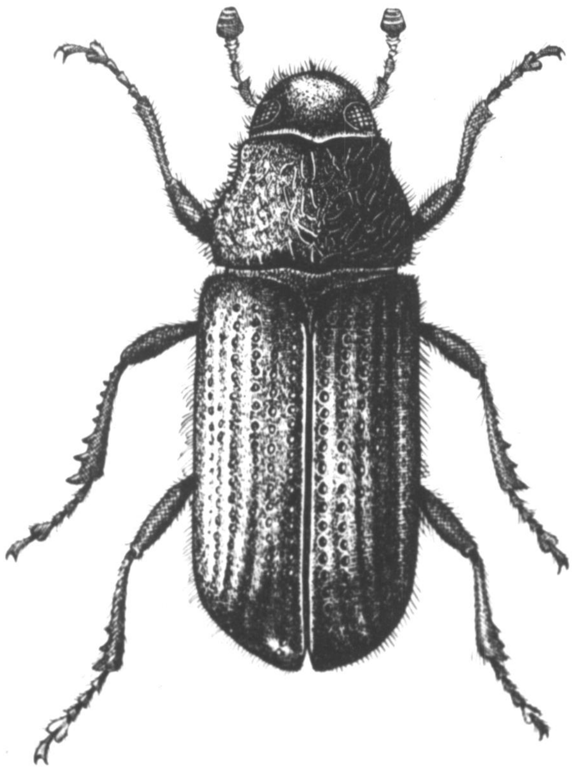

Figure 1. Drawing of the dorsal aspect of the Douglas-fir beetle. (by Hugh Hayes, courtesy of the Forest Research Laboratory, (Oregon State University)

Figure 3 (below). Sexing the insect. Featherweight forceps applied to the elytral declivity as a check to feel the tubercles which are a secondary sexual characteristic of the female.

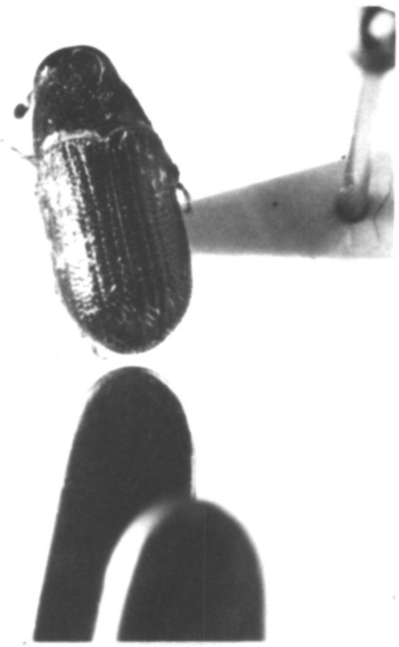

Figure 2. Beetle size. Range in length is between 3.5 and 7 mm.; the average is nearly 6 mm. (19, p. 73). These are males on 18 x 14 mesh screen which covers females that were introduced into the log.

death of trees in groups. Specifically, the photograph is of the east slope of Marys Peak located ten miles west of Corvallis, Oregon. It is the site of much of the research reported herein.

The extent of beetle kill is reported by various authors. Bedard (10, p. 2) records the beetle as having killed trees with an estimated 200,000,000 board feet volume during a three-year period in and adjacent to Tillamook, Oregon burn of 1933. Greeley, Wright, and Pope (52, p. 23) in 1953 observed that such a two- or three-year period had been typical for a Douglas-fir beetle epizootic. Concern, however, was expressed for the situation then at hand in which exceptionally heavy blowdown, 8.9 billion board feet effected during the winter of 1951-52, was present for invasion by beetles already in progradation as a consequence of there being abundant windthrow two winters previous. The latter provided brood material and enabled the population to expand so that a considerable volume (one billion board feet) of standing timber had been killed in the summer of 1951 and now held broods capable of saturating the recent windthrow. Again the beetle population could expand and there was apprehension that it would now reach such proportions that it would not show the same pattern of retrogradation as before.

As summarized in Figure 4, however, the standing tree acreage judged to have epidemic infestation of the Douglas-fir beetle in Washington and Oregon was initially high but did taper off.

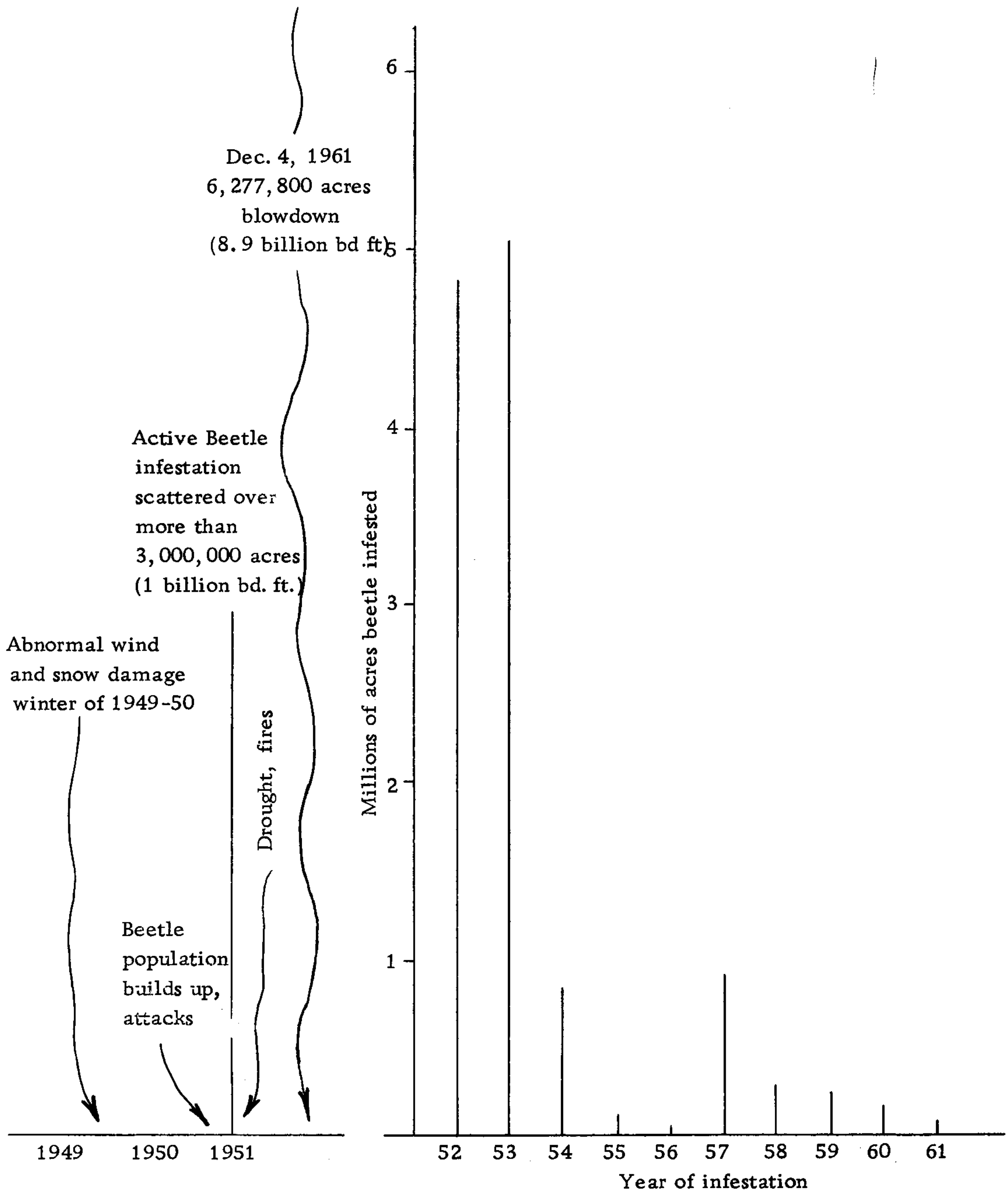

Figure 4. Trend of Douglas-fir beetle investigation in Oregon and Washington since 1950. Compiled from Buckhorn and Orr (14, p. 12), Greeley, Wright, and Pope (52, p. 2-4, 16), Orr (105, p. 18), and Whiteside (150, p. 27).

Nevertheless, the beetle population remains and produces a tree kill over an appreciable acreage each year. An extremely abundant windthrow resulting from storms in October 1962 afforded the beetle population a new ecological advantage and caused concern that it would increase in size again (105, p. 18).

Biology

The distribution map included by Hopkins in his 1909 paper shows distribution of the beetle throughout the range of Douglas-fir. He listed three hosts for the beetle: "Pseudotsuga taxifolia, P. macrocarpa, and Larix occidentalis" (57, p. 125). Pseudotsuga taxifolia (Poir) Britt. is now recognized as P. menziesii (Mirb.) Franco.

Chamberlin (19, p. 66) mentions attacks of the Douglas-fir beetle in Abies and western hemlock, Tsuga heterophylla (Rafn.) Sarg., and describes the host trees in these cases as more or less accidental. Wright is stated by Johnson (66, p. 3) to have reported the beetle attacking Brewer spruce, Picea breweriana S. Wats. Johnson also mentions his seeing the beetle enter western redcedar, Thuja plicata Donn, which was lying near logs of Douglas-fir (68). The author was in the company of Johnson when such an observation was made; it is of note that the Douglas-fir logs were undergoing attack and were well dispersed amongst the redcedar logs. Of significance to one experiment reported herein, the beetle has apparently not ever been noted to be associated with pine.

The weakened host condition identified with beetle attack has suggested preparation of trap trees as a tool with which to control the Douglas-fir beetle. However, precise knowledge as to how to prepare host material so that it could serve as traps has been lacking. Furniss (43, p. 6) wrote in 1959,

> Trap trees may eventually prove to be useful in combatting Douglas-fir beetle infestations. However, their use now would be on a hit-or-miss basis and could be expected to produce variable results depending upon circumstances. While the attractiveness of felled trees is well established, the amount, distribution, and timing of cutting remain to be determined in relation to density and distribution of anticipated beetle population.

Workers at the Intermountain Forest and Range Experiment Station (135, p. 24), continuing to study methods of treating trees to make them more effective as traps for the Douglas-fir beetle, recently employed ammonium sulfamate to kill trees which then were invaded.

Walters (146, p. 9) observed that logging operations can provide trap trees. "Logging should be continuous in time and area. Fresh slash should be laid down on contiguous areas to absorb beetles emerging from slash of the previous year."

Given success with traps, Hopkins (58, p. 34) felt apprehensive that they might cause attack to be induced in nearby healthy trees and thus initiate rather than prevent an outbreak. Recently, Johnson and Pettinger (71, p. 2) have concurred. Specifically, for the Douglas-fir beetle, they state, "Thus it appears that beetles attack nearly indiscriminately in the immediate vicinity of down trees. All trees up to three feet distant were attacked."

Like most but not all Dendroctonus, the Douglas-fir beetle has a one-year life cycle (58, p. 18-19). Beetle flight for the establishment of brood in new host material will occur with favorable weather conditions through the spring and summer (10, p. 7-9; 38, p. 2; 58, p. 108; 93, p. 2).

Major flight activity is more towards the spring, as early as April, and then tapers off with release of overwintered adults completed by June or July. A second peak in flight activity occurs in July and August (10, p. 7-9; 38, p. 2). McCowan and Rudinsky (93, p. 2) observed the latter's continuance into mid-September. The second flight peak is made up of late-maturing adults from broods established the previous summer and, in part, from beetles which already have made a spring attack in the current year and will now establish a second brood. Beetle flight capability is 20 to 30 miles, but most are believed to fly only a mile or so when there is preferred host material within that radius (84, p. 309).

Bedard (9, p. 2) describes the female beetle as responsible for excavation of the entrance tunnel. Male beetles crawl over the bark surface searching for mates and when a female is found excavating a hole will stand by and follow her into the tunnel as she progresses. Bedard (9) continues,

> Fertilization takes place when about an inch of egg gallery has been excavated in the inner bark. After fertilization, the female continues the egg gallery and the male either continues on with this female, assisting her in the disposal of the frass, or he leaves the gallery and wanders off in search of another mate.

In connection with the second flight of beetles which have excavated galleries and established a brood, Vité and Rudinsky (140, p. 165) quote an unpublished report by Bedard, old females "are capable of laying fertile eggs without another fertilization." McMullen and Atkins (94, p. 199) observed that fewer numbers of parent beetles remain within the galleries they have established when attacks per square foot in the log increase. Males leave before females (5, p. 287). McMullen and Atkins (95, p. 1311) note that the proportion of beetles making additional attack flights remains to be determined.

Various studies have included measurements of the intensity of beetle attack, this being facilitated by the clearly seen reddish pile of boring dust at the entry hole.

study	attacks/ square foot	remarks
McCowan & Rudinsky (93, p. 11)	2 - 7	number increased with the height on the tree

study	attacks/ square foot	remarks
Johnson, Wright, & Orr (73, p. 5)	0.43 - 1.0	successful attacks counted; fewer on exposed than on shaded logs; fewer on top of logs than on sides; increased with tree height.
McMullen & Atkins (94, p. 199)	1 - 24	intraspecific crowding study in which lower densities of attack were established by withdrawing log after desired level of attack was reached.

The latter authors noted, "Attack densities of less than three per square foot are seldom encountered in the field because the insect tends to select and congregate in suitable host material" (94, p. 203). A conclusion of their study was that the increase ratio, the number of progeny divided by the number of parents, was greatest in value at the lowest attack density. Increase ratio was observed to decline as attacks per square foot became greater in number (94, p. 202).

A study of the effects of temperature has emphasized the importance of weather as it could influence the yearly cycle of events dependent on different types of beetle activity (119, p. 259-261). Similarly, variation in rate of development has been shown to be temperature dependent (140, p. 161). Ryan (121, p. 521) has shown the effects of different temperatures of cold rest necessary to terminate diapause for this species so that the developmental cycle can be completed.

Photographs of the four major stages of the beetle and the characteristic gallery pattern are provided by Evenden and Wright (38, p. 3), Bedard (10, p. 3, 4), and McCowan and Rudinsky (93, p. 2).

Objectives of the Study

As mentioned above, the beetle is the more consistently identified with fallen and severely weakened host material. It was desired that this study concentrate on evaluating some of the factors in fallen host material that aided or deterred beetle invasion and which might similarly be related to brood development and success. Preferably, work was to be done in the field, but some completmentary laboratory activity was to prove appropriate.

A consideration of phloem moisture as it influences brood development initiated the series of investigations that ranged over a broad base and included several pilot studies which tested new hypotheses that presented themselves. An early impression in the first trees studied, that beetles were variously attracted to the four different host-material treatments, generated a desire to evaluate beetle attraction.

Eventually, various log treatments were empirically tested for field attractance of beetles from the spring flight. One of these, performed by adding beetles to logs, was so influential in inducing attack that it precluded competent evaluation of other treatments. Subsequent investigation sought to evaluate the beetle attractance factor when it was interrelated with various moisture levels in the host material.

Concomitant studies yielded data regarding beetle flight temperature requirements.

Following Vité's (136, p. 48-56) demonstration of quantitative measurement of pine oleoresin flow and Vité and Wood's (142, p. 72-77) study of its effect on beetle entry into sound trees, an assessment was made in fallen Douglas-fir of oleoresin tendency to exude and its influence on beetle entry and brood success.

These objectives were compatible with research needs listed by the Northwest Forest Pest Action Committee (104, p. 13). It was stated for the Douglas-fir beetle that, among other items, more information was needed on:

(a) emergence and flight periods,

(b) influences that attract or repel adults,

(c) beetle susceptibility of individual trees,

(d) influence of pitch flow on brood development.

Previous Work Pertinent to the Objectives

Studies of Host Moisture Related to Scolytid Beetles

Water is a prerequisite for the continuation of life. The amount required varies with the species, each having adapted to an ecological niche in which some relatively fixed range of moisture is available. At the extremes of the range, survival for most members of a species will be difficult and at some point towards the center an optimal state of moisture may be presumed to be definable. The larvae of Scolytidae living within various trees, shrubs, and herbs (109, p. 70) are associated with, and hence adapted to the moderate levels of moisture present in these sites. Moisture-host-scolytid studies, particularly in the case of standing, live trees, have often sought to evaluate climate and climate-dependent soil factors (8, p. 27-28; 53; 96; 100; 132, p. 15). Drought is a weakening agent apparently causal to host susceptibility for many species of Scolytidae. Vité (136, p. 48-57) has recently shown that even momentary changes in tree physiology may be demonstrated with ponderosa pine when environmental moisture factors change.

Other studies have sought to measure the moisture factor in susceptible living host material or in that which had been drastically damaged by girdling or felling. The moisture was evaluated for influence upon brood development, brood success, and/or attractance of adult beetles. For this purpose, moisture had either been expressed directly or as a percentage of the dry weight of plant matter (11, p. 447; 18, p. 9; 59, p. 167; 60, p. 180; 90, p. 481; 136, p. 40), or been inferred from osmotic pressure assessments (28, p. 1409; 99, p. 168-9; 124, p. 74-5), or from a secondary phenomenon of this (136, p. 48-62).

Two authors (106; 123) have sought to relate electrolytic properties of the inner bark to bark beetle considerations.

Martin (90, p. 484) reported phloem moisture values of the order of 50 percent of the phloem dry weight in elm trap logs inhabited by *Scolytus multristriatus* Marsham and *Hylurgopinus rufipes* (Eichoff). His evaluation was that log moisture does not influence beetle entry. Some difference was noted, however, in larval development success of the *Scolytus* species as contrasted with the *Hylurgopinus.* The former requires logs having phloem that still appeared fresh, while the latter could use logs whose phloem was judged dead (90, p. 484, 486).

In a study of moisture as it was contained in the phloem of spring- and summer-attacked trees that were felled in the fall, Inouye (60, p. 175-8) structured a relationship between beetle attack density and sapwood moisture content. A total of four trees each of a different species was studied. *Ips typographus* L. (one beetle species entering these) was seen to be associated with phloem moisture values in the range 53-116 percent, a low one.

Similarly, Pfeffer (110, p. 206) concluded that trees apparently having higher sapwood moisture, as a result of being poisoned in the course of his investigations, were unattractive to *Ips typographus*.

On the other hand, Anderson (4, p. 599) used jack pine, *Pinus banksiana* Lamb, damaged in an ice storm, in a study of *Ips pini* (Say). Snags lacking living branches were attacked, while those with even one three-foot branch had been avoided. The inner bark moisture of the former was almost 100 percentage points wetter than that of the latter. Laboratory studies seemed to confirm the beetle's preference for the wetter host material.

Recently Shepard (125), in caged tests with the Black Hills beetle, *Dendroctonus ponderosae* Hopkins, and three pieces of bark, found that the beetles selected the wetter bark on which to feed.

Contrasting with the above four investigations, Schwerdtfeger (124, p. 70-1) could not establish any correlation between either the moisture of the bark or phloem and the number of Buchdrucker, *Ips typographus*, entries.

Working with the osmotic pressure of the phloem sap, Chararas (30, p. 2110; 31, p. 1918) found an absence of beetle attack in trees where the value of the latter was high (*circa* eight atmospheres). In another study, he demonstrated that bark beetles could also be causal to an increased osmotic pressure in localized regions (29, p. 3613).

Emphasizing oleoresin exudation pressure, which is an expression of the turgor of the epithelical cells lining the resin ducts (136, p. 39), Vité and Wood (142, p. 74-6) showed fewer attacks in those trees whose pressure was above six atmospheres.

Merker (99, p. 186-7), however, concluded that trees with osmotic values below, but more particularly, above normal offered the least resistance to scolytid attack. Stating that the osmotic values as such have no influence on the beetles, he laid greater attractivity to scents which would be stronger in concentrated saps.

Turning to studies of host moisture as it relates to scolytid brood development, Denton's study cited by Graham (51, p. 62) indicated that the eastern spruce beetle, Dendroctonus piceaperda Hopk., was able to develop better under moist conditions than was its frequent associate, Ips perturbatus (Eich.). The latter, however, could more easily live under conditions that were too dry for the Dendroctonus.

Thalenhorst (133, p. 43) determined that Ips typographus larvae benefit from less wet phloem conditions; better oxygen availability was suspected to be one of the reasons.

Studying the ambrosia beetle, Trypodendron lineatum Oliv., Kinghorn (78, p. 4), after determining that attack was independent of sapwood moisture level, did find that poor survival was associated with excessive moisture.

Reid (114, Vol. 94, p. 606-9), using laboratory preparations in which egg laying could be observed, has recently shown that the mountain pine beetle, Dendroctonus monticolae Hopkins, stopped laying eggs when the inner bark moisture fell below 105 percent.

Brood survival was related to sapwood moisture. There was increasing beetle success up to the 35 percent moisture level. At this point, however, survival decreased (114, Vol. 95, p. 233). Blackman (12, p. 39) similarly related brood survival for this beetle to moisture present in host material. Best survival was in "moist" inner bark with decreasing success in "medium", "dry", and "very dry" conditions.

Beal and Massey (8, p. 26-7) cite brood losses sustained by the southern pine beetle, Dendroctonus frontalis Zimm., and the western pine beetle, D. brevicomis LeConte, when phloem moisture reached high levels, "resulting from defoliation and interference with the proper functioning of the tree."

Miller and Keen (101, p. 27, 71), reviewing the unpublished report of the study by Beal on Dendroctonus brevicomis, cite the high mortality of brood that occurred in study logs which had phloem moisture values of 200 to 300 percent.

Anderson (4, p. 601) measured approximately similar brood survival over the considerable range of inner bark moisture present in field situations but determined that Ips pini did suffer high mortality when subjected to very low and very high moisture conditions produced in the more extreme treatments. Struble and Hall (131, p. 12), for Ips confusus LeConte, which attacks several of the western pines, report, "No consistent correlations were evident between the number of beetles produced in lopped and unlopped logs even though consistent differences in moisture were shown."

Vité (136, p. 57-8) found that water injection, which may be regarded as a more extreme treatment, often led to fermentation of the cambium which, in turn, created unfavorable conditions for brood development. In this study, where branches were present and phloem moisture was only slightly above normal, egg deposition and development of brood were not suppressed.

Attractance of Scolytid Beetles

Observations of the relationship of Douglas-fir beetle attack into its host species, individual trees, and intended trap trees have been cited above (see p. 7 , 8). A discussion of moisture as it might affect general scolytid response to host material has also been presented (see p. 13 - 17). In this section, other factors responsible for scolytid host orientation are considered.

Trap trees and studies of them date to the earliest writers on forest insects because, as known centers of attraction, traps appeared useful in control operations (58, p. 33). Deliberately weakened trees could elicit attack, and studies to the present time have sought to determine how most effectively to prepare host material (1, p. 431; 12, p. 60-3; 30, p. 2109; 42, p. 416; 89; 103; 126).

An understanding of the factors associated with beetle attack is involved. Similarly, Miller and Keen (101, p. 40-45, 300) present the review of a 50-year history of work that sought to comprehend the attack pattern of one Dendroctonus species, the western pine beetle D. brevicomis LeConte. They cite studies in which consideration was given to the following,

- host circumstance
  - windthrown vs. felled trees vs. top-killed standing trees
  - slow growth trees
  - artificially topped trees
  - girdled trees
  - root-pruned trees
  - lightning scarred trees
  - fire scorched trees

- tree constituents
  - sugars and their decomposition products
  - fermented phloem
  - pH of phloem sap
  - turpentine and bark oils

- influence of the beetle on the tree
  - beetles boring in the phloem region
  - concentrations of beetles on a tree
  - pitch masses arising from beetle entry
  - the theory of Person (107, p. 696-699) wherein initial attack by beetles, in response to volatile aldehydes or esters, vectors yeasts into the phloem where ferments are produced that bring a large secondary attack of beetles.

The 1960 review of these authors nevertheless concluded (101, p. 353) "...nor has much progress been made in determining why the beetles are attracted to certain trees and not to others. Or is this merely a matter of host resistance and susceptibility? If a definitely attractive substance could be found, it would open up a new field of control in baiting and trapping."

The general picture in Scolytidae is that there is specificity for a limited number of host species and, further, for a particular physiological condition of the host (116, p. 327-329). The former may be explained by the hypothesis offered by Fraenkel (40, p. 1466), "The food specificity of insects is based solely on the presence or absence of these odd (secondary) compounds in plants which serve as repellents to insects (or other animals) in general and as attractants to those few which feed on each plant species." After a study of the toxicity of three pine resins to *Dendroctonus brevicomis* and *D. jeffreyi* Hopkins, Smith (128, p. 369) has hypothesized that bark beetles can tolerate the resin of their hosts but can not tolerate that of a nonhost. Similarly Francke-Grosmann (42, p. 418) cites the work of Kangas indicating that adult *Dendroctonus micans* died in an atmosphere saturated with fresh resin from healthy trees of Sitka spruce while the beetles usually seem to be attracted by resinous wounds of conifers. Mirov (102, p. 61) records volatile oil composition as different in each of the hundred pine species. Two terpenes, alpha and beta pinene, are resin factors commonly present.

Graham and Werner (50, p. 3) report the gas extraction of volatile constituents and the use of these to obtain preferential response by ambrosia beetles. However, the two pinenes, while present in Douglas-fir extracts, could not be shown in later experimentation to be an attractive factor for Trypodendron lineatum (Oliv.), and the authors thought that the two compounds might even be deterrent (148, p. 3).

Pertunnen (108, p. 109), using an olfactometer and two bark beetle species, Hylurgops palliatus Gyll. and Hylastes ater Payk., showed repellence and attractance by alpha pinene depending on the beetle and the concentration of the odor. Chararas (27, p. 1654) similarly found alpha and beta pinene to be repulsive to Ips typographus L., Hylurgops pallinatus Gyll., and Dryocetes autographus (Ratz.) at strong concentrations but capable of being attractive at weak ones. More recently, Chararas and Berton (32, p. 236-239) have developed the method of quantitatively assessing the amounts of each oleoresin constituent and thus were able to show variation between trees. In a downed tree, decreased emanation with time since felling was observed.

Lu, Allen, and Bollen (86, p. 338-342) obtained results judged to be significant wherein the Douglas-fir beetle was attracted to cultures of four yeasts identified as being associated with the beetle. Such would seem to confirm for the Douglas-fir beetle the theory of Person (107, p. 696-699) cited above. In further acceptance of Person's theory for this species, Furniss (43, p. 6) has written, "Opinion is divided as to whether initial attacks occur in especially attractive trees or simply at random. However, there is general agreement that attacks create attractive odors caused by fermenting phloem."

Merker (97, p. 144) reported the attraction of various European beetles from a distance after a trace of phloem sap was added to a sugar solution that in itself was not attractive. The sugar induced prolonged feeding. Hesse, Kauth and Wachter (55, p. 242-244) found one constituent from spruce phloem, the methyl ester of linoleic acid, to have attractant properties for Hylobius abietis L. Recent work reporting the attractance of forest insects to plant constituents, insect produced attractants, and miscellaneous organic compounds has been reviewed and reported by Franke-Grosmann (42, p. 415-420). Jacobson and Beroza (61, p. 1367-1373) have written a more general review on attractants.

Oleoresin and Scolytid Beetles

Many authors (51, p. 69; 58, p. 21; 99, p. 175-82; 116, p. 340; among others) support a traditional concept that flows of oleoresin deter the entry of scolytid beetles into an intended host; the flows are a principal factor causing abortive attacks. Dendroctonus species entering pine and spruce manipulate the oleoresin flow into an externally visible pitch tube. Hopkins (58, p. 21) states,

> The beetle's power to resist the repelling effects of the resin that flows into the freshly excavated entrances and galleries in the living bark and to dispose of it by forming pitch tubes at the entrances is most remarkable.

But such tubes are not identified with the Douglas-fir beetle in its host tree (10, p. 2; 58, p. 21). In the place of tubes, speaking for the Northern Rocky Mountain region, Furniss (43, p. 3) describes pitch streamers extending from Douglas-fir beetle entries in standing trees which are visible 30 to 50 yards away. Streamers are, however, also seen on many trees in the coast region (93, p. 4).

Chararas (28, p. 1407), however, has recently dismissed the importance of oleoresin flow in deterring scolytid attack by arguing that if some insects are drowned, this is a matter only of an accidental phenomenon occurring about ten days after insect entry.

> La sécrétion des résines, considérée autrepois par certains auteurs allemands comme un moyen de défense de l'arbe contre l'attaque des Scolytidae, n'est en réalité que la réaction mécanique à un traumatisme; si quelques insectes s'y noient parfois, il s'agit là d'un phénomène accidentel, la sécrétion se manifestant en règle générale après la pénétration des insects. C'est ansi que chez l'épicéa, riche en résine, les écoulements apparaissent un dizaine de jours après l'attaque, alors que l'insecte a déjà pratique sa galerie et meme commencé à pondre; chez le sapin, pauvre en résiné, il existe cependant une faible sécrétion et, dans ce cas, l'attaque des branches par *Cryphalus piceae* Ratz. prépare le terrain pour *Pityokteines curvidens* Germ.

To confirm the traditional opinion, however, the pressure with which oleoresin exudes has been related by Vitéand Wood

(142, p. 72-8) to pine resistance to Dendroctonus monticolae Hopk. and D. brevicomis Lec. Vité (136, p. 39) had demonstrated oleoresin exudation pressure in a standing ponderosa pine to be subject to manipulations which altered the state of water balance in the tree; epithelial cells lining the resin ducts are able to express full turgor if adequate water is available from the sapwood transpiration stream.

Rudinsky (115, p. 9) and workers in the Intermountain Region (135, p. 23) have measured oleoresin exudation pressures in standing Douglas-fir trees and related these to resistance of the Douglas-fir beetle.

Oleoresin generally is effective in overwhelming and suffocating bark beetles (51, p. 69; 101, p. 13). Smith (128, p. 366-9; 130, p. 130) studying Dendroctonus brevicomis Lec. determined that oleoresin vapors in sufficiently strong concentrations can be toxic if from a tree other than a host species. Not being deterred by the oleoresin of their host, beetles could be theorized to be attracted to the latter because of emanated resin factors. The work of various authors who have given consideration to this last hypothesis has been discussed in the section on attraction above (see p. 21).

MATERIAL AND METHODS

Beetles

Sources

Together with supplies of host material, a quantity of Douglas-fir beetles was basic to the conduct of this study. These could be obtained either by laboratory rearing or from field logs. In either case, an understanding of the required cold rest as shown in Ryan's (121, p. 521-522) diapause studies of the species was essential.

For rearing, recently cut three-foot logs brought to the laboratory were made to receive about 15 attacks through confinement in a small cage with 30 beetles; half of these were females. At laboratory temperatures (75° F.) the amount of time to establish brood and for most individuals to reach the adult form was 80 days. The cold rest could be as short as 40 days if the temperature was fixed at 43° F. Cold storage was continued until five to ten days before the beetles were intended for use, this latter time period being that needed by the insects to emerge from the log.

Cold storage also afforded a means of holding the brood in infested logs which were winter cut into manageable lengths and brought to the laboratory. The bark only of infested logs could also be collected and its contained beetles in diapause also placed in cold storage until five to ten days prior to use.

Sexing

In beetle manipulation and tallies where precision was not required, a given population sample could be presumed to be half male and half female (9, p. 8). The sexes are quite alike in appearance but do possess characteristics by means of which they can be distinguished. Chapman (20, p. 2, 3) described the high degree of accuracy obtainable by listening for the stridulation unique to males. Lyon (88) differentiated sexes by examining the seventh abdominal tergite which is modified in males and is the stridulation organ. Hopkins (57, p. 73) defined the difference between males and females in those species of Dendroctonus he grouped in subdivision II C. "Females: interspaces of elytral declivity rugose. Males: interspaces of elytral declivity smooth." Chapman (20, p. 3) credits McCowan and Rudinsky with finding the roughness distinguishable to human touch. Very recently, Jantz and Johnsey (63, p. 1328-1329) have described the high degree of accuracy obtainable through microscopic examination of the elytral declivities.

Sexing was important in conducting investigations relating to this thesis: a combination of listening for the stridulation and feeling the elytral declivity was used. Featherweight forceps, as listed by Ward's (147, p. 80) and used in handling the living beetles to avoid damage to them, proved the ideal tool for checking the rugosity of the declivity (Figure 3).

Controlled Introduction

Where it was essential to direct the entry of individual beetles and beetle pairs, this was done with one of a variety of confinement devices that restricted beetle activity to a fixed location on a log. Three-inch diameter cylinders an inch high, fitted with screen on the exterior and sponge rubber next to the log, proved the more difficult to manipulate and tie in place. Small- to medium-sized cans could be made to provide a secure and light tight seal if they were fitted into a circular groove made in the bark by rotating a similar can by hand (Figure 5d) or at high speed with an electric drill. Number 000 gelatin capsules, as used in the pharmaceutical industry, were efficient in that they could be secured tightly using a number three insect pin that pierced the capsule and was pressed into the bark. In all of these cases, entry was best facilitated if a one-eighth inch hole was drilled at an angle through the bark (Figure 5a). The holes were generally entered readily by individual beetles of either sex and by beetle pairs even when the host material was not Douglas-fir (Figure 5b). For multiple introductions, the easiest confinement procedure was to cover the beetle entered into the drilled hole with 18 x 14 mesh wire screen held in place with 1/2-inch staples (Figure 5c). In the field attraction studies, this technique was much

a.

b.

c.

