

AN ABSTRACT OF THE THESIS OF

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Title: A CONTRIBUTION TO THE BIOLOGY OF *PSEUDOHYLESINUS NEBULOSUS*

(LECONTE) (COLEOPTERA:SCOLYTIDAE), ESPECIALLY IN RELATION

TO THE MOISTURE STRESS OF ITS HOST, DOUGLAS-FIR

Abstract approved:

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Professor Julius A. Rudinsky

The study (1) describes the life cycle of *P. nebulosus*, (2) examines stimuli that may cause the beetles to locate brood material, and (3) establishes the relationship between moisture stress in Douglas-fir and colonization by *P. nebulosus* and other meristem insects.

(1) Development of *P. nebulosus* goes through the egg stage, three larval instars, and the pupal and callow adult stages. Teneral adults emerge from late spring through fall, disperse, and feed in tissues of live Douglas-fir twigs before attaining sexual maturity. Progeny initiated in early spring may become capable of reproduction and initiate colonization of susceptible host material in fall. *P. nebulosus* overwinters in all stages except the egg and pupal stages, hibernating in feeding tunnels or galleries of newly colonized breeding sites. The main breeding period is the early spring. Females begin gallery construction.

(2) The flight of immature beetles is governed by temperature, but is induced by light and appears primarily oriented toward light. Positive photic response appears to overpower response to vegetative stimuli.

Temperature induces a reversal in the beetle's photic response at two thresholds (15.5°C and 34°C). Decrease of light intensity to 17 f.c. induces a light negative and thigmotactic response. Two temperatures (19°C and 34°C) limit the range for flight take-off, which occurs only under conditions inducing positive phototropism in the beetle.

Field tests failed to attract flying immature beetles to materials known as highly attractive to mature beetles. In laboratory tests, walking beetles responded to ethanol vapors in darkness but were unresponsive in the light. Circumstantial evidence suggests that the beetles alight into Douglas-fir crowns by chance and respond to feeding stimuli under condition-favoring negative phototaxis and thigmotaxis.

The flight of mature *P. nebulosus* differs from the flight of immature beetles primarily in orientation. Field tests showed strong response by mature *P. nebulosus* to fresh Douglas-fir twigs and stem sections as well as to certain monoterpene solutions and ethanol.

Ethanol was also attractive to *Pseudohylesinus grandis* Sw.; *Dendroctonus pseudotsugae* Hopk.; *Hylastes nigrinus* (Mann);

Gnathotrichus spp.; *Trypodendron lineatum* Oliver; and *Anisandrus pyri* (Peck). This suggests the possibility that ethanol is a constituent of primary host-attraction also to other scolytids besides timber beetles as suggested by others.

The bimodal flight pattern of mature *P. nebulosus* and its possible causes are discussed. It is possible that trees under midday moisture deficits may become a temporary attraction source and 'absorb' part of the airborne population.

(3) Diurnal and seasonal changes in moisture relations of Douglas-fir were determined by Scholander's pressure chamber technique of measuring plant moisture stress (PMS) in vascular plants. The ecological interpretation of PMS, determined at dawn and at midday, is discussed.

The relationship between PMS in Douglas-fir and colonization by meristem insects was established by correlating the infestation status of a tree with its PMS (diurnal minimum) condition. PMS thresholds were found which indicate whether a host tree is in a condition (a) inducive; (b) tolerant, or (c) abortive to initial colonization by *P. nebulosus*, *Scolytus unispinosus* Lec., *D. pseudotsugae* (Scolytidae), and *Melanophila drummondi* Kirby (Buprestidae). These PMS thresholds appear specific for each insect species. The relation between the cardinal PMS condition in the insect-host relationship and other physiological parameters of the tree, such as photosynthetic activity, cell division, etc., are

discussed. Only trees under PMS levels indicative of physiological condition with curtailed integrative processes become inducive to attacks by meristem insects. Ecological, silvical and entomological conclusions based on the obtained results may be important in forest management considerations regarding reduction of damage caused by bark beetles.

A Contribution to the Biology of the *Pseudohylesinus*
nebulosus (LeConte) (Coleoptera:Scolytidae), especially in
Relation to the Moisture Stress of its Host, Douglas-fir.

by

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A CONTRIBUTION TO THE BIOLOGY OF THE
PSEUDOHYPHESINUS NEBULOSUS (LECONTE)
(COLEOPTERA:SCOLYTIDAE), ESPECIALLY IN
RELATION TO THE MOISTURE STRESS
OF ITS HOST, DOUGLAS-FIR

INTRODUCTION

Bark beetles are among the most destructive forest insects known. They decimate millions of board feet of coniferous timber yearly. For example, in Washington and Oregon alone, some 74 billion board feet of Douglas-fir were killed during four major outbreaks of the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins in the period from 1950 to 1969; in addition, the losses during non-outbreak conditions averaged 10 million board feet annually (Furniss and Orr, 1970).

Factors leading to Douglas-fir beetle outbreaks were recently reviewed (Johnson and Belluschi, 1969). The key factor is believed to be the large beetle population amassed in years following severe blow-downs or other calamities that provide a surplus of breeding material (Furniss, 1936; McCowan and Rudinsky, 1954; Wright and Lauterbach, 1958).

As with other bark beetles, the amount and distribution of host material suitable for colonization may greatly affect the extent of tree mortality caused by a given Douglas-fir beetle population. It follows that factors predisposing trees to attack have to be understood and the stand condition qualitatively and quantitatively assessed to predict the extent of damage and to determine measures to reduce the damage.

The role of other subcortical feeding insects associated with Douglas-fir in predisposing hosts to attack by *Dendroctonus pseudotsugae* has received little attention. Some of the associated bark beetles known to colonize Douglas-fir blowdowns in large numbers are: the Douglas-fir hylesinus (*Pseudohylesinus nebulosus* Lec.), the one-spined scolytus (*Scolytus unispinosus* Lec.), and a Buprestidae (*Melanophila drummondi* Kirby). It is noteworthy that progeny of *Pseudohylesinus nebulosus* and *Scolytus unispinosus*, emerging from downed trees, infest new breeding material before Douglas-fir beetles complete their development.

Little is known about the ecological role of these insects. They are considered unimportant, but reports that some of these species kill young trees or tops of mature trees (Chamberlin, 1958) suggest their possible importance in providing outbreak foci for *D. pseudotsugae*.

Objectives

The general objective of this study was to study the host selection behavior of *Pseudohylesinus nebulosus* with some attention to associated subcortical insects. In detail, the specific objectives were as follows:

- (1) To describe the life cycle of *P. nebulosus* in Western Oregon.

- (2) To determine the nature of stimuli that induce and govern flight of *P. nebulosus* and cause the flying beetle to locate brood material.
- (3) To assess moisture stress conditions in Douglas-fir as related to *P. nebulosus* and other subcortical insect colonization.

Research on these objectives was initiated in January, 1966 and terminated in spring 1968. Field studies were conducted primarily in the McDonald Forest near Corvallis, Oregon, with comparative observations in old-growth stands in the Mary's Peak area, near Philomath. Laboratory work was done at the Forest Entomological Laboratory of the Department of Entomology at Oregon State University.

The field and laboratory research was supported by National Science Foundation Grant #30-4417 directed by Dr. J. A. Rudinsky. Data analysis and manuscript preparation was supported from the candidate's private resources and with assistance by the Weyerhaeuser Corporation.

LITERATURE REVIEW

The Douglas-fir Hylesinus, *P. nebulosus*

Pseudohylesinus nebulosus was described by LeConte (1859) as *Hylesinus nebulosa*. Swaine (1918), in a generic revision, transferred the species to *Pseudohylesinus* and refers to it (p. 75), "...as a

slender species, with strong color-markings in dark and reddish-brown; the male very densely clothed with stout scales; the epistomal lobe strongly developed; length 2.8mm; width, 1.2mm. The supposed female has interspace 9 on the declivity less strongly serate, and the elytral scales decidedly elongate and becoming plumose towards the base."

P. nebulosus is associated with Douglas-fir, *Pseudotsuga menziesii* Mirb. (Franco), and its range corresponds with that of its host (Chamberlin, 1958). Among scolytids associated with Douglas-fir, it is the earliest to breed in spring, according to Daterman, Rudinsky and Nagel (1965). It is a monogamous species with the female initiating the gallery. There are three larval stages and the pupal stage (Walters and McMullen, 1956). Emergence of new beetles was observed as early as mid-May (Chamberlin, 1918; 1958). In interior British Columbia, there is one generation per year (Walters and McMullen, 1956) with a partial second generation in Oregon and on the British Columbia Coast (Hopping, 1928; Chamberlin, 1918). Chamberlin (in Walters and McMullen, 1956) reports two generations per year in Southern California.

P. nebulosus is considered to be a secondary insect; it is found primarily in slash and thin-barked material (Walters and McMullen, 1956). Chamberlin (1918; 1958) however, reported that beetles frequently killed the tops of healthy mature Douglas-fir in the Willamette Valley of Oregon.

Host Selection by Scolytidae

Mechanisms by which insects find their hosts may be viewed as a sequence of stimulus-response chains (Wigglesworth, 1950; Dethier, 1953; Thorsteinson, 1960) with chemoreception playing the key role in final recognition of the host plant (Schoonhoven, 1968). Dethier (1953) and Thorsteinson (1960) associate the following behavioral patterns with host selection by phytophagous insects: (1) dispersal; (2) orientation to the food; (3) biting response; and (4) continuous feeding.

With Scolytidae, flight is essential in the stimuli-response chain leading to host location. Scolytid flight consists of two distinct phases, the dispersal and the aggregation phase (Gara and Vité, 1962; Southwood, 1962). The orientation of flying scolytids in each phase is distinct, as each phase has an unique ecological function. The dispersal phase ensures displacement of new adults, increasing the chances for a part of the brood to encounter and respond to stimuli leading to initial host finding. According to Southwood (1962), a beetle in the dispersal (or migratory) phase of the flight does not respond to any vegetative stimulus, such as food, mate or shelter. It means that the

flight of scolytidae, during the dispersal phase, must be governed by physical factors such as temperature and light. The ability of scolytidae to respond during flight to vegetative stimuli appears to be physiologically induced. For instance, *Trypodendron lineatum* (Oliv.) needs flight exercise to lower the threshold level for olfactory perception sufficiently for olfactory stimuli to overpower the dominating effect of light (Graham, 1959). Once the beetle encounters an olfactory stimulus in a concentration above the threshold level for perception, it orients its flight toward the stimulus and enters into the aggregation flight phase.

Scolytidae aggregate on host material primarily through olfactory responses governed by host odors and insect-produced pheromones. Some workers believe that the initial attack (by pioneer beetles) involves random selection (Vité and Wood, 1961; Berryman and Ashraf, 1970), other that colonization is induced by odors from the host (Person, 1931; Pertunnen, 1957; Chararas, 1959; Chapman, 1962; 1963) under a certain physiological condition (Browne, 1952; Heikkinen and Hrutfiord, 1965; Rudinsky, 1966b; Francia and Graham, 1967; Graham, 1968; Goeden and Norris, 1967; Moeck, 1970; Cade, Hrutfiord and Gara, 1970). Some Scolytidae are believed to respond to host odors alone (Perttunen, 1957); others, upon contact with the host tissues, release an attractive substance that synergizes the host volatiles (Anderson, 1948; McMullen and Atkins, 1962; Meyer and Norris, 1967; Rudinsky, 1963; 1966; Rudinsky and Daterman, 1964; Silverstein *et al.* 1966; Vité, 1962; Vité *et al.* 1964;

Wood, 1962; 1963). Certain metabolites of host tissue seem to affect attractant production (Pitman, 1966). In general, the behavior involved in host location varies among species and can vary even within a species as modified by such factors as population density, physical environment, or the insect's physiological condition (Atkins, 1966a; Borden, 1967; Gara, 1963; Graham, 1959).

Beetles respond upwind to sources of attraction, and areas of more intense attraction amass the greatest number of beetles (Chapman, 1962; Gara, 1963). Experiments designed to explain how scolytids orient upwind to a source of attraction have been less fruitful. Person (1931) proposed that chemo-anemotaxis toward airborne gradients of attractive substances is involved in host selection, an oversimplified assumption if one considers the characteristics of air movement in a forest (Chapman, 1963). Wright (1958) proposed that insects orient their flight by the frequency of olfactory encounter, and that as intervals between chemostimulations increase, klinokinetic movements place the insects back on the odor track. Wind is, in the context of Wright's theory, only a carrier of information.

Host Disposition to Colonization by Scolytidae

Circumstantial and scientific evidence linking bark beetle attack with trees in a moisture deficient condition, regardless of its cause, has been available for some time (Blackman, 1924; Craighead, 1925;

Kraemer, 1949; 1950; 1953; Merker, 1956; Zwölfer, 1957; Chararas, 1959; Miller and Keen, 1960; Schimitschek and Wienke, 1963; Stark and Cobb, 1969).

Considerable research was conducted on the role of oleoresin in host-bark beetle relationship and is reviewed in more detail by Rudinsky (1962) and Stark (1965). Attention focused on: (1) the role of oleoresin in host defense to bark beetle colonization (Caird, 1935; Merker, 1960; Miller and Keen, 1960; Reid, 1963; Reid and Gates, 1970; Smith, 1961); (2) the role of oleoresin as a possible attractant (Chararas, 1959; Heikkinen and Hrutfiord, 1965; Rudinsky, 1966b; Jantz and Rudinsky, 1966); (3) the possibility that intraspecific variation in monoterpene composition might be a factor in resistance to bark beetle attack (Smith, 1966); and (4) the role of oleoresin exudation pressure (OEP) in predisposition of trees to bark beetle colonization (Vité and Rudinsky, 1960; Vité, 1961; Vité and Wood, 1961; Rudinsky, 1962; Vité and Rudinsky, 1962; Wood, 1962; Wood and Stark (in Stark, 1965). Attention to the OEP was spurred by earlier works (reviewed by Stark, 1965) in which the moisture condition in trees was correlated with the osmotic pressure of epithelial cells lining the resin ducts and with OEP. Since oleoresin is regarded as the major factor influencing the success of initial bark beetle attack, oleoresin exudation pressure, as an expression of both water balance of the tree and its oleoresin flow, appeared suited to provide a dependable indication of the trees' disposition to bark beetle attack (Vité, 1961).

Workers using the OEP to relate moisture deficiency to bark beetle attack showed a positive relation between "low" pressure trees and successful bark beetle attack and conversely a negative relation between "high" pressure trees and successful attack. It appeared that the information on the trees' OEP is of predictive value as to its disposition to colonization by bark beetles; the work by Wood and Stark (in Stark, 1965) showing a large number of successfully attacked trees in the "high" pressure tree category indicates, according to Stark (1965), that the risk classification or OEP determinations are not always satisfactory for stand resistance assessment. Stark (*ibid.*) suggests the possibility that "high" pressure trees are overcome during low pressure periods and stresses the need to demonstrate experimentally the pressures at which trees are overcome by a particular bark beetle species. The present study attempts in part to provide some answers to this question.

BIONOMICS OF *PSEUDOHYLESINUS NEBULOSUS*

(Part I)

MATERIAL AND METHODS

Study Area

Field studies were conducted primarily in the McDonald Forest near Corvallis, Oregon. The forest is a typical part of the western coniferous biome and forms a transitional zone between the drier Willamette Valley in the east and the moist belt along the Pacific Coast to the west. Elevations range from about 76 to 550 meters. The soils are predominantly red-brown latosols. Alluvial soils, typical of the lower, flat parts of the forest, are thin and lie close to the parent material. The stands are mainly composed of second-growth Douglas-fir. On exposed sites, with thin soil layers, patches of oaks commonly intermingle with the Douglas-fir trees. Grassy openings with groups of sapling and pole-sized Douglas-fir and oak trees are frequently found in the southern part of the forest. In general, the stands appear thrifty, but each year beetle-killed trees can be found easily.

The area is characterized by mild, rainy winters and warm, occasionally dry summers. Average monthly temperatures^{1/} range from 5°C in January to 17.7°C in August. Annual precipitation averages about 1135mm of which some 80 percent occurs between October and March. The

^{1/}Recorded at a meteorological station located about three kilometers east of McDonald Forest.

summer of 1967, during which studies on host tree condition bark beetle relationships were conducted, was characterized by an unusually prolonged period of drought, unusually high temperatures and low humidities. Temperatures ranged from 5.7°C, the monthly January average, to 21.6°C, the monthly August average. Total 1967 precipitation amounted to 903mm with 21mm in May, 19mm in June, none in July and August and only 21mm in September.

In the spring of 1966, there was an ample supply of brood material in form of snow-broken tree tops scattered throughout pole-sized stands. Thinning and logging activities conducted in the southern part of the forest from 1966 through late spring of 1967 provided a continual fresh supply of brood material. Accordingly, it is reasonable to assume that during the study period, the area contained an increased population of Scolytidae as well as other subcortical-feeding insects associated with Douglas-fir.

Life History of *P. nebulosus*

In order to study the beetle's host selection behavior as influenced by factors of host susceptibility, it was first necessary to determine the life cycle of *P. nebulosus* in the study area. Trees were periodically felled and incidence of infestation noted. Brood material was placed (1) into rearing cages kept in the field under open and shaded conditions and (2) into temperature controlled rearing chambers. The logs were dissected periodically and brood development charted.

Infested material was caged together with freshly cut material to study *P. nebulosus* reemergence behavior.

Response to temperature and light. To determine the ambulatory and flight response of *P. nebulosus* under varying temperature and light intensity levels, freshly emerged beetles (15 to 25 at a time) were placed either on a log surface or on a sheet of plywood. The response of these test insects was recorded together with light and surface temperature conditions.

Beetles used for these observations were taken from two different preemergence temperature regimes. One group emerged from logs kept in the shade, the other group originated from brood-material exposed to sun.

To determine the effect of temperature and light intensity on the diurnal emergence pattern, infested logs were placed into a sun-exposed insectary unaffected by the shade of nearby standing objects. Emerging beetles were collected at half-hour intervals and the log and air temperatures measured with thermistors connected to a portable recorder. Light intensities were determined with a mobile Tru-Lux light meter^{2/} especially adapted to low light intensities.

^{2/}Gosseau and Company, GMBH, Erlangen, Germany.

Response to Olfactory Stimuli

Field tests. To determine whether *P. nebulosus* locates its brood material by volatile, host-produced substances, a series of tests were carried out in April of 1967.

A 90-year-old Douglas-fir stand in the northern part of the study area was chosen for the attraction study site location. The stand covers approximately 8 hectares in the midslope of a westerly oriented hillside. It is bordered on the west and north by an old clearcut; a young pole-sized Douglas-fir stand borders the study site on the south and east. There was no current or recent logging activity within about a one-mile radius from the test site.

Test procedure. Test materials were separately placed in wooden cages (30x30x90cm) covered with densely meshed polyvinyl screens. The cages and the test materials, placed on 120x120cm plywood sheets, were stationed 25m apart on a northerly oriented logging road leading through the testing site. Each testing station was numbered. The test materials were randomly assigned to a test station. The test materials were exposed simultaneously (within a 15-minute interval). Beetles landing on screens covering the test material were periodically (usually at hourly intervals) removed and placed into tin boxes.

Test materials. Synthetic compounds: (1) ethyl alcohol (95%); (2) butyl alcohol (70%); terpenes^{3/}; (3) α -pinene; (4) β -pinene; (5) limonene; (6) D-camphene; (7) geraniol. The terpenes were diluted to a 3% concentration (B.V.) in each of the two alcohols. The liquid compounds were dispensed into large-mouth (4cm diameter) vials. Changes in compound concentrations and the amount evaporated during test periods were not determined. Testing of these synthetic compounds was prompted by earlier reports that found *D. pseudotsugae* responsive to α -pinene (Heikkinen and Hrutfiord, 1965) and to α -pinene and limonene diluted in ethyl alcohol (Jantz and Rudinsky, 1966; Rudinsky, 1966a).

Douglas-fir materials: (1) fresh twigs (branches from sapling-sized Douglas-fir cut immediately before testing); (plant moisture stress was determined with the pressure chamber technique at the start and the end of the testing period as described in Part II of this work); (2) one-day-old twigs (branches from sapling-sized trees, cut 24 hours before testing); (3) uninfested stem sections; (4) infested stem sections. To obtain the uninfested and infested stem sections, a pole-sized Douglas-fir was felled three days prior to the test. A part of the stem in the crown region was covered with a wire screen to prevent colonization by *P. nebulosus* or other insects. Three days after the tree was cut, two stem sections of similar size (7200 cm² of bark

^{3/}Technical grade; K and K Laboratories, Inc., Plainview, New York.

surface on each) were sawn off and their cutting face sealed with wax; one section was uninfested by any insect (taken from the wire screen protected stem portion), while the other was infested by *P. nebulosus* (the beetles had entered the phloem region but not the cambial region). The tree was under a moisture stress of 21 atm., when the sections were sawn off. The attractiveness of the infested and uninfested stem section was bioassayed over a period of 20 days; (5) blank cages (included also in bioassays of synthetic compounds).

Laboratory test. The following test was designed to determine the olfactory response of walking, sexually immature *P. nebulosus* in presence and absence of photic stimuli.

The bioassay was conducted in a bi-ramous olfactometer. It consisted of a plastic chamber with a circular, perforated bottom into which two plastic tubes were inserted from opposite directions. On the outside end of each tube, a light bulb was mounted and an inlet for an air hose attached. An electric air pump forced an even air stream into the tubes. One hose carried air alone, while the airstream in the other hose passed through a vial partly filled with ethanol (95% conc.) before entering into the tube. Freshly emerged beetles (from material kept for three months under 4-5°C) were placed in groups in the center of the chamber and exposed simultaneously to both untreated air and that with ethanol vapors for 30 minutes. The test was conducted in darkness, except for the lights at the end of each tube, then repeated

in total darkness; the room temperature during the test was 22-23°C. Each group of beetles, ranging from 16 to 60, was tested only once.