Figure 5. Beetle introduction techniques.

(a) Drilling of 1/8-inch holes for beetle introduction

(b) Placing beetles into the holes.

(c) Wire screen as used in many of the replicates to confine and protect the introduced beetles.

(d) Metal can retainer fitted into a circular groove in the bark.

d.

used, being effective not only to contain pre-entered females but also to prevent their being mated or preyed upon.

It should be noted that there is a fractional failure of beetles to enter the log whatever technique is used. This failure ordinarily is not indicated at the outset.

Isolation of logs receiving controlled entries was often necessary. In the laboratory, this could be accomplished by moving the preparations into a separate room or, for greatest security against chance entry, to a separate building. This procedure was used where it was desired that only a fixed number of beetle pairs be established in the study logs.

Laboratory isolation was used also to preserve the virginity of entered females for three days while they made full entry into logs intended for a field attraction study. In two other cases, the isolation was achieved directly in the field by wrapping the logs in heavy wrapping paper (Figure 6). Further replicates in the same line of experimentation accomplished the isolation of the unmated female by the stapled screen technique mentioned above.

Observation of Field Attack

Frequent counts were made in order to determine if, in a certain study, a given treatment of host material would receive more attacks than another. Visits were made at least weekly during the attack season. More often, especially in the later studies, visitations were two and three days apart. Primary interest was in those attacks which were new and would be clearly indicated by reddish piles of frass. These were marked with colored staples at the time of counting. A different color spray paint was used to prepare the staples used each week. Besides conveniently allowing for this coding, staple marking had the additional advantage of great speed (Figure 7).

Analysis of Brood Success in the Host

Attempts during the first summer's study to excise bark sections at intervals to check the relative success of larval development in the various treatments were shortly discontinued. Larvae of known age could be found but, in the numbers obtainable from small excisions, offered no difference as between host material treatments. Large bark samples taken from the study trees would have so altered the latter that they would not have been worthy of continued study as the treatments they were intended to be. Furniss (44, p. 486) has noted this disadvantageous circumstance "... the removal of infested bark is a destructive process which prevents remeasurement of the same insects at a later time."

Evaluations of brood successes in the several investigations were thus made by stripping bark from study material when beetle

Figure 6 (left and below). Paper wraps on logs used to quarantine them while treatment (introduction of a fixed number of beetles) was made certain.

Figure 7. Attack marking techniques.

(a) Painting sticks of ataples various colors for use in marking attacks of each inspection with a different color.

(b) Inspection and marking of attacks.

a.

b.

development was in the teneral adult stage. A circumferential section of bark three to five feet long was removed. The number of adult galleries could then be counted (Figure 8).

In some cases, this datum was checked against the record marked on the exterior bark surface at the time of the spring attack. Except in those logs where oleoresin interfered with beetle entry, the fall gallery count was judged to be a reliable substitute for the final count of spring attack when it had not been observed.

A gallery's initial brood was counted as that represented by the first instar larval mines. The end-of-summer more mature brood could be tallied according to developmental stage, i. e. teneral adult, pupa, or larval instar.

Counts were made also of the predaceous larvae of the dolichopodid fly Medetera aldrichii Wheeler, the predaceous larvae of the clerid beetle, Enoclerus sphegeus (Fab.), and of cocoons of the braconid wasp parasite, Coeloides brunneri Viereck.

Host Material

Trees Used and Sources

A variety of Douglas-fir host material was used. Consideration for the study being undertaken influenced the selection of material, but this had to be within limits of availability and, in many cases,

Figure 8. Removal of bark in the fall to assess brood success. The samples shown here were part of the 1959-1960 Woods Creek study.

Above: sample from top of November cut tree section. It had a simulated root connection but no limbs. In the sample area there were 1.63 attacks per square foot; brood survival was 47 percent.

Below: sample from bottom of November cut tree section. It had neither root connection nor limbs. In the sample area there were 0.65 attacks per square foot; brood survival was 51 percent.

with attention paid to the feasibility of hand manipulation.

date and location (also see Figure 30)	material	treatments
Phloem Moisture Studies		
Spring, summer, 1959. Monmouth Peak. S 15, T9S, R7W, Willamette Meridian. 20 miles NW of Corvallis Elevation 2400 ft. (Fig. 9)	4 trees windthrown the previous winter. 3-ft. basal diameter. 150- foot long. 160-years age.	One of four treatments designed to affect phloem moisture applied to each tree.
Fall, winter, 1959-1960. Corvallis laboratory	2 trees from McDonald Forest near Corvallis. Cut Sept. 25 and Feb. 20. 14-inch basal diameter.	One of four treatments designed to affect phloem moisture applied to each of several 3-ft. logs cut from the two trees.
Winter, spring, summer 1959-1960. Woods Creek S 10, T12S, R7W, W.M. 10 miles west of Corvallis. Elevation: 1300 ft.	8 trees, two on each of 4 dates spaced through the winter were cut. 15- 20-in. basal dia. 80-ft. long. 60-yrs. age. Old growth bark partially up bole.	Trees were cut into half length. One of four treatments designed to affect phloem moisture was applied to each tree section.
Beetle Attraction Studies		
Spring, summer, 1961. East Trail on Marys Peak. S 5, T12S, R7W, W.M.	7 trees from McDon-Forest cut in March. 13- 15-in. basal dia. 55-years age. Old growth bark over most of bole length used.	Each tree yielded 12 to 20 three-ft. logs. Each log received a treatment which might affect the response a beetle would make to it.

date and location	material	treatments
Beetle Attraction Studies (continued)		
Spring, summer, 1961. Various sites on the east slope of Marys Peak.	7 trees each cut at a different time through the spring and summer. 13- 18-in. basal dia. 55- 150-years age. Old growth bark over most of the bole length used.	Each tree yielded 18 to 27 three-ft. logs. Each log (except controls) was treated by introducing into it a few beetles of controlled sex in order to produce different log treatments.
Spring, summer, 1962. Miller Ridge road on Marys Peak. S 24, T12S, R7W, W.M.	4 trees cut April 19, 20, 1962 from McDonald Forest. 10- 15-in. basal dia. 85- 95-years age. Old growth bark over most of bole length used.	3 of the trees yielded 16 three-foot logs. The other yielded 20. Logs received four treatments (Table 2).
Oleoresin Effects Studies		
Summer, 1960 to summer, 1962. Woods Creek, as above.	10 standing trees. 13- 40-in. diameter at breast height.	Gages inserted to measure oleoresin exudation pressure.
Spring, summer, 1960. East Trail Road on Marys Peak. S 15 & 22, T12S, R7W, W.M. 10 miles west of Corvallis.	6 large diameter trees windthrown the previous November. 3- 4-ft. basal dia. 200 ft. long.	Gages installed to measure o. e. p. Trees observed for beetle attack and brood success.
Summer, 1961. East Trail on Marys Peak. S 15.	One standing tree.	O. e. p. measured, then tree girdled through sapwood. Meanwhile beetles forced to attack through confinement under screen.

Additionally, six more trees of three other species were used in attractance studies.

time and location	material	treatment
Summer, 1961. East Trail on Marys Peak.	Western hemlock. 17-in. basal dia. 125-years age. Cut at the site July 7, 1961.	The 20, three-ft. logs were divided into two groups. Logs of one group each received a few introduced females.
Summer, 1961. East Trail on Marys Peak	Grand fir. 8-in. basal diameter. Cut in Corvallis July 14, 1961.	8, twelve-inch logs divided into two groups. Logs of one group each received a few introduced female beetles.
Summer, 1961, East Trail on Marys Peak.	Grand fir. 11-in. basal diameter. Cut from McDonald Forest Aug. 1, 1961.	10, three-ft. logs divided into two groups. Logs of one group each received a few introduced female beetles.
Spring, summer, 1962. Miller Ridge road on Marys Peak.	Western hemlock. 14-in. basal dia. 120-years age. Cut at the site, May 12, 1962.	22, three-ft. logs divided into two groups. Female introductions made into one group.
Spring, summer, 1962. East Trail on Marys Peak.	Grand fir. 15-in. basal dia. 170-years age. Cut at the site May 18, 1962.	8, three-ft. logs divided into two groups. Female introductions made into one group.

Spring, summer, 1962 Miller Ridge on Marys Peak	Ponderosa pine. 11-in. basal dia. 30-years age. Cut from McDonald Forest plantation May 14, 1962	8, two-and-one-half foot logs divided into two groups. Female introductions made into one group.

In making attacks, Douglas-fir beetles generally ignore bark whose thickness is less than 0.3 inches. Those few attacks which do occur in thin bark are unsuccessful (93, p. 11). Old growth bark is sufficiently thick and provides fissures on its exterior whose niches afford an anchor point for the initiation of beetle entry. Thus, particularly for the attraction studies, logs having old-growth bark were sought; they provided the most valid host material. Logs with such bark could be obtained from some 13- to 15-inch basal diameter trees which were as young in age as 55 years (Figure 10).

Phloem Moisture Studies

Treatment of the Host Material

Beetle success in trees as they might have been differently damaged in the course of being windthrown was a major interest in these studies. In preparing treatments, it was intended that there be representations of trees which, on the one hand, lost their crown or, on the other hand, retained it; also, a root connection with the soil might or might not be retained. Three sets of procedures were used.

The Monmouth Peak trees, windthrown in January 1959, were selected and prepared on May 16 (Figure 9). Two of the trees had kept their crown on falling. One of these, already more disturbed in the root region by the fall than the other, was cut through at the root collar to interrupt moisture uptake. The other trees had shattered their crowns in falling and were thus left without any transpiring surface. One of these was cut at the base.

Treatments analagous to the above were applied to short logs used in laboratory studies and to the series of 16 half-tree sections of the Woods Creek study.

Nine three-foot logs were cut from one tree to provide material for laboratory experimentation begun in September. A second tree, supplying eight logs, was cut and study started in February. In each case, cutting of the logs was managed so that on some of them a limb was left attached. This was intended to correspond to the crown of an intact tree. Root connections were simulated by using one and a half inch pipe nipples as an injection device for the placement of water into the base of four logs (Figure 10). To deter moisture loss from the exposed ends of the log sections, the ends were coated with an application of molten paraffin.

Within both the September and February groups of logs, four treatments were applied. Two logs had attached limbs and a simulated root connection. Two logs had limbs only; two others had just the root connection. The remaining logs (3:September, 2:February)

Figure 9. Site of the windthrown trees used in the Monmouth Peak study. Trees bordering the clear-cut area were especially subject to windthrow.

Figure 10. Logs as differently prepared for laboratory experiments.

Figure 11. Detail of simulated root connection as applied to half the treatments at Woods Creek.

had neither root connections nor limbs.

For the Woods Creek study, eight trees were cut during the winter of 1959-60. Two trees were cut every six weeks, starting on November 7. All were cut through at their mid-length so that two treatments were produced by each tree. These were felled so that most of the limbs were retained and thus the top sections all had limbs. To half of the limbed upper sections simulated root connections were fitted (Figure 11). Similarly, in half the cases involving the limbless, basal section, the same kind of root connection was made. Thus, for each felling date there existed one of the following:

Code	Treatment		Source
A	simulated root connection,	no crown	first tree
B	simulated root connection,	crown	first tree
C	no root connection,	crown	second tree
D	no root connection,	no crown	second tree

The 16 tree sections were present in the ground pattern diagramed in Figure 12 prior to the spring warming which allowed the first Douglas-fir beetle flights.

The third set of techniques was adaptable to short logs and could be used to provide three levels of moisture: wet, control, dry. In a 1961 study all three levels were used. The 1962 beetle-attraction study employed the treatments for wet and control.

Logs receiving the wet treatment were paraffined at one end and were then set upright in a tub of water for two and a half weeks, at which time they were removed and paraffin then applied to the

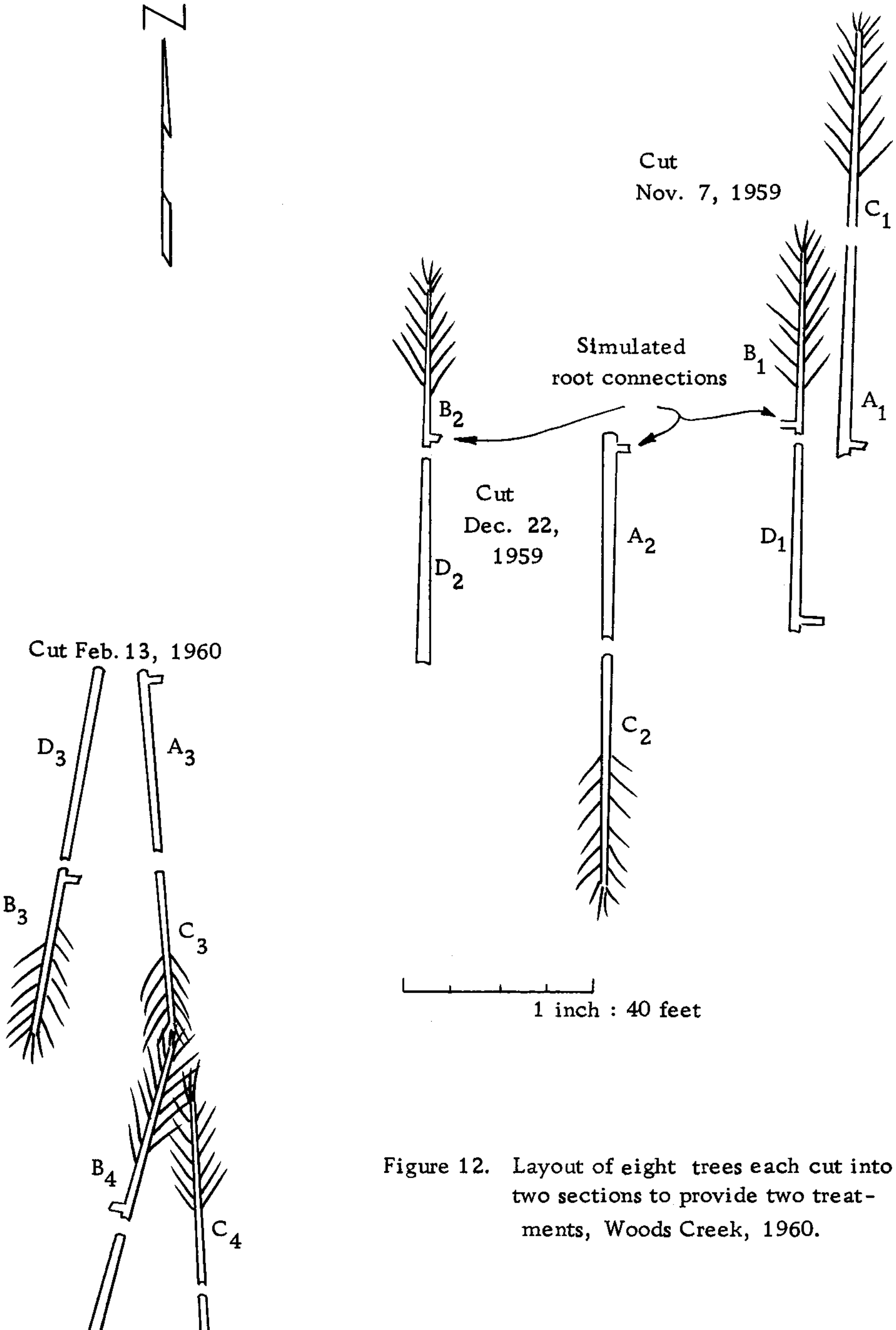

Figure 12. Layout of eight trees each cut into two sections to provide two treatments, Woods Creek, 1960.

basal end. For multiple treatment of large numbers of logs, it was economic to use six mil polyethylene sheeting which could be drawn up on the sides of the logs, tacked in place, and thereby made to contain a two- or three-inch depth of water in which the logs soaked.

In the dry treatment, the log ends were not paraffined and the logs were laid so as to give free circulation of air to the ends, drying being thus encouraged. After two and a half weeks, the log ends were sealed with paraffin.

Control logs had their ends paraffined shortly after cutting and received no other treatment save being stored in the same room with the classes above while they were being treated.

Moisture Assessment

The treatments designed to produce variously wet phloem were followed with tests at intervals that measured moisture content and helped evaluate effect of the treatment.

Sampling of the phloem was accomplished by means of a large punch, fabricated from a section of one and a half inch pipe that was driven through the outer bark to the cambium (Figure 15). The outer bark was trimmed away and the phloem-cambium sample was brought to the laboratory in stoppered vials for moisture measurement. Punch holes left in the bark were sealed with paraffin.

Weights of the sample while wet and after drying at 90° C. to constant weight were established and moisture determined by subtraction. The latter is expressed as a percentage of the dry weight. The balance used was accurate to yield values of three significant figures.

This procedure conforms to that of many authors as previously mentioned (see p. 14). Chalk & Bigg (18, p. 9), while using a different technique for assessing the distribution of moisture in Douglas-fir, observed that the orthodox procedure has the advantage for certain purposes in that it gives an indication of the actual amount of water in the stem.

Moisture Sampling Points

Earlier studies had shown water to move in a restricted path up Douglas-fir trees (54, p. 358-359; 141, p. 35). In the initial Monmouth Peak study therefore, moisture samples were taken from four sides of the tree, subsequent studies took samples only from one side. Three loci were sampled in each of the Woods Creek half-tree treatments; base, mid-length, and top. Consideration was given to having the sampling point not in line with the simulated root connection when it was used.

In the three-foot logs, single samples were taken at mid-length and, again, out of line from the root injection when it was used.

Treatment of Logs for the Attractance Studies

Following the inconclusiveness of observations made of differential attack on the Monmouth Peak and Woods Creek trees in 1959 and 1960, respectively, a new study was initiated to measure beetle response to logs presenting a variety of different stimuli. In the absence of prior demonstration of clear-cut beetle response to differently treated host material, an approach that was largely empirical was used.

Logs were cut March 20-22, 1961 in the Oregon State University School of Forestry's McDonald Forest. These were brought to the laboratory in Corvallis for treatment. Each of the series of 13- to 15-inch basal diameter trees was cut into 12 to 20 three-foot logs. To the logs of one tree, three or four treatments were applied; the treated logs of one or two trees provided the material for a trial. The logs were randomized for determination of the treatment each was to receive. In all cases, treatment included paraffining the log ends.

Randomization in the case of each trial produced the scheme for treatments shown in Figure 13.

For the trial of logs of different colors the code in Figure 13a indicates an enamel paint application to the logs of two trees as follows:

OR	BL	RE	YE	WH	VI	CO	GR	YE	RE	CO	WH	VI	GR	BL	OR	X	X

YE	VI	OR	GR	WH	RE	BL	CO	CO	GR	YE	VI	OR	RE	BL	WH	X	X

A. Colors applied to the logs of four replications for a beetle response to colors test

C	S	P	S	C	P	P	S	C	S	P	C

P	C	S	C	P	S	S	C	P	S	P	C

B. Logs treated to provide different host material odors, eight replications

CV	KN	H	CO	H	KN	CO	CV	CV	KN	H	CO	CO	CV	KN	H	CO	KN	H	CV

C. Treatments applied to logs to provide miscellaneous altered stimuli, five replications

C	D	W	C	D	W	C	D	W	C	D	W	C	D	W

D. Logs treated to provide a different moisture levels, five replications

C	♂	PR	♀	I	PR	I	♀	♂	C	PR	♂	I	C	♀	PR	I	♂	♀	C

E. Logs treated with different introductions of beetles; this material was laid out in a single replication

Figure 13. Treatments applied in five tests of beetle attractance to logs, spring, 1961. Within a test, treatments were directed by randomization

RE:	Red	WH:	White
YE:	Yellow	GR:	Green
OR:	Orange	VI :	Violet
BL:	Blue	CO:	Control
X :	Unpainted		

A quart of paint was used in spray painting four logs their designated color. This rate of application gave reasonably good coloration. Non-pigmented Enameloil[1] was applied at the same rate to the controls.

The test for response to log odors used the logs of two trees; each log received one of three treatments determined by randomization and coded in Figure 13b.

P: entire log dipped into molten paraffin which was to serve as a sealant.

S: log was cooked in a soil sterilizer for eight hours, with steam pressure at 15 p. s. i., log ends paraffined.

C: control; no treatment except to coat the log ends with paraffin.

Also for this test a series of old logs which had been used for laboratory rearing, and from which the broods had emerged, were selected. The bark on these was still intact and similar in appearance to that of the fresh logs. Diameters of the old logs were similar to those of the fresh ones.

All logs of the four treatments in this test were provided with

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[1] Trademark: Benjamin A. Sipe Company, Philadelphia, Pa.

foot-square wire screens bordered with Deadline[2], a tacky material in which insects become entangled. The design was to have served as an instrument for recording beetle visitation to the log apart from that which resulted in entry.

In the third test, stimuli that logs offer were altered in miscellaneous ways. In Figure 13c, the treatments made are coded as follows:

CO: control logs, no treatment save paraffining the ends to preserve moisture, as in all cases below.

CV: logs covered with brown fabric which altered their appearance and touch.

KN: logs on which the rough outer bark was shaved away, yielding a different appearance and touch.

H : logs hidden from overhead by an 18- by 48-inch khaki painted piece of plywood nailed to the log.

Logs having different phloem moisture content were prepared for the fourth test as indicated by the code in Figure 13d. The method used has been described earlier (See p. 41).

W: moisture increased

D: moisture decreased

C: control

The fifth test in this series used logs in which the treatment was simply to introduce small numbers of beetles in different

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[2] Trademark: California Spray Chemical Company

combinations indicated by the code in Figure 13e.

PR: beetle pairs introduced; one pair into each of six holes

♀ : six unmated female introductions; one in each of six holes

♂ : six male introductions; as above

I : a number of beetles were mascerated with water and this mixture was inoculated six times into each log.

C : control, no treatment except, as above, the log ends were paraffined.

The beetles had been laboratory reared and emerged from their brood log after passing through diapause (see p. 26). Introductions were equally spaced on a line running the length of the log. For two days in the laboratory the introductions were guarded by 000 gelatin capsules held in place by a number three insect pin. All beetles had entered the bark and produced frass at the time capsules were removed.

After treatment the logs were set out in the field so that they might be tested for reception of differential attack. The experimental design in the case of the first four tests was to use the logs of a test to produce a series of replicates. The logs of each replicate were distributed over an area about 200 square feet (Figure 14). The particular area used was selected because a field beetle population was observed to be present. A large windthrown tree in the vicinity was under attack.

This plan for distribution of the study material served from

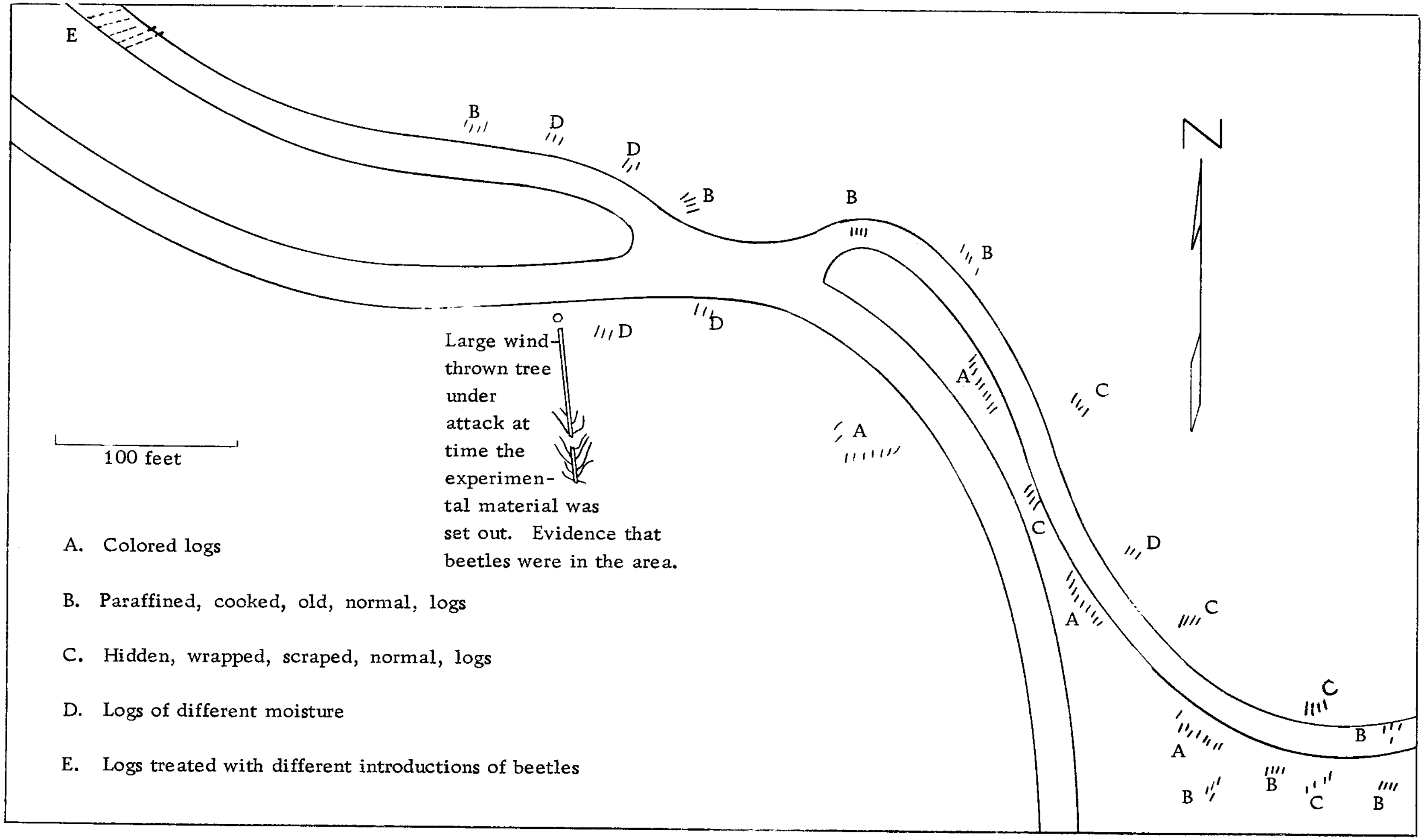


Figure 14. Dispersal of the replications of the experiments testing beetle attraction to variously prepared logs

the first of April until June 16, when, with few attacks having been seen, a more concentrated layout of material was used. The four to eight logs of a treatment which had made it possible to have four to eight replications were now gathered together. In the case of each test, replication was abandoned to substitute, instead, a single trial where each treatment was represented in larger amounts.

The fifth test, of beetle response to logs already containing a few beetles, was set out later than the other four tests and employed only the large trial arrangement of host material. The results read in June 1961 from this particular test showed it to be a line of investigation that was most warranted for further experimentation.

Accordingly, the experiment was successively duplicated eight more times in 1961 before beetle flight activity was seen to cease in mid-August.

In the subsequent trials, two of the treatments of the initial test were abandoned. These were the male introduction and innoculum ones. It was not thought necessary to continue them: any attractant effect of introduced males or innoculum would show up in other treatments which were to be better represented in each trial because the test material would be spread among three treatments instead of five.

The subsequent trials were substantially alike, but were carried out at different times. This was necessary because laboratory-reared beetles needed to effect the beetle introductions were not abundant and could only be used as they became available. The varying number of beetles fixed the number that could be used for the treatments of a replication. However, never fewer than three introductions per log nor more than six were made.

Labor demands incidental to preparing new replications and reading the data as it developed from those already begun also mitigated against coincidental replication.

In the initial and the first two subsequent trials entered beetles were denied escape for two to three days after introduction by a gelatin capsule pinned in place. When the logs were set out in the field (initial trial) or stripped of their protective paper wraps as shown in Figure 6, (two successive trials), the capsules were removed and at that time the test was underway. In the several later trials with Douglas-fir and other host material, wire screening was stapled in place over the entry immediately after introducing the beetles (see p. 28).

After the initial trial, trees were cut at convenient locations in the field. It was incumbent that the various log treatments be laid out where cover was such that uniform accessibility for attacks would be allowed while at the same time there would be shade protection from solar radiation. Figures 16 and 17 picture the use of an abandoned roadway and brush-free site used for the layout of

Figure 15. Tool used for sampling phloem for percent moisture determination.

Figure 16. Logs of the three treatments as laid out in one of the replications testing for attractance due to a beetle factor.

Figure 17. The two treatments of the hemlock experiment. The logs into which female Douglas-fir beetles were introduced and which were the only ones to receive attacks are at left.

logs of the different treatments. The sites were in four different general areas and are shown on the map, Figure 30. A second replication was not initiated at an area until attack activity had ceased in the replication previously set out there.

Tree age ranged from 55 to 150 years; basal diameters were from 13 to 18 inches. In addition to the latter variation in size, there were differences in usable tree length. Therefore, the surface bark area of the treatments was different between replications. Within each replication, however, each treatment had the same bark surface area in so far as uniformity of tree shape and designation of logs by randomization allowed.

Two of the felled trees were made to provide two replicates each. This was done by reserving the logs cut from the butt half to one replicate and logs cut from the top half to another.

A summary of the variations in treatment technique which were used as new replications were prepared and predictability of success emerged from older trials is given in Table 1.

In 1962, study of beetle-induced attractance was continued. The noteworthy treatment revealed in 1961, namely the introduction of a few unmated mature female beetles, was made to be one of the factors in a factorial experiment. The beetles used came from the bark of the 1961 study material which had overwintered in the field. Log moisture, represented by two levels, was the concomitant

Table 1. Variation in treatment techniques of the nine replications. Beetle attractant factor experiment, 1961.

Replicate	Felling details	Treatment details	Security of introduced beetles	Initiation of field attack
1	tree cut March 20, 2 months prior to treatment	done in the laboratory; 5 treatments prepared (see p. 48)	gelatin capsules used as retainers in the initial stage only	placed in field to receive attack four days after treatment
2	tree cut, treatment begun on same day	done in the field; logs wrapped in paper; 3 treatments (see p. 51)	paper covers (Fig. 6) on logs until beetles in capsule retainers had made a secure entry	paper wraps removed and logs opened to attack one day after treatment
3	"	"	"	paper wraps removed two days after treatment
4) from & same 5) tree	"	done in field; introduced beetles retained and guarded by metallic screen tacked in place; 3 treatments	screen retained beetles throughout the trial; screening also on controls to simulate an equal appearance	logs open to attack immediately after cutting and preparation
	"	"	"	"
	"	"	"	"
8) from & same 9) tree	"	"	"	"

factor. The experimental scheme is presented in Table 2. The procedure used is in accordance with that described in a standard textbook dealing with statistical inference (85, p. 309).

Table 2. Four treatments for a two-factor (introduction of females and log moisture) log attractance study, 1962

	Log moisture factor	
Introduction of female beetles factor	logs soaked 16 days; 6 ♀ Douglas-fir beetles introduced into each	logs not soaked; 6 ♀ Douglas-fir beetles introduced into each
	logs soaked 16 days; no beetles introduced	logs not soaked; no beetles introduced

Techniques Used in the Study of the Effects of Oleoresin

The gage technique employed by Vité (136, p. 42) was adapted to make determinations of the oleoresin exudation pressure in standing and fallen Douglas-fir trees. A commercial gage intended for measurement of hydraulic pressures was fitted with a short nipple of 1/8-inch commercial pipe size (actual outside diameter: 0.40 inch, actual internal diameter: 0.27 inch). This was forced into a 5/16-inch hole drilled along a diameter of the tree bole in such a fashion that the pipe nipple tapped its own threads as it moved into the wood (Figure 18). To allow early equalization of pressure and determination of its value, the holes were sometimes back-filled with high-density solutions of glucose or sodium silicate. Vité (136, p. 43) with ponderosa pine, similarly employed glycerol or simply reduced the internal diameter of the pipe nipple by inserting therein a close-fitting piece of plastic tubing.

Gages were inserted in the standing trees at breast height on a shaded side. Sound trees with diameters ranging from between 13 and 40 inches at the four and a half foot height were used.