Diurnal Flight Pattern

To determine the effect of environmental factors such as temperature, light intensity, air movement and olfactory stimuli on the beetles' diurnal flight pattern, four study plots were established as follows: Plot A - a thrifty Douglas-fir stand, seemingly without suitable brood material; Plot B - a thinned Douglas-fir stand with the fresh cut trees left on the ground; Plot C - fresh Douglas-fir slash in the open; Plot D - a snow-damaged patch of Douglas-fir (winter 1965-66), consisting of broken tops, snow-bent stems and uprooted trees.

The 1966 study plots were located in a 25 to 35-year-old post-pole-sized Douglas-fir stand on a flat ridge-top in the northern part of the study area. The plots in 1967 were located in the southern part of the study area in a 70 to 80-year-old Douglas-fir stand on a southwesterly hillside.

To obtain an estimate of the *P. nebulosus* flight intensity under the environmental conditions in each study plot, the beetles were collected into rotary nets. The aerial net-trap assembly, essentially the same as described by Gara and Vité (1962), consisted of a rotary net, diameter 38cm, mounted on a 180cm high stand and rotated at 60 revolutions per minute, powered by a gasoline generator. One net-trap

assembly was installed on each plot in 1966; two assemblies per plot were operated in 1967. The nets were operated daily during spring whenever daily maximum temperatures could potentially exceed 10°C; they were emptied at half-hour intervals during critical flight periods and hourly during favorable conditions. The trapped scolytids were identified and their numbers recorded. The air temperature and wind velocity at 180cm above the ground was determined at the start and end of each sampling period by mercury thermometers and Dwyer-type windmeters. Foxboro hygrothermographs, sheltered 76cm above the ground, also recorded ambient air and humidity conditions.

To determine seasonal variations in the diurnal flight pattern, net sampling was conducted at six- to fourteen-day intervals during May. In June, July and August more intensive sampling was resumed in connection with studies on *Scolytus unispinosus* by Echols (unpublished data, 1967). Net-trap collections on Plot B were resumed during the period of *P. nebulosus* brood emergence.

Seasonal Flight Pattern of Scolytidae Associated with Douglas-fir

Information on the seasonal flight pattern of other subcortically feeding insects associated with Douglas-fir was obtained during observations on *P. nebulosus* and during simultaneous observations on *S. unispinosus* by Echols (unpublished data, 1967). They supplemented the data reported by Daterman *et al.* (1965).

RESULTS AND DISCUSSION

Life History of *P. nebulosus*

Temperatures permitting, *P. nebulosus* selects brood material from fall until mid-spring; the peak of *P. nebulosus* attack occurs in early spring. Teneral beetles emerge from late spring until late fall. Upon dispersing from the breeding site, the beetles feed on twigs of live Douglas-fir to attain sexual maturity. Progeny initiated in early spring complete development by fall and are ready to initiate a second generation. The seasonal history of *P. nebulosus* life cycle is shown in Figure 1. Observations in this work are similar to those in other studies on *P. nebulosus* (Chamberlin, 1958; Walters and McMullen, 1956) with the exception of the maturation feeding habit, which was found for the first time as reported by Stoszek and Rudinsky (1967).

Host Colonization. Observations on *P. nebulosus* host selection behavior revealed that both females and males are responsive to host attraction. Trees felled in the morning (on days with conditions favorable for *P. nebulosus* flight), had, by the afternoon, large numbers of *P. nebulosus* beetles crawling on their stems and branches. With decreasing light intensity, an increasing number of females were found motionless and seemingly arrested at bark crevices and bark indentations. The females soon were joined by one or even two male beetles. Mating was not observed; it may have occurred at dawn, outside the gallery. The earliest signs of initiated boring activity

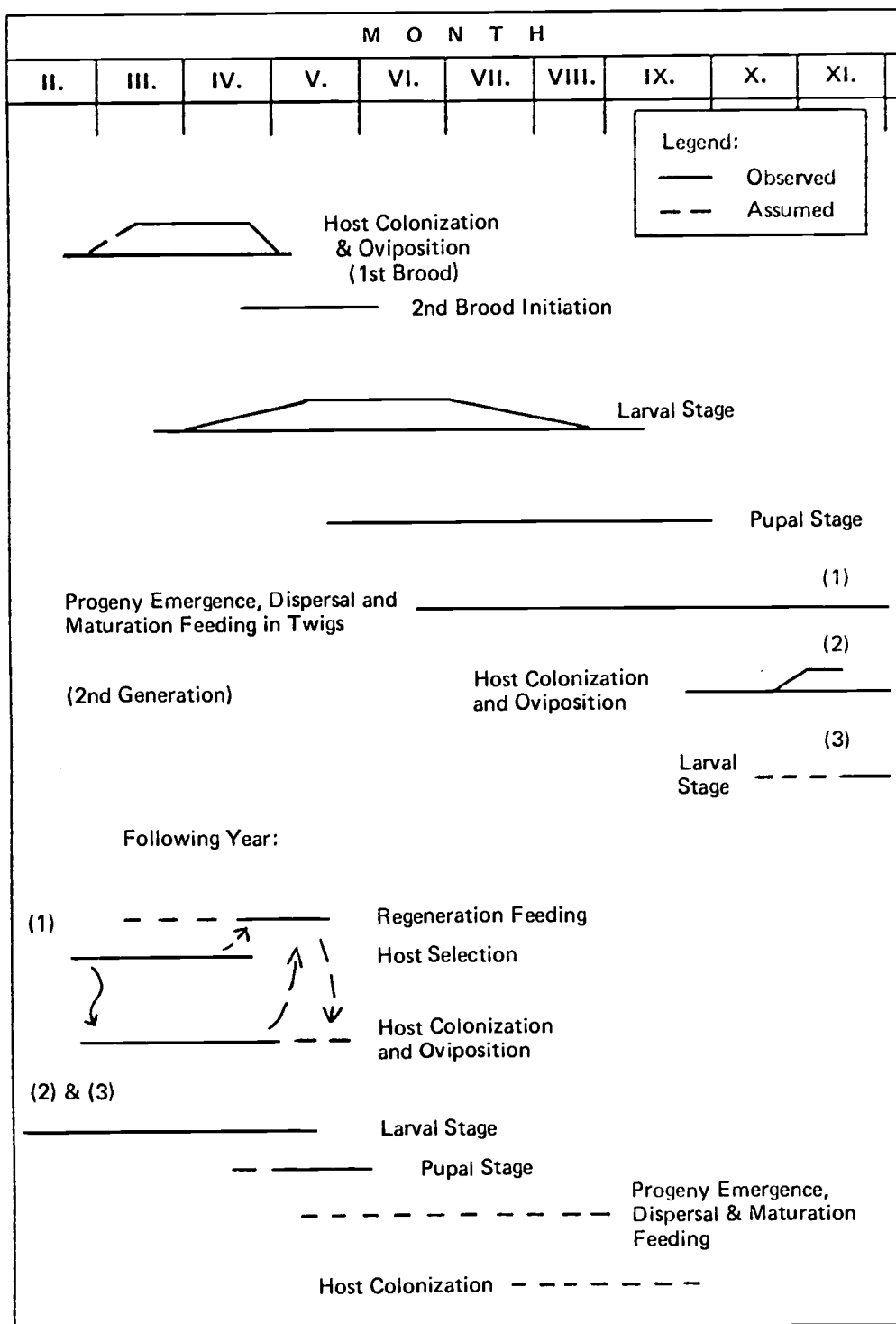


Figure 1. Seasonal life history of *Pseudohylesinus nebulosus* Lec. in western Oregon.

were found the morning after the beetles located the brood material. The female initiated gallery construction and, followed by the male, mined the egg gallery scoring the cambial layer slightly or not at all. Simultaneously with gallery construction, eggs are laid singly into alternately cut notches in the gallery. Upon completing the upper branch, the female starts to mine the downward-directed, egg-gallery branch.

Gallery description. The completed egg gallery is longitudinal, parallel with the grain of wood, and characteristically biramous. The gallery length and the number of eggs laid vary. Galleries with an average length of 55mm contained an average of 29 eggs, but often, particularly in tops of standing trees, unusually long galleries were found that contained up to 80 eggs per gallery. The egg galleries initiated during late fall and early spring colonization do not score the wood. Galleries constructed on trees felled in May were found to score the xylem tissues rather deeply. The egg gallery is kept free of frass; a reddish-brown pile of borings on the bark surface distinguishes the breeding site of *P. nebulosus* from that of similar scolytids on Douglas-fir.

The larvae feed at first perpendicularly to the egg gallery and later turn up or down in a longitudinal direction, parallel to the branches of the egg galleries where they originated. The pupal chambers are located in the outer phloem region, phloem thickness permitting.

Immature stages. Development of *P. nebulosus* goes through the egg, three larval instars, pupal and the callow adult stages (Walters and McMullen, 1956). Results of laboratory and field observations show that the rate of development is temperature dependent (Table 1 and Table 2). Observations on caged material showed that reemerging females initiate second brood production. Galleries constructed by the reinfesting beetles scored the xylem tissue deeply. Walters and McMullen (1956) found only 10.2 percent of parent beetles present inside galleries with brood in an advanced development stage. Since all the beetles found were dead, it was concluded that the rest died shortly after leaving the gallery.

In the course of the study, callow adults emerged in mid-June; peak of emergence, however, occurred from July through August. Emergence of second brood progeny was found to continue through the fall.

The emerging beetles were found to have an even sex ratio; out of 613 specimens examined, 300 were females. The elongate and plumose scales on female elytra and the stout elytral scales on males, described by Swaine (1918), proved reliable for sex determination.

Maturation feeding. Freshly emerged beetles were caged with thin-barked stem sections. The beetles entered the bark, usually at an injured place, and constructed short galleries deeply scoring the xylem. Often three to ten beetles were found crammed in one feeding

niche; Walters and McMullen (1956) considered these niches as overwintering sites. The beetles failed to breed. Dissection revealed poorly developed ovaries (with ovarioles lacking follicle differentiation) and a lack of fat body.

The search for possible maturation feeding sites met with success when callow adults were introduced into cages containing potted, four-year-old Douglas-fir seedlings. The beetles mined the twigs and constructed tunnel-like shelters by chewing out a cavity and feeding on xylem and inner bark tissues. The twig mining habit was subsequently recognized in the field. Twigs on Douglas-firs of any size, age (except current year growth) or vigor were found to provide shelter and food for the beetles. In stands with high populations of emerging *P. nebulosus* the ground was literally covered with twigs broken off by feeding injury. A characteristic notch on the cut end of the twigs distinguishes the work done by teneral *P. nebulosus* beetles.

Beetles feeding for about 50 days in the tissues of four-year-old Douglas-firs (under constant temperature of 21°C) entered stem sections encaged with the seedlings and laid viable eggs. Dissection of beetles that have passed through this feeding period revealed an increase in the amount of fat body and enlargement of testes or ovaries; the ovaries had ovarioles with distinct follicle differentiation.

In the field, the first sign of completed maturity; i.e., colonization of brood material, was observed sporadically by the end of

TABLE 1. Duration of *Pseudohylesinus nebulosus* development under constant temperatures.

Developmental Stage	Duration in Days	
	21°C	15.6°C
Egg	5	6
Larva I	5	9
Larva II	5	8
Larva III	12	17
Pupa	13	13
Sex. Immature Adult	58	-
(Maturation Feeding)	(50)	-
TOTAL:	About 98 Days	-

TABLE 2. Seasonal history of *Pseudohylesinus nebulosus* in 1966.

Activity or Developmental Stage	Brood Material			
	Sunny		Shaded	
	Observation Date	Duration in Days	Observation Date	Duration in Days
Colonization Initiated	3-25		3-25	
(Egg & Larval Stage)		77		98
Pupal Stage	6-10	10	6-30	21
Callow Adults	6-21		7-20	
Emergence	6-25		8-1	
Maturation Feeding	Was not determined			
(New) Colonization	9-22	94 ^{4/}		
TOTAL:		181 Days		

^{4/}Uncertain whether initiated by progeny originated in spring of 1966.

September in 1966 and 1967. The first mass colonization was observed on warm sunny days in November, 1967, following a cold and rainy October.

Regeneration feeding in twigs. At the end of April, 1967, a large number of twigs freshly bitten off by *P. nebulosus* was observed on the ground in the northern part of the study area -- an obvious evidence that *P. nebulosus* resumed feeding in twigs. Interestingly, this was not found in the southern part of the study area. Later, from mid-May till early June, a noticeable amount of bitten off twigs showed up in the southern but not the northern part of the study area. This indicated either the emergence of callow adults or resumed feeding by adults that have reemerged from breeding sites. The latter possibility appeared more plausible as second instar larvae were the most advanced stage found in galleries initiated in early spring.

This assumption was tested with mature beetles (collected in April and kept under 5°C refrigeration in tin boxes with moist filter paper until the first week of June) placed under gelatine capsules and affixed with padding to twigs of potted, five-year-old Douglas-fir seedlings. The beetles burrowed into the twigs and fed on the tissues in the same manner as the callow adults during their maturation period. Several beetles that were inside the twigs for one week were dissected and their body cavity contents compared with those of "starving" beetles. Besides the obvious difference that the digestive tract of

beetles from inside the twigs was full of tissues and that of "starving" beetles was empty, there was a marked buildup of fat body in the twig-fed beetles compared to the "starving" beetles.

P. nebulosus reemerging from successfully colonized (and caged) Douglas-fir were released into cages with potted, four-year-old Douglas-fir seedlings. Some of the beetles resumed feeding in twigs in the same manner as callow adults or the "starving" beetles in previous tests.

Overwintering stage and habits. *P. nebulosus* was found to overwinter in all but the egg and pupal stage. Most of the immature beetles spent the winter inside the hollowed out twigs, conveniently sheltered during the cold-induced hibernation and feeding to maturation during the warmer periods. The sexually mature beetles, if successful in breeding material colonization prior to the onset of cold weather, overwinter in the egg galleries; otherwise, they conceivably hibernate under bark crevices, in litter on the ground, or inside the twigs. Both the immature and mature beetles may change, temperatures permitting, the hibernation place.

Flight and Related Response Behavior of Sexually Immature Beetles

Response to temperature and light intensity. The effect of temperature on the phototrophic response of *P. nebulosus* is shown in Figure 2. There were two temperature levels, 15.5°C and 34°C, at which

the beetles changed the photic response from light negative to a light positive and vice versa. The thresholds for photic reversal were derived by plotting the percentage of light positive beetles under a particular temperature (from Appendix, Table A and Table B) against the observed temperature. (This approach was suggested by the work of Taylor, 1963.)

Light intensity of 17 f.c. (Figure 3) was determined as the threshold at which the beetles reverse their photic response independent of temperature. The threshold was graphically derived from observations in Appendix, Table A, as were the temperature thresholds for photic reversal.

The effect of temperature on the take-off capability of *P. nebulosus* is shown in Figure 4. Similar to the positive phototropism, the ability of *P. nebulosus* to take off is limited by a lower and upper temperature threshold, 19°C and 34°C, respectively. The threshold levels were determined from observations in Appendix, Table A and B in a manner similar to the thresholds for photic reversal.

Interestingly, the take-off temperature threshold of beetles that have emerged from shaded sites (19°C) is lower than the take-off threshold of beetles from breeding material kept in sun-exposed cages (27°C). Beetles that emerged from shaded material were able to crawl at temperatures at which the beetles from sun-exposed sites were still immobile (Appendix, Table A and Table B). These differences in mobility and in flight readiness are similar to those reported by Atkins, who found

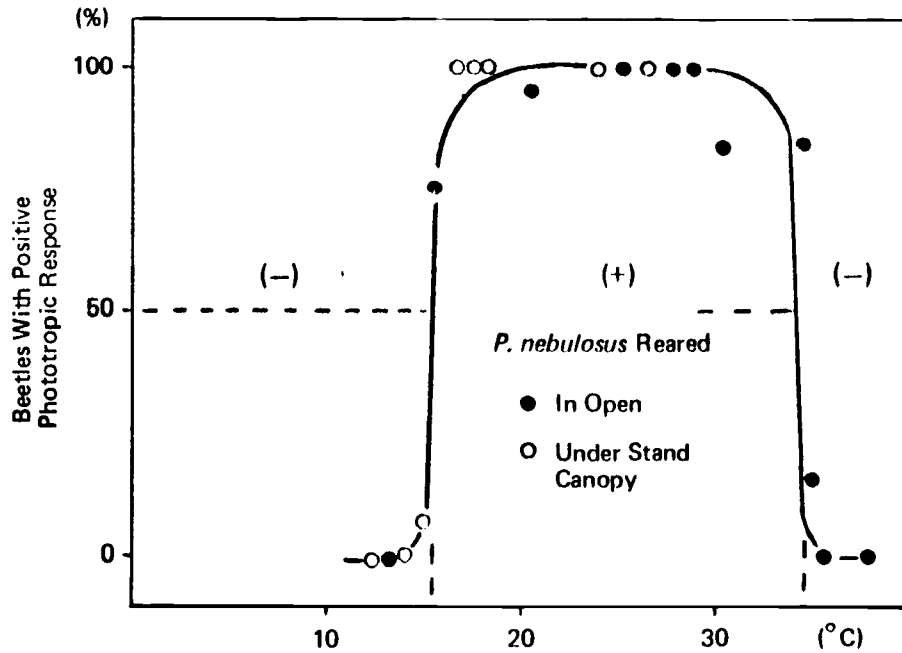


Figure 2. Temperature Thresholds for Reversal of Photic Response by Sex. Immature *Pseudohylesinus nebulosus* Beetles.

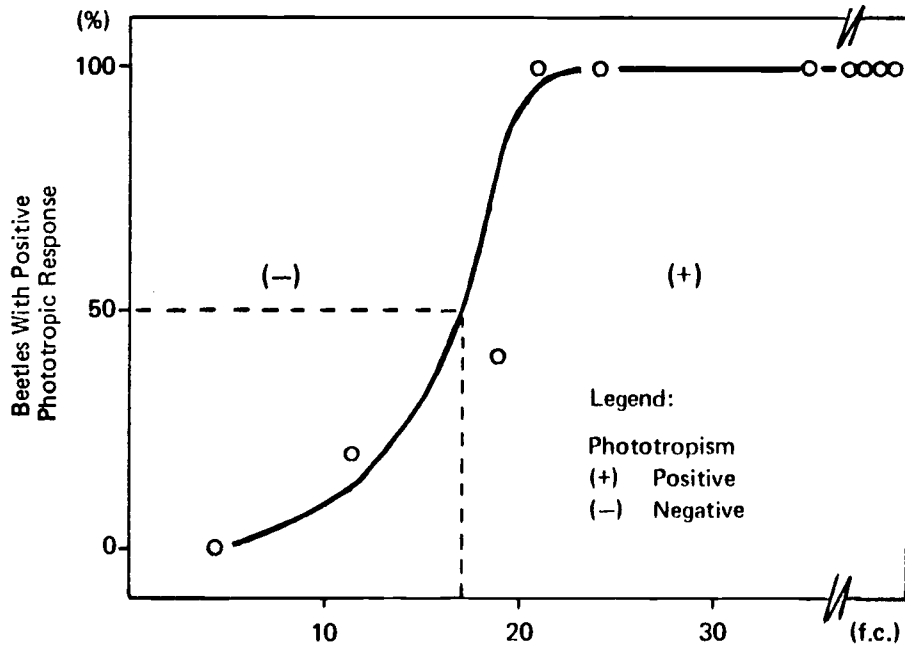


Figure 3. Light Intensity Threshold for Reversal of Photic Response by Sex. Immature *Pseudohylesinus nebulosus* Beetles.

(1966b) that Douglas-fir beetles with a higher fat content took off more readily than beetles with a lower amount of fat. In a later study, Atkins (1967) showed that beetles exposed to higher preemergence temperatures had less fat than beetles kept under cooler temperatures.

The diurnal pattern of *P. nebulosus* emergence correlated with air and bark surface temperatures and light intensities, shown in Figure 5, substantiates the accuracy of above discussed observations. The effect of temperature on the ambulatory response of sexually immature *P. nebulosus* is shown in Figure 6. The locomotive activity is characteristically limited by two temperature thresholds similarly as observed on other scolytids (Rudinsky and Vité, 1956; Francia and Graham, 1967; McMullen and Atkins, 1962; Shepherd, 1966). It is noteworthy that only positively phototrophic beetles are apt to resume flight, whereas negative phototrophic beetles exhibit thigmotactic reactions.

Response to olfactory stimuli.

Response of walking beetles. The response of walking, freshly emerged beetles to air-alone and ethanol vapors (Table 3) indicate that *P. nebulosus* beetles, without light stimulus are attracted to ethanol vapors but are less responsive when exposed to light. The results suggest that the response to light dominates over response to olfactory stimuli.

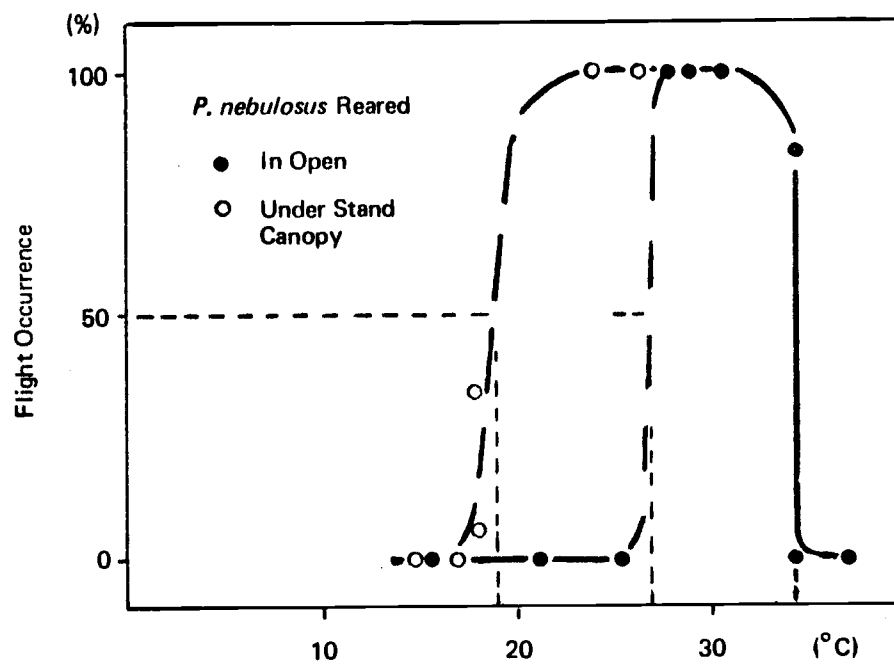


Figure 4. Flight Take-Off Temperature Thresholds of Emerging *Pseudohylesinus nebulosus*

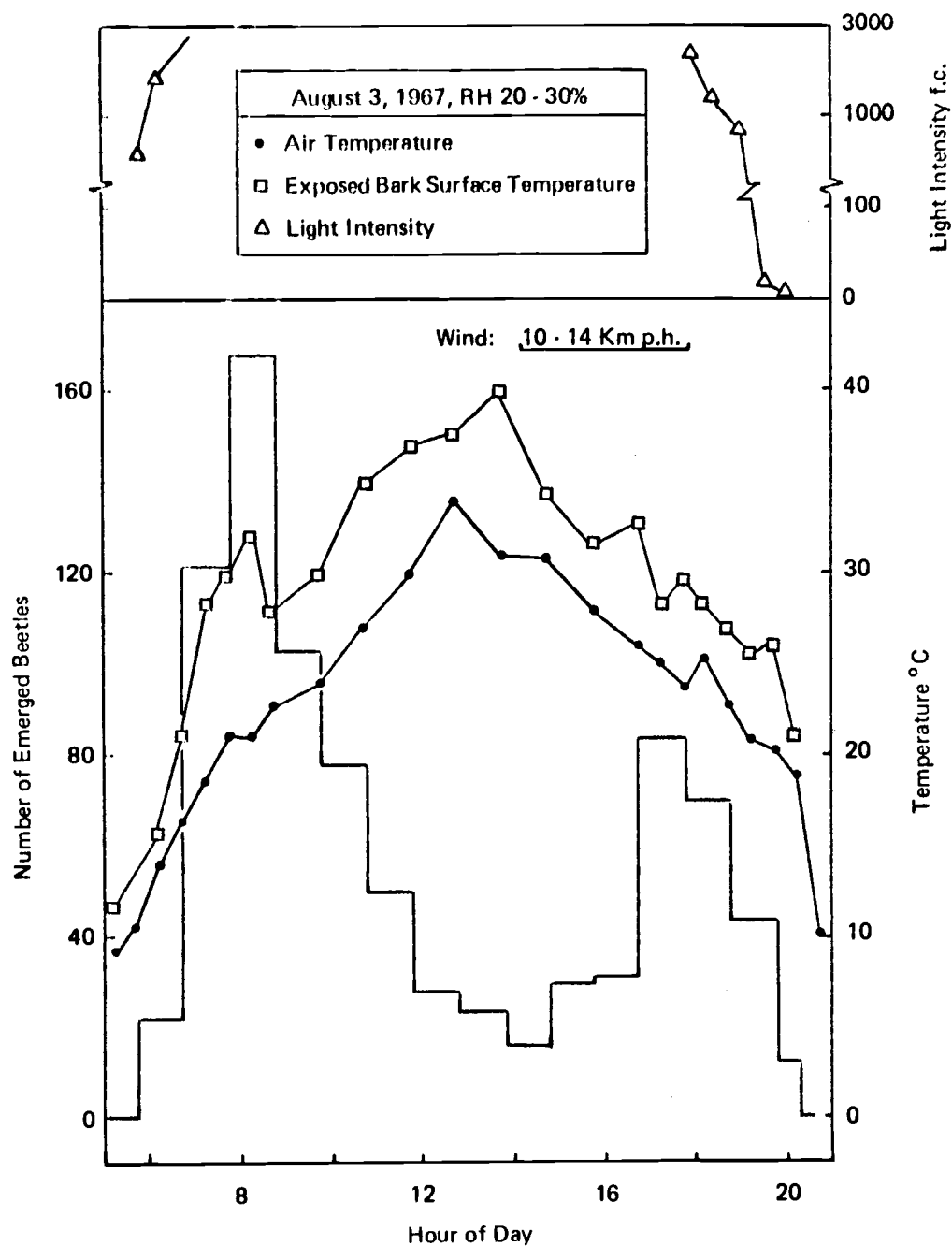


Figure 5. Temperature, Light Intensity and Diurnal Emergence Pattern of *Pseudohylesinus nebulosus*.

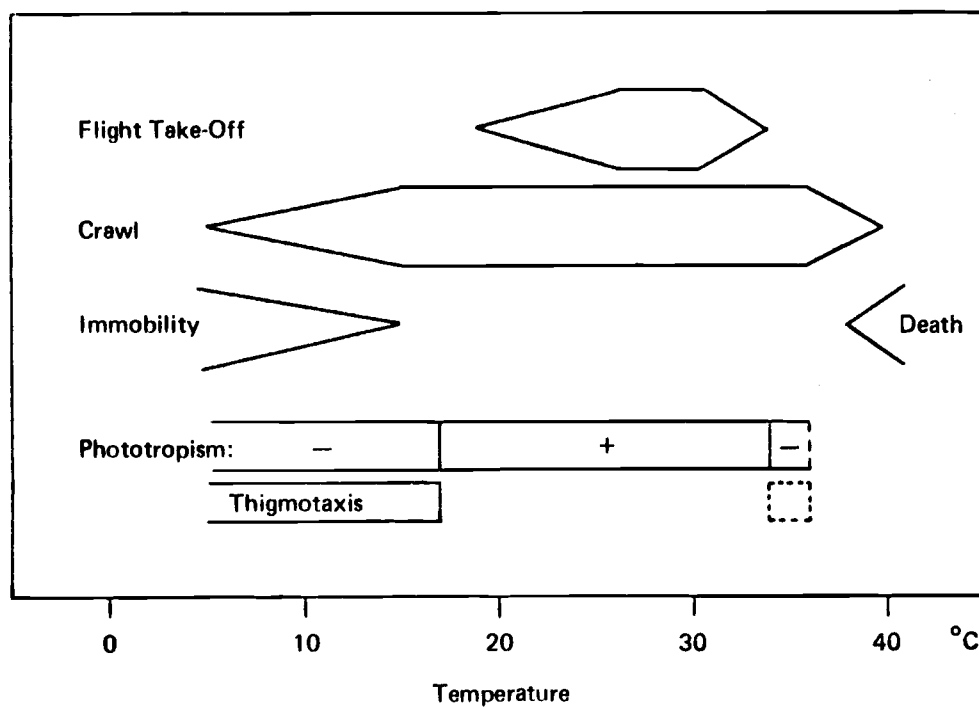


Figure 6. Temperature and Ambulatory Responses of Sex-Immature *Pseudohylesinus nebulosus* Beetles.

Response of flying beetles. Efforts to attract emerging immature *P. nebulosus* to material and compounds known as highly attractive to flying sexually mature beetles failed. Tested were freshly cut twigs and ethyl alcohol placed under wooden frame cages. The cages were installed in a stand with plenty of slash from which large numbers of *P. nebulosus* beetles were emerging and in an open field upwind from an introduced slash pile with large numbers of emerging beetles. Not a single beetle was found to respond to the materials.

Flight orientation.

The beetles that took off during observations on the effect of temperature and light on beetle response were in almost every instance visually trailed. It was easy to keep the flying beetle in sight for about 10-20 meters during midday, owing to the fact that the beetles directed their flight invariably toward the sky in a spiral-like fashion. Beetles observed to take off in the evening could be trailed for a distance of five to ten meters, which was sufficient to determine that at sunset the beetles flew in a semi-horizontal direction toward the sun. Wind direction (gusts up to 3 km per hour) seemed to have no effect on flight orientation, except for an eventual mechanical shift in direction.

These observations suggest that the post-emergence flight of *P. nebulosus*, in its initial phase at least, is directed toward the highest light intensity.

TABLE 3. The response of walking, sexually immature *P. nebulosus* to olfactory stimuli in presence and absence of light.

LIGHT		DARKNESS	
Number of Beetles Responding to		Number of Beetles Responding to	
Ethanol	Air	Ethanol	Air
31	17	29	8
37	24	35	12
31	29	14	2
TOTAL: 99	70	78	22
Ratio:	1.4:1	3.5:1	

Flight and Related Response Behavior of Mature Beetles

Response to temperature and light intensity.

From numerous casual observations on mature beetles, it became apparent that, as with the immature beetle, the reversal in photic response is dependent upon temperature or light intensity, and the ambulatory responses are temperature governed and limited by two threshold levels. No attempts were made however to determine the threshold levels, with the exception of the flight continuation temperature threshold.

A threshold of 12.5°C was determined as the minimum necessary for mature *P. nebulosus* to continue in flight. The graphical determination shown in Figure 7 is based on trapping results (by the rotating net assembly) correlated with air temperatures during the trapping periods. Each trapping period was classified as either 1, if one or more beetles were caught or 0, if none were caught (Appendix, Table C). The trapping periods were then grouped according to the prevailing temperature and the percentage of occasions with flight plotted against temperature (after Taylor, 1963).

Response to olfactory stimuli.

To determine whether airborne sexually mature *P. nebulosus* locate brood material by volatile host-produced substances, synthetic compounds and portions of Douglas-fir were field bioassayed. In accordance

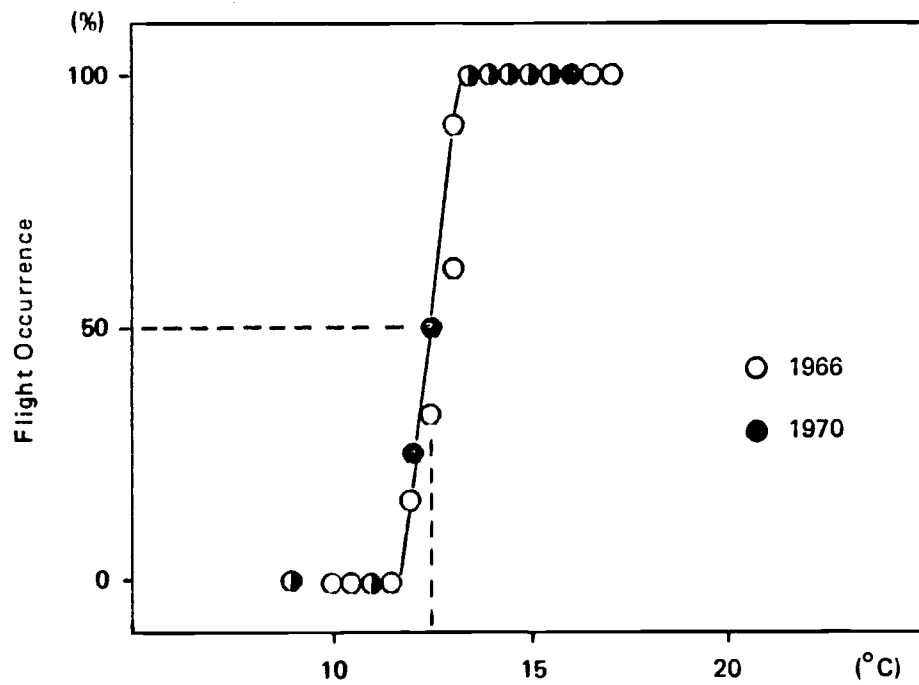


Figure 7. Temperature Threshold for Flight-Continuation by Sexually Mature *Pseudohylesinus nebulosus* in Early Spring.

with the objective, the results are qualitatively evaluated, and no quantitative assessment was made.

Response to synthetic compounds. The responses of *P. nebulosus* to volatile emissions from (1) ethyl alcohol, (2) butyl alcohol, (3) terpene solutions in butyl alcohol are summarized in Table 4; responses grouped under one test number (Test I or Test II) and date are comparable since the compounds were simultaneously tested.

From results in Table 4, it is evident that ethyl alcohol *per se* and terpenes diluted in ethyl alcohol attract *P. nebulosus*. Butyl alcohol *per se* was unattractive to flying *P. nebulosus* under the test conditions. Interestingly, *P. nebulosus* beetles responded to all the tested terpene solutions in butanol (perhaps with exception of geraniol). Ethyl alcohol tested in early May, when other Scolytidae in addition to *P. nebulosus* were in flight, proved attractive to the following species: *Anisandrus pyri* (Peck), an ambrosia beetle associated with hardwoods; *Dendroctonus pseudotsugae*; *Hylastes nigrinus* (Mann), a bark beetle breeding primarily in Douglas-fir roots; *Pseudohylesinus grandis* Sw., a bark beetle associated with Douglas-fir and some other coniferous trees; *Pseudohylesinus nebulosus* and to *Gnathotrichus* spp. The results are shown in Table 5.

The attractiveness of ethanol to the Douglas-fir beetles is a puzzling contradiction of observations by others. Rudinsky (1966a) and

TABLE 4. Response of airborne *P. nebulosus* to volatiles from ethyl alcohol, butyl alcohol and terpene solutions in ethyl and butyl alcohol.

Test			Test Material -- Number of <i>P. nebulosus</i> Attracted							
No.	Date	Temp. °C	95% Ethanol	Ethanol with 3% Conc. (b.v.) of						Check
				α -P.	β -P.	Limon.	D-Camp.	Geran.	Df-Oleor.	
I.	4.1.	11-13	2	17	23	47	6	11	-	0
	4.2.	12-15	208	213	299	503	167	241	75	1
	4.3.	12-13	2	2	6	5	5	2	2	0
	4.6.	11-16	68	156	156	201	49	53	148	0
		TOTAL:	280	388	384	756	267	307	225	1
			95% Ethanol	Butanol with 3% Conc. (b.v.) of						Check
				α -P.	β -P.	Limon.	D-Camp.	Geran.	Df-Oleor.	
II.	4.7.	13-19	28	44	15	10	21	9	47	2
	4.11.	11-15	52	46	6	8	7	-	46	3
	4.23.	10-16	22	1	0	6	0	2	3	1
		TOTAL:	102	91	21	24	29	11	96	6

TABLE 5. Response of some airborne Scolytidae to ethyl alcohol.

Insect Species	No. of Beetles Attracted				Ethanol Total
	May 5, 1967		May 6, 1967		
	Ethanol	Control	Ethanol	Control	
<i>Anisandrus pyri</i>	81	0	61	3	142
<i>Dendroctonus pseudotsugae</i>	48	1	55	6	103
<i>Gnathotrichus</i> spp.	4	0	2	0	6
<i>Hylastes nigrinus</i>	5	0	24	0	29
<i>Pseudohylesinus grandis</i>	126	5	30	4	156
<i>Pseudohylesinus nebulosus</i>	42	0	47	3	89
<i>Trypodendron lineatum</i>	0	0	1	0	1

Range of air temperatures during test periods: 5.5.:16.7-19.4°C; 5.6.:17.8-20.0°C.

Jantz and Rudinsky (1966) tested the response of *D. pseudotsugae* to various terpenes in ethanol solutions and to ethanol alone. The beetles were found unresponsive to ethanol, but highly responsive to some terpenes dissolved in ethanol. The same lack of response of *D. pseudotsugae* to ethanol is shown in a recent report involving laboratory and field bioassays of *trans*-verbenol (Rudinsky *et al.*, 1972). The reason for this difference is not known.

The attractiveness of ethanol to ambrosia beetles (Scolytidae) is well documented. Hardwoods treated with ethanol induced heavy attacks by ambrosia beetles (Buchanan, 1941; Browne, 1952). Ambrosia beetles of the genera *Xyleborus* and *Platypus*, associated with tropical hardwoods, were found strongly attracted to ethanol dispensed at concentrations ranging from 95 to 30 percent (Samaniego and Gara, 1970). Ethanol was found to be a feeding and tunneling stimulant for *Xyleborus ferugineus* (Norris and Baker, 1969). Graham (1968) proposed, based on the evidence from earlier studies, to isolate the compound of Douglas-fir attractive to *T. lineatum* (Graham and Werner, 1956; Werner and Graham, 1957; and Francia and Graham, 1967), that attractant production by a host was a result of changes in cell metabolism from an aerobic process to an anaerobic one. The metabolic change occurs when the oxygen content in water of the tree's conductive tissues is depleted. This idea was substantiated by Moeck (1970) for *T. lineatum* and by Cade *et al.* (1970) who found ethanol in naturally attractive and anaerobically treated conifer wood; the beetles responded to

ethanol in both field and laboratory bioassays. The response of bark and ambrosia beetles to ethanol determined in this work suggests that Graham's idea applies to a number of bark beetles as well as to ambrosia beetles.

Response to Douglas-fir material. The fresh twigs, under plant moisture stress conditions ranging from 16 to 36 atm. at the start and the end of the bioassay period, respectively, attracted substantially more *P. nebulosus* than the twigs cut one day earlier (a total of 189 beetles compared to 19 beetles during a 180-minute period). The response pattern is shown in Figure 8. To assess the attractiveness of tested materials, the response elicited by the twigs was expressed in percent of the response shown by *P. nebulosus* to ethanol during the same time intervals.

The transformed results (Figure 9) indicate that the attractiveness of freshly cut twigs increases sharply, reaches a peak, then declines again; the old twigs exhibit a low and steadily declining attractiveness. It is possible that the sudden increase in moisture stress upon twig severance triggers certain metabolic processes (perhaps in terms suggested by Graham, 1968) that result in attractant production. Further reduction in moisture contents of the tissues changes metabolic processes and the attractiveness of the material declines.

P. nebulosus responded in high numbers to both the uninfested and infested stem sections from the crown portion of felled, pole-sized

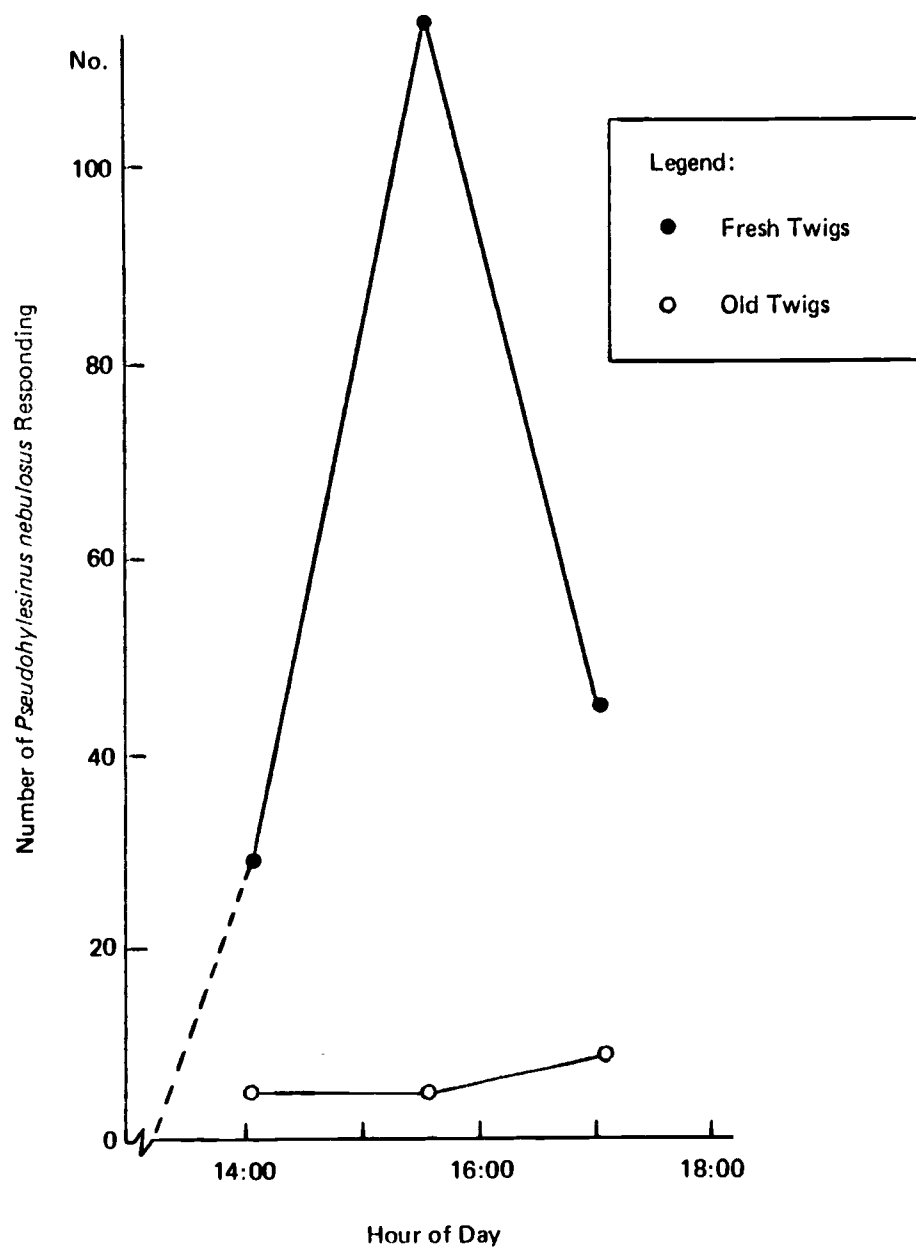


Figure 8. Response Pattern of *Pseudohylesinus nebulosus* to Fresh and One-Day-Old Cut Douglas-fir Twigs.