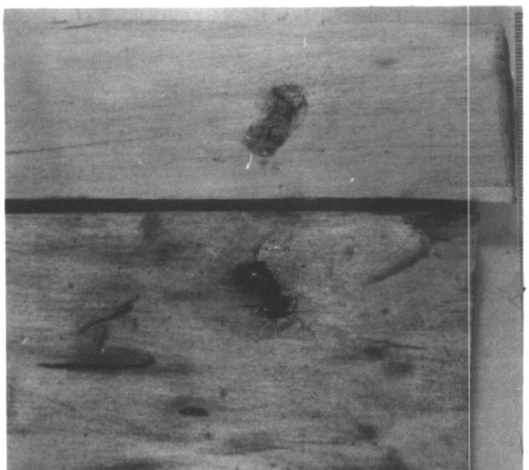
One standing tree, apart from these, was fitted with a gage and two days later girdled through to the heartwood so that the effect of this drastic surgery on oleoresin exudation pressure might be observed (Figure 19). At the same time, beetle attacks were forced into the tree so that some assessment might be made as to their entrance in relation to the pressures read.

The fallen trees had been windthrown in December 1959. Six trees were used; they had basal diameters of 3. 5 to 4. 5 feet and lengths of approximately 200 feet. The trees were relatively intact with the bole and roots a unit although, in each case, a section about 30 feet long had broken free from the top. In three cases, a fair number of the limbs below the broken out top remained attached to the trunk.

The 200 pounds per square inch limit gages initially installed recorded no pressure through late March and were replaced with

Figure 18 (above). Hydraulic gage tapped into the underside of a fallen tree and recording an oleoresin exudation pressure of about 16 p. s. i.

Figure 19. (right above). Experimental reduction of oleoresin exudation pressure. As measured in the intact tree, the pressure was 40 p. s. i. Following a deep girdle, this dropped to zero in a month's time. Only then did forced beetle attacks succeed.



a.

b.

Figure 20. Oleoresin influence on beetles.
(a) Bark removed from sapwood revealing an abortive attack. Beetle just penetrated to cambium. Oleoresin now in gallery.
(b) Three galleries in which oleoresin is judged to have interfered with the adults as well as with development of the brood.

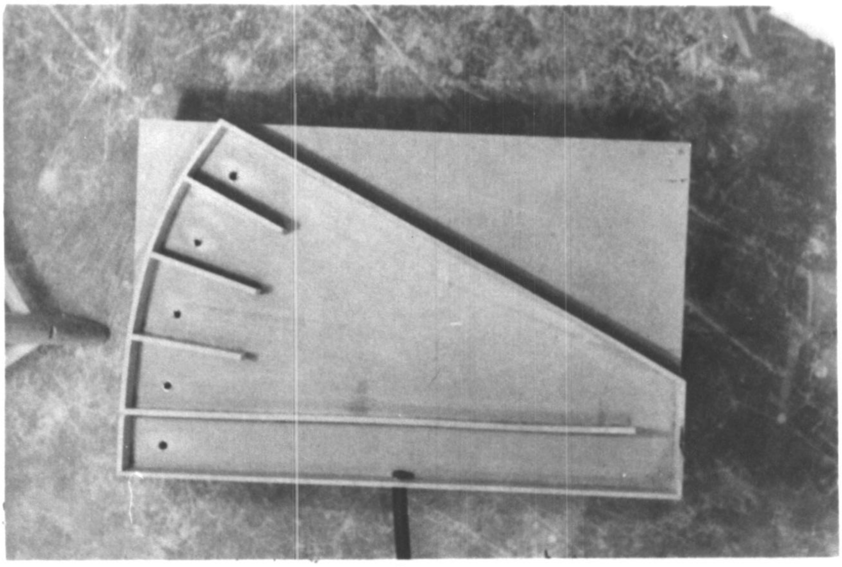
15 p. s. i. limit units. Biweekly visits were made through midsummer to note the pressures indicated by these gages.

These trees were observed also for beetle attacks which were recorded from late April to July 11. A five-foot section of each fallen tree was marked off near the installed gage and attacks were counted and marked in this area. For each tree, other areas in the upper part of the intact trunk and in the broken off section were similarly studied. In the fall, bark was removed from the study areas in order to judge success of beetle entry and of established broods (Figure 20).

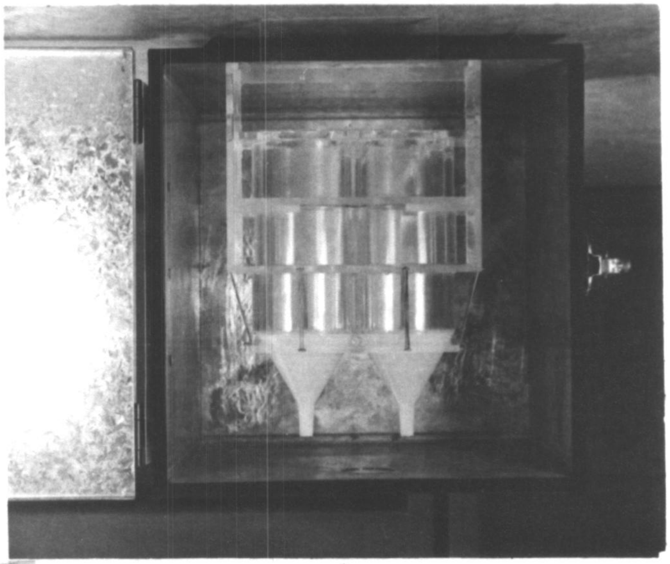
Olfactometric Devices

To gain an insight into beetle chemotactic behavior, two designs of laboratory olfactometers were used. One of these, a sector-arena made of tempered hardboard, was original (Figure 21a). The other, of plastic, was a modification of that of Wilson & Bean (154) (Figure 21b). No positive results were obtained by the author with these apparatuses and thus none will be reported here. Nevertheless, the experimentation proved useful in helping to shape the design for field studies described above.

In the field, a metal box large enough to receive a three-foot long, 12-inch diameter log was used. This was fitted at one end with a six-volt electric-motor-powered fan similar to those used



a.



b.

(a) Sector arena-type laboratory olfactometer.

(b) Olfactometer with restricted arena. After Wilson & Bean (154).

c.

(c) Log with introduced females contained within a metal box. Air extracted vapors from the log and these were released via holes in the second box.

Figure 21. Olfactometric devices.

in automobile heaters. A hose was led from the opposite end to a closed wooden box four inches thick and having a top measurement of two by four feet. The top contained multiple 1/8-inch perforations through which vapor could flow (Figure 21c).

A later trial used two such arrangements close by each other to provide a control; i. e. a log having received no treatment was placed in one box, a log whose treatment was to have a dozen unmated females introduced into it was present at the same time in the other box.

RESULTS

Factors Influencing Beetle Attack

Phloem Moisture Levels in Fallen Host Material

The four Monmouth Peak trees and the sixteen tree sections studied at Woods Creek showed various levels of phloem moisture. There was variation between trees and, as time passed, within a tree. To some extent, differences could be related to treatment. Trees and sections lacking a crown region or branches were wetter than those on which some transpiration surface had been retained. Yet, even when foliage was present, moisture values could reach beyond the moderate level of 150 percent. The presence or absence of a root connection (Monmouth Peak) or a simulated root connection (Woods Creek), as for an effect on moisture level, was of little consequence. On the other hand, as seen at Monmouth Peak and in the six trees of the oleoresin-effects study, the presence of an intact natural root together with some crown components was identified with the retention of a viable appearance of the phloem for a longer duration. Figure 22 graphs the phloem moisture changes of the Monmouth Peak trees through the summer of study. Figure 23 similarly shows the curves representing phloem moisture change in the sixteen tree sections at Woods Creek during the winter of

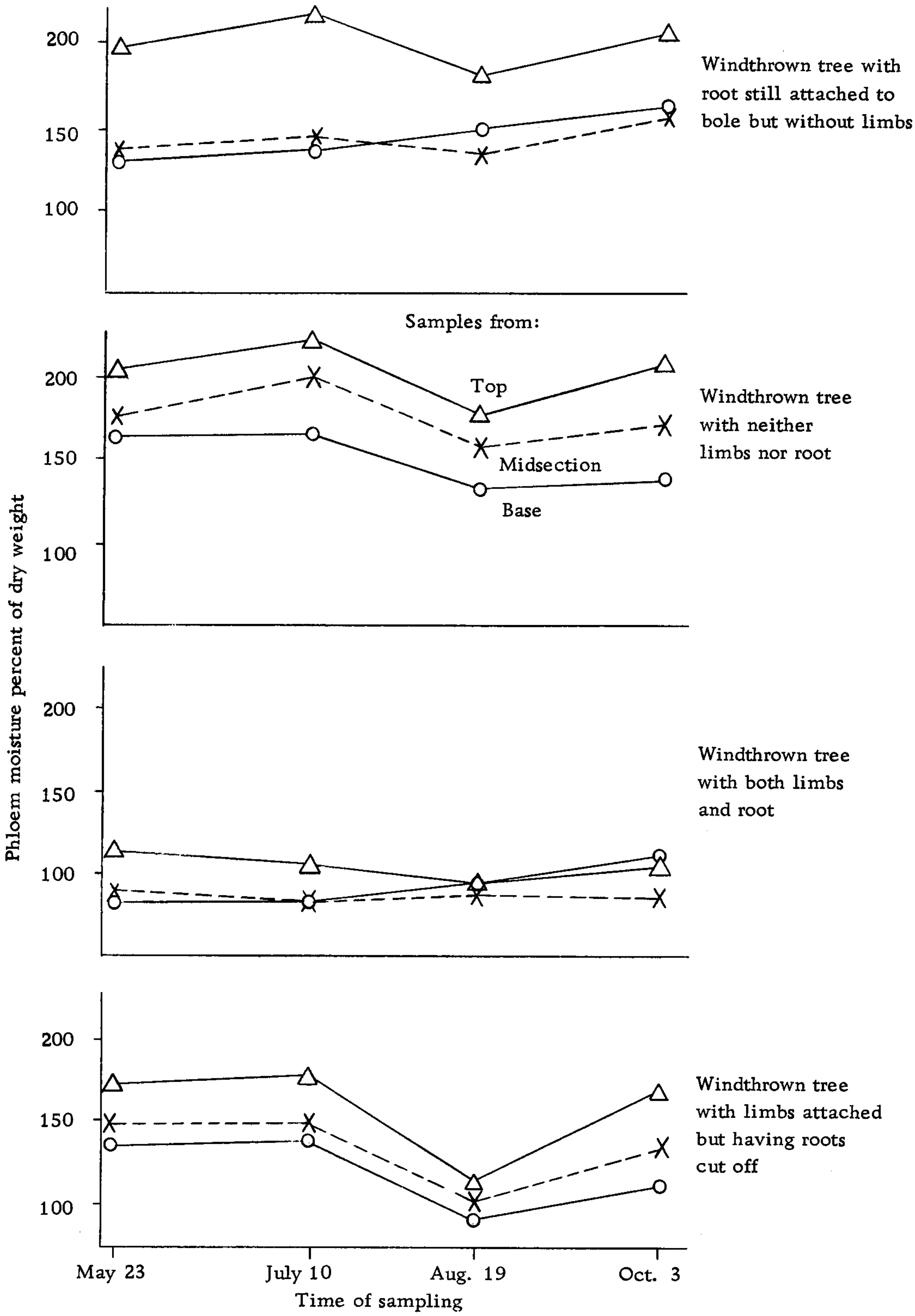


Figure 22. Phloem moisture values, Monmouth Peak trees, 1959. The trees had been windthrown in January and received treatment preparations on May 16. Each moisture value plotted is the mean of the determinations from four samples taken from around the bole.

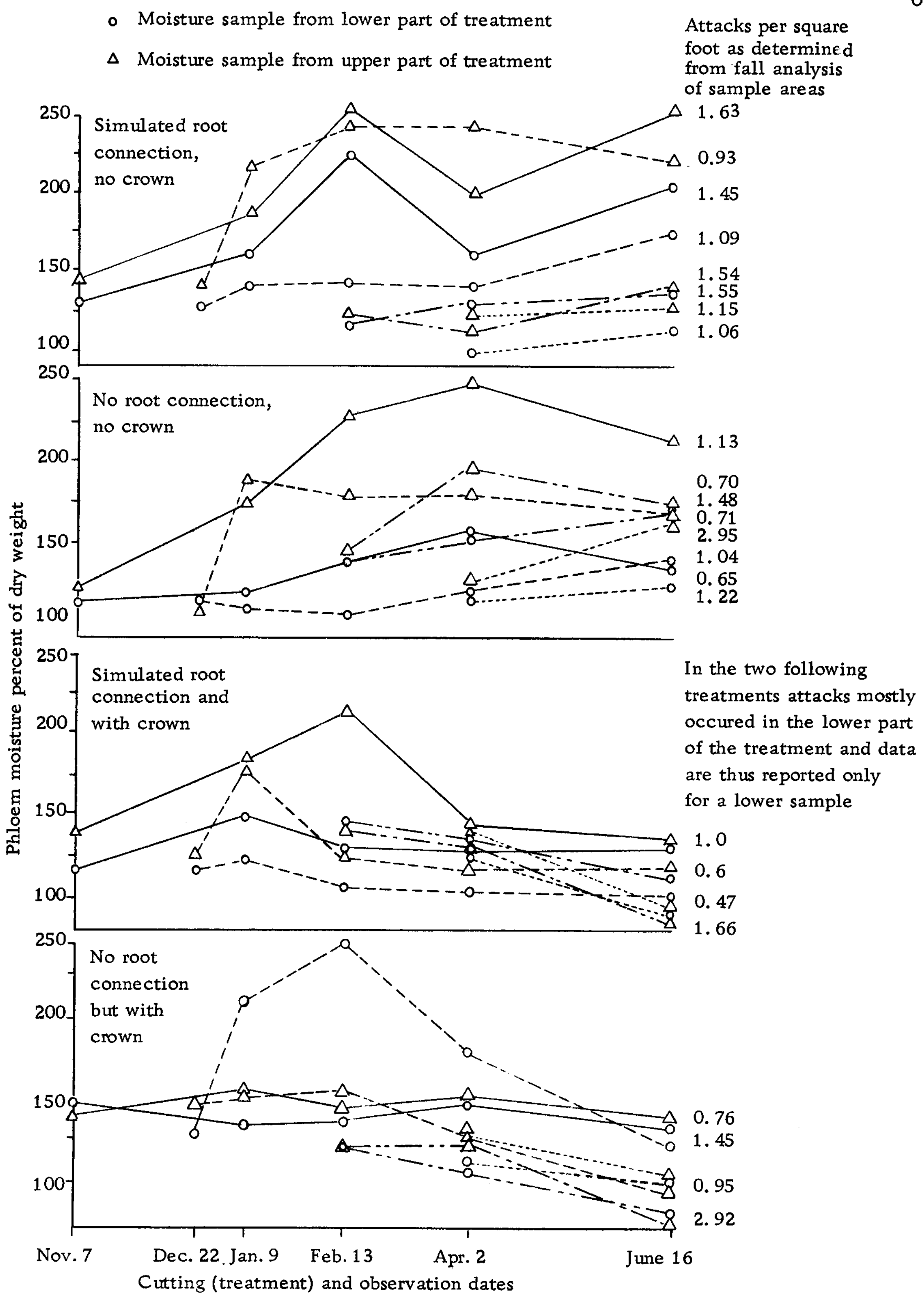


Figure 23. Phloem moisture change in 16 treatments of host material. Preparations were made four times during the winter of 1959-60. Beetle attack densities, recorded at right, show a lack of correlation with the various levels of moisture.

1959-60 from the time of cutting through early April, when the attack season started, to June 16. In both cases, there was demonstrated to be appreciably higher moisture in the upper parts of the tree or half-tree treatments. From the above two studies, it may be said that, generally, moisture values ranged between 95 and 250 percent of phloem dry weight. The latter value tended to represent a maximum. After phloem moisture reached this level it fell off. A comparison with the determinations of Graham (Figure 1, appendix) from standing living trees shows these to have values that lie in the lower half of the range for fallen trees.

The results obtained with short logs in this same line of experimentation differed to the degree that an increase in phloem moisture was effected by simulated root connections (Figures 24 & 25). The drying action of a transpiring surface, now represented by a single limb, was again noted.

In a later study, logs of various moisture levels were produced by butt soaking, on the one hand, and exposure to drying, on the other. A middle moisture condition could then be obtained in those logs with paraffined ends which were neither soaked nor dried (Table 3A).

A yet later 1962 study, employing logs from four trees, used two treatments which affected log moisture: soaking and not soaking (Table 2). Phloem moisture determinations made in a sampling of

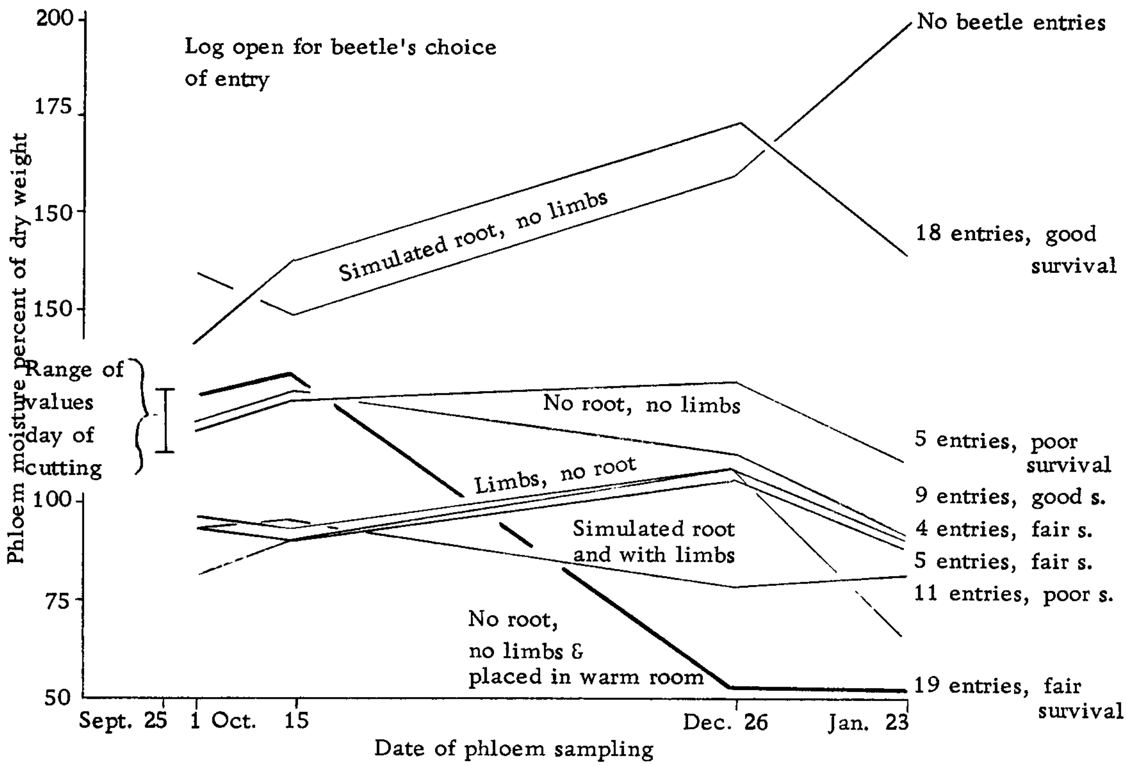


Figure 24. Phloem moisture change and brood success in logs of the first laboratory experiment.

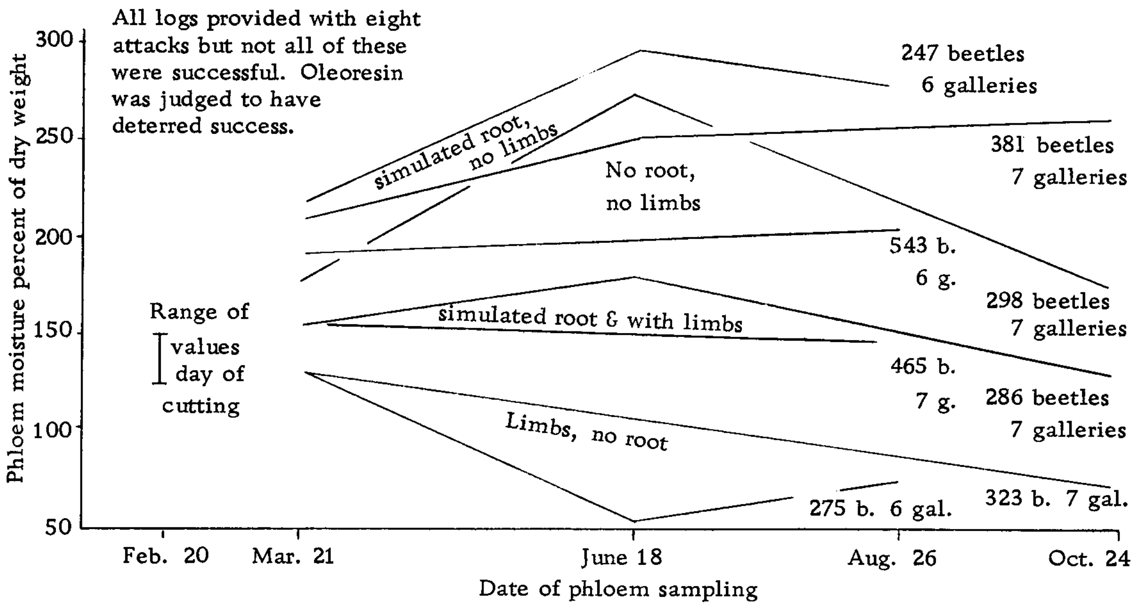


Figure 25. Phloem moisture change and brood success in logs of a second laboratory experiment.

Table 3. Phloem moisture values present in short logs following different treatments. Part A: Three-way treatment; after 19 days. Part B: two-way treatment; treatment period was 16 days.

% moisture values in different logs receiving the treatment indicated.

	Part A	
logs soaked	control; log ends paraffined	log ends exposed to drying
131	100	74
112	95	61
112	107	60
198	120	67
194	107	81

Part B

logs soaked			logs not soaked		
May 10, end of treatment	July 7	Aug. 19	May 10, end of treatment	July 7	Aug. 19
		Tree A			
149	154	140	122	132	97
152	161	122	117	132	165
156	127	140	108	112	140
163	140	-	119	149	-
-	-	80	-	-	139
-	-	97			
-	-	114			
		Tree B			
170	146	64	115	138	158
178	126	74	122	138	136
190	140	-	125	164	-
165	170	-	115	166	-
-	-	87	-	-	137
-	-	87	-	-	116
		Tree C			
122	123	134	105	116	112
116	139	82	105	138	96
108	114	-	102	113	-
107	135	-	102	101	-
-	-	84	-	-	86
-	-	68	-	-	102
		Tree D			
156	122	83	103	131	116
139	144	108	118	123	116
139	135	-	101	125	118
146	144	-	117	143	-
-	-	132	-	-	130
-	-	76	-	-	-

logs from this experiment are reported in Table 3B.

In all cases, soaking increased phloem moisture, but a variation between the logs of one tree as compared with those of another was shown. Also demonstrated was an appreciable moisture increase in the phloem of logs not soaked after an interval of two months (Table 3B). This corroborates the finding of an increase in phloem moisture in the no-root-connection, no-crown tree, and tree-section treatments at Monmouth Peak and Woods Creek (Figures 22, 23).

Phloem Moisture Relationship to Douglas-fir Beetle Attack

Four experiments, through four summers, demonstrated that beetle attack density was not influenced by the various levels of phloem moisture which are present in recently fallen timber.

Table 15 includes the attacks per square foot as determined from fall analysis of the Monmouth Peak trees. These data are inconclusive when related to the moisture determinations (Figure 22).

An attempt to continue this line of study in the laboratory greenhouse was unsuccessful because the recently emerged beetles that were used responded more to photo stimulus and largely failed to enter the study logs at all. Graham (48, p. 283) working with the ambrosia beetle *Trypodendron lineatum* and Vité, Gara, and Kliefoth (139, p. 43) with *Ips confusus* relate similar experiences. In recent study, Graham (49, p. 519) has found that air swallowing during flight dampens the phototactic response.

The Woods Creek study established the several treatments shown in Figure 12 for selection by the 1960 spring flight of beetles. The variables of basic treatment and time of cutting produced, by the start of the attack season, a wide range of phloem-moisture values (Figure 23). Figure 26 shows beetle attacks as they were recorded week by week at Woods Creek. Attempts to relate the Douglas-fir beetle attack record to the phloem-moisture data were inconclusive.

In the attack season of 1961, the five replicates having short logs of three moisture treatments (Figure 13d, Table 3A) received only ten Douglas-fir beetle attacks. Six of these were into one of the dry logs, three into a wet log, and one into a control log. Yet, a shorter log from the same tree left without treatment at another location received ten attacks.

Beetles of other species did, however, record a selective attack. As shown in Table 4, the wet logs were invaded by Gnathotrichus ambrosia beetles and a Dryocetes species and a Hylastes one. This observation was verified the following year in a study that lends it added importance (see p. 74). Also noted in Table 4 is that sour-phloem, an inner bark decay condition discussed below (see p. 77), was found only in the wet logs, the ones recording the selective attack by the Gnathotrichus, Dryocetes, and Hylastes beetles. This finding, likewise, was supported by observation in the next year's

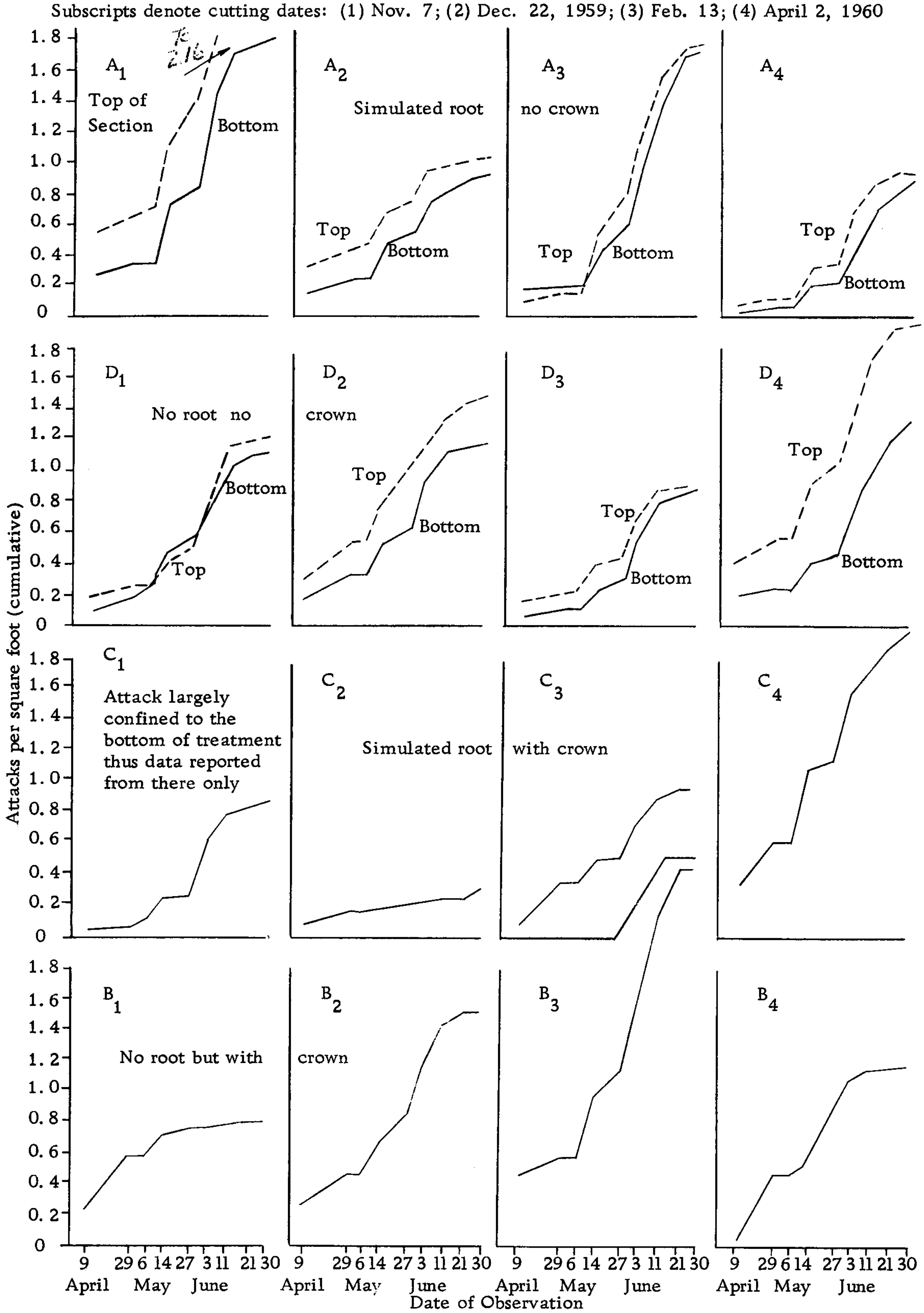


Figure 26. Progress of beetle attacks on 16 tree-section treatments, Woods Creek, 1960.

Table 4. Beetles found in fall analysis of logs receiving different moisture treatments. The logs are the ones having the moisture values cited in Table 3A.

Log Number	Douglas-fir Beetle Entries	Gnathotrichus Ambrosia Beetle Entries	Dryocetes & Hylastes Entries	Buprestid Larvae Found	Sour-Phloem*
		Soaked Logs			
3	0	49	6	0	yes
6	0	32	3	0	yes
9	0	20	18	0	yes
12	3	65	5	0	yes
15	0	40	29	0	yes
		Controls			
1	0	0	0	0	
4	0	0	0	4	
8	0	0	0	0	
10	0	0	0	10	
13	1	0	0	7	
		Logs Exposed to Drying			
2	6	0	0	0	
5	0	0	0	20	
7	0	0	0	0	
11	0	0	0	0	
14	0	0	0	17	

* A phloem decay condition which is discussed later in this thesis.

study.

Buprestid beetle larvae, almost surely Melanophila drummodi Kby. (75, p. 171), were found only in the control and dry logs.

During the attack season of 1961, other experimentation produced evidence of a female beetle attractance factor which greatly influences the numbers of Douglas-fir beetles attacking a log. A later experiment, during the attack season of 1962, sought to compare attractivity of wet logs as opposed to controls while in both cases the female factor was present in half the cases and not present in the other half (Table 2).

Figure 27 shows the progression of attack in the four treatments of each trial. For the convenience of conserving space, logarithmic scale is used for time, as measured in days, commencing May 21. This was the day on which the first attacks in these logs must have occurred. May 26, the day attacks were first counted, thus represents the sixth day following initiation of attack and a logarithmic scale would read 6.0 at that date while May 27, being the seventh day, would read 7.0, and so forth.

The graphical analysis presented in Figure 27 confirms analysis made by statistical means. While there is significance at the one percent level for attacks received in those logs which had had female beetles introduced into them as their treatment, there was not significance, even at the five percent level, as between the logs

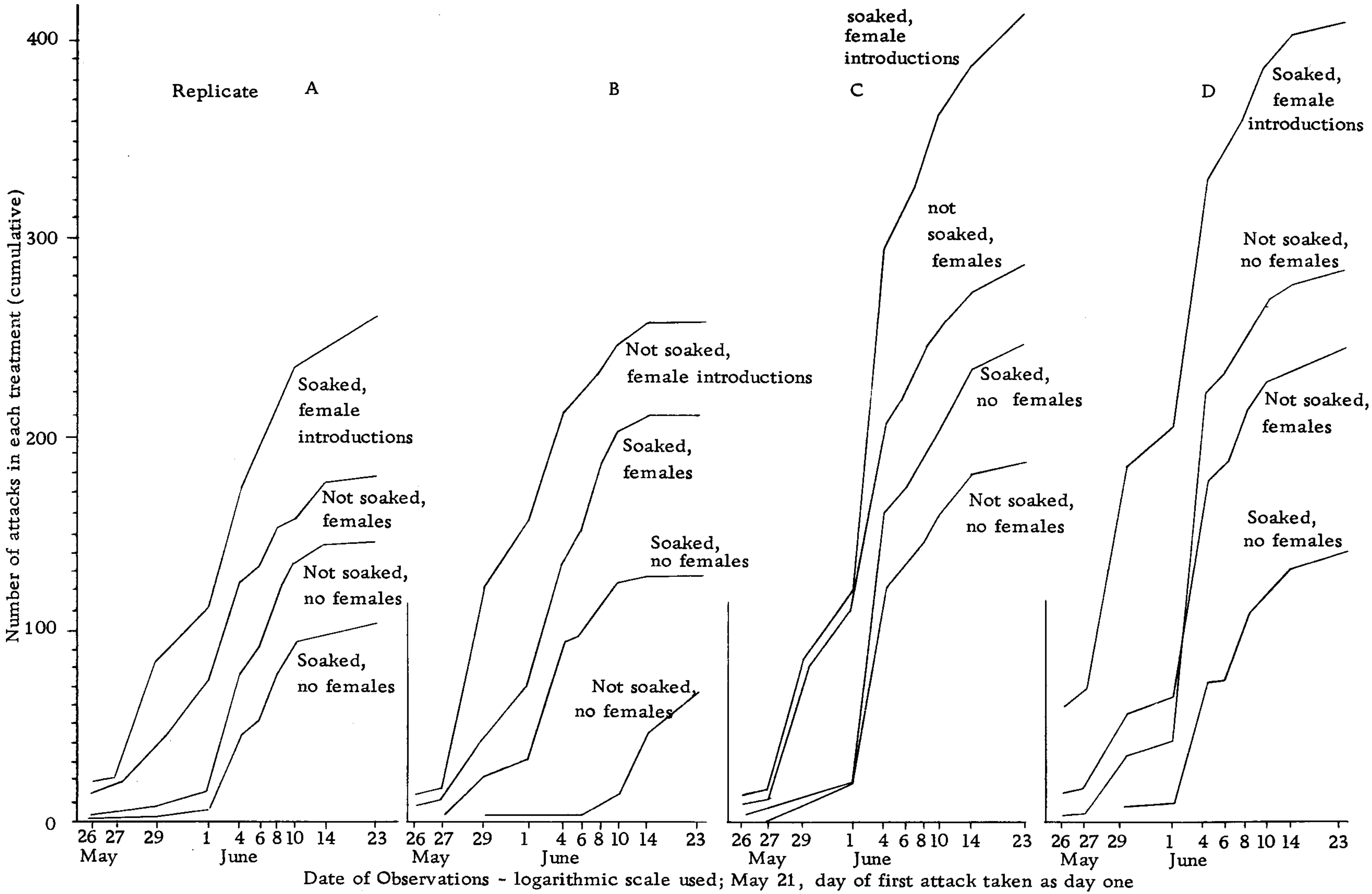


Figure 27. Field attack in four replications of the four-treatment 1962 soaked- and not-soaked log experiment.

which had been soaked and those which had not been soaked.