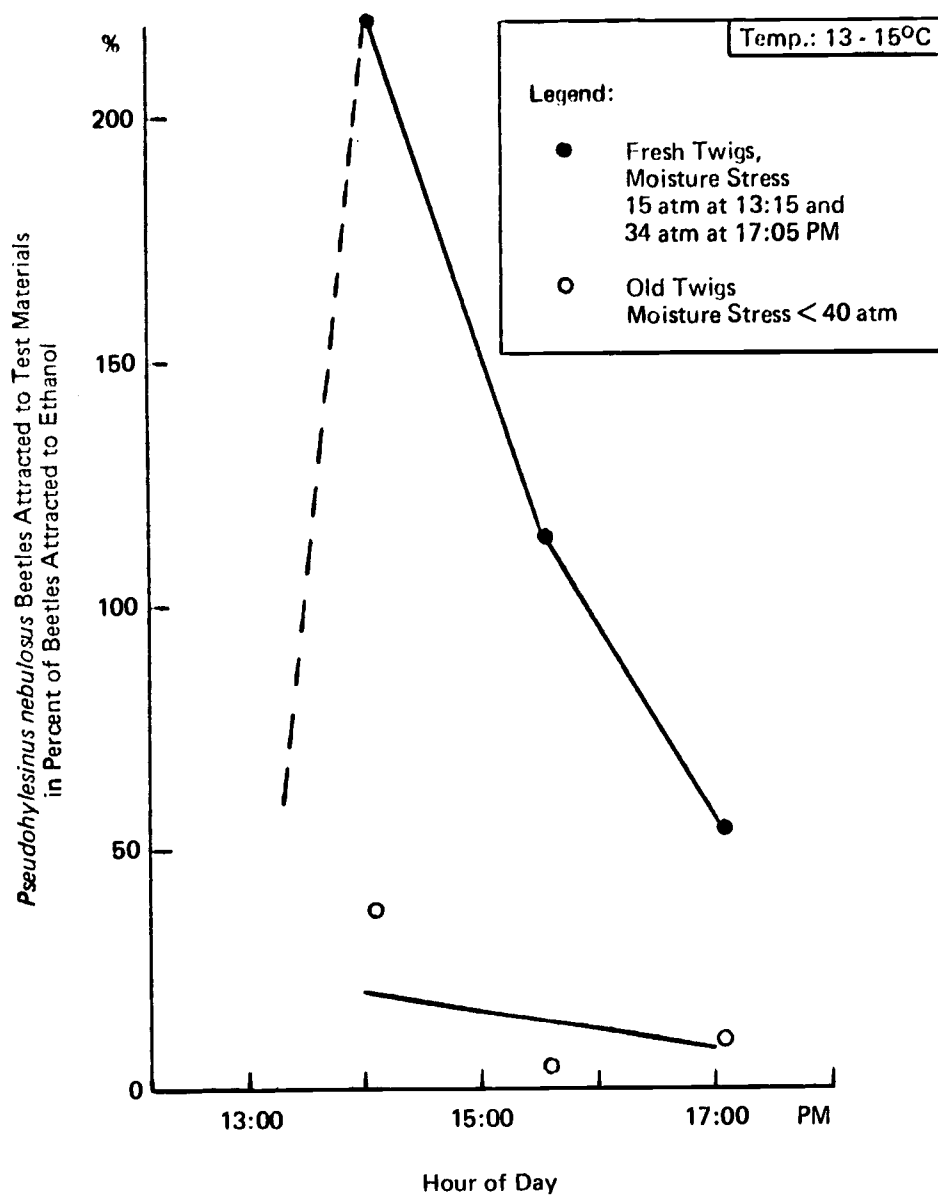


Figure 9. Attractiveness of Fresh and One-Day-Old Cut Douglas-fir Twigs to *Pseudohylesinus nebulosus*.

Douglas-fir. The stem sections initially colonized by *P. nebulosus* were at first (shortly upon severance of the stem section from the crown region of the felled tree) substantially more attractive to the flying beetles than the uninfested stem sections. This is apparent from tests on three different dates involving simultaneous bioassay of infested and uninfested Douglas-fir material of the same bark surface area (Table 6). As in the case of the severed Douglas-fir twigs, the attractiveness of infested and uninfested stem sections was expressed in percent of the number of beetles attracted to ethanol during the same bioassay periods. The results shown in Figure 10 indicate that attractiveness declined sharply with time in both the uninfested and infested stem sections. The infested material was initially substantially more attractive than the uninfested material. Ten days following the initial attack and severance from the crown region, the attractiveness of the infested stem section appeared equal to that of the uninfested section and from then on attractiveness of both materials continued to decline at a slow and steady rate.

The marked difference in initial attractiveness of infested stem sections compared to the uninfested ones could have been caused by increased primary or host attraction due to tissue injury resulting from beetle colonization or by a pheromone of the invading beetles. These possibilities were not studied further. The subsequent decline in attractiveness of both materials is most likely related to changes

in the materials' metabolic processes following the severance from the crown region.

The diurnal and seasonal flight pattern.

The daily flight patterns of sexually mature *P. nebulosus* are shown in Figure 11 and Figure 12. The number of beetles trapped into the rotating nets reflects the size of the airborne beetle population and its response to flight orienting stimuli. The diurnal flight patterns support the earlier discussed observations on *P. nebulosus* response to temperature, light and olfactory stimuli. The number of trapped beetles increases sharply with temperature increase above the flight continuation temperature threshold. Conversely, the number of trapped beetles decreases sharply with temperature decrease toward the flight continuation temperature threshold. Apart from these correlations, temperature seems to have little direct effect on the size of the airborne beetle population as reflected by the number of beetles trapped. This is apparent on histograms in Figure 11 (March 25, study plot A, B, C, D) where flight increase corresponds at first with temperature increase, then later in the day (from about the 13:00 to 15:00 hours) the flight intensity (as reflected by the number of beetles caught) is reduced despite continuing temperature increase. On some plots, particularly on clear sunny days, a distinct decrease in the number of trapped beetles in the early afternoon is followed by a substantial increase in beetle numbers during trapping periods later in

TABLE 6. Response of flying *Pseudohylesinus nebulosus* to uninfested and initially infested Douglas-fir material.

<u>Testing</u>			<u>No. of Beetles Attracted to</u>	
<u>Date</u>	<u>Hour</u>	<u>Temp. °C</u>	<u>Uninfested Stem Sections</u>	<u>Infested Stem Sections</u>
3.22.	15:00	-	5	22
	16:00		0	18
	17:00	-	1	4
TOTAL:			6	44
4.2.	13:40	13°	3	10
	14:40	-	11	215
	16:20	15°	50	138
	17:40	-	15	58
TOTAL:			79	421
			<u>(Hour)</u>	
4.6.	15:20	15.6°	77 (14:55)	70
	17:25	-	11 (17:10)	79
	18:20	-	7 (18:05)	14
TOTAL:			95	163
SUM TOTAL:			180	628

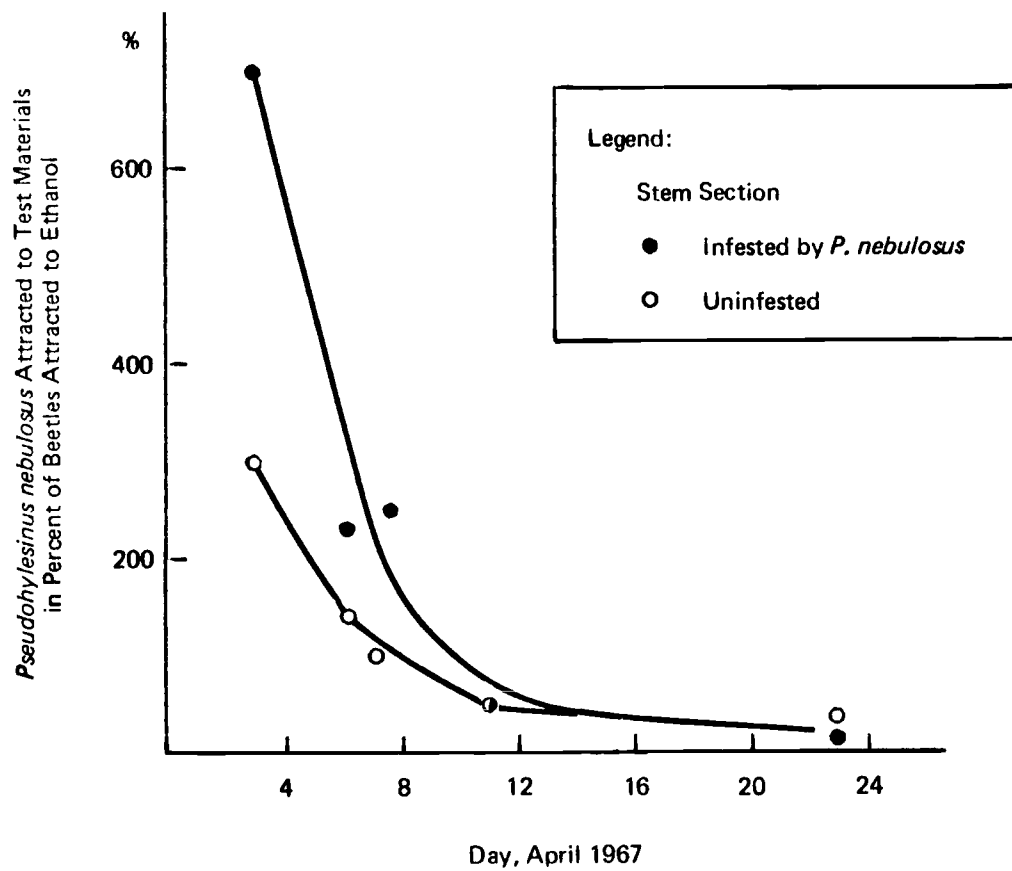


Figure 10. Attractiveness of Infested and Uninfested Douglas-fir Stems to *Pseudohylesinus nebulosus*.

the afternoon (Figure 11; March 25, study plots A, C, D; Figure 12; April 2, study plot C; April 1, study plot B). A similar midday reduction of scolytid flight intensity during warm weather was reported by other workers (Gara and Vité, 1962; Rudinsky, 1963; Rudinsky and Daterman, 1964; Vité, Gara and Kliefoth, 1964; Daterman *et al.*, 1965; Gara, Vité and Cramer, 1965; Zethner-Moller and Rudinsky, 1967) who attributed the midday decline to the inhibited flight activity by high temperatures. The bimodal flight pattern of *P. nebulosus*, or rather the midday decrease in numbers of trapped *P. nebulosus* beetles, does not appear to be the result of temperature and light intensity interference with the beetles' flight. This assumption is based on the inference that the beetles' hibernation and take-off places (foliage, twigs and branches of live Douglas-fir trees) were unlikely to reach temperatures exceeding the upper threshold for flight take-off (Figure 4) under the cool air temperatures recorded during periods with the midday decrease in numbers of trapped beetles (Figure 11, 12). Since observations in this study have not shown high light intensities to inhibit flight of *P. nebulosus*, it is unlikely that light intensity interactions are involved in the midday decrease of trapped beetles.

Chapman (1967) proposes that the bimodal pattern of the daily flight of scolytids results primarily from impaired tracking of attractive odor plumes by the beetles due to strong air turbulence around midday, particularly on clear sunny days. The midday decline in numbers of *P. nebulosus* trapped (beetles responding to the slash on the ground)

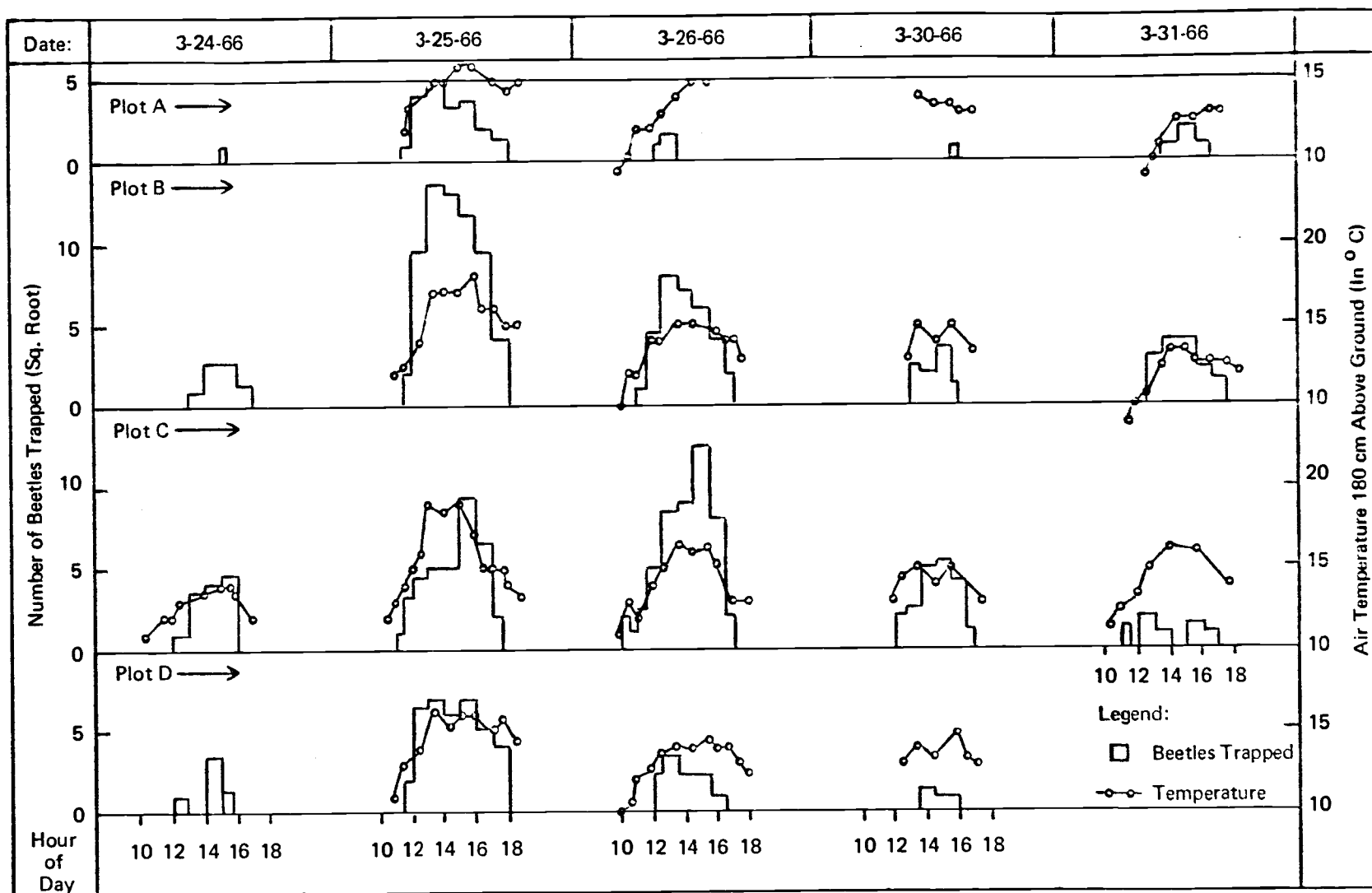


Figure 11. The Diurnal Flight Pattern of Sexually Mature *Pseudohylesinus nebulosus* in 1966.

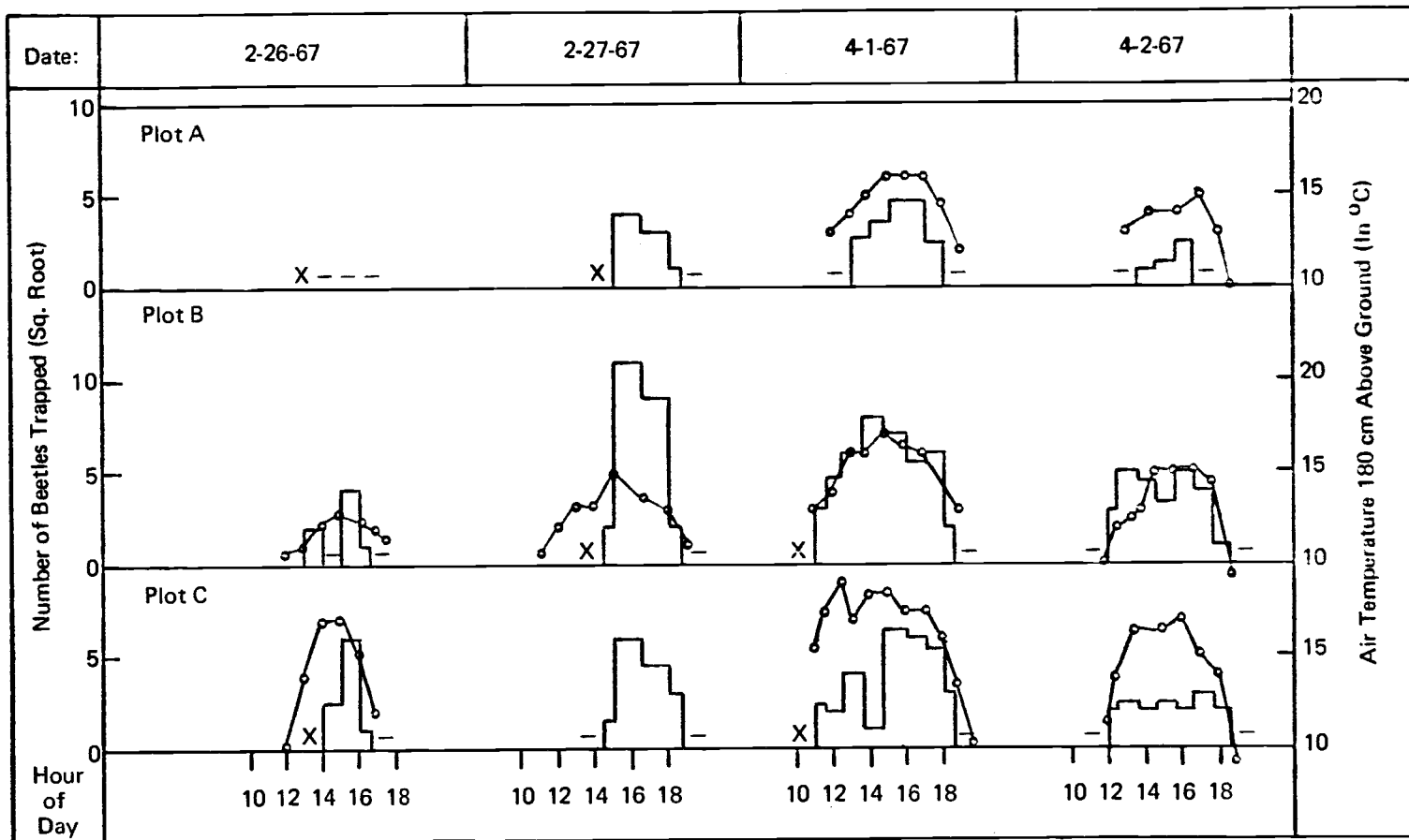


Figure 12. The Diurnal Flight Pattern of Sexually Mature *Pseudohylesinus nebulosus* in 1967.

seems explainable in terms of Chapman's (1967) theory. There is however another plausible explanation complementary to Chapman's observation, namely that other sources of attraction - sources with a short-lived, temporary attractiveness - compete, from about midday to midafternoon, with the "permanent" sources of attraction and "absorb" part of the airborne beetle population. This theory is based on study results, discussed later, suggesting the possibility that Douglas-fir trees under midday-midafternoon moisture deficits may become the source of temporary attraction.

The seasonal flight pattern of sexually mature *P. nebulosus* during spring periods of 1966 and 1967 is shown in Figure 13 and Figure 14, respectively. The size of the airborne beetle population is reflected by the number of beetles caught in net traps located near attraction sources. To obtain more comparable results, the daily catch was divided by the number of trapping hours with temperatures favorable to flight. The flight-favorable weather conditions in early spring of 1966 and a region-wide large supply of snow-broken tree tops enabled the beetles to locate brood material within several days. In 1967, a combination of cool weather and lack of suitable brood material resulted in the prolonged flight period shown in Figure 14. According to the attraction study results noted earlier, *P. nebulosus* beetles were searching for breeding sites until the first week of May. These observations correspond with those made earlier by Daterman *et al.* (1965) and with general observations reported by Chamberlin (1958).