A July 7 phloem sampling showed that those logs which had been soaked for 16 days, two months earlier, possessed phloem which was becoming sour while the drier logs did not. This observation, together with the one noted earlier (see p. 69 , was corroborated by separate sour-phloem studies to be reported below (see p. 77).

Phloem Moisture and Selectivity by Other Scolytids

The 1962 study results just cited were in line with those of studies from the three previous years; the Douglas-fir beetle could not be observed to show preferential attack in logs of any particular moisture level. It is noteworthy, however, that while this was being ascertained for the Douglas-fir beetle, at the same time and in the same study material, other scolytid beetles (*Hylastes*, *Dryocetes*, and especially *Gnathotrichus*) were observed to concentrate their attack in the wet logs. First note of these other beetles in the various replicates was June 4, 6, and 8. A June 30 approximation of the number of ambrosia beetles in the four treatments of the four replications is given in Table 5.

On August 19, the bark of all the logs was removed so that a more definite count of the differential attack by ambrosia beetles in the wet and and dry logs was possible. These data too are included in Table 5.

Table 5. Ambrosia beetle (Gnathotrichus sp.) entries in soaked as opposed to unsoaked logs. All treatments consisted of four, three-foot logs except that in replicate c there were five logs per treatment. Six Douglas-fir beetle females were introduced into each log of the female introduction treatments. The count of entries is approximate.

Replicate	Date of Count	Log Treatment: Soaked (begin to develop sour-phloem): ♀ Douglas-fir Beetles Introduced*	Soaked: No ♀ Introductions	Not Soaked (no sour-phloem): ♀ Douglas-fir Beetles Introduced*	Not Soaked: No ♀ Introductions
a	June 30	45	55	0	0
	Aug 19	170	590	8	0
b	June 30	75	145	0	0
	Aug 19	260	610	2	5
c	June 30	160	205	0	0
	Aug 19	440	500	12	1
d	June 30	55	80	0	0
	Aug 19	170	410	0	3

* Logs with introduced ♀ Douglas-fir beetles received greater numbers of Douglas-fir beetle attacks as shown in Figure 27.

Two of the treatments were soaked logs, two were unsoaked (Table 2). Hylastes, Dryocetes, and Gnathotrichus had attacked all the logs in the former treatments. One of the soaked treatments and one of the unsoaked had been concomitantly treated with introductions of female Douglas-fir beetles. This made these logs attractive to other Douglas-fir beetles (see p. 93). While still great in number, a smaller number of ambrosia beetles entered the wet logs treated with female Douglas-fir beetles.

The ambrosia beetles were determined to be of the two *Gnathotrichus* species, *G. sulcatus* LeConte and *G. retusus* LeConte, after the method of Johnson (58, p. 239) in which an 0.057-inch diameter probe is too large for the beetle's gallery while an 0.052-inch diameter probe should fit. The timing of the attack into the logs also serves for identifying these species from the other principal ambrosia beetle in the region, *Trypodendron lineatum.* The *Gnathotrichus* species are in flight in the summer, whereas the *T. lineatum* population largely confines flight activity to the spring (67, p. 3, 4; 112, p. 92, 94; 120, p. 1345-1347). Species determination of the other two beetles was based upon collected adults and made from Chamberlin (19, p. 114-116, 188-191). They are *Hylastes nigrinus* (Mannerheim), and *Dryocetes septentrionis* Mannerheim. Bright (13, p. 108) holds the latter to be a synonym of *D. autographus* (Ratzeburg).

In summary, logs made somewhat wetter by 16- or 19-day butt soaking elicited an attack response by members of the general *Hylastes, Dryocetes,* and *Gnathotrichus.* The Douglas-fir beetle, on the other hand, showed no discrimination between the soaked logs and their drier controls. Soaked logs tended to initiate sour-phloem.

These results are corroborated by incidental observations from two other studies where windthrown trees developed sour-phloem. Pertinent data are presented in Tables 15 and 19. Table 15 cites Dryocetes as having been associated with the decayed phloem in part of the host material while in Table 19, ambrosia beetles were the associate.

Log Age

Log Aging and Phloem Change

Sour-phloem may develop as a log ages. It has been noted that soaked logs may do this also. The soaked logs in Table 3B, shown to be selectively attacked by ambrosia beetles in Table 5, were observed to have incipient sour-phloem when sampled in July, two months after soaking. Table 4 also reports sour-phloem found in soaked logs of a similar, earlier experiment. In Douglas-fir sour-phloem, the inner bark attains a pronounced reddish coloration, has a soft, stringy consistency, and presents a blend of odors sometimes reminiscent of fruits (apple, strawberry) and at other times suggesting acetaldehyde. It is well seized to the sapwood underneath so that bark removal is difficult.

The term "sour-phloem" is taken from colloquial and other references to "sour-sap" and "sour-cambium". Blackman (12, p.

36) for ponderosa pine in relation to the Black Hills beetle states,

> Frequent light rains accompanied by warm weather at the time when the larvae are in their first and second instars appear to produce a change in the inner bark often spoken of as "souring of the sap" which is fatal to a large percentage of the young larvae.

Keen (75, p. 154), discussing the genus Hylurgops, mentions its species as often being referred to as sour-sap beetles. Chamberlin (19, p. 118) describes the genus as, "most often found in dead trees, especially trees or logs having wet, sour-sap cambium." The fermented phloem discussed by some authors (87, p. 336; 107, p. 697) might be accepted as equivalent to sour-phloem. Vité (136, p. 57) cites a "sour-cambium condition" in his experiment with water injection. Acidity implied by the term sour would be justified in the light of study showing the pH value to be 3.04, whereas healthy tree phloem yielded a pH of 5.45 (115, p. 7).

In addition to the soaked logs, sour-phloem had been seen to appear erratically in the host material of various studies. These were:

Monmouth Peak study

a. tree without roots and without limbs
b. tree without roots and with limbs
c. upper region of the tree with root, without limbs

Laboratory log studies

a. logs with simulated root connections and without limbs, three of the four cases

Woods Creek

a. in July in treatments cut the previous November and December and having neither simulated root connection nor limbs.

b. as above but in treatments having simulated root connections

c. in September localized in the basal area of a section without root connection, with limbs

Oleoresin exudation study of six large diameter windthrown trees (see p. 87)

a. broken out section detached from the crown region, four out of six cases

Laboratory study showed sour-phloem development to be inherent in the phloem. Circular, Petri-dish size phloem samples were placed in Petri-dishes with varying amounts of water (0, 5, 10, 15 ml.) and sealed. Seals were of two types: (1) pressure-sensitive tape was used to join the top dish to the bottom, (2) dishes were set in molten paraffin to effect an air-tight seal.

Both series of dishes were subjected to 500,000 Roentgens in the Oregon State University irradiator, available information in late 1961 being that this was a lethal dose for micro-organisms, a limited number of rare forms excepted.

Within two weeks after preparation (one week after irradiation), there was a noticeable darkening of the phloem samples in the tape-sealed Petri-dishes. This is tentatively identified as oxidative melanization; the tape seals not being as air-tight as the wax seals, some entry of oxygen could have been allowed. To substantiate this, the darkening of the phloem was most intense in the samples to which no water hadbeen added and least intense in the samples having 15 ml. added water, which is thought to have deterred oxygen diffusion.

Four weeks after preparation, in all of the wax seals, but only in these, phloem disintegration equivalent to that of sour-phloem had occurred. The intensity of souring had increased with the amount of water added.

Efforts to identify or further characterize the causal agent of sour-phloem were not successful.

In summary, it may be said that the sour condition is promoted with time by moisture and anaerobic conditions and is not deterred by a radiation dosage of 500,000 Roentgens. The appearance of sour-phloem in the three-foot logs which were butt soaked sustains this view. Time is a factor in two ways. When conditions are suitable for the development of sour-phloem, souring is furthered with time. Secondly, drier phloem not yet sour may, with time, increase in moisture so that souring might be initiated (Figures 22-25).

One Study of Log Age as It Relates to Beetle Attack

Evidence that log age *per se* might not serve to identify the logs most suitable for attack is provided by the Woods Creek experiment. Data of this study have been presented (Figure 26). Subscripts on the labels of the several curves denote different host-material cutting dates. From one to four these were, respectively, November 7, 1959; December 22, 1959; February 13, 1960; and April 2, 1960. All tree sections lay in the same immediate area (Figure 12). There were no beetle attacks in them as of April 2. All sections, however, had received some attack as of April 9. Beetle flight for this could have been allowed on the warm days of April 4, 5, and 6 (Figure 32).

The several curves in Figure 26 summarize the progress of attack. As shown by the curves, Douglas-fir beetle-attack density was independent of the time since cutting, which ranged from nil to five months.

Oleoresin and Beetle Attack

For orientation to the technique, oleoresin-exudation pressure measurements were made in ten standing trees. The values observed (Table 6), do not vary from those shown for the same tree species by other authors (135, p. 23; 115, p. 9).

Of interest, the table records the long-term utilization of these gages installed in Douglas-fir. This contrasts with the experience in pine where solidification of oleoresin may occur within 24 hours, necessitating frequent changing and cleaning of gages for continued pressure determination (136, p. 43). In Douglas-fir,

Table 6. Oleoresin-exudation pressure in pounds per square inch as measured in ten standing Douglas-fir trees at Woods Creek. Sodium silicate was used in the cases noted to fill space when the gages were installed.

			1960		1961				1962		
Tree No.	Filler Used	Initial Pressure	Jul 28	Oct 1	Jan 7	Apr 11	Jul 18	Dec 21	Apr 13	Jul 28	Aug 24
1	yes	10	25	55	91	76	71	90	87	52	52
2	yes	10	46	57	104	87	48				
3	yes	20	13	32	123	66	38	30	26	22	20
4	yes	5	30	44	110	60	40				
5	yes	17	37	26	65	60	67	70	66	44	
6	yes	17	40	22							
7	no	0	1	45	108	55					
8	no	0	8	20	55	57	46	68	74	36	36*
9	no	0	18	9	0						
10	no	0	6	23	45	44	43	55	48	30	30*

*Gages 8 and 10 were full of fluid oleoresin and fell to zero pressure when they were removed.

oleoresin retains its fluid consistency for a much longer period; two of the installed gages in this study yielded pressure readings regarded as valid for two years.

A later investigation used a standing tree which recorded 40 pounds per square inch oleoresin-exudation pressure (Figure 19). A deep girdle into this tree caused the pressure to drop, but a month passed before it reached zero. During this time, 36 female beetles were forced to attack the tree by being confined under screening. In time, nine made known escapes, ten more probably escaped, six were seen to have encountered a flow of resin which came into the entry holes; 11 made an apparently satisfactory entry.

When adapted to exudation pressure determinations in wind-thrown trees, weak values were expected, and 15 pounds per square inch limit gages were used. Table 7 contains the record of six such gages installed and read on trees which were three to four feet in basal diameter.

High-density glucose syrup was used as a hydraulic filler and, when confined, produced an initial reading that in three cases dropped in value before rebuilding to levels regarded as reliable representations of the pressures present. In two cases, trees three and four, the pressure readings were without this equilization to zero. The gage of tree number one apparently recorded no pressure other than that of the confined syrup.

Table 7. Oleoresin exudation pressures read from 15 pounds per square inch limit gages in six large windthrown trees, 1960.

All trees had limited root connection with the soil. Four of the trees, as noted, had retained some of the lower crown foliage. In all cases, the upper crown had been completely detached from the tree.

Tree No.	Relative No. of Limbs Attached To Bole	Pressure in Pounds per Square Inch On:							
		Mar 27	Apr 16	Apr 30	May 6	May 27	June 13	June 27	July 11
1	many	2. 5	0. 8	0. 6	0	0	0	0	0
2	some	2. 5	0	4. 6	8. 5	10. 5	4. 3	2. 8	1. 3
3	none	3. 0	8. 5	15. 0	17. 0	7. 0	2. 0	1. 3	0
4	none	0. 2	0. 5	1. 0	0. 8	0	0	0	0
5	some	1. 2	0	0	1. 5	0	1. 3	1. 8	1. 4
6	some	1. 5	0	0	1. 6	6. 0	11. 0	16. 0	5. 2

It is not intended that the values presented in Table 7 be taken as pressures generally present throughout the windthrown trees. They are simply determinations at particular points on the various boles. The main value of the readings is in the demonstration that, even in badly weakened windthrown host material, there could exist a small but measurable pressure.

The trees were now observed for the number of beetle entries that appeared through the spring. These were examined in the fall to determine what success the entered beetles had experienced. Attack was first noted April 29 and continued to July 11. The counts presented in Table 8A are from a five-foot-long sample area in the basal part of each windthrow adjacent to the point where the pressure gages had been installed. Tree number five, situated in the sun, received no Douglas-fir beetle attacks but, on the other hand, was alone in containing a large number of buprestid attacks.

Of pertinence at this point is the number of abortive attacks wherein the beetle(s) did not get to the cambium or produced only a short gallery from which no larvae developed. Figure 20a shows an entry which reached only to the cambium; it then became filled with oleoresin. The appearance is not unlike the abortive attacks of the Douglas-fir beetle shown by Bedard (10, p. 4, 5) on the one hand, and said to be due to excessive moisture under the bark, and those of _Ips spinidens_ in hemlock demonstrated by Merker

Table 8. Oleoresin interference with the Douglas-fir beetle in six windthrown trees which recorded minor oleoresin exudation pressures. Detached crowns from some of the trees developed sour-phloem and this was associated with poor brood development and survival as reported in Table 19.

Part A: sample area near base of tree, contiguous to placement of gages which recorded the pressures cited in Table 7.

Part B: sample area about 150 feet above base of the tree.

Tree No.	Sq. Ft. in the Sample Area	Attacks		Abortive Attacks		Galleries Showing Oleoresin Interference With Brood	Brood	
		in the Sample Area	per Square Foot	Not Reaching the Cambium	Short Gallery No Larvae Develop		Established per Sq. Ft.	Survival Per-cent
				Part A				
1	43	23	.53	1	3	5	37	17
2	46	18	.39	5	8	5	5	12
3	38	9	.24	5	3	1	trace	0
4	38	18	.47	4	9	5	2	4
5	55	0	-	-	-	-	0	-
6	43	25	.58	0	8	8	47	39
				Part B				
1	31	38	1.21	0	1	0	51	60
2	35	73	2.08	0	12	18	66	15
3	30	43	1.43	0	8	6	40	77
4	30	28	.93	0	1	8	58	36
5	45	57	1.26	0	3	12	63	22
6	35	52	1.48	1	3	0	94	48

(99, p. 178-179), where they are interpreted as being due to resinosis.

Study of a second five-foot sample area near the top of the intact stem showed a much greater number of attacks and, with a consequent wider dissipation of oleoresin flow, a reduction in beetle suffererance to the oleoresin (Table 8b).

A third five-foot sample, taken from a segment broken out of the top of each of the trees, was also examined. It contained no evidence of resinosis but instead, in four out of six cases, showed an entirely different phenomenon, well established sour-phloem, the development of which was discussed above (see p. 77). The sour-phloem affected brood-development; data from the broken-out tops (Table 19) are thus discussed below under Factors Influencing Brood Development and Survival (see p. 124).

The oleoresin study served to emphasize the need for proper technique when determining the frequency of abortive attack. Entries that were clearly evident by means of their pile of reddish frass in the spring, unless marked at that time, could not be observed in a later analysis. Frass darkens and is blown or washed away. By itself, the small beetle entrance hole is not sufficient for finding an aborted entry.

Similarly, it may be noted that if, during the fall analysis, all the attacks which were marked in the spring are easily located, it is likely that there was no great oleoresin interference with beetle attack. Such was true in the Woods Creek host material and the broken off top sections of the windthrown trees in the oleoresin study. Oleoresin exudation pressures expectedly could not be demonstrated at loci in these study materials.

The influence of oleoresin on entry was also seen in other studies where it interfered with experimental design which required beetle introduction into freshly cut logs. The incidents are cited below to afford further comment on the action of oleoresin on beetle entry.

In one of the laboratory log studies, it was desired to get eight evenly spaced attacks into each of eight logs. Some of the beetle pairs refused to enter at the loci where they were first confined. After a day, they were moved a short distance or replaced. At one site, five repetitions were necessary before an apparently normal entry was made. The logs were of four different treatments (see p. 39) but no one type of treatment, as judged by the number of refusals, could be considered more advantageous to the beetles than another. While six or seven of the eight attacks in each log were successful, oleoresin was judged to have interfered with the others noted in Figure 25.

In another case, a study was initiated where 108 beetle pairs of different brood origin were confined with spacing into 18 logs of the same tree. The desire was to observe the establishment and development of brood by the beetle pairs. The entries appeared normal. The logs were thus set aside for 45 days, at which time the bark was removed and it was found that 82 attacks were abortive. The beetles were dead, they did not enter in eight cases and in the rest produced galleries which were less than three inches in length and had no brood. Oleoresin was present in each of the entries albeit in small amounts and, at the time of examination, hardened.

In the course of the field study involving beetle attractant factors (see p. 48), the essential treatment was to have a few females introduced into a log. Various versions of this experiment were performed in Douglas-fir 14 times. In one case, however, the expected attacks by the field population did not follow the introduction of the females. The trial was abandoned ten days after its initiation and bark removed so that the introductions could be examined. A droplet of oleoresin was found in the short (less than one-half inch) entrance gallery of many of the introductions. Out of 15 female beetles introduced, six were dead, two had escaped, and several others had attempted escape as evidenced by excavations on the bark surface under the protective screen. Five of the females made exploratory workings under the bark, apparently to produce a gallery in another direction.

Oleoresin exudation then, even though minimal in short logs, may locally interfere with beetle entry. It is a factor to contend with in experiments requiring forced entry of beetles.

Various Log Treatments Used to Measure Beetle Attraction

Four studies, carried out in the attack season of 1961, designed to provide an insight to beetle orientation mechanisms were inconclusive. A fifth study, however, did produce data of significance, as will be shown shortly.

As followed from the first of April to June 23, 1961, the 36 logs of different color and their controls (Figure 13a) evidenced not a single attack.

The 32 logs of the test for presumed host-material odors (Figure 13b) were largely not invaded. Of the total of 29 beetle entrance galleries, 21 occurred in one control log; two other controls acquired four and one, respectively, while three of the paraffined logs each received one.

In a third test, where the logs received miscellaneous treatments (Figure 13c) one hidden log had eight attacks, another hidden log, four. A control and a cloth-covered log each received one attack.

The fourth test (Figure 13d), (Table 3 A) was similarly inconclusive because too few Douglas-fir beetle attacks were evidenced. The logs had been treated to provide different moisture levels. The limited data that evolved have been commented on above (see p. 69).

Nevertheless beetle attacks were continually noted on a large windthrown tree in the immediate area where all the host material for the above tests was distributed (Figure 14). Further, the host material being used was evidenced to be acceptable; logs from, and stumps of, the trees which had been cut in March for the tests were attacked throughout the spring at the felling site.

Attraction Results from Beetles Entered into a Log

The fifth test, one with logs already containing a few introduced beetles, was first performed with the several other attractance studies of the spring of 1961 (Figure 13). Logs of one March-cut tree were retained in the laboratory until placed in the field June 1, at which time the designated treatments (see *fifth test*, p. 48) were completed.

A June 9 tally of field beetle attacks is included with that of subsequent weeks in Table 9A. These data are also presented graphically as the first set of curves in Figure 29. Among the logs within a treatment, there was variation as to the numbers of beetles making attacks as shown in part B of Table 9.

Table 9. Field beetle attacks on logs having different treatments involving previously introduced beetles. The logs were placed in the field June 1, 1961. This was the initial trial (first replicate) of an experiment subsequently repeated, with three of the treatments, eight times.

Part A. Total number of new attacks made on the four logs of each treatment.

Part B. Total number of beetle attacks on logs of various treatments between June 1 and July 7, after which no more attacks were received.

Part A

Date of Examination For New Attacks	Treatment*				
	I	♀	C	♂	Pr.
June 9	8	80	29	8	2
18		11			1
26	1	1			
July 7			1		

Part B

Treatment*									
I		♀		C		♂		Pr.	
Log No.	Attacks	Log No.	Attacks	Log No.	Attacks	Log No.	Attacks	Log No.	Attacks
5	3	4	49	1	13	2	5	3	1
7	6	8	37	10	9	9	3	6	1
13	0	15	2	14	0	12	0	11	0
17	0	3	4	20	8	18	0	16	1

*Treatments
I : infusion of mascerated beetles introduced six times into each log
♀ : six female beetles introduced into each log
C : control
♂ : six male beetles introduced into each log
Pr: six pairs of beetles introduced into each log.

Douglas-fir Used to Demonstrate a Female Beetle Attractance Factor

As described under Materials and Methods, the results from this initial trial commended that the experiment be replicated. Two treatments thought not necessary were eliminated (see p. 51). The successive trials were conducted as long as it was evident that beetles were attracted to newly prepared treatments through June and July to mid-August.

Data from nine replications are presented graphically in Figures 28 and 29. The former, analagous to a series of snapshots, presents the number of attacks received in each treatment at the end of a period of time (one week) following initiation of the trial. The latter, a moving picture, is a more complete presentation. It shows the changes as they occurred with the passage of time in each trial.

Both Figures 28 and 29 demonstrate that treatments containing a few introduced females are preferentially attacked when compared to treatments where males were introduced in addition to females and to treatments having no introductions. Further, of the latter two treatments it may be said that logs containing paired beetles were not more attractive than logs containing no beetles. Since each new entry is initiated by a female, it follows that the attractant factor produced by unmated females is for other similarly unmated members of the same sex. There is, however, attraction also of

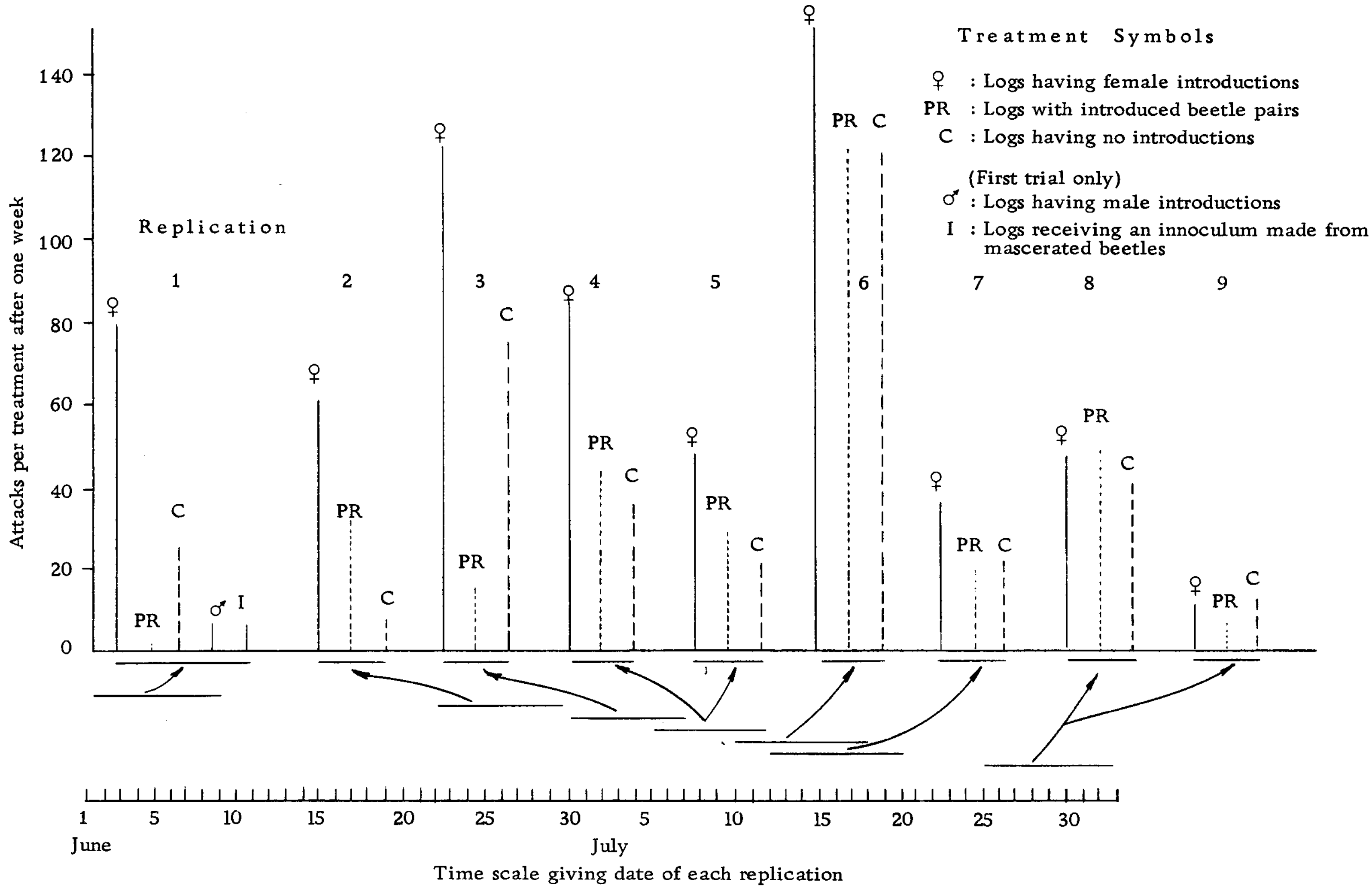
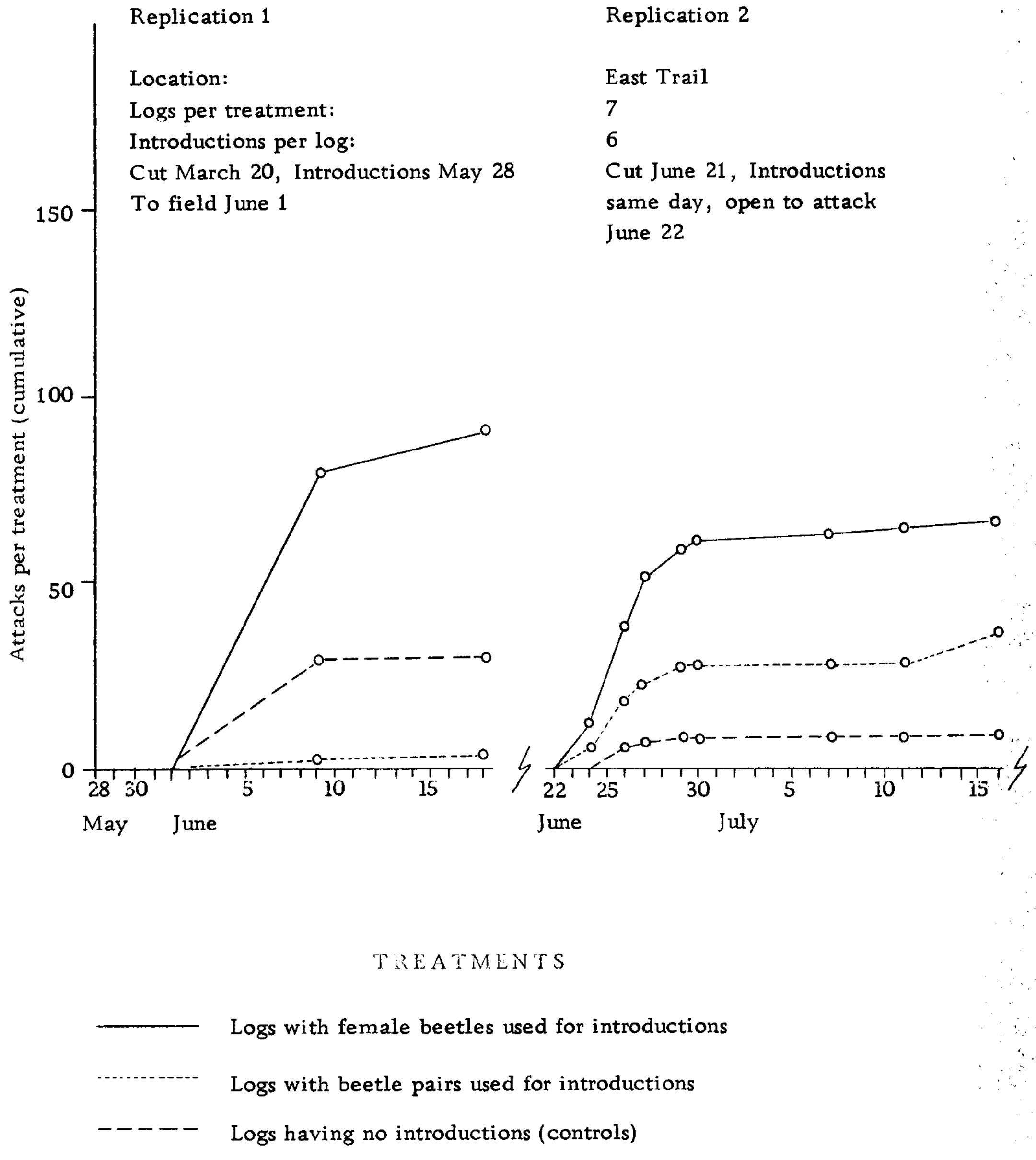


Figure 28. Nine replications of an experiment showing attractance of logs containing unmated female beetles. Counts shown are those existing in the logs of a trial one week after its initiation.