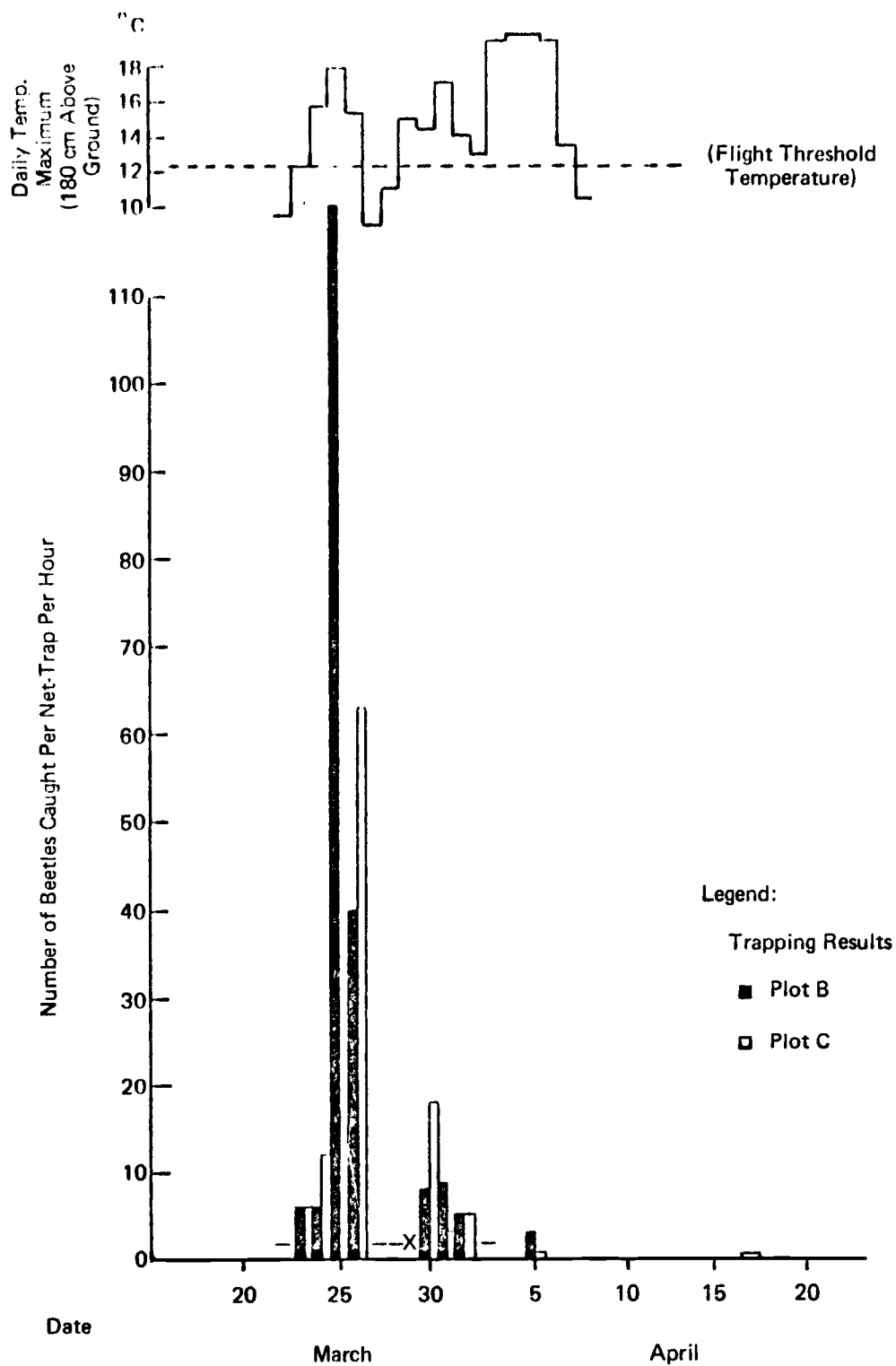


Figure 13. Spring Flight Pattern of Sexually Mature *Pseudohylesinus nebulosus* (1966).

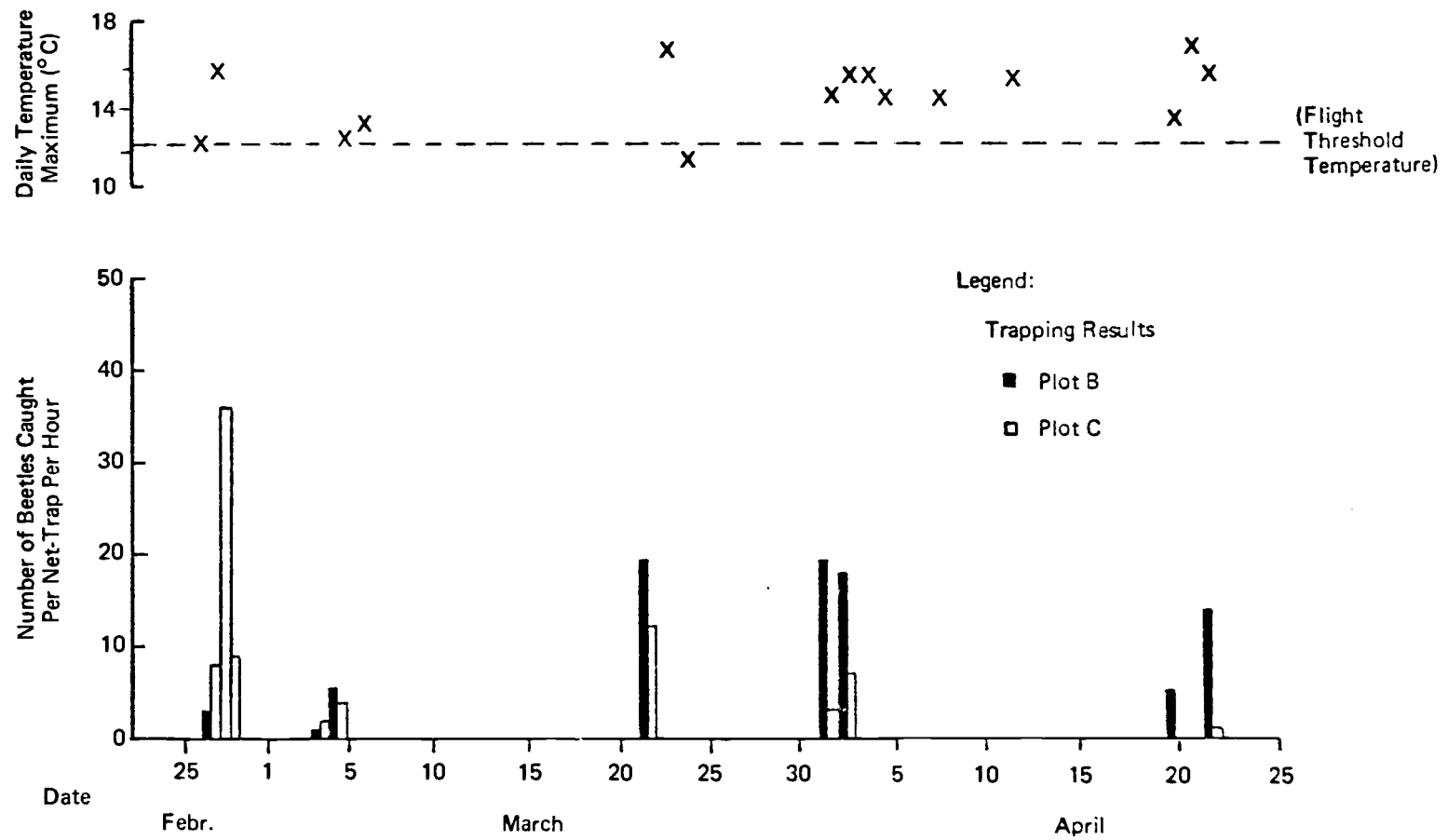


Figure 14. Spring Flight Pattern of Sexually Mature *Pseudohylesinus nebulosus* (1967).

CONCLUSIONS

The obtained results provide a basis for the following theoretical conclusions regarding the flight of *P. nebulosus* beetles. The flight of sexually immature beetles is limited by a lower and upper temperature threshold (Figure 4) and by light intensity (Figure 3). Only beetles with a positive photic response, which is temperature dependent (Figure 2), resume flight. The photic stimulus dominates the responses of beetles to other stimuli; positive phototropic beetles are unresponsive to other stimuli, except temperature.

The beetles orient their flight toward the highest light intensity. The phototropic flight orientation is likely to carry the beetles into air strata in which wind direction and velocity is apt to affect decisively flight direction and distance.

The lack of response of airborne immature *P. nebulosus* to compounds known as highly attractive to airborne, reproduction-capable beetles, indicates that immature beetles do not respond, while in flight, to vegetative stimuli. This suggests that immature beetles alight into Douglas-fir crowns by chance, similarly as do the twig feeding *Scolytus quadrispinosus* saw beetles, according to Goeden and Norris (1965). The presumed chance encounter with the host tree may occur through collision with branches or twigs shortly after takeoff or later, when flight continuation is limited by temperature or low light intensity. Upon landing on Douglas-fir, the beetles respond to feeding stimuli

under conditions favoring negative phototaxis and thigmotaxis, such as low or high temperatures (Figure 6) or low light intensities. This inference is based on the experiment showing walking beetles to be responsive to ethanol when bioassayed in absence of light and unresponsive to ethanol in presence of light (Table 3).

The mature beetles are capable of perceiving olfactory stimuli while in flight. The beetles change, upon perception of olfactory stimuli, their orientation from photic to chemotactic and guide their flight toward the source of attraction. This inference is based on results of field-bioassays showing that airborne *P. nebulosus* are highly responsive to ethanol, terpene solutions in ethanol and in butyl alcohol, and to Douglas-fir twigs and stem sections (Table 4, 5, 6; Figure 8).

The post-emergence flight of sexually immature *P. nebulosus* appears to have the attributes by which Southwood (1962) characterizes insect migration; Southwood states (page 174) "...the animal leaves the population territory or habitat in which it has previously lived and whilst engaged in such movement does not respond normally to any vegetative stimulus, such as food, a mate or shelter." The migratory character of the post-emergence flight evidently enables *P. nebulosus* to keep pace with changes in location of its habitat and it reflects the degree of habitat impermanence (aspects that contributed to the evolution of migratory movements, according to Southwood). On

the other hand, the flight orientation of sexually mature *P. nebulosus* does not conform to the specifications characterizing migration. It shortens the mean distance between neighboring individuals and ultimately results in convergence of beetles on susceptible brood material.

RELATIONSHIP BETWEEN DOUGLAS-FIR
MOISTURE STRESS CONDITION AND
COLONIZATION BY SOME SCOLYTIDAE
AND BUPRESTIDAE

(Part II)

MATERIAL AND METHODS

Moisture Stress Determination, Technique and Procedure

Direct measurement of water relations in trees can be accomplished by a number of techniques as summarized by Barrs (1968), Boyer (1969) and Kramer (1969). The pressure chamber technique reintroduced by Scholander et al. (1965) to measure moisture relations in woody plants directly, easily and reliably appeared best suited for the use in studies on the relation between moisture condition in trees and bark beetles. The technique, originally described by Dixon (1914), is based on the cohesion theory of water movement within vascular plants and in effect measures the pressure needed to force a broken water column back to the severed woody surface of a leafy twig. The results obtained with Scholander's technique are comparable with other direct techniques and sufficiently close to the more elaborate techniques to justify its use in studies where rapid determination of water status is essential (Boyer, 1967; Waring and Cleary, 1967).

To determine the moisture stress in Douglas-fir, the pressure chamber instrument and technique designed and described by Waring and Cleary (1967) was used. The term plant moisture stress (PMS) expressed in positive units was adopted (Waring and Cleary, 1967; Cleary, 1971; Philip, 1966; Kramer, 1969) for its clarity and convenience.

As described by Waring and Cleary (1967) the water column within the vascular system of a woody plant is generally under tension. The tension results from the inability of the plant to replenish rapidly enough the water lost by evapotranspiration. When a twig is severed, the broken water column withdraws into the tissues for a short distance. By placing the leafy twig in a chamber, with the cut end protruding through a seal for viewing and by exerting pressure into the chamber, the water column is forced back to the cut surface. The pressure at which water is observed is assumed to be the tension on the water column before the twig was cut.

The pressure chamber is simple in operation. The twig is cut (or shot off) from the tree, the bark and phloem are stripped back a short distance from the cut surface, and the exposed xylem is slipped through a rubber stopper and inserted into the cover that is screwed to the body of the chamber. Nitrogen gas, under pressure, is gradually applied through a pressure regulator with help of flow-regulating valves. When water first appears on the cut surface, the flow-regulating valves are closed and the pressure reading is recorded. Then the bleeder valve is opened to vent the system and prepare it for the next sample. The entire procedure takes, at most, one minute.

For routine PMS observations, two sample twigs were measured; each was taken from about the same level but from different aspects in the crown. A shotgun was used to shoot down twigs from tall trees.

If the difference between the recorded pressure in the samples was within 1 atm., the lower reading was recorded; when a larger difference occurred, a third sample was measured and again the lower reading of two samples within the 1 atm. range was recorded. When the measurements still exceeded the 1 atm. limit, all three readings were recorded.

As recommended by Waring and Cleary (1967), errors in measurement were reduced by (1) using two- or three-year-old twigs with smoothly cut ends; (2) measuring the PMS in the sample within four minutes after it has been severed from the tree; (3) not allowing the cutoff twig to protrude for more than 0.5 centimeters from the pressure chamber; (4) increasing gas pressure at a steady rate of about 1 atm. per second. There was no correction made for the error due to the osmotic potential described by Boyer (1967).

Changes in Douglas-fir Moisture Stress and Relations to Colonization by Scolytidae

To determine the diurnal moisture stress pattern in Douglas-fir and its seasonal changes, trees were selected so as to encompass the widest possible range of site condition and tree characteristics. The sample trees included individuals of different age, size and position in stand; trees growing on moist and on exposed sites, on places where water deficit was likely to occur because of logging or other activities of man and on sites where "beetle-killed" trees frequently

appeared in past years. Some trees were subjected to periodic observations throughout the year, but most of the trees were subjected to PMS observations in late summer, when the effect of the 1967 drought became apparent.

A total of 49 mature Douglas-fir trees were subjected to PMS examination in 1967; some of these trees were reexamined in the spring of 1968. Trees with the highest PMS values at or near the end of the summer drought were singled out and felled during the spring of 1968. On each felled tree, the bark and phloem tissues from larger limbs, the midcrown stem, the midbole and the butt region were peeled off to determine eventual infestation by subcortically feeding insects. Recorded were successful or unsuccessful (aborted) attacks by Scolytidae and Buprestidae and the inference on the season of attack initiation. Then, the trees' moisture stress condition determined during *P. nebulosus*, *D. pseudotsugae* and *S. unispinosus* host selection periods was correlated with the trees' infestation status in respective periods.

Sapling and post-sized trees were inspected for signs of attack during peak flight periods of *P. nebulosus*, *D. pseudotsugae* and *S. unispinosus*. At the end of the 1967 drought, on September 16, post-sized Douglas-fir trees growing scattered on a grassy hillside were found under attack by *S. unispinosus*. Examination of 20 trees had been completed when a brief rain altered the water relations of the

stand. To determine the rain's effect on the trees' moisture stress and on subsequent scolytid behavior, the trees under observation prior to the rain were reexamined four days after the rain terminated. A linear regression between the pre-rain PMS levels and the post-rain PMS levels was made. The plant moisture stress and infestation status of another 16 post-sized trees on the same locality was added to the record; their pre-rain PMS condition was estimated by their post-rain PMS status. The PMS and infestation status of some of these trees was reexamined the following winter or spring.

Moisture Stress in Douglas-fir and Maturation Feeding by *P. nebulosus*

To determine whether the sexually immature beetle prefers to feed on trees under certain physiological conditions, the following test was conducted:

Thirty potted and well-established four-year-old Douglas-fir trees with shoot growth completed were divided into three equal groups. Each group received a different watering schedule to attain the following moisture status: group A trees, a turgid condition, with plant moisture stress levels not exceeding 7 atm.; group B trees, a semi-stressed condition, with plant moisture stress levels ranging between 14-20 atm.; and group C trees, a highly stressed condition, with plant moisture stress levels exceeding 34 atm.

On August 15, the test trees were placed under a 1 m-high wooden frame cage covered with a wire screen of dense mesh. Stem sections with emerging *P. nebulosus* were added into the cage. By evening, about 200 to 300 beetles had emerged and were found on the screened walls and the ceiling. Prior to sunset, the beetles were forced off from the screens in an attempt to increase the chances for seedling infestation (soon afterwards it appeared that all beetles were back on the screens). Two days later, August 17, each seedling was inspected to determine the attack incidence and other related aspects. To prevent infestation by additional beetles, breeding material and free-crawling beetles were removed from the cage. Trees in group A were watered and with the other seedlings returned back to the original position in the cage. Four days later, August 21, the trees were inspected again.

Host Material Characteristics and Colonization by Scolytidae

To determine the preference of *P. nebulosus* and other scolytids to such host material characteristics as bark thickness, stem diameter and stem position in regard to the crown, the following experiment was set up. Two groups of Douglas-fir were felled in late winter - early spring of 1967. The first consisted of 12 trees, 80 years old, diameter over 50cm, with a thick rough bark and a moderately developed crown. The trees were felled as a part of a preharvest release cut in February, prior to the spring flight of bark beetles. The second

group consisted of 12 trees, 30 years old, that were pole-sized with smooth bark and well-developed crowns. Trees in this group were cut at the onset of *P. nebulosus* spring flight activity.

To alter the trees' condition, stems on six trees in each age group were sawed off at the base of the live crown. The remaining trees were left unbucked. Three trees from each category (age group and treatment) were placed on a clearing; the rest left in shade. The material was inspected in August to determine colonization by bark beetles and other phloem-feeding insects.

RESULTS AND DISCUSSION

Colonization by Meristem Insects and some Physical
Characteristics of Douglas-fir Material

As described, groups of young and old Douglas-fir were felled in early spring of 1967. The tree stems were subjected to (1) different dessication rates and (2) different radiation exposures. All the felled trees, categorized by size, treatment and exposure to direct sunrays, were inspected in August to determine bark beetle and buprestid beetle colonization. The Scolytidae were identified by species, but no attempt was made to identify the Buprestidae larvae. The results are shown in a generalized scheme in Table 7.

The group of trees lying under the stand canopy consistently showed a rather simple colonization pattern. The crown region and part of the bole adjacent to the live crown on unbucked old trees were found to be heavily and exclusively infested by *P. nebulosus*, as were the entire stems of unbucked pole-sized trees and the stems in the crown of both age-size categories. The limbless bole of unbucked trees and the bucked limbless stem sections in the old, large diameter groups were successfully and exclusively colonized by *D. pseudotsugae*. The only exceptions were areas of bark surrounding epicormic branches, which were heavily and successfully infested by *P. nebulosus*; galleries of both species overlapped only over a 2 to 4cm wide area. Stems of young, pole-sized trees, severed from live crowns, were sporadically

infested by *D. pseudotsugae* near the butt. The unfinished parent galleries were later found aborted and the few resulting larvae dead. Some sections became sporadically colonized by *P. nebulosus*, the beetles entering the bark near the cutting face or at points of fresh injury and the resulting larvae failing to complete development. The observations are similar to those reported by Johnson and Zingg (1969).

The group of trees lying exposed to full radiation in the open showed a more complex colonization pattern. The stem parts not exposed to direct sun were infested by the same bark beetle species as the trees in the stand. The exceptions were the shaded parts of pole-sized stem sections which were heavily infested by *P. nebulosus* and not at all attacked by *D. pseudotsugae*. Bark portions exposed directly to midday sunrays were free from attacks by *P. nebulosus* and *D. pseudotsugae* on all trees. On stems with thick and rough bark, the sun-exposed parts were riddled by buprestid larvae; stems and limbs within the crown region were colonized by *S. mispinosus*. Only the thin bark on fully exposed stem portions was free from insect invasion.

Comparing the characteristics of breeding sites preferred by each of the observed scolytids, it is evident that neither bark characteristics, phloem thickness, stem size or age determines the preference of these species; yet each beetle shows a distinct preference for certain breeding site characteristics. *P. nebulosus* prefers bark areas proximal to a "moisture drain" source such as branches with live foliage or bark areas under excessive cuticular transpiration. The preference of

TABLE 7. Scolytidae and Buprestidae colonization and host material characteristics.

Scolytidae and Buprestidae Colonization Intensity						
Douglas-fir		Young (22-27cm DBH)		Old (53-66cm DBH)		
Treatment & Stem Portion	Shaded	In Open		Shaded	In Open	
		Shaded Bark	Sun-Exposed Bark		Shaded Bark	Sun-Exposed Bark
Unbucked tree						
crown	P.n.++	P.n.++	S.u.++	P.n.++	P.n.++	Bpr.++, S.u.+
bole	P.n.++	P.n.++	S.u.+, Bpr.+	D.p.++	D.p.+	Bpr.++
Bucked tree						
crown	P.n.++	P.n.++	S.u.+	P.n.++	P.n.++	Bpr.++, S.u.+
bole	D.p.+	P.n.+	Bpr.+	D.p.++	D.p.+	Bpr.++

LEGEND:

Colonization intensity:

++ High - moderate
+ Low - sporadic

Insects:

P.n. *Pseudohylesinus nebulosus*
S.u. *Scolytus unispinosus*
D.p. *Dendroctonus pseudotsugae*
Bpr. Buprestidae

bark areas surrounding epicormic branches over the rest of the stem exemplifies this point. *D. pseudotsugae* appears to prefer bark areas on stem portions not proximal to the crown and to limbs with "live" foliage. *S. wispinosus* appears to prefer the same tree parts as *P. nebulosus* but simultaneous attacks to the same part of the tree by both species were not observed. *S. wispinosus* appears to tolerate or require bark under higher temperature regimes than *P. nebulosus*. Buprestid larvae were always found in stem portions exposed or semi-exposed to direct solar radiation. They appear to be formidable competitors to *S. wispinosus*.

Diurnal and Seasonal Moisture Stress Changes in Douglas-fir

The diurnal patterns in Douglas-fir moisture stress condition shown in Figure 15 were determined under various atmospheric and soil-moisture conditions over the season.

Two points in the diurnal PMS pattern deserve special attention, the diurnal minimum and the diurnal maximum. The diurnal minimum (or nightly low) obtained during the one-hour period before sunrise reflects the water state of trees in the absence of stomatal transpiration, with transpiration losses replenished to the point limited by factors affecting water absorption and/or redistribution. In trees with unimpaired physiological and morphological ability to absorb and redistribute water, or to control stomatal transpiration, it indicates the *status quo* between the tree and the available soil moisture. The

diurnal maximum (or daytime high) reflects the accumulated difference between the rate at which water is lost through transpiration and the rate at which it is absorbed and redistributed. It occurs on days with conditions highly favorable for evapotranspiration and high soil moisture content in the early afternoon. The values of the PMS maximum are most clearly related to the evaporative demand of the air (Klepper, 1968) and to the physiological-morphological ability of the trees to control excessive transpiration losses. Waring (1970) observed that stomata on Douglas-fir began to close with PMS levels exceeding 17 atm. In this study, transpirational losses were found substantially curtailed at PMS levels of about 20-24 atm., stresses to which the diurnal maxima were limited under undepleted soil moisture conditions (Figure 16). Essentially the same observation was shown for Douglas-fir by Waring and Cleary (1967). Lopushinsky (1969) found that three-year-old Douglas-fir close stomata at 22 atm. No doubt these levels vary with ecotype and tree preconditioning to drought (Zavitkovski and Ferrell, 1970).

There is an increase in PMS values with increase in tree height. The PMS minima determined in twigs from the top of a 28-meter Douglas-fir and in twigs two meters above the ground showed a gradual decrease of 2.5 atm. The observation supports data reported by Scholander *et al.* (1965) and the cohesion theory of water conduction within vascular plants, which implies that pressure on the water column in vascular tissues increases 1 atm. with each 10 meters of height increase. From

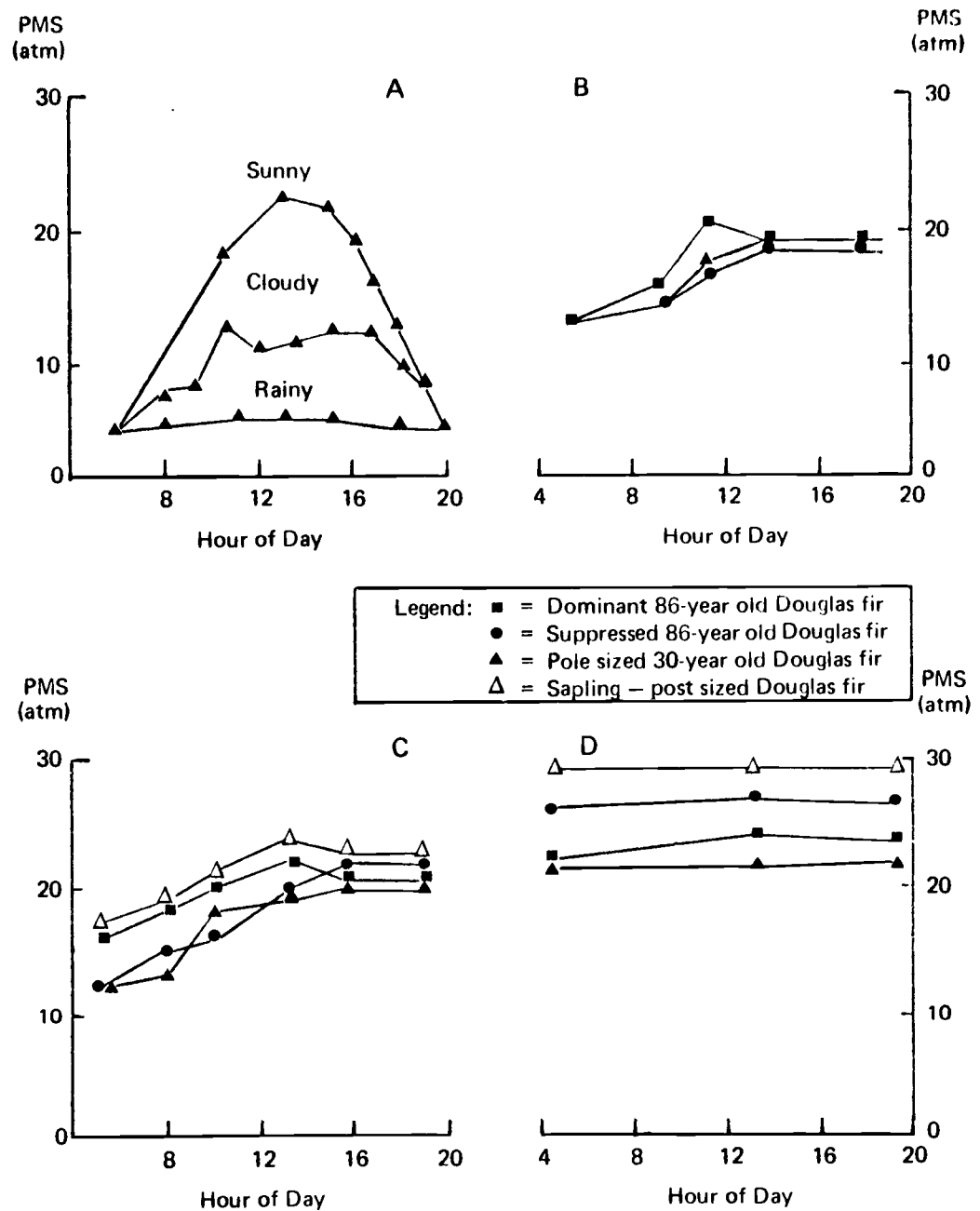


Figure 15. Diurnal PMS Pattern in Douglas-fir Under Large Soil Moisture Contents (A); Decreasing Soil Moisture Contents (B, C); and Depleted Soil Moisture (D).

experience in this study, the minimum PMS levels were not affected by crown aspects. Zaerr (1971) found differences smaller than one-third of an atmosphere between shaded and sun-exposed twigs on the same tree at noon.

The diurnal moisture stress patterns of seemingly healthy Douglas-fir trees determined under high soil moisture content are shown in Figure 15A. Curve (1) characterizes the PMS pattern during an overcast, rainy day; curve (2) exemplifies the PMS pattern during an overcast day; and curve (3) exemplifies the diurnal PMS pattern under clear, sunny days when atmospheric conditions are highly favorable to evapotranspiration and cool soil temperatures impede water absorption. Under the latter conditions, the amplitude between diurnal moisture stress minimum and the diurnal maximum may attain up to 16 atm. and fluctuations in stress, increases or decreases, occur rapidly (up to 4 atm. in one hour).

The diurnal moisture stress patterns under decreasing soil moisture content are shown in Figure 15B, C and D. The difference between the daytime high and nighttime low decreases due to increased minimum PMS levels and continues to decrease with progressing soil moisture depletion. At levels exceeding 24 atm., the diurnal PMS curve flattens out and the PMS minimum approximates the PMS maximum (Figure 15C, D; Figure 16). With continuing lack of precipitation and under conditions favoring evapotranspiration, the PMS values continue to increase and may (on Douglas-fir seedlings) reach to about

48 atm. levels without permanent injury to the tissues (Waring, 1970). Once limitations on replenishment of lost water disappear, the PMS decreases accordingly.

At high soil moisture conditions, there was little variation in PMS minima among healthy trees. As expected, variations among trees in the daytime stress amplitude and patterns were frequent. Different exposure to factors affecting evapotranspiration, likely interrelated with the trees' different ability to regulate transpiration losses and with differences in the rate of water redistribution, certainly accounted for this variation. The lack of precipitation and conditions highly favorable for evapotranspiration resulted, in July of 1967, in an increased variation in PMS minima; a particularly marked increase in PMS could be noted in trees exposed to man-inflicted changes in stand environment (trees near skid roads, fresh cutting lines and road cuts) compared to trees in the undisturbed part of the stand.

The moisture stress deficiency in sampled trees reached the peak in mid-September, at the end of the 1967 seemingly record-setting drought for Western Oregon. The variation in PMS levels among trees following the prolonged rainless period was indeed substantial. For example, the moisture stress levels determined on post-sized Douglas-firs grown scattered on a grassy hillside ranged from 22 to over 44

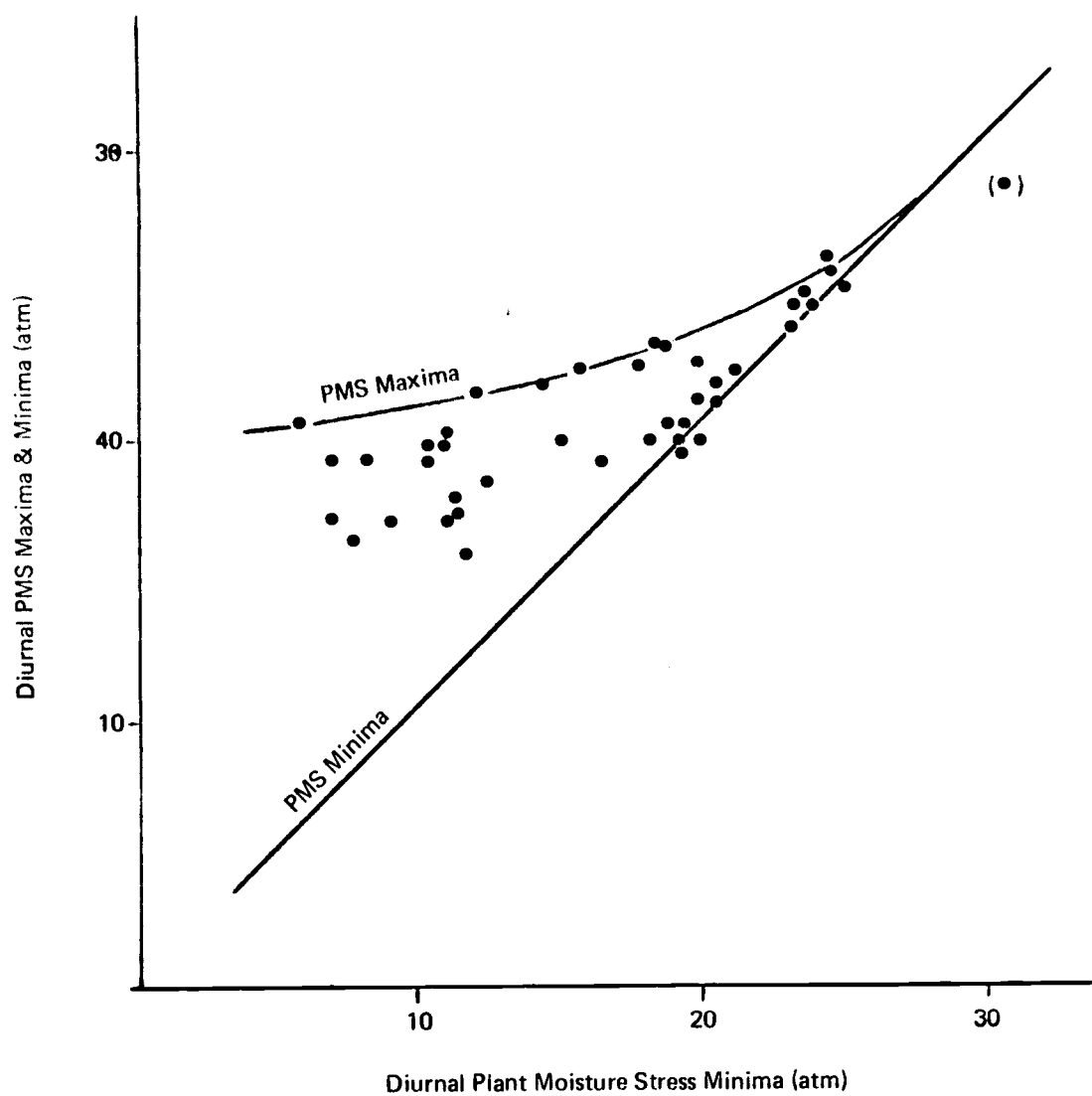


Figure 16. Relation Between Diurnal PMS Minima and Diurnal PMS Maxima in Douglas-fir.

atm.; a group of pole-sized Douglas-firs, lush and vigorous in appearance, grown on a creek alluvium (salmonberry in the undergrowth) attained PMS minima ranging from 20 to 31 atm. A brief rain in mid-September caused a temporary drop in moisture stress (Figure 17), but the trees recovered to fully turgid conditions after the rainstorms in fall replenished the depleted soil moisture.

Relationship between Moisture Stress in
Douglas-fir and Scolytidae and
Buprestidae Colonization

Scolytus wispinosus.

As mentioned, a brief rain interrupted observations on the PMS and infestation status of trees in a stand subjected to initial colonization by *S. wispinosus*. The effect of the rain on the trees' PMS was determined four days later. A high correlation between the pre-rain PMS conditions and the post-rain PMS conditions was established (Figure 17). The infestation status of additional trees from the same stand and similar site condition characteristics was added to the record; the pre-rain PMS of each tree was estimated from the linear equation in Figure 17. The results (Table 8), graphically depicted in Figure 18 by plotting the percentage of infested trees in a PMS interval against the PMS interval, show that Douglas-fir upon reaching a PMS threshold of 29 atm. become subject to initial colonization by *S. wispinosus*. It needs to be added that the galleries initiated on

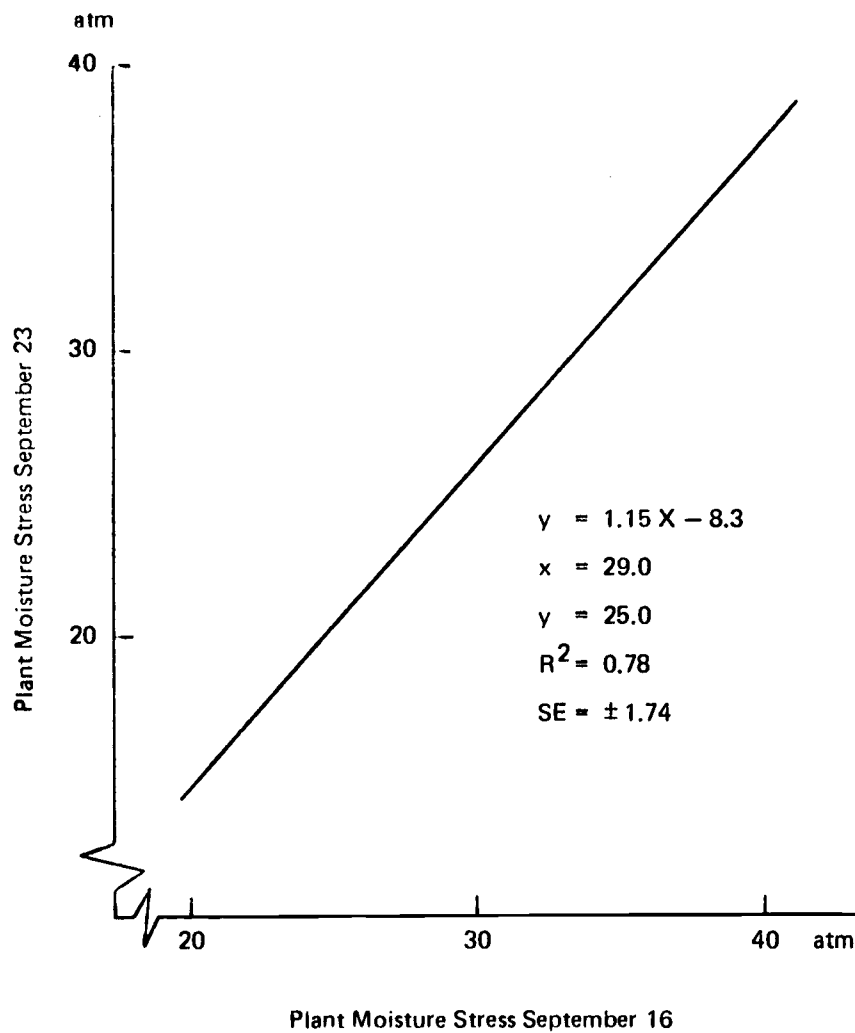


Figure 17. Linear Relation Between Moisture Stress in Douglas-fir Recorded Prior to and after a Brief Rain in September 1967.

trees with PMS near the threshold have not reached the cambium, whereas advanced, egg-containing galleries were found in trees with PMS exceeding 34 atm. The attack density on trees with PMS near 28 atm. was low, increasing on trees under higher PMS.

The results show that Douglas-fir trees under the physiological conditions indicated by the PMS threshold (the lower limit) are susceptible to and inducing initial colonization (the boring activity) by *S. wispinosus*. Furthermore, trees under PMS levels equal to and higher than the threshold appear capable of producing volatiles attractive to flying beetles. This inference is derived from two observations. First, in this study *S. wispinosus* were found crawling in large numbers in stems of trees under PMS levels near 29 atm., while none were found on stems of trees with PMS levels lower than 25.5 atm; second, Echols (unpublished 1967) found that large numbers of *S. wispinosus* responded to caged Douglas-fir twigs cut off a few days before testing, while fresh twigs were unattractive to the beetles.

The status of *S. wispinosus* infestation in Douglas-fir with recovering PMS conditions is shown in Table 9. Graphically depicted in Figure 19, it suggests that Douglas-fir trees with water relations improved beyond 20 atm. PMS abort; i.e., pitch-out, the invasion.

TABLE 8. Moisture stress in Douglas-fir and initial colonization by *Scolytus unispinosus*.

PMS atm.	Number of Trees		% Infested
	Infested	Uninfested	
≤ 23.8	0	8	0
23.9-25.5	0	2	0
25.6-27.2	1	3	25
27.3-28.9	3	3	50
29.0-30.6	2	1	66
$30.7 \leq$	11	2	84
<hr/>			
TOTAL:	19	17	-
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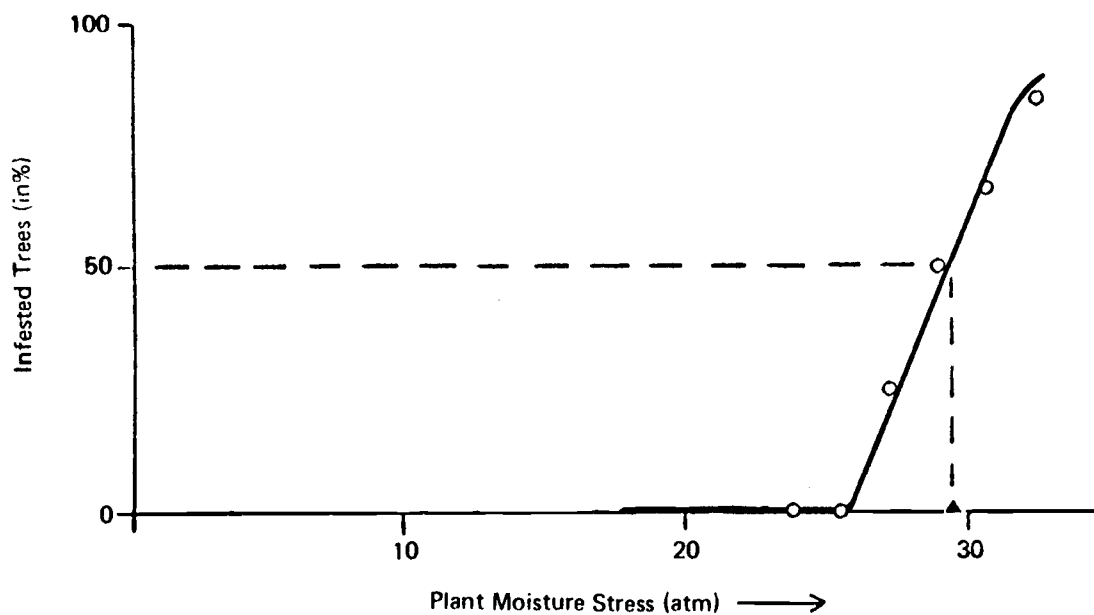


Figure 18. Douglas-fir *Scolytus unispinosus* Relationships: Threshold PMS Indicative of Tree Condition Conducive to Colonization.

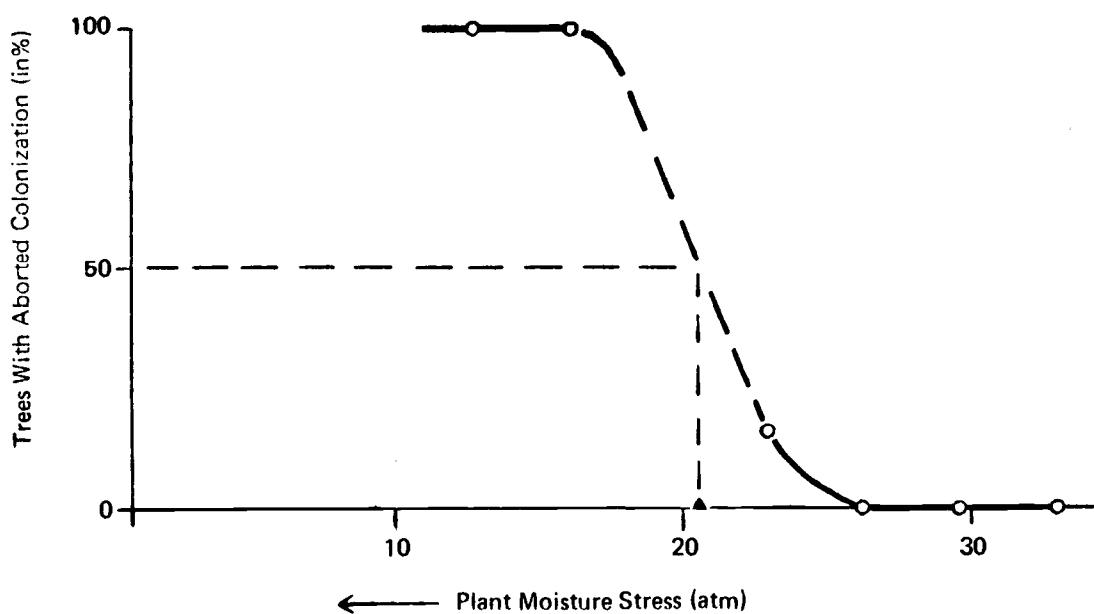


Figure 19. Douglas-fir *Scolytus unispinosus* Relationships: Threshold PMS Indicative of Tree Condition Abortive to Colonization.