Replication 1
Location:
Logs per treatment:
Introductions per log:
Cut March 20, Introductions May 28
To field June 1
Replication 2
East Trail
7
6
Cut June 21, Introductions
same day, open to attack
June 22
Attacks per treatment (cumulative)
150
100
50
0
28
30
5
10
15
May
June
22
25
30
5
10
15
June
July
TREATMENTS
Logs with female beetles used for introductions
Logs with beetle pairs used for introductions
Logs having no introductions (controls)

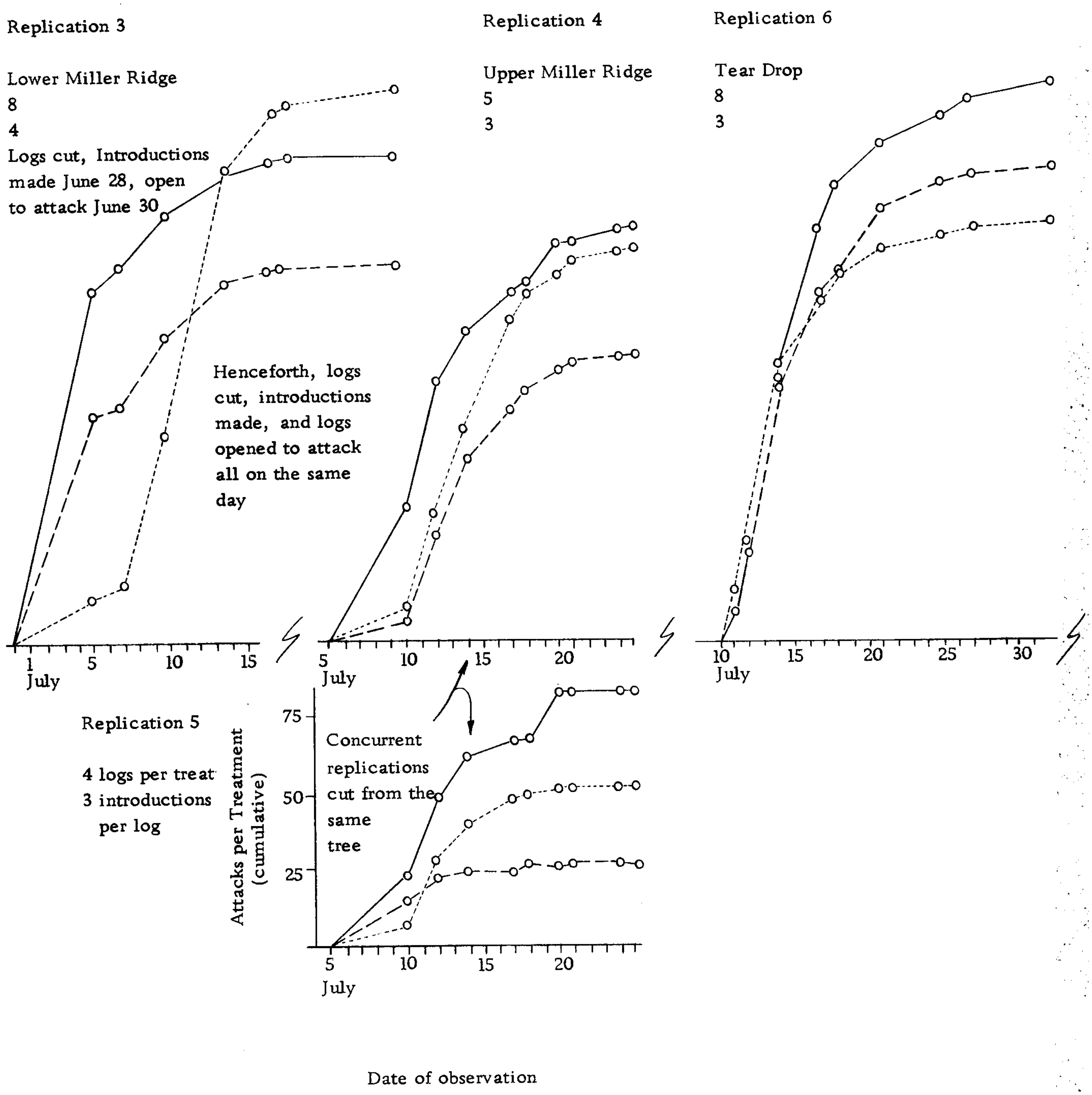
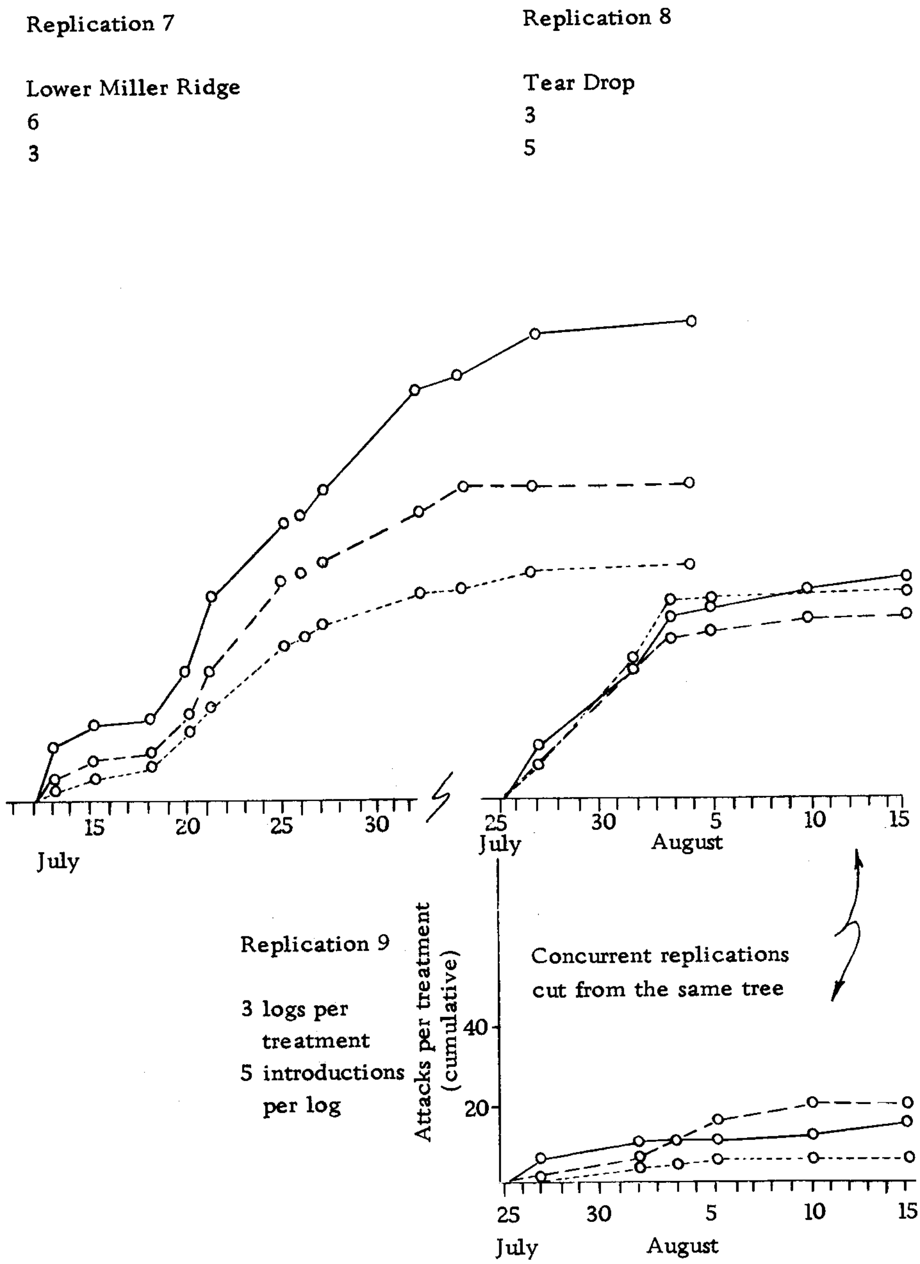


Figure 29. Running record of the field attacks in the nine replications of an experiment showing attractance of logs containing unmated female beetles.



Replication 7
Lower Miller Ridge
6
3
Replication 8
Tear Drop
3
5
15
20
25
30
July
25
30
5
10
15
July
August
Replication 9
3 logs per treatment
5 introductions per log
Attacks per treatment (cumulative)
40
20
Concurrent replications cut from the same tree
25
30
5
10
15
July
August

males; members of this sex could sometimes be seen on the screens directly over the hole which contained an introduced unmated female (Figure 2).

Data from the experiments may be subjected to statistical analysis. It is redundant to do so, however, in the face of graphical presentation of significance. Further, the kinetic properties of the data, demonstrated graphically in Figure 29, would not be so evident when statistical analysis was used. The latter, of necessity, employs data from a fixed moment of time.

A kinetic picture is of value because it presents a concept of interaction between a log and female beetles which, on the one hand, may be entered into it or, on the other hand, may still be in flight.

Logs initially with female beetles attracted more of these and thus tended always to hold the attractive lead. Females in flight, however, could come to the logs of the other treatments and induce the female centered attractance in them. Other females would follow. Generally, the curves representing attacks received run parallel to one another. The third replicate, however, shows a case where there is sharp rise in attractiveness of the logs of one treatment indicating a possible stronger attractive power lodged with some of the females which arrived from the field population. Figure 29 also shows a delay in expression of preference which sometimes occurs; this is the case in the sixth, eighth, and ninth replications. In the latter two instances one may speculate that this may be due to the presence in the field population of greater numbers of beetles making their second flight (see p.9). These may not as actively respond to the female beetle attractant factor and/or as actively produce it in the log themselves.

The graphical presentations use overall attack values as yielded directly by each of the treatments in all of the replicates. In Table 10, on the other hand, conversion was made to attacks per square foot, a unit common in bark beetle investigations. It is useful, in this case, to show the resultant final attack densities for comparison with those of other reports (see p. 10) and conclude that this level of attack is moderate. For other purposes, such conversion is not indicated. Attraction of the field attacking beetles is largely independent of the size of the tree; it relates mainly to the influence of entered, unmated female beetles. The experiments demonstrated in this study show that females could initiate response when their number was as few as 12 and not more than 42 per treatment in one or another of the replications (Figure 29, especially replications two and five).

Notwithstanding the moderate density of attack (Table 10) and the continuing presence of beetles in the field, there is seen to be a failure of beetles to make new entries after a time interval of two to three weeks following initiation of field attack in a trial (Figure

Table 10. Final attack densities in the treatments of the several replications. Female beetle attractant factor experiment, 1961.

Replicate No.	Total Square Feet per Treatment (approximate)	Number of Attacks per Square Foot on Logs Treated by: Introducing Female Beetles	Introducing Pairs of Beetles	Introducing No Beetles (Controls)
1	39	2.4	0.05	0.7
2	55	1.1	0.7	0.1
3	88	1.8	2.1	1.4
4	57	2.5	2.3	1.6
5	35	2.1	1.7	0.7
6	60	3.1	2.3	2.7
7	58	2.1	1.0	1.4
8	40	1.4	1.4	1.1
9	35	0.4	0.2	0.6

27 and 29).

Attractant Tests with Host Material Other than Douglas-fir

Knowledge of the limited range of the Douglas-fir beetle has been summarized by Johnson (66, p. 3); western hemlock, *Tsuga heterophylla* (Rafn.) Sarg., is included as an incidental species in which attacks and even brood development have been reported. Chamberlin (19, p. 66) mentions reports of *Abies* having been attacked by the beetle. Pine, to the author's knowledge, has not been described as associated with this insect.

Hemlock

Once in 1961 and again in 1962, trials were set up to determine whether western hemlock could be made attractive to the Douglas-fir beetle by the introduction of female beetles into the bark. The 1962 test yielded no results but the earlier one did; the evidence is thus considered to have given an affirmative answer to this line of investigation.

The trial used a 125-year-old, 17-inch basal diameter tree that was cut into 20 logs. Ten of these were controls; six females were introduced into each of the other ten. The logs of the two treatments were arranged as in Figure 17. The nearest Douglas-fir host material undergoing attack at the same time was 1,000 feet away, over a 150-foot ridge. It is eliminated as a factor influencing this experiment.

From July 10 to August 10, seventeen Douglas-fir beetle attacks were observed in the female introduction logs as shown in Table 11 A.

In the fall and winter, the bark from these logs was removed for analysis. It was then seen that there had been four additional attacks.

The characteristics of the frass pushed from the entrance, the boring and direction of the gallery, the particular pattern of the branching larval galleries, and the recovery of entered adults verified that the total of 21 attacks made in the hemlock logs having introduced females was made by Douglas-fir beetles. No Douglas-fir activity was at any time seen in the control treatment placed 20 feet away.

Grand Fir

Three trials using host material of grand fir, *Abies grandis* Lind., similar to the two-treatment hemlock experiment were initiated. Tests in 1961, prepared in July and early August, were of no consequence; Douglas-fir beetles did not come to the logs. The 1962 experiment, using a 170-year-old tree of 15-inch basal diameter, provided one noteworthy observation. Nine short logs from

Table 11. Field attacks of the Douglas-fir beetle into unnatural host material which had and had not received introductions of female beetles of the same species

Part A. Western hemlock. 10 three-foot logs per treatment, tree cut and prepared July 6, 1961. Treatments laid out as in Figure 17.

Part B. Ponderosa pine, 4 two-and-one-half-foot logs per treatment. Tree cut May 18, treatments accomplished June 1, 1962.

		Part A Field Attacks Into	
Date of Observation		Logs Which Each Had 6 Female Douglas-fir Beetle Introductions	Logs Which Had No Beetle Introductions
July	10	1	0
	11	2	0
	12	4	0
	14	5	0
	17	0	0
	20	0	0
	27	2	0
August	1	1	0
	3	0	0
	10	2	0
attacks found in later study		4	0
total		21	0

		Part B Field Attacks Into	
Date of Observation		Logs Which Each Had 8 Female Douglas-fir Beetle Introductions	Logs Which Had No Beetle Introductions
June	4	8	0
	6	1	1
	8	4	6
	10	24	18
	14	30	25
	23	21	22
	30	10	8
total		98	80

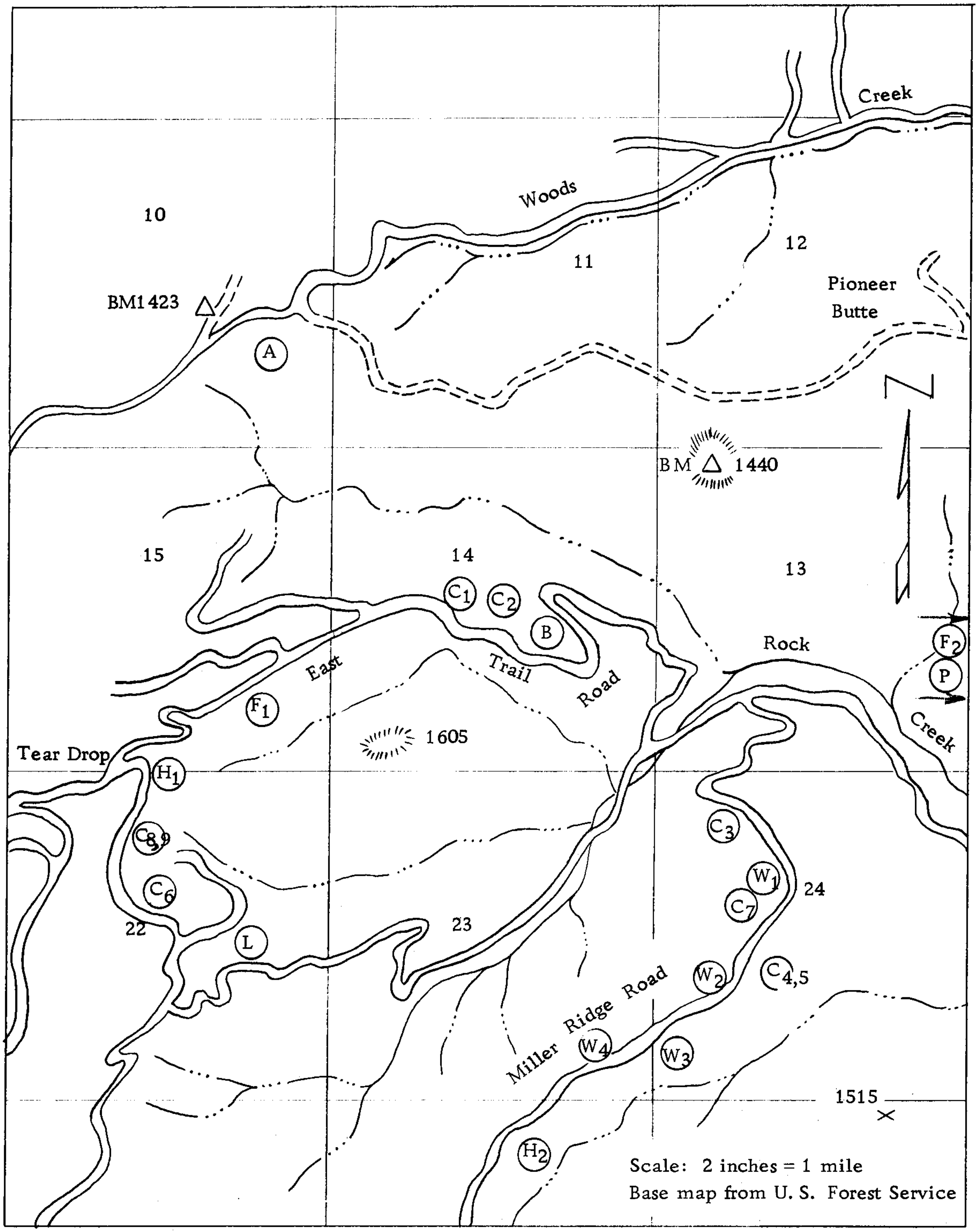


Figure 30. The east slope area on Marys Peak showing locations used for many of the experiments reported in the thesis. A: Woods Creek 1959-60. B: Attractance to variously treated logs, 1961. C_1 - C_9 : Replicates substantiating the female beetle attractant factor, 1961. H, F, P : Tests for female beetle attractant factor when the host material was hemlock, fir, or pine, 1961-62. L : Oleoresin pressure and effects in windthrown trees, 1960. W_1 - W_4 : Tests for attraction of soaked and unsoaked logs, 1962.

the tree were delegated to each of two treatments. Eight females were introduced into each of the logs of one treatment; the other treatment was the control and did not have these introductions.

The important observation was on the day of treatment. Preparation of the logs, including the introductions, had been completed by 10 a.m. At 4:30 p.m. on the same day, a return was made to the experiment. At this time, four male Douglas-fir beetles were seen in place on the screens over the galleries of the introduced females. The logs of the experiment were examined many times through the summer; no other evidence of attraction of Douglas-fir beetles was noted.

Ponderosa Pine

A two-treatment test with eight, two-and-a-half-foot logs of a 20-year-old plantation-grown ponderosa pine, Pinus ponderosa Lawson, was established in the spring of 1962. Four logs were each provided with eight introduced females protected under screen stapled in place. Treatment was completed at 11:30 a.m. As with the one grand fir experiment, the logs were revisited for observation at 4:15 p.m. the same day. At this time, two male Douglas-fir beetles were seen on the screens.

Four logs lacking introduced female beetles were placed 15 feet from the logs with introductions. No other host material undergoing attack by the Douglas-fir beetle was in the immediate vicinity. Field attacks by Douglas-fir beetles into the study logs are recorded in Table 11B.

Use of Field Olfactometer

Two days' use was made of the olfactometric apparatus in which a log containing 20 female entries was held within a metal box and hence hidden from view (Figure 21c). Air blown through the box led to a second box and was released there. The apparatus elicited some response from the field population of beetles as follows:

June 17, 1961: through eight hours, 16 Douglas-fir beetles were taken as they arrived at the apparatus. Half were males. Many beetles did not go to the box through which the air was discharged but came instead to the end cover joint of the box containing the log and traveled along it as though perceiving an odor and searching for the release point. Throughout the day, temperatures ranged between 80 and 92 degrees Fahrenheit.

June 18, 1961: the above apparatus was set out 15 feet from identical equipment containing a control log. Through eight hours, during which temperatures ranged from 60 to 70 degrees Fahrenheit, two males and two females came to the former, while no beetles came to the control.

Continued Study of Experimental Lines Earlier Judged to be Inconclusive

Establishment of the importance of the female beetle attractant factor in the orientation of attack prompted a renewal of study of three earlier investigations which had been inconclusive. Results which both confirm the effectiveness of the female beetle attractant factor and help explain the inconclusiveness of the earlier studies are given below.

Renewed Experimentation with the Colored Logs

As followed from April 29 to June 23, 1961, the 36 logs of different color and their controls (Figure 13d) received not a single attack. Different log layouts were used, including one which was analagous to that of the female beetle attractant factor trial; the logs of a treatment were placed together, treatments were alongside one another. In mid-June phloem appearance was fresh, and moisture values were in the normal range.

On June 23, five females were introduced into one of the logs of each color. Through the next 14 days the logs received a total of 21 attacks, as listed in Table 12.

The net effect was to demonstrate that, on satisfaction of one condition, the introduction of a few female Douglas-fir beetles, logs which had been by-passed by the field beetle population would then be selected for attack. It may be expected that, normally the study logs would randomly, or otherwise, come to receive a few initial attacks; these would elicit further response through the mechanism of the female beetle attractant factor. That these initial attacks were not received is explained by the presence of a large windthrown tree undergoing attack in the immediate vicinity (Figure 14). Its size was such that it may be expected to have had a continuing number of newly arrived and still single females. This made it the attraction center at the expense of the study logs. When one or another of the latter, however, was invaded by female beetles, either naturally or through introduction, limited to moderate attack followed.

Table 12. Field attacks observed on the colored logs. These had been further prepared by introducing five female Douglas-fir beetles into one of the four logs of each color on June 23.

Log	Day of Observation			
	June 26	June 27	June 29	July 7
$white_1$	3		1	
$white_3$	1			
$green_1$	1	1	3	5
red_3			1	
red_4	1			
$blue_1$			1	
$control_3$		1		
$control_2$		1		
unpainted $control_2$			1	

Total attacks from the field population : 21

Re-evaluation of the Woods Creek Data

A first emergence female entered into a log is unmated for at least a short while as she initiates gallery construction. During this period, the female beetle attractant factor is produced; this contributes to the attractiveness of the log. Attack thus follows attack. The more females invading a log, the more attractive it should become. Attacks received by a log during the first few days influence the pattern of beetle response to the log for a time thereafter.

At each inspection, usually spaced a week apart, the 16 treatments of host material at Woods Creek had been observed to have received various numbers of attacks (Figure 26). This attack pattern could not be shown to be related either to phloem moisture or to log age.

In renewed evaluation, the attack data for a given inspection was compared with that of the next succeeding inspection to appraise to what extent current attacks were correlated with and presumably had influence on later attacks.

This evaluation proceeded as follows: In the first inspection of April 9, 400 attacks were counted in the 16 treatments of host material. The bottom section of treatment A_1 had received 24 attacks or 6.0 percent of the total. No new attacks in any of the treatments were evident on April 16 or 23; the weather at this time was too cool to allow beetle flight (Figure 32). On April 29, a total of 205 new attacks was counted. Ten attacks, or 4.9 percent of the total, were into the bottom section of treatment A_1. These data are tabulated in Table 13 together with similarly derived values for all the inspections and treatments.

Table 14 could now be constructed wherein a section's percent of attack for one inspection was tabulated as a value under the section's percent of attack in the previous inspection; i.e., the value 4.9 was tabulated as a function under the value 6.0. In Table 14, the total number of values representing subsequent percentages is 144. This is accountable to 24 sections which were involved in six inspections yielding noteworthy attack values after April 9.

The data from Table 14 may be plotted to yield the scatter diagram shown in Figure 31. An abscissa, x, represents the percentage of attack received in an inspection whereas an ordinate, y, represents the percentage of attack received by the same section in the next subsequent inspection.

The data may also be used in statistical analysis. When this is done, there is confirmation that there are significant differences as to the value of y for the various values of x (one percent level). A test to determine if there is a linear relationship of increasing values of y for increasing values of x fails, however, as derivation from linearity is found to be significant (one percent level).

Table 13. New attacks in the Woods Creek study material as inspected on the dates shown. Attacks received by a log section are computed as a percentage of the total number of attacks noted in that inspection. At: attacks, %: percentage.

Treatment #		Inspection to count new attacks on													
		April 9		April 29		May 6 & 14		May 27		June 3		June 11		June 20-21	
		At	%	At	%	At	%	At	%	At	%	At	%	At	%
A_1	bot	24	6.0	10	4.9	40	8.8	11	5.7	57	10.1	28	7.7	6	3.2
	top	59	14.7	14	6.8	50	11.0	33	17.4	46	8.2	17	4.7	7	3.8
A_2	bot	23	5.7	14	6.8	31	6.8	11	5.7	30	5.3	12	3.3	8	4.3
	top	33	8.2	14	6.8	23	5.1	9	4.7	19	3.4	1	.3	4	2.2
A_3	bot	11	2.2	3	1.5	18	4.0	8	4.2	32	5.7	26	7.1	25	13.5
	top	6	1.5	4	2.0	27	6.0	15	7.9	28	5.0	19	5.2	12	6.5
A_4	bot	5	1.2	2	1.0	13	2.9	2	1.0	21	3.7	23	6.3	13	7.0
	top	7	1.7	5	2.5	15	3.3	3	1.6	32	5.7	12	3.3	6	3.2
D_1	bot	8	2.0	7	3.4	21	4.6	8	4.2	16	2.8	18	4.9	3	1.6
	top	11	2.7	4	2.0	9	2.0	4	2.1	19	3.4	17	4.6	2	1.1
D_2	bot	19	4.7	12	5.9	20	4.4	11	5.7	31	5.5	18	4.9	3	1.6
	top	28	7.0	20	9.8	24	5.3	14	7.3	22	3.9	13	3.5	11	6.0
D_3	bot	4	1.0	3	1.5	7	1.5	7	3.7	19	3.4	15	4.1	5	2.7
	top	11	2.7	2	1.0	13	2.9	2	1.0	16	2.8	9	2.4	4	2.2
D_4	bot	19	4.7	5	2.5	16	3.5	4	2.1	33	5.8	25	6.8	19	10.3
	top	30	7.5	11	5.4	25	5.5	11	5.7	20	3.5	29	7.9	12	6.5
C_1		13	3.2	21	10.2	7	1.5	5	2.6	1	..2	0	0	1	.5
C_2		33	8.2	5	2.5	17	3.7	15	7.9	28	5.0	19	5.2	6	3.2
C_3		20	5.0	6	2.9	16	3.5	9	4.7	18	3.2	27	7.4	16	8.7
C_4		4	1.0	6	2.9	11	2.4	2	1.0	16	2.8	9	2.5	4	2.2
B_1		3	.7	2	1.0	9	2.0	3	1.6	18	3.2	9	2.4	3	1.6
B_2		6	1.5	3	1.5	3	.7	1	.5	3	.5	2	.5	0	0
B_3		5	1.2	16	7.8	10	2.2	1	.5	14	2.5	10	2.7	5	2.7
B_4		18	4.5	16	7.8	28	6.2	2	1.0	25	4.2	8	2.2	10	5.4
Total		400		205		453		191		564		366		185	

Inspections were made on April 16 and 23, but no new attacks were observed on these dates. Because only 30 attacks were observed on May 6, these are grouped with those of the May 14 inspection.

Treatment designations for the code used are given in Figure 26, which is a graphical presentation of the progress of attack into the various sections of the 16 treatments.

Table 14. Percentages of new attack received by a log section in one inspection with similar percentages determined from the next subsequent inspection as functions of these.

	A section on one inspection receiving this percentage of the new attack											
	0	0.2	0.3	0.5	0.7	1.0	1.2	1.5	1.6	1.7	2.0	2.1
in the next subsequent inspection received this percentage of the new attack	.5	0	2.2	0.5	1.0	2.9	1.0	2.0	3.2	2.5	3.4	3.4
				0.5	0.5	1.5	7.8	1.5	5.7		6.0	5.8
				0	2.5	2.9		4.0			2.0	
						2.9		1.5			2.1	
						2.0		0.7			1.6	
						2.8		2.6				
						2.8		3.7				
						4.2						
						3.7						
	2.2	2.4	2.5	2.6	2.7	2.8	2.9	3.2	3.3	3.4	3.5	3.7
	1.5	1.0	3.3	0.2	2.0	2.5	3.5	10.2	1.6	4.6	4.7	7.9
	0.5	2.2	3.7		1.0	4.9	2.4	7.4	4.3	0.3	2.1	3.4
	5.4	1.6	3.5		2.7	2.4	1.0	2.4	3.2	4.6	7.9	6.3
			2.7				1.0			4.1	6.0	
			2.2									
	3.9	4.0	4.1	4.2	4.4	4.5	4.6	4.7	4.9	5.0	5.1	5.2
	3.5	4.2	2.7	5.7	5.7	7.8	4.2	5.9	8.8	2.9	4.7	6.5
				2.8			1.1	2.5	1.6	5.2		3.2
				2.2				3.4	1.6	5.2		
								3.2				
								3.8				
	5.3	5.4	5.5	5.7	5.8	5.9	6.0	6.2	6.3	6.8	7.0	7.1
	7.3	5.5	5.7	6.8	6.8	4.4	4.9	1.0	7.0	11.0	9.8	13.5
	3.3		4.9	10.1			7.9			6.8		
				5.3						5.1		
				5.5						5.7		
				3.5						10.3		
				7.1								
				3.3								
	7.3	7.4	7.5	7.7	7.8	7.9	8.2	8.8	9.8	10.2	11.0	
	3.9	8.7	5.4	3.2	2.2	5.0	6.8	5.7	5.3	1.5	17.4	
					6.2	6.5	2.5			7.7		
						5.0	4.7					
	14.7	17.4										
	6.8	8.2										

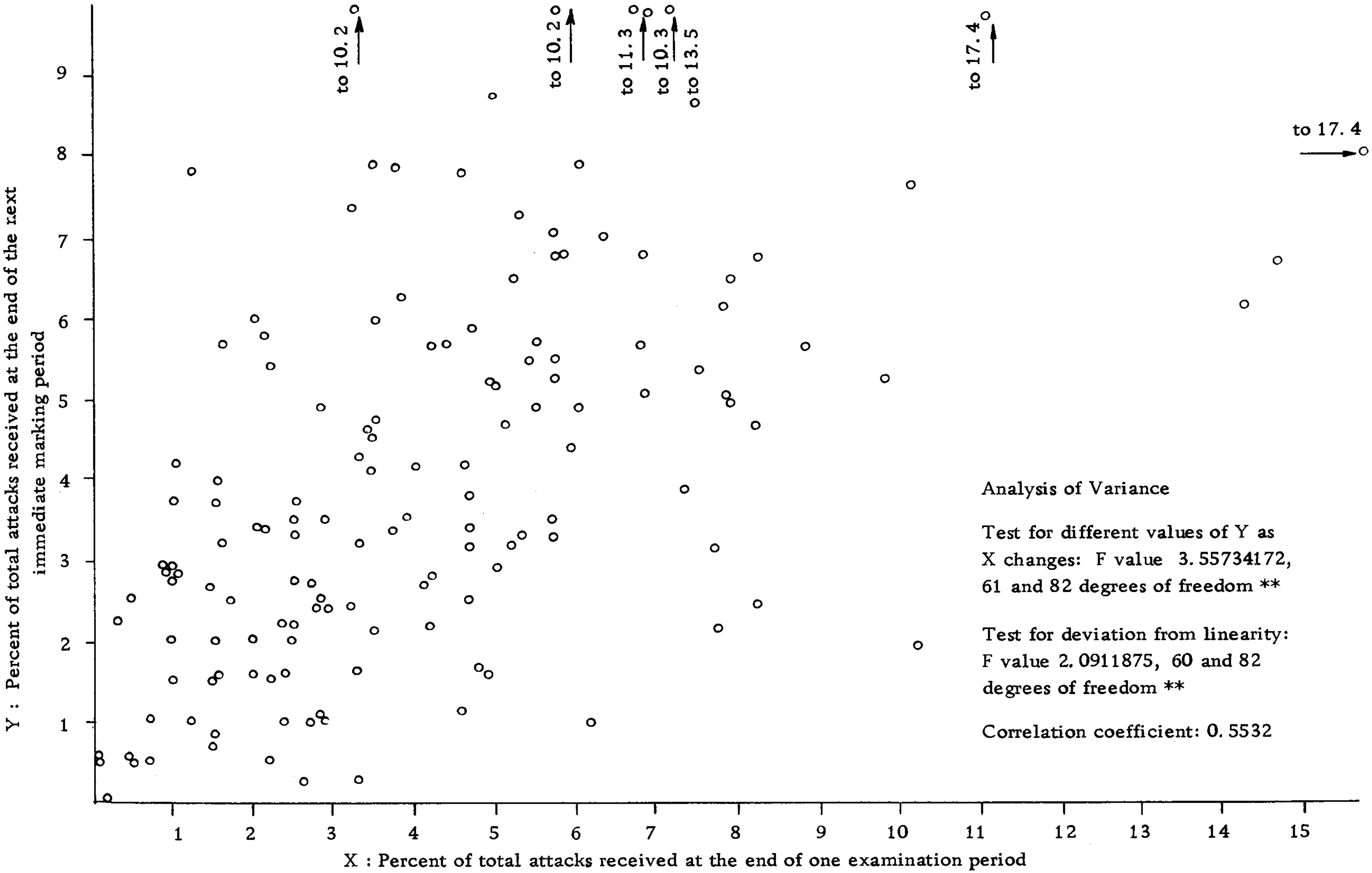


Figure 31. Scatter diagram, renewed examination of the attack data from the 1960 Woods Creek study. The relationship between current and previous attack is presented.

The net effect of the evaluation is to make the Woods Creek attack pattern tenable when explained in terms of operation of the female beetle attractant factor.

Log Moisture Considered in Conjunction with the Female Beetle Attractant Factor

This study, conducted in the attack season of 1962, renewed the effort to determine the importance of log moisture on beetle attack. Knowing that entered females induce attack, both wet and drier logs, each with and without females, were laid out for attack. The record of attack and its lack of significance as between wet logs and drier ones, whether or not the female factor was present in the treatment at the outset, have been described (see p. 72).

Air Temperature and Beetle Attack

Since it is a poikilothermic animal, the Douglas fir beetle's physiological activity is temperature dependent. Rudinsky and Vité (120, p. 262) and Atkins (5, p. 286) report the beetle's flight activity as determined in the laboratory. An air temperature of 20° C. (68° F.) is required for beetles at rest to initiate flight. Both investigations, however, emphasized the importance of solar radiation and the warmth that may be provided by absorption to a beetle in cooler air situations, flight thus being allowed. To facilitate this, emergence holes may be constructed at moderate temperatures. Reid (114, vol. 95, p. 230) has observed such a phenomenon with the mountain pine beetle, *Dendroctonus monticolae* Hopkins.

Once flight is initiated, it might possibly be continued at temperatures as low as 11.5° C. (52° F) (119, p. 263).

Figure 32 charts attacks received by the Woods Creek host material in the advancing spring of 1960. The daily maximum temperatures as determined by a Foxboro hygrothermograph are also recorded.

No attacks were received prior to April 2, but on the 9th of April 400 entries were marked. The temperature maximum through the 7-day time interval was 62° F. (17° C.). From May 14 to 27, the maximum temperature was 56° F. (13° C.); 205 entries were noted. Better activity was seen when temperatures approaching 67° F. (19° C.) were recorded; best activity was shown at temperatures of 76° to 80° F. (24° - 27° C.).

As set forth in Figure 32, after June 3, despite continuously favorable temperatures, beetle attack numbers into the logs decreased. Their number no longer was related to the relative warmth of the air. Two explanations are possible. The number of beetles in flight may have greatly decreased, their emergence from the brood logs being nearly complete. Attractance of all the host material may have decreased, perhaps because of a repellant factor.

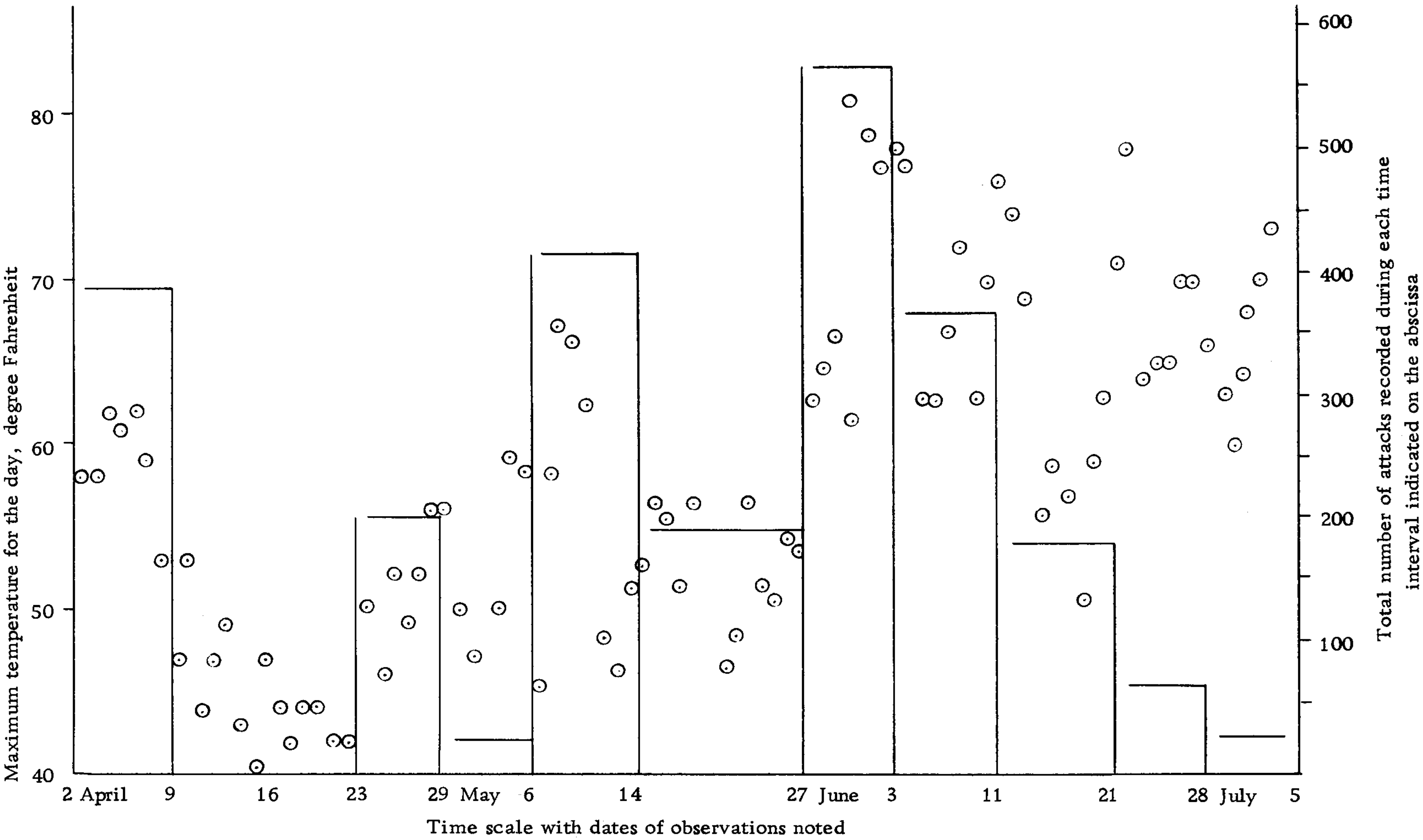


Figure 32. Relationship between air temperature and flight implied from the Douglas-fir beetle attacks recorded at Woods Creek in the advancing spring, 1960.

Substantiation of the possibility of attack at more moderate temperature has recently been reported by McMullen and Atkins (95, p. 1310-1311) in one case and by Rudinsky (117, p. 30) in another.

Factors Influencing Brood Development and Survival

As the experimentation supporting this thesis was largely conducted in the field and since brood development occurs over a period of time, there was an interaction between factors affecting the brood that makes assessment of an individual influence difficult. Results often came to be expressed as observations rather than to be demonstrated numerically.

Phloem Moisture

Variable moisture values produced in different log preparations have been cited (Table 3, Figures 22-25). Assessment of brood success at the various moisture levels in the field was determined from fall analysis. In the laboratory, essentially the same procedure was used; counts were made of brood size after individuals were largely in the adult stage.

Field Studies

In the Monmouth Peak and Woods Creek studies, counts of survivors considered the numbers of larvae, pupae, and adults. Among the various treatments, a larger or smaller number of one stage was not apparent. There was not seen, for instance, a tendency for logs of a given moisture level to have a greater or lesser percentage of larvae and pupae as compared to adults. The case in which sour-phloem might develop in wet host material is an exception to this generalization (see p. 124).

Differences in development rates in the different treatments of host material studied are thus deemed to be narrow. It has already been mentioned that in pilot studies of excised larvae, no difference in rate were discernible. More detailed study using the excision method was precluded for the reason that this would have resulted in extreme alteration of the study material.

Tables 15 and 17 summarize data from the Monmouth Peak and Woods Creek studies. Listed are attacks and initial brood on a unit-area basis. Survival including larvae, pupae, and adults has been computed similarly by unit area and also as a percent of initial brood. Predaceous larvae of *Medetera* and *Enoclerus* per unit area are tabulated as are *Coeloides* parisitized beetle larvae. In Table 15 note is made of the observation of scolytid associates of the genus *Dryocetes* and whether sour-phloem was present. Table 17 lists ambrosia beetle entries per unit area; *Dryocetes* were not evident in this study while sour-phloem was available for only

Table 15. Summary of fall analysis of brood samples obtained from near the butt and top regions of the four trees in the Monmouth Peak study

Location of Sample	Attacks per Squ. Ft. In the Sample Area	No. of First Instar Larvae per Sq. Ft.	No. of Brood Surviving to Fall per Sq. Ft.	Percent Survival	*Medetera* per Sq. Ft. of Sample Area	*Enoclerus* per Sq. Ft. of Sample Area	*Coeloides* per Sq. Ft. of Sample Area	*Dryocetes* Present In Sample Area?	No. of Sq. Ft. In Sample Area	Sour-Phloem Present?
Tree 1, having root connection but without limbs										
butt	2.4	124	28.0	22.5	6.7	1.1	0	0	20	
top	1.6	49	0.4	0.9	1.9	0.7	0	yes	16.6	yes
Tree 2, having neither root connection nor limbs										
butt	1.5	30	3.8	12.4	3.5	0.5	0	many	14.6	yes
top	0.8	28	2.9	10.1	0.7	0.2	0	many	11.4	yes
Tree 3, having root connection and limbs										
butt	1.4*	14	11.0	76.2	0.05	0.05	0	0	18.9	
top	2.1	73	38.0	52.0	0.25	0.2	0.2	0	16.3	
Tree 4, without root connection but with limbs										
butt	0.9	38	1.9	5.0	1.3	0.4	0	yes	15.6	yes
top	0.3	15	2.0	12.6	0.3	0.2	0	many	12.3	yes

* 1.4 attacks per square foot occured but because of what appeared to be interference caused by oleoresin, only 0.5 attacks per square foot were successful.

Table 16. An index to survival of brood when allowance is made for the estimated loss to predation. Monmouth Peak study.

Tree and Section	Number of Brood Surviving to Fall per Square Foot	Percent Survival	Estimated Loss to Predators*	Survival Index**	Phloem Moisture Determination (percent of dry weight) 2 Months After the Onset of Attack (July 10)
	Tree 1, having root connection but without limbs.				
butt	28.0	22.5	29.9	47	136
top	0.4	0.9	14.3	30	220
	Tree 2, having neither root connection nor limbs				
butt	3.8	12.4	14.5	61	168
top	2.9	10.1	4.4	26	226
	Tree 3, having root connection and limbs				
butt	11.0	76.2	0.85	85	85
top	38.0	52.0	3.7	57	108
	Tree 4, without root connection but with limbs				
butt	1.9	5.0	8.6	27	141
top	2.0	12.6	3.6	37	184

*Estimated Loss to Predator = $L_e = 2M + 15E + 1C$

M = number of Medetera per square foot of sample area.
E = number of Enoclerus per square foot of sample area.
C = number of Coeloides per square foot of sample area.

** Survival Index $= \frac{L_e + N_f}{N_1}$

L_e = estimated loss to predators.
N_f = number of brood surviving to fall per square foot.
N_1 = number of first instar larvae per square foot.

Table 17. Summary of the fall analysis of brood samples obtained from the 16 treatments of the Woods Creek Study. Circular bark samples five feet long were examined.

Age of Section (see note below)	Location of Sample	Attacks per Square Foot Over the Whole Section	Attacks per Square Foot in the Sample Area	Number of First Instar Larvae per Square Foot	Number of Brood Surviving to Fall per Square Foot	Percent Survival	*Medetera* per Square Foot of Sample Area	*Enoclerus* per Square Foot of Sample Area	*Coeloides* per Square Foot of Sample Area	Ambrosia Beetle Entries per Square Foot of Sample Area
			A - Treatments with simulated root connection, no crown							
1	base	1.82	1.45	98	54	55	6.0	0.1	0.1	8.4
	top	2.16	1.63	76	36	47	12.9	0.4	3.6	11.6
2	base	0.96	1.09	61	23	38	2.8	1.7	0	14.0
	top	1.04	0.93	70	16	23	3.8	0.4	0	15.0
3	base	1.73	1.55	95	26	27	3.5	1.1	1.5	5.0
	top	1.75	1.54	94	18	19	6.7	0.5	2.2	5.1
4	base	1.02	1.06	100	29	29	3.0	0.6	1.6	0.2
	top	0.95	1.15	99	12	12	6.3	0.9	5.1	0.8
			D - Treatments without root, without crown							
1	base	1.21	0.65	48	25	51	1.2	0.5	0	8.4
	top	1.23	1.13	86	36	43	6.3	0.2	0.4	3.7
2	base	1.20	1.04	86	25	29	2.0	1.6	0.2	10.0
	top	1.49	1.48	85	15	18	3.5	0.4	1.0	2.6
3	base	0.92	0.71	45	29	64	5.7	1.1	0.5	3.1
	top	0.90	0.70	66	11	16	2.2	0.4	7.2	5.9
4	base	1.44	1.22	97	46	47	4.6	0.9	0.2	2.7
	top	2.07	2.95	185	22	13	7.3	0.9	1.1	1.0
			B - Treatments with simulated root connection and with crown							
1	base	0.87	1.0	68	6	11	4.3	0.2	4.2	4.0
2	base	0.31	0.47	36	18	36	2.3	0.7	0.7	2.9
3	base	0.95	0.6	44	15	33	2.2	0.7	2.4	1.9
4	base	1.86	1.66	153	28	18	5.1	0.7	4.1	0.8
			C - Treatments without root but with crown							
1	base	0.80	0.76	50	7	15	2.3	1.0	6.6	2.8
2	base	1.50	1.45	100	21	21	3.4	1.5	5.1	2.5
3	base	2.48	2.92	132	13	10	2.1	0.2	0.7	0
4	base	1.14	0.95	95	10	10	4.2	1.0	1.5	1.5

1 - tree felled Nov. 7, 1959.
2 - tree felled Dec. 22, 1959.
3 - tree felled Feb. 13, 1960.
4 - tree felled Apr. 2, 1960.

Table 18. An index to survival of brood when allowance is made for the estimated loss to predation, Woods Creek study.

Age of Section (see note below), Location of Sample		Number of Brood Surviving to Fall per Square Foot	Percent Survival	Estimated Loss to Predators (see Table 16)	Survival Index (see Table 16)	Phloem Moisture Determination (percent of dry weight) $2\frac{1}{2}$ Months After the Onset of Attack (June 16)
A - Treatments with simulated root connection, no crown						
1	base	54	55	13.6	69	202
	top	36	47	35.4	94	252
2	base	23	38	31.1	89	175
	top	16	23	13.6	42	220
3	base	26	27	25.2	54	139
	top	18	19	22.6	43	138
4	base	29	29	16.6	46	113
	top	12	12	31.2	44	130
D - Treatments without root, without crown						
1	base	25	51	9.9	73	140
	top	36	43	16.0	60	219
2	base	25	29	28.2	62	143
	top	15	18	14.0	34	172
3	base	29	64	28.4	128	169
	top	11	16	17.6	43	172
4	base	46	47	29.9	71	129
	top	22	13	29.2	28	167
B - Treatments with simulated root connection and with crown						
1	base	6	11	15.8	32	135
2	base	18	36	15.8	94	121
3	base	15	33	17.3	74	121
4	base	28	18	24.8	34	91
C - Treatments without root but with crown						
1	base	7	15	26.2	64	139
2	base	21	21	34.9	56	125
3	base	13	10	7.9	16	78
4	base	10	10	19.9	31	96

1: tree felled Nov. 7, 1959. 2: tree felled Dec. 22, 1959
3: tree felled Feb. 13, 1960. 4: tree felled Apr. 2, 1960.

limited observation, as noted on page 79.

Tables 16 and 18 in effect are continuations, respectively, of Tables 15 and 17. In each case, for the several brood-sampling locations, a survival index was calculated which estimates what survival might have been, had no loss to the two principal predators and the one parasite occurred. Also listed in Tables 16 and 18 are phloem moisture values as they were determined in the host study material two months, in the first case, and two and a half months, in the second case, after the onset of attack. The moisture values and the survival indexes have been plotted in the scatter diagram, Figure 33, to demonstrate a lack of correlation between phloem moisture and brood survival. Attempts to use other representations of phloem moisture and relate these to brood success were also inconclusive.

It has already been reported that Douglas-fir beetle attack density did not relate to phloem moisture; the former instead was found to be greatly influenced by a female beetle attractant factor that causes attack to be loaded into logs receiving some initial attack. The factor could thus be causal to that decreased survival which is correlated with crowded broods (94, p. 200-202). On the other hand by building up attractiveness in one log, producing light attack as a result in other host material, the factor could be related to slow beetle development which occurs in phloem that sours because

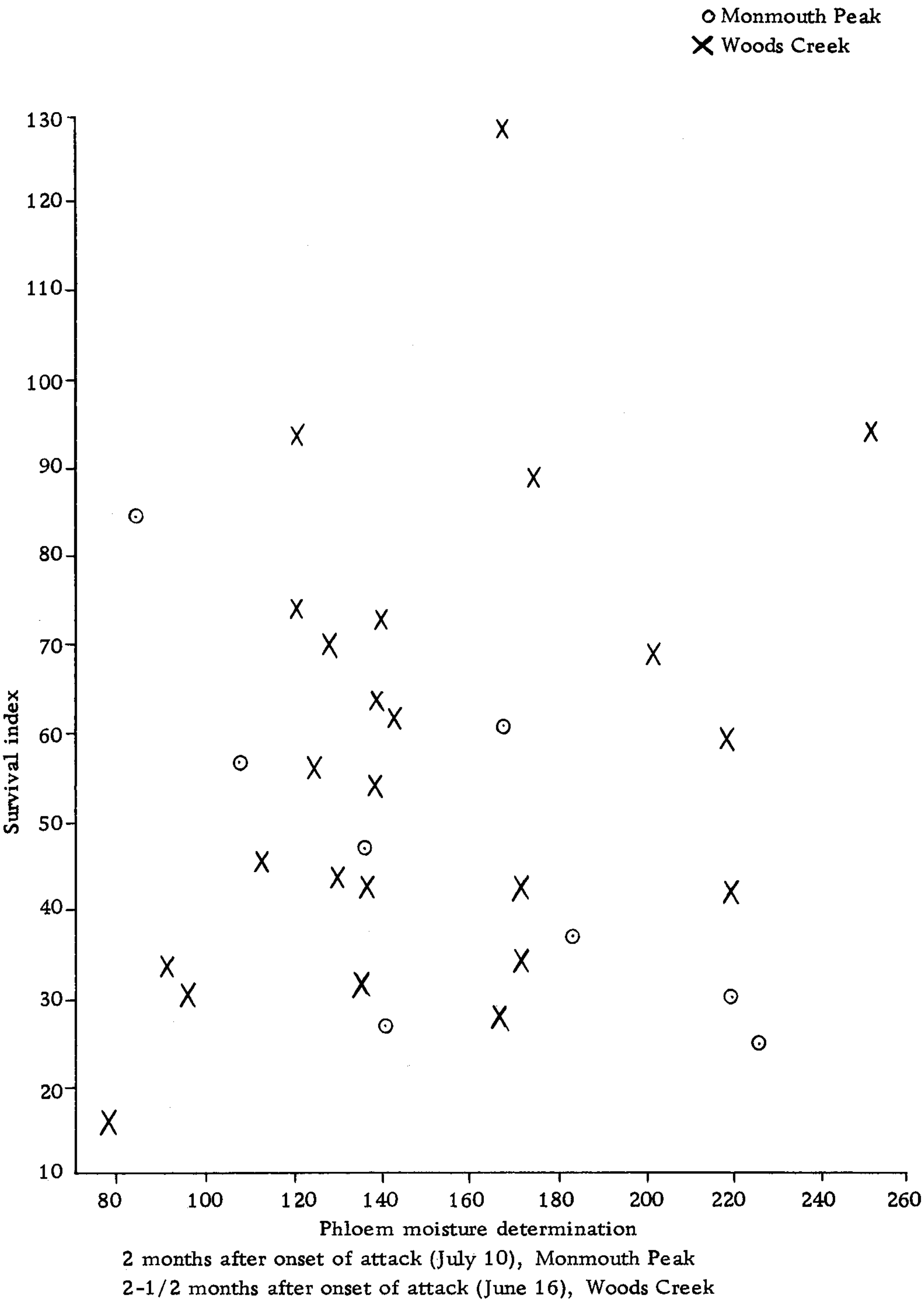


Figure 33. Indifference of Douglas-fir beetle brood success to phloem moisture levels present in two field studies.

the bark has not been sufficiently vented (see p. 124). Limited attack also may result in brood loss because of resinosis of the host (see p. 127). Further, a beetle factor apparently causal to attracting at least some predators to a log (117, p. 28) is thus related to predation loss.

In considering this last point, data from the Monmouth Peak study (Table 15) suggest a linear relationship between attack density and the numbers of Medetera and Enoclerus in fall analysis. However, on making a similar plotting of the data from Woods Creek, the concept is found to be inconclusive and must be set aside.

It remains, however, that predators are present and are a cause of mortality independent of the conditions of moisture encountered in these studies. Tables 16 and 18, together with the moisture values in Figures 22 and 23, sustain this view. No correlation between predator numbers and moisture conditions exists.

Coeloides parasite reduction of beetle brood depends, in large measure, upon bark thickness (115, p. 760-761), a factor which, again, is apart from moisture conditions. Table 17 data sustain this view; greater loss to Coeloides was in the top as opposed to the bottom sections of the A and D treatments. Treatments B and C were cut out of trees above these and, with thinner bark, show even more loss to the parasite.

Laboratory Study

Brood logs used in the laboratory in attempts to study attack patterns were continued in observation; in post development analysis the data shown in Figures 24 and 25 were obtained. Within the range of moisture present in these logs, brood size and survival were likely to be as good at one level as another.

Sour-Phloem

An observation already noted (see p. 77-80) was that abundant moisture in non-living host material might presage, by two months or so, a phloem decay situation termed sour-phloem. It was observed in various host material preparations in the different studies. The cases where sour-phloem influenced brood development and survival of the Douglas-fir beetle are cited below.

The Monmouth Peak data (Table 15) indicated that lower brood-survival values are associated with the presence of sour-phloem.

The 1960 windthrown trees observed in connection with oleoresin pressure studies happened also to have sour-phloem in broken-off sections of the crown region. This was true for four of the six trees in the study, but sour-phloem was not so evident in one of the other units and was clearly not present in the remaining case (Table 19). The greater length of the six trees from which the crowns

Table 19. Beetle and brood success in soured- and unsoured-phloem. The six trees were similar in that they were large diameter, tall ones windthrown the same date. As a result of falling, a sizable portion of the crown broke free of the trunk. The areas studied were part of the broken off sections. The intact stems, from which the crown portions were detached, did not, in any of the six cases, have sour-phloem. Instead, principally in the lower part of the trunk, there was oleoresin interference with the brood. Attack and survival data thus relate to oleoresin influence on invasion and survival and are included in Table 8.

Tree No.	Sour-phloem ?	Phloem Moisture at Time of Analysis (Oct. 1) % of Dry Weight	Douglas-fir Beetle				Ambrosia Beetle Entries in a 2 Sq. Ft. Sample
			Attacks per Sq. Ft.	Brood Estab-lished per Sq. Ft.	Brood Survival to Oct. 1, Percent	Portion of Survived Brood Reaching Adult	
1	yes	160	low	low	low	half	124
2	yes		mod.	low	low	half	123
3	no	106	1.5	103	20	99	0
4	yes	131	low	low	low	half	103
5	yes	71	mod.	low	low	half	127
6	no		2.5	93	30	90	29

Value judgments for entries relating to trees 1, 2, 4, 5 were necessary because the bark was so well seized to the sapwood that it could not be removed to provide an accurate numerical assesment.
Attacks per square foot, low: less than 1; moderate 1 to 2.5.
Brood established per square foot, low: 20 or fewer larvae.
Brood survival to October 1, low: approximately 20 percent or less.

were detached did not have sour-phloem (Table 8).

In the broken-off tops where sour-phloem was present, adult gallery length was shorter and brood size was small. Survival of initiated brood was judged to be low. Definite counts could not be made, however, because no technique was available which would enable expeditious removal of the beetle-infested bark that was tightly seized to the sapwood.

Soaked logs used in 1961 and 1962 field attraction studies were observed to be developing sour-phloem; their unsoaked controls were not. The principal test of 1962 found both soaked and unsoaked treatments to be equally attacked, difference in number of entries depending upon the presence or absence of the female beetle attractant factor (Figure 27).

Late summer removal of the bark in order to analyze brood success was easily done on both the soaked and the unsoaked logs. For the former, this would indicate that the development of sour-phloem was not in the advanced stage seen in other studies. However, odor, color and appearance were of the typical sour-phloem syndrome. Further, the soaked logs had been preferentially attacked by ambrosia beetles (Table 5).

In this case, where the soaked logs showed sour-phloem only in the incipient stage, the size of the established brood, developmental status of individuals, and survival generally, were equivalent to that found in the unsoaked logs.

A similar instance was seen in the Woods Creek study where part of the November- and December-cut material was judged in July to have sour-phloem. The logs had been well attacked, however, and held large brood numbers. In analysis conducted in the fall, the phloem appearance was such that it could not be called sour; survival was good.

Thus, in those cases where sour-phloem became fully established before brood development was completed, it was judged to be associated with small brood size and poor brood success. On the other hand, when the brood could out-pace development of sour-phloem, success of the former was normal.

Oleoresin Interference with Brood Development

The large diameter windthrown trees having the oleoresin exudation pressures recorded in Table 7 and receiving beetle attacks as recorded in Table 8, when analyzed in the fall, showed a number of galleries into which oleoresin had flowed, interfering with progress of the adult beetles and development of their progeny. Thus adult galleries were short; they occasionally branched off or doubled back, suggesting beetle avoidance of a pitch area; a few adults were seen at the gallery teminus blanketed in pitch. Larval galleries similarly would show such interference and, for this reason, the small broods initiated exhibited low survival. The number of broods in the study trees in which oleoresin interference could be observed is appreciable, as noted in Table 8.

In the laboratory, corroboration of the effectiveness with which oleoresin entangled adult beetles was demonstrated by the fatal immobilization of them within 15 minutes. Three-drop samples of the liquid were used. That the viscous and adhesive properties of the oleoresin were causal to this action was shown by essentially as rapid an immobilization when sodium silicate or molasses was used in equivalent amounts in control tests.

DISCUSSION AND CONCLUSIONS

Phloem Moisture

Phloem-moisture values ranging from about 100 percent of dry weight to 250 percent were found in fallen trees. The 100 to 200 percent range was the mode. Within a Douglas-fir, values increased as sampling proceeded further towards the upper part of the trunk. Trees or sections with a transpiring surface had less moist phloem than those without such a surface but this was not seen to be absolute; moisture of 150 percent was often present in the phloem of a fallen unit having limbs.

The results may be compared with those established in other scolytid host species investigations. Anderson (4, p. 599), Beal (in Miller & Keen (101, p. 25)), Beal & Massey (8, p. 27), Reid (114, vol. 94, p. 608), and Vité (136, p. 47), collectively representing four different species of pine, found phloem moisture values generally higher. On the other hand, in elm, Martin (89, p. 304) securred determinations much lower than those in Douglas-fir. A further difference would be that Anderson, and Vité found moisture content in standing host material to decrease with height.

As time since felling increases there are changes in percentage moisture. In Douglas-fir, these generally are upward.

Anderson (4, p. 600) has noted the same phenomenon in a pine species. An exception is possible in Douglas-fir when foliage or a cut log surface allows drying. If phloem percent of dry weight losses do occur, these tend to be minimal and involve spring-felled material more than that dropped in the winter or fall.

Regarding this latter finding, research centering on logging practice in Europe has demonstrated that transpiring crowns left on fallen trees reduce tree weight (39, p. 264-265; 83, p. 87; among others). It thus appears that phloem remains relatively moist in spite of moisture loss from the tree as a whole. Johnson's (70, p. 7) experiments with slabs of Douglas-fir showed phloem to remain wet while its adjacent sapwood dried.

Moisture level could not be related to the pattern of Douglas-fir beetle attack in downed trees. In the field studies, using windthrown and winter-felled trees, the various moisture conditions were found not to relate to the pattern of attack of the Douglas-fir beetle. Laboratory studies, using differentially moist logs, were of no value as beetles responded more to phototactic stimuli, ignored the logs, and thus did not come to distinguish between them. A last field study, rigidly controlled and centering on wet as opposed to normal logs, was striking since it showed that the wet log condition was strongly favored by Gnathotrichus sp. In the same logs, there was also selective attack by Dryocetes autographus and Hylastes *nigrinus* in restricted numbers. Nevertheless, there was not a significant difference in the numbers of Douglas-fir beetle attacks in the wet as compared to the normal logs.

In agreement with the *Hylastes* observations, Chapman (23, p. 4) has noted attacks of *H. nigrinus* in the narrow zone where Douglas-fir logs came in contact with the ground. He concluded, "It appears .... that high bark moisture may be a prerequisite for attack by this species."

To elaborate on the above-mentioned observation of *Gnathotrichus*, the almost exclusive confinement of large numbers of these ambrosia beetles to the two wet-log treatments, in each of the four replicates, indicates preference. This preference would be related to metabolic decay, termed sour-phloem, and not to the presence of extra moisture *per se*. The decay condition develops with time in phloem sealed from the air. Moisture helps implement the seal. Limbed host material, is not necessarily to be eliminated as a site where souring might develop. Host material with attached limbs sometimes became sour although it was not soaked. It was well attacked by *Gnathotrichus*.

Seeming to offer some corroboration to these findings, Johnson (65, p. 510) noted more *Gnathotrichus* attacks in those logs aged longer. However, since time in his study ran to a few years, the loading was in part due to accumulation. In another study of log age and beetle attack, Prebble and Graham (112, p. 105) found their data to give little evidence that the number of *Gnathotrichus* beetles entering logs was associated with a particular cutting period.

Study results involving the other principal ambrosia beetle, *Trypodendron lineatum,* have been more decisive, and for this reason the species deserves note here. *T. lineatum,* however, and *Gnathotrichus sp.* appear to have different characteristic attack procedures. Kinghorn (79, p. 3-4) reports that different preparations of host material, made from the logs of one tree, recorded different numbers of attacks from these two beetle genera even though the log preparations were laid out together. Rudinsky and Daterman (120, p. 1348-1349) have shown *T. lineatum* attractance to host material which contained females of the same species, this being an example of mass attraction analagous to that of the Douglas-fir beetle (see p. 144). In the same study, on the other hand, the *Gnathotrichus* beetles, *G. sulcatus* and *G. retusus,* were not attracted to logs containing females of these two species. Instead, it was clearly shown that these scolytids were attracted to logs which had been infested with females of the Douglas-fir beetle.

Dyer and Chapman (37, p. 3) found that *T. lineatum* attacked soaked logs in about the same numbers as it did unsoaked controls. It is noted, however, that the logs were aged and equivalent phloem conditions could have arisen in the study as a consequence of the time factor. The soaking might have been incidental. For brood production, the soaked logs were unsuitable to the beetle. Kinghorn (78, p. 4), concluded that the presence of moisture does not limit attack but that its lack might do so. In another line of investigation, more Trypodendron attacks were observed in lopped as opposed to unlopped logs (68, p. 3). With regard to log age, the record for T. lineatum indicates that winter-felled logs are more attractive to this species than spring-felled ones (21, p. 3-4; 65, p. 510; 112, p. 105).

To continue the discussion with attention to the primary species in this study, considering phloem moisture *per se*, no moisture levels which were restrictive on the growth and development of the Douglas-fir beetle could be found. Figure 33, summarizing brood success as determined in the field studies at Monmouth Peak and Woods Creek, plots survival indexes. These values are estimates of what survival might have been had there not been loss to predators and the Coeloides parasite. Lack of correlation between survival and moisture is indicated. This lack is also shown in Figures 24 and 25 which summarize laboratory studies where parasites and predators, being excluded, were not present as error factors. Brood survival as subjectively measured in the wet and normal log treatments of the 1962 field study continued to support the concept that survival was independent of phloem moisture levels encountered in these field and laboratory investigations.

These various experiments justify the conclusion that, within the range of phloem moisture values likely to be obtainable in the field, beetle brood survival is about as good at one moisture level as at another. To express the concept differently, mortality would be perceptible where phloem moisture was at some point either below 100 percent or above 250-300 percent of dry weight. As for the lower limit, phloem moisture might drop to 50 percent and still allow fair brood survival. An example of this was observed in one of the laboratory experiments (Figure 24). Miller and Keen (101, p. 71) for another Dendroctonus species, D. brevicomis, state

> Rearing of exposed larvae in dry rooms has demonstrated that they can withstand considerable dessication. It would appear that in nature the moisture stored in the sapwood of attacked trees and logs is passed on to the inner and outer bark in sufficient volume to provide for satisfactory brood development.

Anderson (4, p. 601), working in the laboratory with Ips pini and a more complete spectrum cf moisture values, could produce reduced brood survival at the extremes. However, data of his taken at those levels of phloem moisture which were present in the field would show agreement with the above conclusion. Similarly, Johnson's (69, p. 660) study of Douglas-fir beetle broods reared in slabs of host material showed that where sapwood moisture dropped into the 15 to 20 percent (oven dry weight) range, survival was much reduced. That this treatment might be regarded as extreme is shown by another study of Johnson's (70, p. 7) wherein phloem moisture was found to drop to 15 percent when the value for sapwood reached 11 percent. Good survival was observed in those slabs where the wood side was waxed which prevented undue moisture loss from the sapwood; best furvival of brood was in slabs which were completely waxed (69, p. 660). Completely waxed slabs after two months would have a phloem moisture level of 134 percent (70, p. 7), a moderate level.