The infestation status of mature Douglas-fir and their PMS record from September and mid-October (periods with depleted and high soil moisture contents, respectively) are shown in Table 10. The results support the observations on sapling post-sized trees (Figure 18 and Figure 19).

Pseudohylesinus nebulosus, Sexually Mature Beetles.

The relationship between the moisture stress of Douglas-fir and beetle infestation determined during periods when *P. nebulosus* beetles were known to be selecting breeding sites is graphically depicted in Figure 20. The diagram indicates the PMS of 17 atm. (diurnal minimum) as the threshold beyond which the trees, upon further stress increase, become subject to initial attacks by *P. nebulosus*.

The response of flying *P. nebulosus* to Douglas-fir material (Figure 9 and Table 6) under PMS proximal to the threshold indicates that trees under PMS levels equal to or higher than the threshold are capable to produce volatiles attractive to flying beetles.

The earlier discussed decrease in number of *P. nebulosus* beetles trapped during early midafternoon hours (Figures 11, 12) coincides in time with the PMS in Douglas-fir reaching the diurnal maximum (Figure 15). This suggests a causal relationship. It is possible that trees temporarily exceeding the PMS threshold for even just a few hours become attractive to flying beetles. The attractiveness

TABLE 9. *Scolytus unispinosus* colonization in relation to moisture stress in Douglas-fir.

PMS atm.	Number of Trees With <i>S. unispinosus</i> Colonization		%
	Aborted	Continuing	
≤ 13.5	2	0	100
13.6-16.9	2	0	100
17.0-20.3	-	-	-
20.4-23.7	1	6	16
23.8-27.1	0	5	0
27.2-30.5	0	5	0
30.6 \leq	0	9	0
TOTAL:	5	25	-

TABLE 10. Moisture stress of mature Douglas-fir and *Scolytus unispinosus* colonization.

PMS (atm.)		Colonization		
Mid-September	Mid-October	Successful	Aborted	Uninfested
18	13	-	-	X
19	11	-	-	X
20	9	-	-	X
22	13	-	-	X
23	-	-	-	X
25	17	-	X	
25	39	-	-	X**
25	20	-	-	X**
26	14	-	-	X
27	-	-	X	-
27	37	X	-	-
27	35	-	-	X**
30	24	-	-	X*
31	15	-	X	-

*Limbs and stem in crown region colonized by *P. nebulosus* in fall, 1967.

**Limbs and stem in crown region colonized by *P. nebulosus* in spring and fall, 1967.

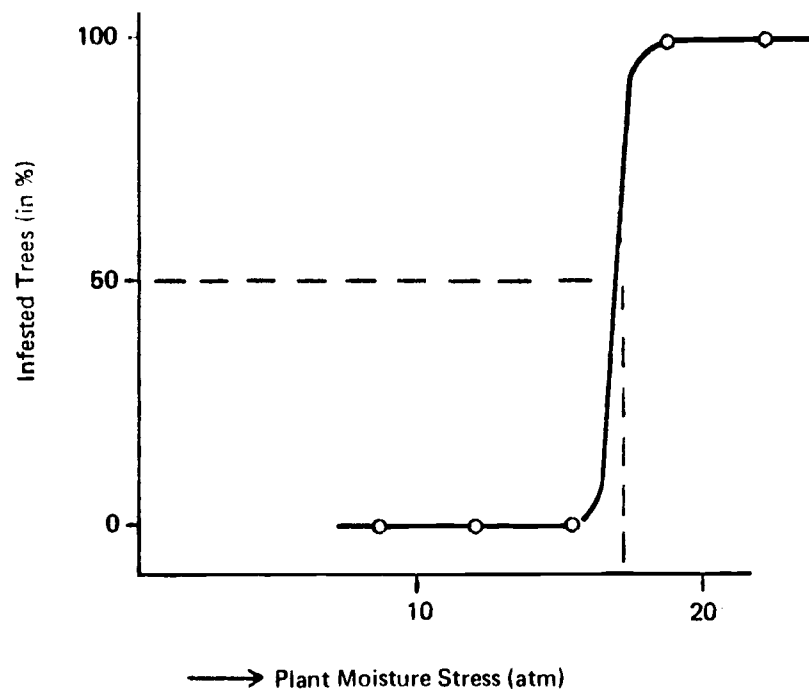


Figure 20. Douglas-fir — *Pseudohylesinus nebulosus* Relationships: Threshold PMS Indicative of Tree Condition Conductive to Colonization.

subsides with PMS recovery and the beetles become responsive to flight-inducing stimuli; the increased number of flying beetles then becomes reflected in the trapping results. The validity of these speculations was not investigated.

Observations on the status of *P. nebulosus* colonization in trees recovering from stress revealed that the beetles continued gallery construction in a tree under 13 atm. (at dawn), a PMS level well below the determined colonization threshold.

Pseudohylesinus nebulosus, Sexually Immature Beetles.

Douglas-fir seedlings in three different PMS categories were caged with fresh emerged *P. nebulosus* to determine the effect of PMS on initiation and continuation of maturation feeding. The results (Appendix, Table E) showed a statistically insignificant difference in feeding site initiation rates among seedlings in the three PMS categories. This suggests that the PMS in Douglas-fir does not affect feeding site selection and feeding initiation by *P. nebulosus*. The reaction of trees to injury or their suitability to feeding continuation varied with the moisture stress condition. The inspection of trees, five days after the beetles started the feeding attack, found 29% of feeding sites in the turgid group (plant moisture stress < 7 atm.) abandoned and filled with resin. The highest incidence of abandoned feeding sites, 36%, was found in the water-deficient dead and drying-out seedlings (or seedling parts). The feeding activity

in the semi-turgid group (plant moisture stress 14-20 atm.) continued seemingly unhampered as the beetles abandoned only 3% of initially constructed feeding niches, (significantly less at the 5% level, than in the turgid and stressed groups).

The tree reaction to the feeding injury and its effect on feeding continuation is ecologically important to the beetle. An adverse reaction undoubtedly increases beetle mortality by entrapments of beetles in feeding tunnels and losses connected with a resumed dispersal flight. The forced feeding interruption is likely to prolong the maturation process. Conversely, the tree condition favoring uninterrupted occupancy of the feeding site is likely to increase the rate of the maturation process. Interestingly, the PMS minima of most mature Douglas-fir determined during August and September of 1967 fall into the PMS range shown as best suited for uninterrupted maturation feeding.

Hot and dry weather during the spring and summer evidently increases not only the temperature dependent development of the larval stages, but through the effects on the host tree condition it affects favorably the maturation process of emerged beetles as well. It is certainly not a coincidence that the PMS threshold indicating the host condition conducive to *P. nebulosus* colonization (Figure 20) lies within the range of PMS conditions shown as favorable for uninterrupted maturation feeding.

Dendroctonus pseudotsugae.

The relation between the PMS condition in Douglas-fir trees and *D. pseudotsugae* colonization is graphically depicted in Figure 21. The PMS level of 15 atm. appears to be the threshold indicative of physiological conditions under which Douglas-fir trees become conducive to initial attacks by *D. pseudotsugae*. Considering the lack of data from trees under PMS within the 13.6-16.9 atm. range (Appendix, Table F), the PMS threshold in Figure 21 must be regarded as a rough approximation.

Observations on the status of *D. pseudotsugae* colonization in trees recovering from stress revealed that the beetles continued gallery construction in trees under 14 atm.; aborted galleries were found in a tree with PMS recovered to 8.5 atm. The results in Figure 22 suggest that trees with moisture conditions improved beyond 12 atm. abort the invasion.

Melanophila drummondi Kirby and other Buprestidae.

Unlike bark beetles, the buprestid beetles lay eggs into bark crevices; upon eclosion, the larvae mine through the bark to feed in the phloem tissues. Lack of external signs indicating initial colonization obviously hinders observations on host condition-Buprestidae relationships. Nevertheless, the following observations provide a limited insight. On a hot midday (35°C) during the first week in June of 1967, stems of two 90-year-old Douglas-fir trees were found literally covered by *Melanophila drummondi* and other buprestid beetles.

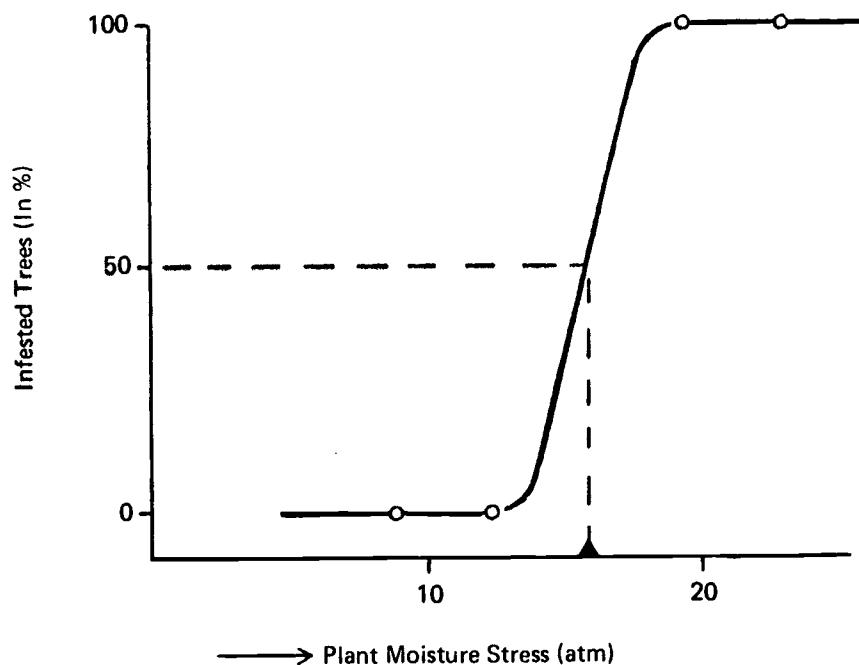


Figure 21. Douglas-fir — *Dendroctonus pseudotsugae*
Relationships: Threshold PMS Indicative of
Tree Condition Conducive to Colonization.

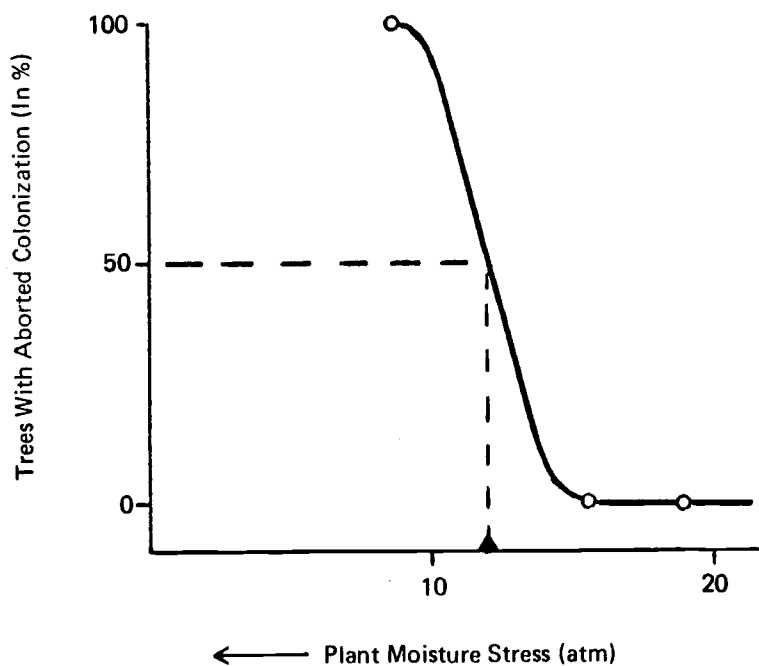


Figure 22. Douglas-fir — *Dendroctonus pseudotsugae*
Relationships: Threshold PMS Indicative of
Tree Condition Abortive to Colonization.

The trees were grown on a southern tip of a patch of timber adjacent to a clearcut; each tree had a moderately developed crown and an average-vigor appearance. Only a few or no Buprestidae at all were seen crawling on stems of adjacent trees. The two "attractive" trees and two of the adjacent, seemingly unattractive trees (No. 1-2 and 3-4, respectively) were subjected to the following observations:

(1) The PMS of each tree was determined in four consecutive days at dawn and at midday; (2) A 3600cm^2 piece of Tanglefoot-covered cheese-cloth was placed on the south exposed stem in the midbole of each tree. Five days later, the sticky traps were removed and the insects trapped on the center 900cm^2 of cloth were identified by species or group, counted and recorded; (3) The PMS of all four trees was periodically measured throughout the season; (4) Their insect-colonization status was determined in spring of 1968.

The relation between the moisture stress condition of Douglas-fir and their attractiveness to *Melanophila drummondi* and other Buprestidae is shown in Figure 23. Trees to which the Buprestidae and their predatory and parasite associates were evidently attracted in mass (tree No. 1 and 2) show a PMS range from 17.6 atm. at dawn to 22 atm. at noon; the PMS at dawn ranged from 17.6 atm. to 20 atm. and averaged 18.8 atm.

The moisture stress conditions of trees found as relatively unattractive to the insects (tree No. 3 and 4) ranged from 9 atm. at dawn to 19 atm. at noon. The stress at dawn ranged from 9 to 11.2 atm.

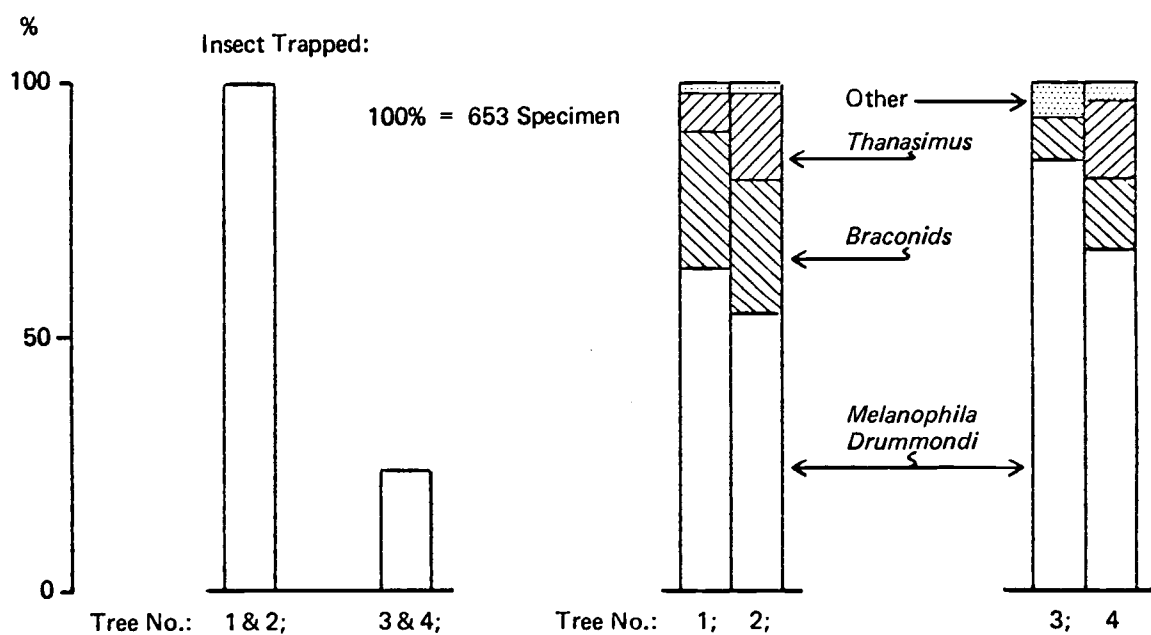
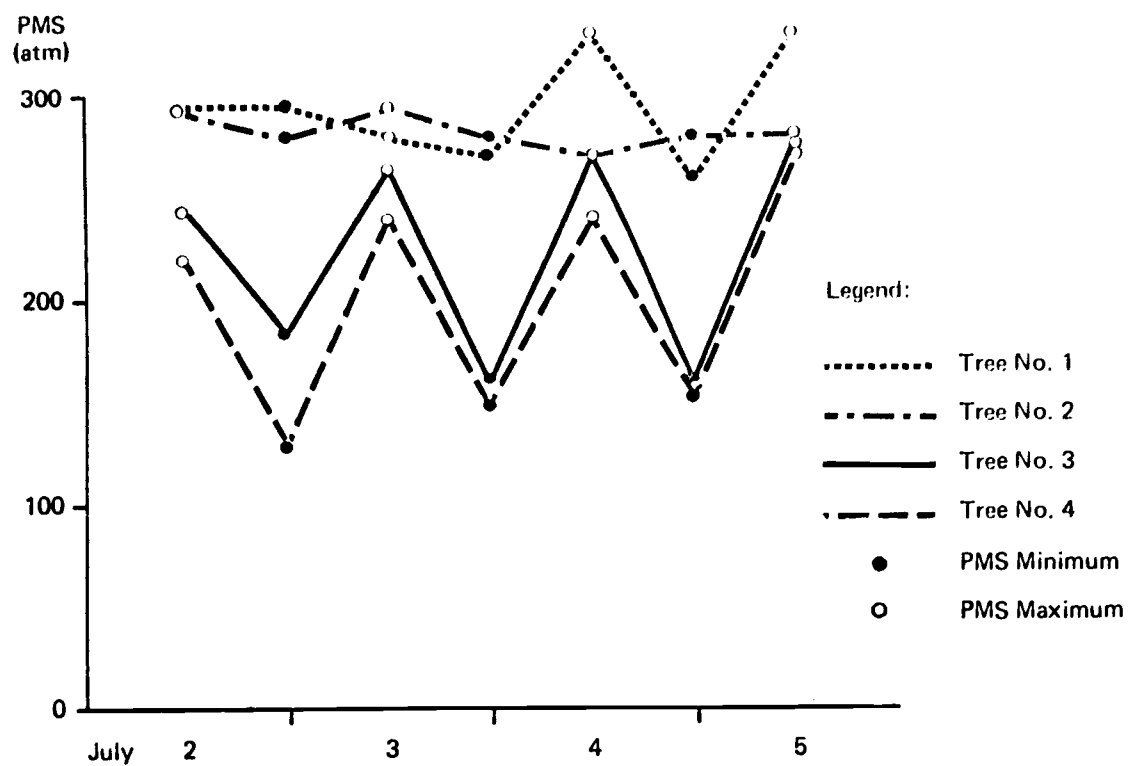


Figure 23. Relation Between PMS of Mature Douglas-fir and Their Attractiveness to *Melanophila drummondi* Beetles and Their Parasite-Predator Complex.

and averaged 10.8 atm.; the stress at noon ranged from 15 atm. to 19 atm. and averaged 17.2 atm.

The colonization status of all four trees was determined in the spring of 1968. On tree No. 1, the phloem tissue on the entire stem was riddled by Buprestidae larvae (and the bark in the midbole stripped by woodpeckers). Its foliage was discolored by June. On tree No. 2 (felled in February), the phloem tissue on the entire limbless stem portion was riddled by Buprestidae larvae (and the bark in the midbole stripped by woodpeckers); the limbs and stem in the crown region were colonized by *S. wispinosus* and *Scolytus tsugae*, in addition to buprestids. In contrast, tree No. 3 showed no apparent signs of injury; growth of new shoots in spring of 1968 was normal. Tree No. 4, felled in February, had the limbs and the stem portion in the crown region free of insect colonization. The stem in the midbole region, particularly its part exposed to midday sunrays, was sporadically and unsuccessfully colonized by Buprestidae larvae (the larval mines were, without exception, filled with resin; the larvae were dead).

The PMS conditions of mature Douglas-fir trees (determined at the end of the rainless period in September) and the Buprestidae colonization status of each tree (determined in spring of 1968 when the sample trees were felled) are shown in Figure 24 (from data in Appendix, Table H). The diagram indicates that 22 atm. (at dawn) is the threshold PMS at which Douglas-fir trees become susceptible to invasion by larvae of Buprestidae.

The status of Buprestidae colonization matched with the trees' PMS condition in late fall of 1967 or spring of 1968 periods with high soil moisture contents, is shown in Figure 25 (from data in Appendix, Table I). The diagram indicates that trees colonized by Buprestidae and capable of recovering from a water deficit to PMS levels beyond the threshold PMS of 16 atm. abort the invasion by engulfing the larvae in resin.

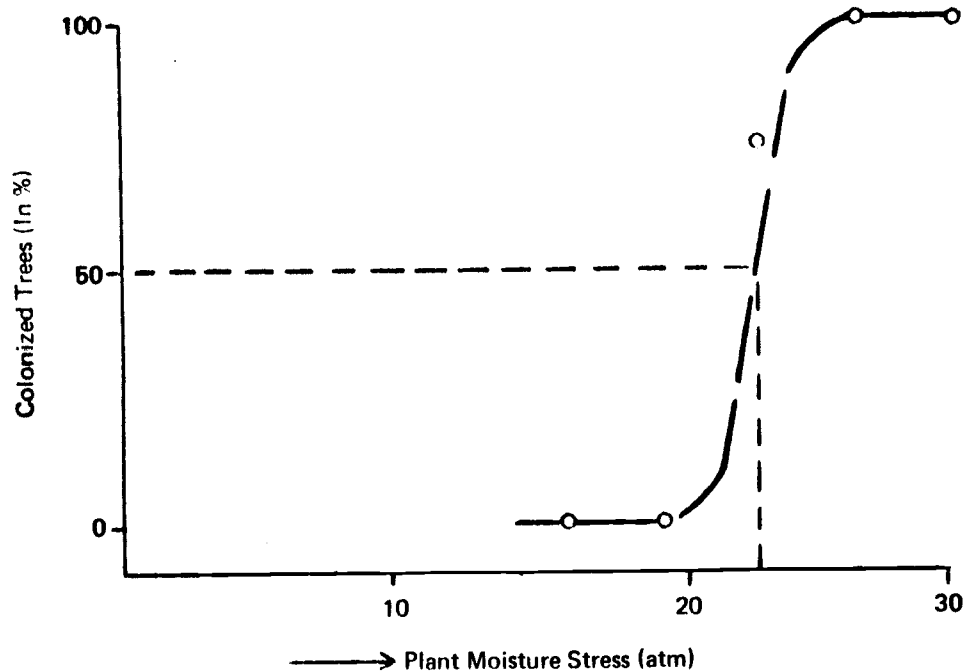


Figure 24. Douglas-fir – *Melanophila drummondi* Relationships: Threshold PMS Indicative of Tree Condition Susceptible to Colonization.