In one sense, moisture was seen to play a role in brood development and survival. Ample moisture in a dying stem along with the retention of an anerobic condition provided by intact bark contributed to the formation of sour-phloem. Moisture helps implement the anerobic seal. However, if the seal is not present, moisture alone will not produce sour-phloem. Conversely, logs in which souring is well developed could be observed even though phloem moisture values were low (Table 19); the seal necessary for the particular kind of phloem change to occur was effected by the relatively intact bark.

The phloem decay condition when present in field host material is associated with deterred brood development and lowered survival. Oxygen levels are low; secondly, sour-phloem itself may be harmful to the larvae.

The moisture levels that precede sour-phloem need apparently be only a little higher than those in sound, healthy stems. Butt soaking of a log for two weeks will cause an increase in phloem moisture percent of dry weight to the extent of perhaps 25 or 50 percent (Table 3). Such logs initiate development of sour-phloem. Time and continued isolation of the phloem from oxygen are necessary to complete the process.

Beal, cited by Miller and Kean (101, p. 71), Blackman (12, p. 36), and Vité (136, p. 57) have noted the three-way association of ample moisture, souring of the inner bark, and interference with larval development. In all three studies, the host tree was ponderosa pine. The beetle species were, respectively, *Dendroctonus brevicomis*, *D. ponderosae* (= *D. monticolae*), and *Ips pini*. Beal and Massey, without mentioning a sour condition, report very high *D. valens* brood mortality in trees where phloem moisture reached the excessive value of 400 percent.

Douglas-fir beetle broods of substantial size initiated concomitantly with the initiation of sour-phloem produce tunneling that admits air beneath the outer bark and interferes with the development of souring. Thereby, the beetles' own survival is promoted. Logs having high phloem moisture, if well tunneled, will not have sour-phloem (Figure 8). Johnson's (70, p. 6) conclusion regarding the likelihood of secondary attack by Douglas-fir beetles would be acceptable to this point of view. Results of his studies showed brood-establishing adults to remain in wetter host material for a longer period of time.

It is possible that the concept of beetles being enabled to make a secondary flight through the regeneration of indirect flight muscles when in unfavorable material (6, p. 31) should be amended. Wet host material can become unfavorable for the beetle species. Oleoresin-exuding host material is unfavorable. It is to the beetle's advantage that such material be attacked in volume. Similarly, it is to the species' advantage to establish the largest broods possible in that unfavorable material which has come to receive limited attack. Lengthened adult galleries and more numerous larval galleries serve to open up the inner bark area in the same way that more massed attack would. In certain classes of unfavorable host material, flight muscles would thus remain degenerated.

Log Age and Attack

Results in this study partly stand in opposition to those recently published by McMullen and Atkins (95, p. 1312-1314). Four ages of host material, produced by cutting trees at six-week intervals through the winter, showed Douglas-fir beetle entries to be independent of cutting date (Figure 26).[3] On the other hand,

[3] The earliest felled trees (making the oldest fallen host material) were cut November 7. It is expected that trees felled earlier, in the summer, would have experienced enough deterioration that they would have received few beetle entries.

McMullen and Atkins, with host material felled at 15-day intervals, obtained a demonstration of beetle preference for the most recently felled material.

Further study to resolve this discrepancy is indicated. The major finding of both studies is with regard to the attractance produced by small numbers of entered and unmated female beetles. Attractance will result whether the females are entered in material freshly fallen or, as seen in the case of the colored log experiment, cut three months earlier. The beetle population itself would be capable of preempting any attractant factors that might be inherent in the host. This would explain the author's failure to obtain data comparable to that of McMullen and Atkins. It then remains unclear how McMullen and Atkins compensated for the influence of the female beetle attractant factor. It is noted that their experiment was conducted in 1957, apparently prior to their insight as to the importance of beetle-induced attractance. Also noted are conflicting reports from the study of *Dendroctonus engelmanni* which underscore the difficulty of assessing what effect log age has on the attack pattern of a *Dendroctonus* beetle (92, p. 3, 4; 103, p. 895).

An alternative interpretation for the data of McMullen and Atkins is that the beetle population is involved in the production of a repellent factor which, in small logs, becomes fully active in limiting attack about three weeks after invasion of the log begins.

Such interpretation would fit the data presented in Figures 27 and 29, as noted on page 97. Repellency of a log could increase until it not only negated the attractance produced by those freshly entered females but also deterred attack into near-by host material.

In the McMullen and Atkins experiment, alternate ten-foot sections along a bole were protected by a covering of factory cotton that was removed 15, 30, or 45 days after each felling date. Attacks into the uncovered sections began on the day of felling. In the case of each tree in the experiment, the number of attacks into the logs which had been left uncovered was approaching the maximum received (attraction was much decreased) when the first of the covered logs was opened to attack. The newly uncovered logs were then observed to receive a much lighter attack (95, p. 1314).

The three-week time interval noted above might be expected to be different with different sizes of host material, various amounts of host material, different habitat temperatures, or with a greater or lesser pressure of numbers from the beetle population.

Recent observations of Johnson (70, p. 8) would not be in disagreement with the above hypothesis. Newly exposed two-month-old host material which had been protected with screens was as well attacked as a freshly fallen tree. Previously exposed logs suffered little additional attack.

Oleoresin

Slight oleoresin exudation pressures were demonstrable in fallen timber and a flow of resin, assumed to be dependent on this pressure of from one to fifteen pounds per square inch, was seen to restrict beetle success. Many attacks were overwhelmed in resin, and not a few were evidenced to be repelled before they penetrated to the cambium. Adult galleries, when established, sometimes showed oleoresin to have hindered brood development and survival.

Oleoresin in this study thus emerges as a deterrent to beetle success, both in terms of attack and brood development. There remain the studies of other workers (27, p. 1654; 50, p. 3; 108, p. 105-107; 128, p. 369) which show oleoresin constituents to be responsible for attraction to, or at least identification of, possibly suitable host material. Chapman (25, p. 675-676) has recently shown discrete selection by many scolytids from amongst several log odors released in the field. It is possible that oleoresin is the source of these odors. If only as a model, such action would have validity because oleoresin is a repository for volatile constituents that vary with the tree species, and, while oleoresin is generally a deterrent, it provides a mechanism for identification of a host by those insects which are more or less specific to it. The restricted point of balance that an insect occupies with regard to its host is emphasized.

A study of Furniss is of interest because standing trees having substantial oleoresin for exudation were much more attacked than windthrown trees in the same investigation (44, p. 488-490). Different ecological considerations exist for the Douglas-fir beetle in southern Idaho than in western Oregon. In Idaho, windthrown Douglas-fir host material varies in quantity from year to year and is rare in fringe areas (44, p. 491). Contrasting with the attack observations in Idaho, McGowan and Rudinsky's (93, p. 11) study on the coast indicated that windthrown trees were slightly more densely attacked than standing ones.

One is thus led to hypothesize a somewhat greater tolerance of the intermountain Douglas-fir beetle for oleoresin. However, since the resin appears to kill by entanglement and occlusion of the spiracles a direct resistance to the viscous fluid is not suggested. Rather, the beetle population would appear to accept higher oleoresin presence thresholds and is able to survive these because of attraction generated by attacking females for other members (males and females) of the population. "This mechanism in their (the beetles') behavior which induces mass attacks is the main reason why bark beetles are able to kill living trees" (84, p. 310). Massed attack into a tree dissipates the flow of oleoresin; this increases the possibility that an individual beetle will not encounter an entangling quantity of the fluid.

It may be of the essence that there is, in most years, in the coastal Douglas-fir enough naturally fallen timber to sustain the available beetle population. These fallen trees with low oleoresin exudation pressure at best, with lesser resin flow, do not as rigorously select the population for the above tolerance to (greater acceptance of) resin. "In logs or dead trees, a light population of beetles can thrive" (84). Thus only when especially abundant fallen timber is present, to produce abundant broods, is there a Douglas-fir beetle population large enough to contain a sufficient number of oleoresin-tolerant beetles to present a threat to standing trees. On entering a standing tree, these better adapted individuals have, as later arriving associates, oleoresin-intolerant beetles which produce broods that merge with those from the fallen timber to continue to keep the oleoresin-tolerant population well diluted by the oleoresin-intolerant ones.

Air Temperature and Flight and Attack

As a consequence of viewing the attack record of the beetle in connection with the attraction studies, entries were seen from beetles which could only have arrived by flight when recordings showed the air temperature not to have been higher than 62° F. or even 56° F.

This point must be given at least small note, since it allows revision of temperature values that would be considered in future studies when the possibility of beetle attack is being appraised.

Study with Olfactometers

In connection with the phloem moisture-attraction studies and other attraction studies, olfactometry suggested itself as a useful means of experimentation. However, for this author the use of such apparatus in the laboratory yielded no significant finding. In hindsight, it may be said that such would be so because of the number of unknowns involved in this kind of experimentation. Jacobson and Beroza (61, p. 1370) have recently noted the finesse that the test of materials for attraction of insects requires.

Proper olfactometer design, its technique of use, the applicable odors, and proper beetle condition (49, p. 519) had to be determined more or less at the same time. As events have developed, the studies of Wood and Vité (156, p. 91-94) and Vité and Gara (138, p. 260-264) with _Ips confusus_ and _Dendroctonus brevicomis_, McMullen and Atkins' (95, p. 1315-1319) experiments with the Douglas-fir beetle, and studies with the same species described herein, demonstrated strong attractive factors deriving from within the beetle populations. Establishment of attractive odors was thus the initial break in a vicious circle centering on olfactory orientation.

With knowledge of these attractants, it has been possible to use laboratory olfactometers, constructed as part of this study, and to demonstrate beetle response therein (117, p. 34; 139, p. 41). Wood (155, p. 141-143) has recently employed an arena-type olfactometer to demonstrate response by Ips confusus to the attractant produced by the male of that species.

Attractance Generated by the Female Beetle

The important role that the Douglas-fir beetle population itself plays in the attack of the species into its host has been demonstrated in this study. Logs containing relatively small numbers of unmated female beetles were significantly more attractive than logs from the same tree initially having an equal number of beetle pairs or logs initially having no beetles at all. This was experimentally shown with logs from different individual host trees, at different locations, and at different points in time.

The number of unmated beetles was 12 to 42; these were introduced into three-foot logs of which there were three to eight in the various trials.

The various trials employed logs laid out in the field, and beetles from field broods produced the entry holes that were counted and became the data. Experimental procedure was thus analagous to natural situations. Additional insight as to the pattern of attack into a log was provided. Attracted females, for instance, also induce attraction in whatever log they enter; experimental data, therefore, were ever changing. Nevertheless, differential attraction was clear. Logs initially with female beetles attracted more of these and tended always to hold the attractive lead.

By extrapolation, a short log containing a single successfully entered female would be expected to have at least some of this beetle-centered attraction. Such a log was seen in one experiment designed for other purposes (see Various Log Treatments Used to Measure Beetle Attraction, p. 85). Of 95 three-foot logs laid in a ten-acre site (Figure 14), few received any entries at all and this was after mid-May. The one log, however, had received an attack by a beetle that was noted on April 29. Then by May 13, seven more attacks were received. In all, this log experienced 21 attacks. The few other logs in which beetles were noted at later dates either showed a similar, albeit restricted, development of attack or may be explained as having received the initial solitary entry so far into the season that they then held too little attractance to draw in competition with other logs having more entries that were available in the vicinity.

True attractance, corresponding to the definition of Dethier, Browne, and Smith (35, p. 135), is exhibited in the response of beetles of both sexes. Males, however, additionally demonstrate themselves to be arrested when they have arrived proximal to the entry of a yet unmated female.

The attractance of the female Douglas-fir beetle is analagous to that of the male beetle in *Ips pini,* revealed by Anderson (4, p. 596-597) and not fully appreciated for more than a decade until Wood and Vité (156, p. 93) investigated the host-selection behavior of *Ips confusus.*

In 1961, the year of experimental demonstration of the female factor for the Douglas-fir beetle reported herein, Vité and Gara (137, p. 175-181; 138, p. 252-269) used field olfactometers and mechanical catching techniques to demonstrate the effectiveness of the male-produced attractant for *Ips confusus* and *Ips ponderosae* as well as to show the existence of a female-produced attractant for *Dendroctonus brevicomis.* In all cases, there was attraction of both sexes. Knowledge of this experimentation during the summer of 1961 served to confirm the study reported here and to obviate the need to conduct experiments to prove more completely that there was not auditory or visual stimulus in a log by the unmated female.

It was also of benefit to be aware of the experience of Kline (82, p. 18-19) (also see Appendix, p. 179), another graduate student at Oregon State University. In using logs of three treatments for a field study of predators of the Douglas-fir beetle, noteworthy beetle attraction to preparations which contained unmated females was observed.

A recent publication by McMullen and Atkins (94, p. 1315-1319) reveals their insight into knowledge of the Douglas-fir beetle attractant factor in studies of the effect of initial attack dating to 1959. This work in British Columbia and the Oregon studies described herein, carried out independently of one another, validate the concept of the female beetle attractant factor in widely scattered segments of the population.

While Allen (3, p. 9) has questioned the concept that the female Douglas-fir beetle does not stridulate, any sound from her outside of chewing and body movement remains unproved. Thus, since it is the prior entered and still unmated female that elicits attack, an auditory stimulus for the attractive force is ruled out. Visual stimulus could scarcely be operative since a log with beetle pairs introduced into it has the same appearance, with reddish boring dust at the entry holes, and yet is significantly less attractive. Further, a log can be hidden within a metal box having air moving through it and continue to be attractive (see p. 104).. The recent studies of Rudinsky (117, p. 34-35) which include extraction of the attractive substance from frass of entered, unmated Douglas-fir beetle females and its use in field olfactometers further prove odor-centered attraction.

It has long been clear that the female Doulgas-fir beetle enters a log first and is followed by the male (10, p. 7). With this knowledge, one could deduce that an olfactory sex attractant would make such a system operable, i. e., the male on perception of the female-produced attractant would be released to move towards her. The attractant, being a beetle-produced substance discharged to the outside to act among individuals of the same species would qualify to be designated as a pheromone, as described by Karlson and Butenandt (74, p. 39). Pheromones are stated to be one kind of chemical releaser. Wharton, et al. (149, p. 1062) have noted that specific sex attractants are produced by numerous animal species. Investigations centering on pheromones found in other species of insects in Lepidoptera, Coleoptera, Hymenoptera, and Hemiptera have been reviewed by Jacobson and Beroza (61, p. 1367-1373) and Karlson and Butenandt (74, p. 45-50).

"Attractants, " Jacobson and Beroza state, "may be classified as sex, food, or oviposition lures" (61, p. 1367). The sexual attractants of Scolytidae, now becoming apparent in the genera Ips, Dendroctonus, and most recently Trypodendron (120, p. 1348-1350), are different from those previously conceived, however, in that attraction is not exclusively for the opposite sex. Introduced or early arrived Dendroctonus virgin females, for instance, bring other females as well as males to the log being attacked. The attractant, operating as a pheromone, would thus conform to Wilson's (152, p. 107) use of the term "social releaser." Allee (2, p. 22-29), discussing the schooling of fish, the flocking of tropical birds, and the grouping of stags of Scottish deer, notes that these are examples of social life developed to high level and specifically are not extensions of family relations. In scolytidae there may be seen a biochemical basis for this aggregating type of social behavior.

Very recent work by Rudinsky and Daterman (120, p. 1350-1351), as previously mentioned (see p. 132), has shown that the two *Gnathotrichus* species, *G. sulcatus* and *G. retusus*, are attracted both to logs which have been infested with females of the Douglas-fir beetle and also to an ethanol extract of frass obtained from females in a log. The indications are that this is a case of interspecific attraction. This attraction characteristic of *Gnathotrichus* together with its attack pattern demonstrated in wet as opposed to dry logs presents an intriguing problem which is outlined in the appendix.

Effectiveness of the Attractant

Logs containing introduced unmated female beetles placed 15 to 20 feet from logs having either pairs of introduced beetles or logs with no introductions were demonstrated to receive significantly greater numbers of attacks. The latter two log treatments did come to contain females which arrived from the field population and the logs thus became more attractive. The number of attacks in them, however, continued to be fewer. Females arriving in the logs with females added to the attractant capacity, which initially was related solely to the introductions; logs with introduced females held the lead (Figures 27 and 29).

Since there was relatively narrow spacing between the logs of different treatments, discrete selection by the beetles from the field population was demonstrated. A high aggregating power from the attractant is indicated. Similarly, Vité and Gara (138, p. 262) attest the aggregating power lodged in related scolytid species attracted to and caught in their field olfactometers employing logs containing unmated beetles.

Note was made in the Introduction (see p. 7) of Douglas-fir beetles attacking western redcedar logs which were dispersed with logs of Douglas-fir undergoing attack. From this, it may be hypothesized that the female beetle attractant factor emanating from the Douglas-fir so directed beetle response that there was lessened discrimination for the two diverse types of logs. Experimentation demonstrated that female beetles introduced into hemlock and pine logs will induce attack by other Douglas-fir beetles into host material not normally accepted. Thus, the female attractant factor can be produced in abnormal host material and can prevail over whatever mechanism a searching beetle might have for identifying its preferred host from tree factors alone.

As for experimentation with grand fir, attractance was seen although it was only of males. These were seen on the screen covering the female introductions. Hypothesizing that there is a single attractant produced by the unmated female beetle to which both males and females are responsive, then extrapolation will allow that it will later be possible to demonstrate female attraction to grand fir. To the point, it is not improper that males alone were observed on the screen for this is the case even when Douglas-fir is the host material. Males are attracted to unmated females; when these are sheltered by screening, a male may often be seen arrested in position directly over the female entry, even remaining there while being killed by solar radiation (Figure 2). The attraction of females, on the other hand, is to the log in general and not to specific loci on it. Indeed, there is a dispersal of entries over the log surface suggesting that each female seeks its own extended territory.

The limited production of attractance by females in fir and hemlock provides evidence on which to support the hypothesis that acceptability of host material is prerequisite to the degree with which pre-entered females produce their attractant. Strengthening this view, Rudinsky (117, p. 34-35) has extracted the attractive substance of the Douglas-fir beetle from frass of entered unmated females. The studies of Wood (155, p. 142-143) and Vité, Gara, and Kliefoth (139, p. 47-49) showed the beetle attractance factor of *Ips confusus* also to be associated with frass resulting from feeding upon host material. More recently, Pitman and Vité (111, p. 225-226) have demonstrated that the hindgut epithelium of males of this species is of different structure from that of the females.

A large log already receiving beetles continued as the most attractive locus even though the 95 three-foot sections relating to various attraction experiments were also present in the same 10-acre area. As shown in such a project, attraction arising from entered females is so intense that designing experiments to test for other possible attraction stimuli, *i. e.*, those owing to host materials, may be difficult.

This statement is made notwithstanding McMullen and Atkins' (95, p. 1312-1314) report of significant attractance of Douglas-fir beetles to fresher logs as opposed to older ones. Discussion on this point appears above (see p. 137 - 138).

The wet-log - normal-log study of 1962 was designed to correct for the preemptive influence of the female beetle attractant factor. Some of the logs in each of the two moisture treatments were further prepared by introducing female beetles into them. The results showed no difference as between the wet and normal logs in amount of Douglas-fir beetle attack. The wet logs, it has been noted, initiate sour-phloem; old logs similarly tend to become sour. The experience demonstrates the difficulty of assessing different levels of attraction that might be inherent within the log, that is, those that might be exclusive of the attractance produced by female beetles.

Advantage to the Species

Viewing the attractant as a device for congregating numbers of the species, it is appropriate to speculate as to what selective advantage this affords.

1. A female joining other females which were still unmated and attracting males might better insure that she would be mated.
2. In a tree having oleoresin exudation pressure and thus providing resistance to attack, the olfactory biocommunication to other individuals and the convergence of these on a tree helps insure that the general beetle attack in that tree will be successful. Mass entry of beetles dissipates the oleoresin flow. Conditions for each individual entry are then more favorable.
3. Mass attack insures the opening of the under bark area to air so that the brood will have adequate oxygen for respiration. Also, development of sour-phloem will be

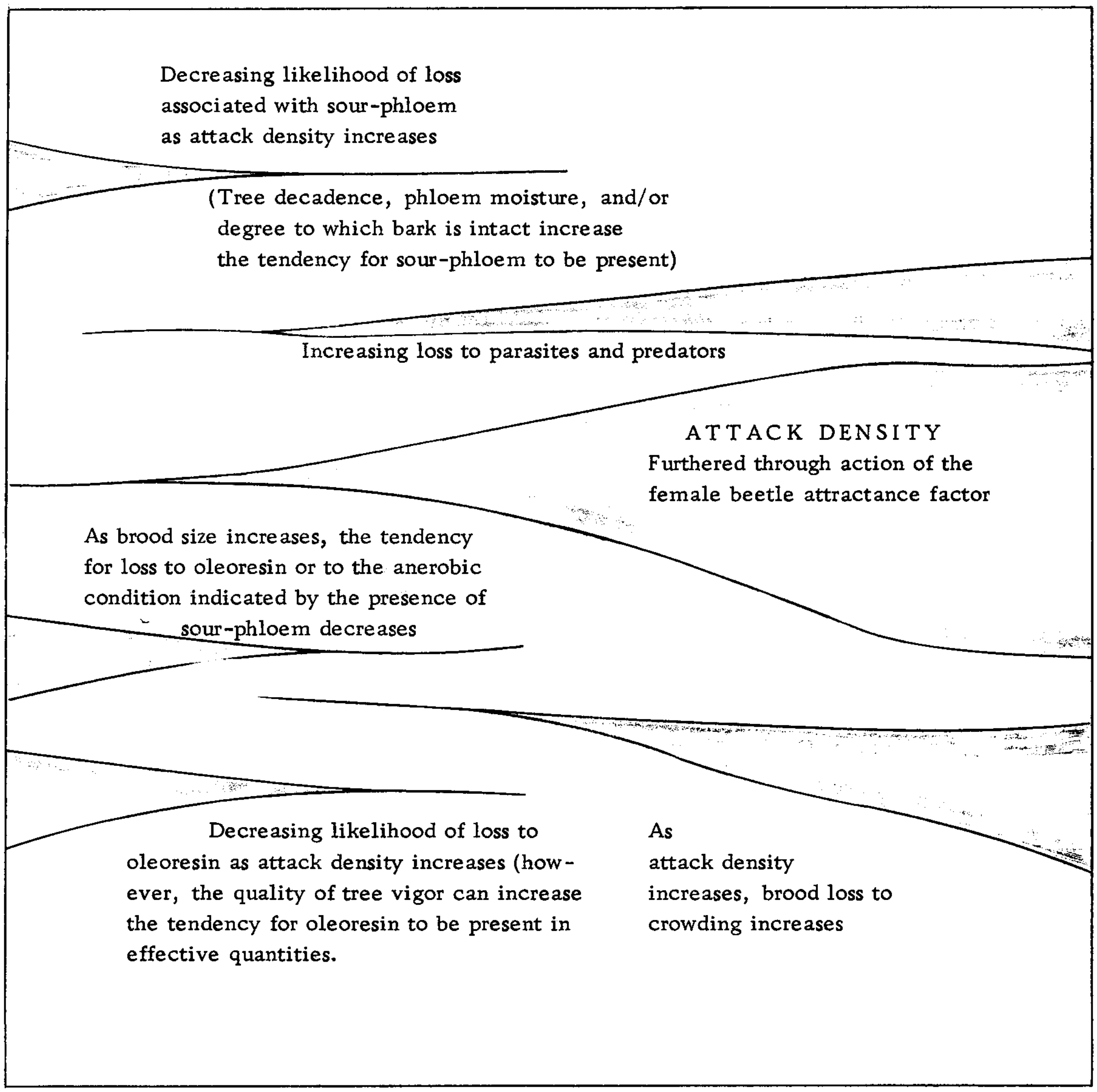


Figure 34. Diagramatic Presentation of the Interaction of Factors Discussed in the Thesis.

forestalled. More optimal conditions for larval growth are produced.

It is recognized that there is some paradox in a condition which demands close spacing of brood to the end that individuals might be successful. Intra-specific crowding will induce a measure of mortality. The advantage of the population having been well established equips it better to sustain this mortality.

The welfare of the species is implemented in yet another way. By massing a large number of individuals on a single piece of host material, the species makes efficient use of that material. When circumstances are such that part of the population is carried to standing trees, the beetles do not do what they might otherwise appear capable of doing: initiate a limited number of attacks in each of a great number of trees. The beetle is thus a prudent parasite, placing minimal demands on its host tree species. It is restrained from killing off the entire host population and thereby insures its own survival. Parasites exist only so long as their hosts.

Advantage to Control

For the moment, knowledge of the gregarious pattern of attack, and the female-centered olfactory communications system which makes such a pattern possible, serves to make intelligible many incongruous observations of the past. These would include beetle avoidance of suitable host material, as was true in the case of the 95 experimental logs which were ignored in favor of the large, previously attacked windthrow. Also the attack of seemingly repellent logs like those of western redcedar in a particular situation where these were dispersed in amongst Douglas-fir logs undergoing attack is now explainable (see p. 150).

Concentration of attack in one locality can now be understood. On the other hand, the summary statement of Furniss (43, p. 6) "... there is general agreement that attacks create attractive odors caused by fermenting phloem" is set aside. Bedard's (9, p. 7-9) observation that 60 percent of the Douglas-fir beetles present in attacked trees were females is of interest. Attacking females induce males as well as others of their sex to come to the entered tree. Some of the imbalance between the two sexes, in the first days of attack particularly, may reflect a tendency by female beetles to be more strongly responsive to the attractant. The paradox of Atkins and McMullen's (7, p. 3) demonstration of significant beetle preference for logs laid on the ground over those stood on end, while one standing log was seen to have the greatest density of attack, can now be understood. The standing log may have been earlier attacked; it may have come to contain females especially strong in the ability to produce attractant.

The concept that weakened and fallen timber expectantly will harbor beetle attack is made more valid since this kind of host material best enables successful entry of first-attacking females; these produce their attractant which, in turn, induces further attack. Specifically, weakened host material sustaining attack will come to be the attractive locus. Continued attack will tend to center at this locus. Adjacent healthy trees may be expected to receive some of the arriving beetles. By and large, this will be infrequent, however. The antagonistic effect of exuded oleoresin in the standing trees, together with the relative absence of this antagonism in the fallen host material, will result in continued attack in the latter as long as such material is present. There will be attack also in other material, perhaps at a distance, that is similarly weakened and will sustain successful attack.

One observation is of interest here. A pair of standing trees had four short logs containing introduced females placed at their bases. The trees, like the logs, came to receive attack by the Douglas-fir beetle. Four attacks were made into one tree, upwards of 50 were made into the other. These were first noted a month after attacks had been initiated in the logs having introduced females. The logs had absorbed 409 attacks and were part of a replicate, whose treatments were 20 feet apart, that received a total of 1,080 attacks. The majority of beetles entered the logs.

Since both standing trees were vigorous ones, able to supply a copious oleoresin flow, they survived the attacks. Thus, to the point, the conclusion of Johnson and Pettinger (71, p. 7), "For practical purposes, the results of this study show the importance of removing windthrown and felled timber in the spring and early summer prior to infestation by bark beetles, " should be countered. It is proper to regard fallen timber as a reservoir of suitable host material which will receive the beetle population and divert it from healthy trees. Good practice, on the other hand, will continue to dictate removal of this infested material at some time before emergence of developed brood the following spring.

Beetle-induced attractance provides clues for the design of trap trees that would be more consistently effective. Where values will warrant the cost, beetles may be reared and a few females can be entered into host material in the field much as was done for the treatments in this study. Such a log should then be a focal point of the beetle attack. A residual insecticide, as demonstrated by Rudinsky, Terrier, and Allen (118, p. 951), may be applied to the surface of such logs to serve as a toxicant to those beetles attracted to the trap log. This design should make a log useful for a longer period of time and obviate the need to destroy developed broods in it.

One may speculate that eventually there will be identification of the attractant, as has been done in the case of the attractive material produced by the females of gypsy moth, Porthetria dispar

(L.) (62, p. 1011) and the silkworm, Bombyx mori (L.) (16, p. 84). More recently, Wharton et al. (149, p. 1062) have obtained a material from the cockroach, Periplaneta americana (L.), that is similar in action.

In this connection, however, the effort necessary to isolate the gypsy moth attractant, known to exist for 60 years, is of interest. Females, or segments of them, or benzene extracts of these, had been much used during most of this time as baits for traps in connection with distribution studies (15). The hindmost abdominal segments from 500,000 females were used for the stock which eventually yielded 20 milligrams of liquid attractant and 3.4 mg. of another factor which was crystalline (62, p. 101). For advantage, these workers had a larger species than the Douglas-fir beetle to work with, knew where the attractant was located in the body, and that it was present in all females recently emerged from pupation. The insects did not need to respond to a series of stimuli as does the Douglas-fir beetle in entering the bark of a host log before producing the attractant. Still, the isolation serves more to promise a similar eventual success with the beetle attractant than to question it.

Should the material one day be available in quantity, the possibilities in adapting it to control operations, either with a toxic agent or in trapping devices (89, p. 353), could allow highly specific control. Research effort to find the attractant is worthy of support that might be forthcoming since it is consistent with the type of control advocated by critics, such as Carson (17), who have argued against excessive use of insecticides.

BIBLIOGRAPHY

1. Adlung, K. G. Über die Ergebnisse der im Schwarzwald 1958 und 1959 durchgeführten Freilandversuche zur Anlockung von Borkenkäfern mit Lockstoffen. Zeitschrift für Angewandante Entomologie 45:430-435. 1960.

2. Allee, W. C. The social life of animals. Rev. ed. Boston, Beacon Press, 1958. 233 p.

3. Allen, Donald G., Robert R. Michael and Solon A. Stone. Sounds of Douglas fir beetle activity. Corvallis, Oregon Forest Lands Research Center, Aug. 1959. 18 p. (Research Note No. 36)

4. Anderson, Roger F. Host selection by the pine engraver. Journal of Economic Entomology 41:596-602. 1948.

5. Atkins, M. D. A study of the flight of the Douglas-fir beetle, Dendroctonus pseudotsugae Hopk. (Coleoptera: Scolytidae) I. flight preparation and response. Canadian Entomologist 91:283-291. 1959.

6. Atkins, M. D. and S. H. Farris. A contribution to the knowledge of flight muscle changes in the Scolytidae. Canadian Entomologist 94:25-32. 1962.

7. Atkins, M. D. and L. H. McMullen. Selection of host material by the Douglas-fir beetle. Canada. Dept. of Agriculture. Science Service, Forest Biology Division. Bi-Monthly Progress Report 14:3. Jan:Feb. 1958.

8. Beal, James A. and Calvin L. Massey. Bark beetles and ambrosia beetles (Coloeptera: Scolytoidea) with special reference to species occuring in North Carolina. Durham, 1945. 177 p. (Duke University. School of Forestry. Bulletin 10)

9. Bedard, W. D. Douglas fir beetle investigations. 1931. 22 numb. leaves. (U. S. Dept. of Agriculture. Bureau of Entomology. Forest Insect Field Station, Coeur d' Alene)

10. ________________. The Douglas-fir beetle. 1950. 10 p. (U. S. Dept. of Agriculture. Circular 817)

11. Beran, O. Forstentomologische Untersuchungen aus dem Gebiete von Lunz. III. Untersuchungen über den Verlauf der absoluten Feuchtigkeit in der Kambialzone liegender Fangbäume. Zeitschrift für Angewandte Entomologie 20:442-448. 1934.

12. Blackman, M. W. The Black Hills beetle, Dendroctonus ponderosae Hopkins. 1931. 177 p. (New York State College of Forestry Bulletin vol. 4, no. 4. Technical Publication No. 36)

13. Bright, Donald E., Jr. Bark beetles of the genus Dryocetes (Coleoptera:Scolytidae) in North America. Annals of the Entomological Society of America 56:103-115. 1963.

14. Buckhorn, W. J. and P. W. Orr. Forest insect conditions in the Pacific Northwest during 1959. 1959. 37 p. (U.S. Dept. of Agriculture. Forest service. Pacific Northwest Forest and Range Experiment Station, Portland)

15. Burgess, Emory D. Development of gypsy moth sex-attractant traps. Journal of Economic Entomology 43:325-328. 1950.

16. Butenandt, A., R. Beckman and D. Stamm. Über den Sexuallockstoff des Seidenspinners, II Konstitution und Konfiguration des Bombykols. Hoppe-Seyler's Zeitschrift für Physiologische Chemie 324:84-87. 1961.

17. Carson, Rachael. Silent spring. Cambridge, Houghton-Mifflin, 1962. 368 p.

18. Chalk, L. and J. M. Bigg. The distribution of moisture in the stem in Sitka Spruce and Douglas-fir. Forestry 29:5-21. 1956.

19. Chamberlin, W. J. The Scolytoidae of the northwest: Oregon, Washington, Idaho and British Columbia. Corvallis, Oregon State College Press, 1958. 208 p.

20. Chapman, J. A. Sex determination by stridulation sounds in the Douglas-fir beetle. Dendroctonus pseudotsugae. Canada. Dept. of Agriculture. Science Service, Forest Biology Division. Bi-Monthly Progress Report 11:2-3. May-June 1955.

21. Chapman, J. A. A note on felling date in relation to log attack by the ambrosia beetle Trypodendron. Canada. Dept. of Agriculture. Science Service, Forest Biology Division. Bi-Monthly Progress Report 17:3-4. Sept. -Oct. 1961.

22. ________________. Field studies on attack flight and log selection by the ambrosia beetle Trypodendron lineatum (Oliv.) (Coleoptera:Scolytidae). Canadian Entomologist 94:75-92. 1962.

23. ________________. Attacks by the bark beetle, Hylastes nigrinus Mannh. (Scolytidae), on Douglas-fir logs. Canada. Dept. of Agriculture. Science Service, Forest Biology Division. Bi-Monthly Progress Report 18:4. Nov. -Dec. 1962.

24. ________________. Attraction of the bark beetle Dolurgus pumilus Mannerheim to a barrel previously containing commercial B. H. C. Canada. Dept. of Agriculture. Science Service, Forest Biology Division. Bi-Monthly Progress Report 19:3. Jan. -Feb. 1963.

25. ________________. Field selection of different log odors by scolytid beetles. Canadian Entomologist 95:673-676. 1963.

26. Chapman, J. A. and J. M. Kinghorn. Studies of flight and attack activity of the ambrosia beetle, Trypodendron lineatum (Oliv.), and other scolytids. Canadian Entomologist 90:362-372. 1958.

27. Chararas, C. Rôle attractif de certains composants des oleoresines à l'égard des Scolytidae des résineux. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences. 247:1653-1654. 1958.

28. ________________. Les variations de la pression osmotique des coniferes facteur déterminant la pénétration des Scolytidae (Insectes Coléoptères). Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences 248:1407-1410. 1959.

29. ________________. Recherches sur le déséquilibre physiologique des branches de coniferes par les Coléoptères Scolytidae. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences. 248:3612-3614. 1959.

30. Chararas, C. Relations entre la pression osmotique et le rôle de la plante-hôte a l'égard des Coléoptères Scolytidae. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences 249:2109-2111. 1959.

31. ________________. Variations de la pression osmotique de Picea excelsa à la suite des attaques de Dendroctonus micans Kug. (Coleoptera Scolytidae). Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences. 251:1917-1919. 1960.

32. Chararas, C. and A. Berton. Nouvelle méthode d'analyses des exhalaisons terpéniques de de Pinus maritima et comportement de Blastophagus piniperda (Coleoptera Scolytidae). Revue de Pathologie Végétale et d'Entomologie Agricole de France 40:235-243. 1961.

33. Chauvin, Rémy. Physiologie de l'insect. 2d ed. Paris, Institute National de la Recherche Agronomique, 1956. 621p.

34. Craighead, F. C. Interrelation of tree killing bark beetles and blue stain. Journal of Forestry 26:886-887. 1928.

35. Dethier, V. G., L. Barton Browne and Carroll N. Smith. The designation of chemicals in terms of the responses they elicit from insects. Journal of Economic Entomology 53: 134-136. 1960.

36. Doane, R. W., et al. Forest insects. New York, McGraw-Hill, 1936. 463 p.

37. Dyer, E. D. A. and J. A. Chapman. Brood productivity of ambrosia beetles in water-soaked logs. Canada. Dept. of Agriculture. Science Service, Forest Biology Division. Bi-Monthly Progress Report 18:3. Sept.-Oct. 1962.

38. Evenden, James C. and Kenneth H. Wright. Douglas-fir beetle. 1955. 4 p. (U. S. Dept. of Agriculture. Forest Pest Leaflet 5)

39. Forestry the world over. Forestry Abstracts 15:262-265. 1954.

40. Fraenkel, G. S. The raison d'etre of secondary plant substances. Science 129:1466-70. 1959.

41. Fraenkel, G. S. and Donald L. Gunn. The orientation of animals. Oxford, Clarendon Press, 1940.

42. Francke-Grossman, H. Some new aspects in forest entomology. Annual Review of Entomology 8:415-483. 1963.

43. Furniss, Malcom M. Reducing Douglas-fir beetle -- how it can be done. 1959. 6 p. (U. S. Dept. of Agriculture. Forest Service. Intermountain Forest and Range Experiment Station, Ogden. Research Note no. 70)

44. ________________. Infestation patterns of Douglas-fir beetle in standing and windthrown trees in southern Idaho. Journal of Economic Entomology 55:486-491. 1962.

45. Gara, R. I. Studies on the flight behavior of Ips confusus (Lec.) (Coleoptera: Scolytidae) in response to attractive materials. Boyce Thompson Institute for Plant Research. Contributions 22:51-66. 1963.

46. Furniss, Malcom M. and J. P. Vité. Studies on the flight patterns of bark beetles (Coleoptera: Scolytidae) in second growth ponderosa pine forests. Boyce Thompson Institute for Plant Research. Contributions 21:275-290. 1962.

47. Gibson, Archie L. Test of bark-penetrating insecticides to control the Douglas-fir beetle. Journal of Economic Entomology 50:267-268. 1957.

48. Graham, K. Release by flight exercise of a chemotropic response from photopositive domination in a scolytid beetle. Nature 184:283-284. 1959.

49. ________________. Air swallowing: a mechanism in photic reversal of the beetle Trypodendron. Nature 191:519-520. 1961.

50. Graham, K. and A. E. Werner. Chemical aspects of log selection by ambrosia beetles. Canada. Dept. of Agriculture. Science Service. Forest Biology Division. Bi-Monthly Progress Report 12:3. Jan.-Feb. 1956.

51. Graham, Samuel Alexander. Forest Entomology. 3d ed. New York, McGraw-Hill, 1952. 351 p.

52. Greeley, A. W., K. H. Wright and R. B. Pope. Final report on the 1952 blowdown and bark beetle survey in the Douglas-fir region of Oregon and Washington. 1953. 33 p. (U. S. Dept. of Agriculture. Forest Service. Pacific Northwest Forest and Range Experiment Station, Portland)

53. Hall, Ralph C. Environmental factors associated with outbreaks by the western pine beetle and the California five-spined pine engraver in California. Proceedings of the Tenth International Congress of Entomology, Montreal, 1956. 4:341-347. (1958)

54. Hendrickson, W. H. and J. P. Vité. The pattern of water conduction and tracheidal alignment in Douglas-fir. Boyce Thompson Institute for Plant Research. Contributions 20: 353-362. 1960.

55. Hesse, Gerhard, Herbert Kauth and Rudolf Wachter. Frasslockstoffe beim Fichtenrüsselkafer Hylobius abietis. Zeitschrift für Angewandte Entomologie 37:239-244. 1955.

56. Heirholzer, Otto. Ein Beitrag zur Frage der Orientierung von Ips curvidens Germ. Zeitschrift für Tierpsychologie 7: 588-620. 1950.

57. Hopkins, A. D. Contributions toward a monograph of the scolytid beetles. I. The genus Dendroctonus. 1909. 164 p. (U. S. Dept. of Agriculture. Bureau of Entomology, Technical Series, no. 17, Part I)

58. ________________. Practical information on the scolytid beetles of North American forests. I. Barkbeetles of the genus Dencrotonus. 1909. 169 p. (U. S. Dept. of Agriculture. Bureau of Entomology, Technical Series, no. 83, Part I)

59. Huckenpahler, B. J. A comparison of several methods of making moisture determinations of standing trees and logs. Journal of Forestry 34:165-168. 1936.

60. Inouye, M. Studies on the relation between bark beetle attack and moisture content of the sapwood forest in Hokkaido, Japan. Ministry of Agriculture and Forestry. Forestry Experimental Station, Meguro. Bulletin 68:167-180. 1954.

61. Jacobson, Martin and M. Beroza. Chemical insect attractants. Science 140:1367-1373. 1963.

62. Jacobson, Martin, M. Beroza and W. A. Jones. Isolation, identification and synthesis of the sex attractant of the gypsy moth. Science 132:1011-1012. 1960.

63. Jantz, Orlo K. and Richard L. Johnsey. Determination of sex of the Douglas-fir beetle Dendroctonus pseudotsugae Hopkins (Coleoptera:Scolytidae). Canadian Entomologist 96:1327-1329. 1964.

64. Johnson, Norman E. Field identification of ambrosia beetles attacking coniferous timber in the Douglas-fir region. Canadian Entomologist 90:236-240. 1958.

65. ________________. Ambrosia beetle infestation of coniferous logs on clearcuttings in northwestern Oregon. Journal of Forestry 56:508-511. 1958.

66. ________________. Douglas-fir beetle: A problem analysis. Centralia, Wash., 1960. 19 p. (Weyerhaeuser Co. Forestry Research Center. Forestry Research Note no. 29)

67. ________________. Reduction of risk of losses by the Douglas-fir beetle and ambrosia beetles: An interim guide. Centralia, Wash., 1960. 8 p. (Weyerhaeuser Co. Forestry Research Center. Forestry Research Note no. 34)

68. ________________. Ambrosia beetle attacks in young-growth western hemlock. Canada. Dept. of Agriculture. Science Service, Forest Biology Division. Bi-Monthly Progress Report 17:3. Sept.-Oct. 1961.

69. ________________. Rearing of Douglas-fir beetle broods in waxed slabs. Annals of the Entomological Society of America 55:659-663. 1962.

70. ________________. Factors influencing the "second attack" of the Douglas-fir beetle - progress 1960-1962. 1963. 14 p. (Weyerhaeuser Co. Forestry Research Center. Forestry Research Note no. 53)

71. Johnson, Norman E. and Leon F. Pettinger. Douglas-fir beetle attacks in living trees as influenced by the presence of fresh windthrow. Centralia, Wash., 1961. 8 p. (Weyerhaeuser Co. Forestry Research Center. Forestry Research Note no. 37)

72. ________________. Overwintering mortality of Doulgas-fir beetles in infested logs, exposed bark and forest litter in western Washington. Centralia, Wash., 1961. 11 p. (Weyerhaeuser Co. Forestry Research Center. Forestry Research Note no. 42)

73. Johnson, Norman E., K. H. Wright and P. W. Orr. Attack and brood survival by the Douglas-fir beetle in four types of windthrown trees in western Washington. Centralia, Wash., 1961. 8 p. (Weyerhaeusser Co. Forestry Research Center. Forestry Research Note no. 40)

74. Karlson, Peter and Adolf Butenandt. Pheromones (ectohormones) in insects. Annual Review of Entomology 4:39-58. 1959.

75. Keen, F. P. Insect enemies of western forests. Rev. 1952. 280 p. (U. S. Dept. of Agriculture. Miscellaneous Publication no. 273)

76. Kennedy, J. S., C. O. Booth and W. J. S. Kershaw. Host finding by aphids in the field. III. Visual attraction. Annals of Applied Biology. 49:1-21. 1961.

77. Kinghorn, J. M. Fall notes on timber deterioration study. Canada. Dept. of Agriculture. Science Service, Forest Biology Division. Bi-Monthly Progress Report 5:4. Sept.-Oct. 1949.

78. ________________. Sapwood moisture in relation to Trypodendron attacks. Canada. Dept. of Agriculture. Science Service, Forest Biology Division. Bi-Monthly Progress Report 12:3-4. Sept.-Oct. 1956.

79. ________________. An induced differential bark-beetle attack. Canada. Dept. of Agriculture. Science Service, Forest Biology Division. Bi-Monthly Progress Report 13:3-4. Mar.-Apr. 1957.

80. Kinghorn, J. M. and J. A. Chapman. The effect of Douglas-fir log age on attack by the ambrosia beetle, Trypodendron lineatum (Oliv.). Proceedings of the Entomological Society of British Columbia 54:46-49. 1957.

81. Kliefoth, R. A., J. P. Vité and G. P. Pitman. A laboratory technique for testing bark beetle attractants. Boyce Thompson Institute for Plant Research. Contributions 22:283-290. 1964.

82. Kline, L. N. Insect enemies of Dendroctonus pseudotsugae Hopk.: Identification of their immature stages and distribution in standing trees. Master's thesis. Corvallis, Oregon State University, 1963. 122 numb. leaves.

83. Lehos, Harri. Havupuiden rasünkaato (Summer felling of conifers). Metsataloudellinen Aikakauslehti :87. 1954.

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

85. Li, Jerome C. R. Introduction to statistical inference. Ann Arbor, Edwards Brothers, 1957. 553 p.

86. Loschiavo, S. R., S. D. Beck and D. M. Norris. Behavioral responses of the smaller European elm bark beetle, Scolytus multistriatus (Coleoptera:Scolytidae) to extracts of elm bark. Annals of the Entomological Society of America 56:764-768. 1963.

87. Lu, D. C., Donald G. Allen and Walter B. Bollen. Association of yeasts with the Douglas-fir beetle. Forest Science 3:336-342. 1957.

88. Lyon, R. L. A useful secondary sex character in Dendroctonus bark beetles. Canadian Entomologist 90:582-584. 1958.

89. Martin, Charles H. Preliminary report of trap-log studies on elm bark beetles. Journal of Economic Entomology 29:297-306. 1936.

90. Martin, Charles H. Effect of phloem condition and phloem moisture on the entry of Scolytus multistriatus. Journal of Economic Entomology 39:481-486. 1946.

91. Mathers, W. G. Douglas-fir beetle. Canada. Department of Agriculture. Science Service, Forest Biology Division. Bi-Monthly Progress Report 7:3. May-June 1951.

92. McComb, David. Relationship between trap tree felling dates and subsequent Engelmann spruce beetle attack. 1955. 4 p. (U.S. Dept. of Agriculture. Forest Service. Intermountain Forest and Range Experiment Station, Ogden. Research Note no. 23)

93. McCowan, Vaughan F. and Julius R. Rudinsky. Biological studies on the Douglas-fir bark beetle: Millicoma Forest Tree Farm, Coos Bay, Oregon. A progress report. Rev. 1958. Centralia, Wash., 1954. 21 p. (Weyerhaeuser Co. Forestry Research Center)

94. McMullen, L. H. and M. D. Atkins. Intraspecific competition as a factor in natural control of the Douglas-fir beetle. Forest Science 7:198-203. 1961.

95. ________________. On the flight and host selection of the Douglas-fir beetle, Dendroctonus pseudotsugae Hopk. (Coleoptera: Scolytidae). Canadian Entomologist 94: 1309-1325. 1962.

96. Merker, E. Das Wetter der Jahre 1939 bis 1950 and sein Einfluss auf die Massenvermehrung des grossen Fichtenborkenkäfers in Südbaden. Allgemeine Forst-und Jagdzeitung 123:213-233 and 124:1-22. 1952-53.

97. ________________. Lockstoffe und Nährstoff in Wirtspflanzen einiger Waldschädlinge. Allgemeine Forst-und Jagdzeitung 124:138-144. 1953.

98. ________________. Jahrelanger Widerstand von Amerikanischen Hemlockstannen gegen die Angriffe einheimischer Borkenkäfer. Allgemeine Forst-und Jagdzeitung 125: 209-217. 1954.

99. ________________. Der Widerstand von Fichten gegen Borkenkäferfrass. Allgemeine Forst-und Jagdzeitung 127: 129-145; 168-187. 1956.

100. Merker, E. and H. Muller. Die Abhängigkeit des Frasses der Fichtenborkenkäfer vom Bodenklima. Allgemeine Forst- und Jagdzeitung 123:16-20. 1951.

101. Miller, J. M. and F. P. Keen. Biology and control of the western pine beetle. 1960. 381 p. (U. S. Dept. of Agriculture. Forest Service. Miscellaneous Publication 800)

102. Mirov, Nicholas T. The fragrance of pines. Atlantic Monthly 204:60-61. 1959.

103. Nagel, R. H., David McComb and F. B. Knight. Trap tree method for controlling the Engelmann spruce beetle in Colorado. Journal of Forestry 55:894-898. 1957.

104. Northwest Forest Pest Action Committee. An evaluation of forest insect and disease. Research needs in Oregon and Washington. Part I. 1953. 27 p.

105. Orr, P. W. Forest insect conditions in the Pacific Northwest during 1962. U. S. Dept. of Agriculture. Forest Service. Insect and Disease Control Branch, Division of Timber Management, Pacific Northwest Region. 1963.

106. Parr, Thaddeus. Voltage gradient in trees as an indicator of susceptibility to insect attack. Journal of Forestry 41:417-421. 1943.

107. Person, H. L. Theory in explanation of the selection of certain trees by the western pine beetle. Journal of Forestry 29:696-699. 1931.

108. Pertunnen, Vilho. Reactions of two bark beetle species, Hylurgops palliatus Gyll. and Hylastes ater Payk. (Coleoptera:Scolytidae) to the terpene α-pinene. Suomen Hyönteistieteellinen Aikakauskirja Annales Entomologici Fennici 23:101-110. 1957.

109. Peterson, Alvah. Larvae of insects. Part II. 4th ed. Ann Arbor, Edwards Brothers, 1960. 415 p.

110. Pfeffer, A. Der Verlauf des Borkenkäferbefalles und der Holzfeuchtigkeit von künstlich zum Eintrocknen gebrachten Fichtenstämmen. Zeitschrift für Angewandte Entomologie 41:196-207. 1957.

111. Pitman, G. B. and J. P. Vité. Studies on the pheromone of Ips confusus (Lec.) I. Secondary sexual dimorphism in the hindgut epithelium. Boyce Thompson Institute for Plant Research. Contributions 22:221-226. 1963.

112. Prebble, M. L. and K. Graham. Studies of attack by ambrosia beetles in softwood logs on Vancouver Island, British Columbia. Forest Science 3:90-112. 1957.

113. Reid, R. W. Moisture changes in lodgepole pine before and after attack by the mountain pine beetle. Forestry Chronicle 37:368-403. 1961.

114. ________________. Biology of the mountain pine beetle, Dendroctonus monticolae Hopkins, in the East Kootenay region of British Columbia. I, II, III. Canadian Entomologist 94:531-538. 1962. 94:604-613. 1962. 95:225-238. 1963.

115. Rudinsky, J. A. Factors affecting the population density of bark beetles. In: Proceedings, 13th Congress, International Union of Forest Research Organizations, Vienna, 1961. Part 2, vol. 1. Vienna, 1962. Sept. 24, no. 11, p. 1-13.

116. ________________. Ecology of Scolytidae. Annual Review of Entomology 7:327-348, 1962.

117. ________________. Responses of Dendroctonus pseudotsugae Hopkins to volatile attractants. Boyce Thompson Institute for Plant Research. Contributions 22:23-38. 1963.

118. Rudinsky, J. A., L. C. Terriere and D. G. Allen. Effectiveness of various formulations of five insecticides on insects infesting Douglas-fir logs. Journal of Economic Entomology 53:949-953. 1959.

119. Rudinsky, J. A. and J. P. Vité. Effects of temperature upon the activity and the behavior of the Douglas-fir beetle. Forest Science 2:259-267. 1956.

120. Rudinsky, J. A. and G. E. Daterman. Field studies on flight patterns and olfactory responses of ambrosia beetles in Douglas-fir forests of Western Oregon. Canadian Entomologist 96:1339-1352. 1964.

121. Ryan, Roger B. Termination of diapause in the Douglas-fir beetle Dendroctonus pseudotsugae Hopkins (Coleoptera: Scolytidae), as an aid to continuous laboratory rearing. Canadian Entomologist 91:520-525. 1959.

122. Ryan, Roger B. and Julius A. Rudinsky. Biology and habits of the Douglas-fir beetle parasite, Coeloides brunneri Viereck (Hymenoptera: Braconidae), in western Oregon. Canadian Entomologist 94:748-763. 1962.

123. Schimitschek, E. Folgen der Einbringung fremder Holzarten im Nordwestdeutschen (besonders Küstennahen) Raum. Bericht über die Tagung. Nordwestdeutscher Forstverein 20:26-63. April, 1959. (Abstracted in Forestry Abstracts 20:no. 2048. 1959)

124. Schwerdtfeger, F. Pathogenese der Borkenkäfer-Epidemie 1946-1950 in Nordwestdeutschland. Schriftenreihe der Forstlichen Fakultät der Universität Göttingen, Band 13/14, 135 p. 1955.

125. Shepherd, R. F. Distribution of the Black Hills beetle over the host tree and factors controlling the attraction and behavior of the adult. Dissertation Abstracts 21:1001. 1960.

126. Sierpinski, A. A trial of standing trap trees to control secondary insect pests of Scots pine. Prace Instytut Badawczy Leśnictwa 248:211-223. 1962. (Abstracted in Forestry Abstracts 24:no. 3945. 1963)

127. Smith, Frederick E. and Edward R. Baylor. Color responses in the Cladocera and their ecological significance. The American Naturalist 87:49-55. 1953.

128. Smith, Richard H. The fumigant toxicity of three pine resins to Dendroctonus brevicomis and D. jeffreyi. Journal of Economic Entomology 54:365-369. 1961.

129. ______________. Preferential attack by Dendroctonus terebrans on Pinus elliotti. Journal of Economic Entomology 56:817-819. 1963.

130. Smith, Richard H. Toxicity of pine resin vapors to three species of Dendroctonus bark beetles. Journal of Economic Entomology 56:827-831. 1963.

131. Struble, George R. and Ralph C. Hall. The California five spined engraver, its biology and control. 1955. (U.S. Dept. of Agriculture. Circular 964)

132. Thalenhorst, Walter. Die Borkenkäfer-Katastrophe in Deutschland. Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz 60:15-19. 1953.

133. ________________. Grundzüge der Populationsdynamik des grossen Fichtenborkenkäfers Ips typographus L. Schriftenreihe der Forstlichen Fakultät der Universität Göttingen, Band 21, 126 p. 1958.

134. Thorsteinson, A. J. Host selection in phytophagous insects. Annual Review of Entomology 5:193-218. 1960.

135. U.S. Dept. of Agriculture. Annual Report, 1961. 48 p. (Forest Service. Intermountain Forest and Range Experiment Station, Ogden)

136. Vité, J. P. The influence of water supply on oleoresin exudation pressure and resistance to bark beetle attack in Pinus ponderosa. Boyce Thompson Institute for Plant Research. Contributions 21:37-66. 1961.

137. Vité, J. P. and R.I. Gara. A field method for observation of olfactory responses of bark beetles (Scolytidae) to volatile material. Boyce Thompson Institute for Plant Research. Contributions 21:175-182. 1961.

138. ________________. Volatile attractants from ponderosa pine attacked by bark beetles (Coleoptera: Scolytidae). Boyce Thompson Institute for Plant Research. Contributions 21:251-273. 1962.

139. Vité, J. P., R.I. Gara and R. A. Kliefoth. Collection and bioassay of a volatile fraction attractive to Ips confusus (Lec.) (Coleoptera: Scolytidae). Boyce Thompson Institute for Plant Research. Contributions 22:39-50. 1963.

140. Vité, J. P. and J. A. Rudinsky. Contribution toward a study of Douglas-fir beetle development. Forest Science 3:156-167. 1957.

141. ________________. The water conducting systems in conifers and their importance to the distribution of trunk injected chemicals. Boyce Thompson Institute for Plant Research. Contributions 20:27-38. 1959.

142. Vité, J. P. and David L. Wood. A study on the applicability of the measurement of oleoresin exudation pressure in determining susceptibility of second growth ponderosa pine to bark beetle infestation. Boyce Thompson Institute for Plant Research. Contributions 21:67-68. 1961.

143. Walters, J. Investigations of the Douglas-fir beetle. I. Tree classification. Vernon, B. C., Canada. Dept. of Agriculture. Science Service, Forest Biology Laboraotry, 1954. 68 p.

144. ________________. Douglas-fir beetle associated with winter injury. Canada. Dept. of Agriculture. Science Service, Forest Biology Divisions. Bi-Monthly Progress Report 11:4. July-Aug. 1955.

145. ________________. A system of indirect control of the Douglas-fir beetle Dendroctonus pseudotsugae Hopk. Master's thesis. Vancouver, University of British Columbia, 1955. (Abstracted in Forestry Chronicle 34:326-327. 1958)

146. ________________. Biology and control of the Douglas-fir beetle in the interior of British Columbia. Vernon, B. C., Canada. Dept. of Agriculture. Science Service, Forest Biology Division. Publication 975. 1956. 11 p.

147. Ward's Biological Supplies Catalog no. 621. Rochester 3, N. Y. Ward's Natural Science Establishment. 1962.

148. Werner, A. E. and K. Graham. Volatile wood constitutents in relation to ambrosia beetles. Canada. Dept. of Agriculture. Science Service, Forest Biology Division. Bi-Monthly Progress Report 13:3. July-Aug. 1957.

149. Wharton, Denis R. A., et al. Isolation of the sex attractant of the American cochroach. Science 137:1062-1063. 1962.

150. Whiteside, J. M. Report of forest insect surveys in Oregon and Washington, season of 1955. Portland, Ore., U. S. Dept. of Agriculture, Forest Service. Pacific Northwest Forest and Range Experiment Station, 1955. 55 p.

151. Wilson, Edward O. Source and possible nature of the odor trail of fire ants. Science 129:643-644. 1959.

152. ________________. Biocommunication. In: Encyclopedia of the Biological Sciences. New York, Reinhold, 1961.

153. Wilson, Louis F. Attraction of wood boring insects to freshly cut pulpsticks. 1961. 2 p. (U. S. Dept. of Agriculture, Forest Service. Lake States Forest Experiment Station. Technical Note 610)

154. Wilson, Louis F. and James Bean. A modified olfactometer. Journal of Economic Entomology 52:621-624. 1959.

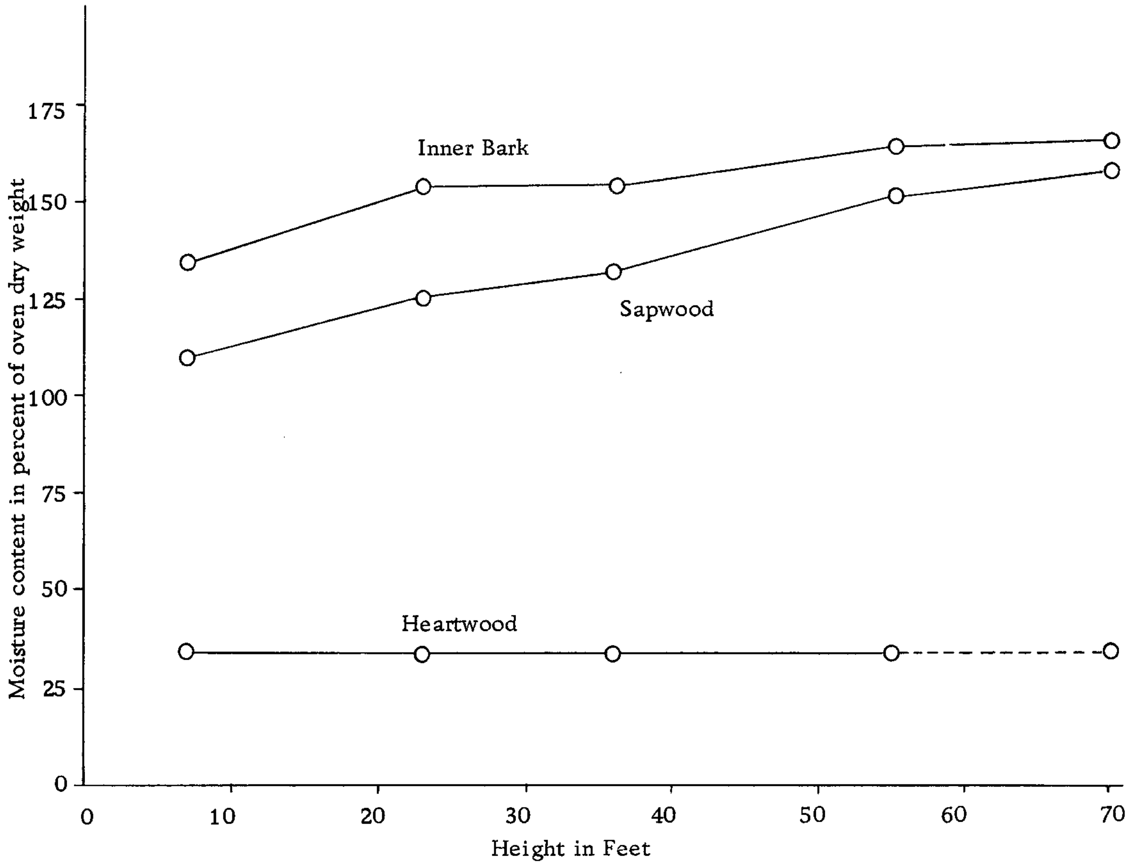
155. Wood, David L. The attraction created by males of a bark beetle *Ips confusus* (LeConte) attacking ponderosa pine. The Pan-Pacific Entomologist 38:141-145. 1962.

156. Wood, David L. and J. P. Vité. Studies on the host selection behavior of *Ips confusus* (LeConte) (Coleoptera: Scolytidae) attacking *Pinus ponderosa*. Boyce Thompson Institute for Plant Research. Contributions 21:79-96. 1961.

157. Wood, Stephen L. A revision of the bark beetle genus *Dendroctonus* Erichson (Coleoptera: Scolytidae). The Great Basin Naturalist 23:1-117. 1963.

158. Wygant, N. D. Engelmann spruce beetle control in Colorado. In: Proceedings of the Tenth International Congress of Entomology. Montreal, 1956. Ottawa, 1958. 4:181-184.

APPENDIX



Appendix
Figure 1. Average Moisture Content of Inner Bark, Sapwood, and Heartwood of Ten Co-dominant Douglas-fir Trees. Sections of the Trees, Cut at Black Rock, 25 Miles Northwest of Corvallis Were Brought to the Laboratory. Large Pieces Were Used for Determinations

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Appendix Table 1. Attractance associated with the female Douglas-fir beetle demonstrated in another study. This data evolved from a study conducted by LeRoy N. Kline, another graduate student at Oregon State University. Mr. Kline allowed the author to examine his experiment and to read the data from it.

For a field study of predators of the Douglas-fir beetle, logs were supplied with introduced beetles. Females exclusively were used for one treatment; pairs of beetles were used for a second treatment. Control logs not having introduced beetles were also used. Logs, cut from the same tree, were three feet in length. When females were introduced, their number was approximately 25 per log. A like number of beetle pairs were involved when introductions for the pairs treatments were made. Four logs were prepared for each treatment, providing material for four replications.

After the beetles were in place, a wire screen cylinder was mounted around each log so there was three inches clearance between the log and the screen. The screen was secured to the log at the top and bottom in such a manner as to prevent beetle escape, entry, or predation. A viscous, sticky material was applied in random cross-hatched pattern in equivalent manner to each of the surfaces of the screens of all the logs.

Beetles attracted to the logs became entangled in the sticky material. A count of them is the data recorded.

Logs placed in field on June 1.		Treatment											
		Log With ♀				Log With Pairs				Control Log			
Dates of Observation		in replicate				in replicate				in replicate			
		1	2	3	4	1	2	3	4	1	2	3	4
June 15	♀ caught	5	4	9	6	1	2	2	2				2
	♂ caught	12	3	28	24	1		1	2				1
June 27	♀ caught	2	4	17	12		1	1					
	♂ caught		2	11	21	1						1	

Some Notes in Regard to the Attack Pattern of Gnathotrichus sp.

Two of the species, G. sulcatus and G. retusus, are attracted to logs containing female Douglas-fir beetles (120, p. 1350).

The genus attacked logs which had been soaked. Excluding small numbers of exceptions, Gnathotrichus sp. did not attack unsoaked logs (Table 5). This was true even when the unsoaked logs contained Douglas-fir beetles (Table 5 and Figure 27).

Gnathotrichus sp. exhibited greater attack in those soaked logs which had the lesser number of Douglas-fir beetles (Table 5 and Figure 27).

As for timing of the attack, the Gnathotrichus beetles increased the number of their entries into the particular (wet) logs of the experiment as the new entries of the Douglas-fir beetles were decreasing.

Gnathotrichus sp.	As of the Date Indicated	Douglas-fir beetle
First attacks had occurred: one or two per 3 foot log.	June 4, 6, 8	Had reached approximately 50 percent of the total of 3540 attacks that would occur in the study logs of the experiment.
Two to 20 attacks present in various wet logs	June 14	Attack 90 percent complete.
Ten to 35 attacks present in various wet logs.*	June 23	Attack 99 percent complete.
24 to 300 attacks present in various wet logs.*	August 16	No attacks after June 30.

*There were four or five logs per treatment; hence the values of 45 to 205 attacks per treatment (June 23 data) and 170 to 610 attacks per treatment (August 16 data) as shown in Table 5.