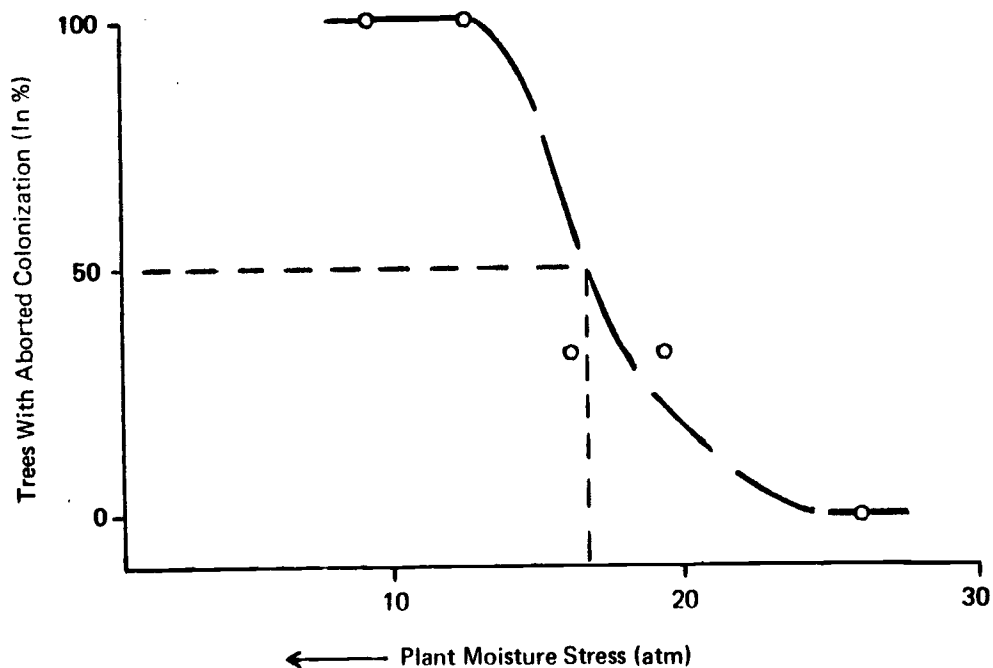


Figure 25. Douglas-fir – *Melanophila drummondi* Relationships: Threshold PMS Indicative of Tree Condition at which Pitch-Oozing Fills the Larval Mines.

CONCLUSIONS

The results obtained in this study clearly confirm the previous belief that the physiological condition of the host tree, as indicated by and related to its internal moisture stress, affects the tree's disposition to colonization by subcortically feeding insects.

The relationship between the moisture stress in Douglas-fir and colonization by scolytid and buprestid beetles is shown in a generalized diagram in Figure 26. First, Douglas-fir trees or their parts become susceptible and conducive to initial colonization by *P. nebulosus*, *D. pseudotsugae*, *M. drummondi* and *S. wispinosus* upon reaching a certain threshold PMS, which appears specific for each insect. Second, initially colonized trees capable of reversing their moisture deficit abort the insect invasion upon recovery to a certain threshold PMS level, which appears also specific for each insect.

The PMS threshold indicative of host condition conducive to initial colonization and the PMS threshold indicative of conditions abortive to the beetle infestation appear to set the upper and lower limit, respectively, to a physiological condition under which initiated colonization continues but the tree *per se* appears incapable of inducing new attacks.

The relationship between the PMS condition of the tree and its colonization by meristem insects, as shown in this study, accords with previous observations relating Douglas-fir beetle colonization to the

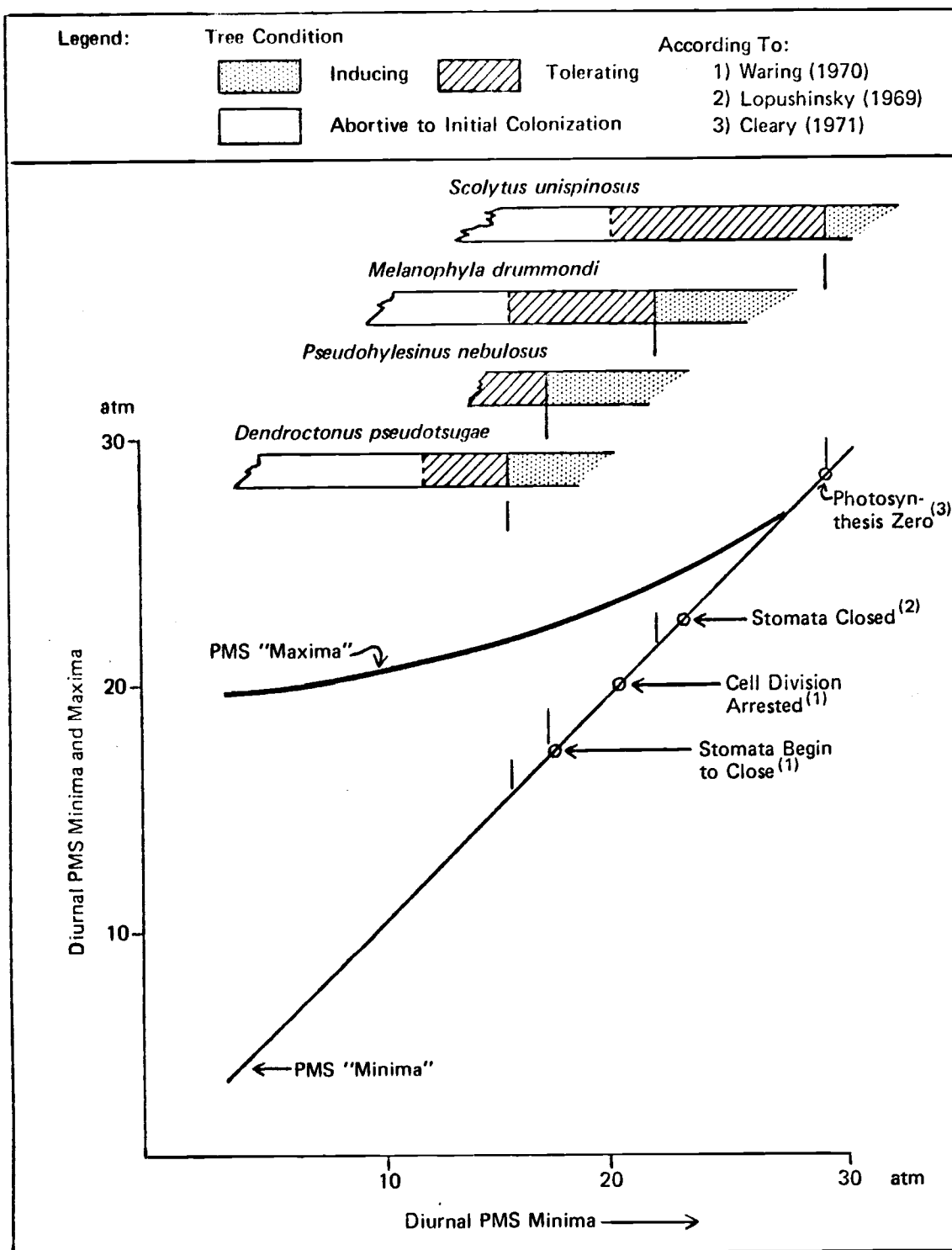


Figure 26. Douglas-fir Moisture Stress – Scolytidae and Buprestidae Relationships.

host trees' OEP (Rudinsky, 1966b). Both studies show that trees under moisture deficient conditions, characterized by certain thresholds, are susceptible to bark beetle colonization. Both emphasize the dynamical nature of the trees' moisture relations and the reversibility of the trees' disposition to bark beetle attack. There is, however, a readily apparent difference between both techniques. The installation of pressure gauges to determine the OEP is laborious, and OEP determinations are time-consuming and readily obstructed by resin crystallization. The pressure chamber technique, on the other hand, enables a direct, easy, rapid and reliable determination of moisture stress in any part of the trees' crown region. More important, the PMS values are comparable with moisture stress parameters obtained by other standard techniques. For these reasons, the pressure chamber technique is highly suitable for studies of the relation of host condition and meristem insect colonization.

Numerous studies have correlated PMS in Douglas-fir with other physiological parameters. This enables one to relate some of the cardinal points in the host-insect relationship to other physiological characteristics of the tree. For example, the PMS thresholds at which Douglas-fir become conducive to initial colonization by *D. pseudo-tugae* and *P. nebulosus* are close to the PMS level at which, according to Waring (1970), Douglas-fir begin to close stomata. The PMS thresholds at which Douglas-fir become attractive to buprestid beetles and enable penetration of the phloem tissues by their larvae are near PMS levels which arrest cell division (Waring, 1970) and close stomata in

Douglas-fir. (Waring and Cleary, 1967; Lopushinsky, 1969.) The PMS threshold at which *S. uniapinosus* initiates colonization appears to correspond with PMS levels at which Douglas-fir completely stop photosynthesis, as data in Cleary's (1971) report indicate.

The PMS threshold indicative of tree conditions abortive to *S. uniapinosus* is close to the PMS at which cell division becomes arrested; interestingly, it lies close to the PMS thresholds at which Douglas-fir become conducive to colonization by *P. nebulosus* and attractive to *M. drummondi*. The threshold PMS at which larvae of Buprestidae are pitched-out appears to correspond with PMS levels at which cell division in Douglas-fir is resumed. It appears that PMS in Douglas-fir trees has to recover to levels under which the integrative processes are fully resumed to induce abortion of initial colonization by *D. pseudotsugae* and *P. nebulosus*.

In short, the initial attack of bark beetles and buprestid beetles associated with Douglas-fir appears to be induced by and directed to trees in a PMS condition in which integrative processes are severely curtailed (Fry, 1965; Cleary, 1971; Zavitkovski and Ferrell, 1970); and as the report by Brix (1962) suggests, respiration increasingly exceeds photosynthesis. Conversely, the trees' increasing capability to abort initial colonization corresponds with improving PMS conditions and the correlated resumption of integrative processes. The ability of attacking beetles to tolerate PMS recovery to certain, apparently

species-specific thresholds, seems to manifest the adaptation of each species to the hosts' defensive mechanisms.

The distinct breeding site preference exhibited by each of the observed insect species, discussed earlier (Table 7), suggests that other factors beside the critical PMS condition also determine whether the whole tree or certain parts of it become colonized by a particular insect species. The host tree compounds eliciting in beetles the chain of responses leading to colonization are evidently products of metabolic processes specific to certain PMS conditions and other as yet unknown host characteristics. In what respect the processes are different in trees or tree parts in an "unattractive" state from that in the "attractive" state needs to be determined. The attractiveness of ethyl alcohol to a number of bark beetle and ambrosia beetle species (shown and discussed in the chapter on bionomics of *P. nebulosus*) provides a possible clue that anaerobic respiration is involved in production of primary attractants. Should this indeed be the case, Graham's (1968) proposal about the role of anaerobic respiration in primary attraction could be valid for Scolytidae as a group. Heikkinen and Hrutfiord (1965) suggested (based on results of olfactometer bioassays of *D. pseudotsugae* response to α -pinene and β -pinene) that tissue specificity to a bark beetle species may be given by the ratio of certain terpene fraction in the tissue, resulting from water deficit-triggered metabolic changes

that differ in the hole from that in the stem of the crown region. The latter suggestion appears complementary to the former; both certainly need further research attention.

As is apparent from Figure 26, some species initiate colonization of trees in which photosynthesis and cell division still takes place, even though at a conceivably reduced rate. It may be said that these species are responding to "marginally weakened" trees. Other species initiate colonization of trees under comparatively high moisture deficits with photosynthesis and cell division completely stopped.

It appears that during seasons with favorable moisture conditions, only trees irreversibly and permanently damaged by factors such as root-rot, disrupted photosynthate translocation to support root growth, lack of oxygen in the root zone, or trees with stomatal aperture damaged by air pollution will attain the marginally weakened condition. The study by Stark and Cobb (1969) relating successful bark beetle infestation to root-rot and air pollution damage in pine stands supports this idea. Trees under such condition have a theoretically low chance to recover from the stress and abort the colonization. The beetle invasion only speeds up the death of the tree.

In seasons in which soil moisture becomes progressively depleted, a high number of seemingly healthy trees may reach the marginally weakened condition. Since the capability to uptake and redistribute water or to control its loss is unimpaired in healthy trees, the trees

are in a temporary and reversible weakened state, a state that is subject to rapid change because of rain or decreased evapotranspiration. Trees in such condition theoretically have a high chance of recovering from the water deficit and a high chance of aborting the beetle colonization. This happens frequently as manifested by the incidence of pitch-defects in Douglas-fir from aborted and overgrown beetle attacks (Belluschi *et al.*, 1965).

Undoubtedly, the host tree and its changing condition exercised evolutionary pressure on the biology and habits of subcortical feeding insects. Ecologically important is the relation between PMS levels at which an insect initiates colonization and the insects' main breeding seasons. It is unlikely that a scolytid associated with marginally weakened Douglas-fir would have a breeding period confined entirely to the high summer and early fall periods of high PMS. Its progeny survival would be adversely affected by the reversible nature of the tree condition. For instance, *P. nebulosus*, shown to respond to trees in a marginally weakened condition, is known to initiate colonization from late fall through early spring. Its progeny emerges throughout summer, a period with a high incidence of trees in a marginally, but temporarily weakened condition. The emerging beetles are sexually immature and do not initiate colonization of breeding sites. The beetles, upon dispersal, enter into Douglas-fir twigs and feed to gain maturity. The sexual immaturity of emerging beetles appears as an adaptation, resulting from the pressure exercised on the

progeny by the reversible nature of marginally weakened trees during summer and from competitive advantage gained from association with marginally weakened trees during "safe" periods. The galleries constructed by the beetle and larvae do not score the wood, and the pupal chambers are also located inside the phloem tissues. These habits appear to be a behavioral adaptation of apparent survival value, interconnected with the evolved association with marginally weakened trees.

The bionomics of *S. unispinosus* seems to provide another example of selection pressure exercised by the host condition. *S. unispinosus* initiates colonization during seasons with progressively depleted soil moisture contents and by associating with trees under relatively high PMS; i.e., 29 atm., (reached by healthy Douglas-fir only in extremely droughty years), it avoids colonization of temporarily weakened trees. The relatively wide range between the threshold PMS level indicative of conditions conducive to *S. unispinosus* attack initiation and the PMS levels at which the trees abort the eventual colonization (compared to that by buprestids or *D. pseudotsugae*) seems to ensure a greater chance for successful completion of the infestation. The xylem-scoring habit of both beetle and larvae appears to be an interconnected behavioral adaptation impairing local xylem conductivity and decreasing the possibility for abortion of attack.

D. pseudotsugae is another species that responds to marginally weakened trees. It colonizes the host from spring until early summer.

The ability to produce a strong pheromone attraction, triggering a mass attack that ultimately weakens irreversibly the marginally and often temporarily weakened trees, appears as another adaptation that evolved as a result of the selection pressure exercised by the host condition (as demonstrated by Rudinsky, 1966b).

Theoretically, the economically most important pests among subcortically feeding insects associated with Douglas-fir are species capable of colonizing and irreversibly weakening trees in the marginally weakened condition. The prime candidate in this respect appears to be *D. pseudotsugae*, particularly the part of its population that searches for breeding sites in late spring and summer (the late emerging brood and reemerging females). *P. nebulosus* may also become destructive should a part of its population reach sexual maturity during droughty summers. Buprestids appear as a pest to be concerned with, particularly in "second growth" even-aged stands subjected to drastic stocking reduction. Attempts to evaluate separately the importance of each species, however, make little sense from the ecological as well as economic standpoint. The host-insect relationships of the species associated with Douglas-fir are interrelated to the extent that the injury caused by colonization of one species predisposes the tree (or certain parts of it) to attack by another species.

Meaningful predictions on the extent of beetle-caused tree mortality and stand hazard ratings have to be based on (1) accurate assessments of the seasonally changing moisture relations in the stand,

and (2) estimates of the beetle population interpreted in terms of host-insect relationships such as those analyzed in the present study. Remote sensing techniques seem to have the capability of solving the first and prime part of the task, perhaps with ground support by the pressure chamber method. Development of methods to monitor insect populations no longer seems a technically formidable task with the use of attractants in survey traps.

Similarly, measures to reduce the hazard of bark beetle attack need to be oriented toward the host condition. First of all, there is need to delimit stands vulnerable to bark beetle colonization and to identify the factors responsible for the weakened state. Bark beetle hazard prevention has to be an integral part of forest managerial planning. In young stands, treatments to increase stand productivity have to be assessed in terms of their direct and indirect, short- and long-term effects on stand disposition to bark beetle colonization. Stand vulnerability to bark beetle colonization has to become a prominent factor in harvest priority designations.

Application of silvicultural or other forest management techniques to reduce bark beetle damage may often prove impractical from forest management standpoint or to be a long-term task. In such instances, employment of techniques affecting beetle behavior to prevent successful colonization of vulnerable stands seems the only route available. Recent progress in alteration of bark beetle behavior through the use of attractants and particularly through the use of compounds deterring colonization promises success in this alternative.

BIBLIOGRAPHY

- Anderson, R. F. 1948. Host selection by the pine engraver. *Journal of Economic Entomology* 41:596-602.
- Atkins, M. D. 1966a. Behavioral variation among scolytids in relation to their habitat. *Canadian Entomologist* 98:285-288.
- Atkins, M. D. 1966b. Laboratory studies on the behavior of the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins. *Canadian Entomologist* 98:953-991.
- Atkins, M. D. 1967. The effect of rearing temperature on the size and fat content of the Douglas-fir beetle. *Canadian Entomologist* 99:181-7.
- Barrs, H. D. 1968. Determination of water deficits in plant tissues. In: water deficits and plant growth, ed. by T. T. Kozlowski. Academic Press, New York. Vol. 1:235-368.
- Belluschi, P. G., N. E. Johnson and H. J. Heikkinen. 1965. Douglas-fir defects caused by the Douglas-fir beetle. *Journal of Forestry* 62:252-256.
- Berryman, A. A. and M. Ashraf. 1970. Effects of *Abies grandis* resin on the attack behavior and brood survival of *Scolytus ventralis* (Coleoptera:Scolytidae). *Canadian Entomologist* 102:1229-1236.
- Blackman, M. W. 1924. The effect of deficiency and excess of rainfall upon the hickory bark beetle. *Journal of Economic Entomology* 17:460-70.
- Borden, J. H. 1967. Factors influencing the response of *Ips confusus* (Coleoptera:Scolytidae) to male attractant. *Canadian Entomologist* 99:1164-93.
- Boyer, J. S. 1967. Leaf water potentials measured with a pressure chamber. *Plant Physiology* 42:133-137.
- Boyer, J. S. 1969. Measurement of the water status of plants. *Annual Review of Plant Physiology* 20:351-364.
- Brix, H. 1962. The effect of water stress on the rates of photosynthesis and respiration in tomato plant and loblolly pine seedlings. *Physiologia Plantarum* 15:10-20.
- Browne, F. G. 1952. Suggestions for future research in control of ambrosia beetles. *Malayan Forester* 15:197-206.

- Buchanan, W. D. 1941. Experiments with an ambrosia beetle, *Xylosandrus germanus* (Bldf.). *Journal of Economic Entomology* 34:367-9.
- Cade, S. C., B. F. Hrutflord and R. I. Gara. 1970. Identification of a primary attractant for *Gnathotrichus sulcatus*. *Journal of Economic Entomology* 63:114-115.
- Caird, R. W. 1935. Physiology of pines infested with bark beetles. *Botanical Gazette* 96:709-33.
- Chamberlin, W. J. 1918. Bark beetles infesting the Douglas-fir. Oregon Agricultural College, Experiment Station. Station Bulletin 147, 39p.
- Chamberlin, W. J. 1958. The Scolytidae of the Northwest: Oregon, Washington, Idaho and British Columbia. Corvallis, Oregon: Oregon State College Press 208p.
- Chapman, J. A. 1962. Field studies on attack flight and log selection by the ambrosia beetle *Trypodendron lineatum* (Oliv.) (Coleoptera:Scolytidae). *Canadian Entomologist* 94:74-92.
- Chapman, J. A. 1963. Field selection of different log odors by scolytid beetles. *Canadian Entomologist* 95:673-676.
- Chapman, J. A. 1967. Response behaviour of scolytid beetles and odour meteorology. *Canadian Entomologist* 99:1132-1137.
- Chararas, C. 1959a. L'attractivité exercée par les Conifères a l'égard des scolytids et la role des substances terpéniques des olérésines. *Rev. Pathol. Vegetale* 38:113-129.
- Chararas, C. 1959b. Relations entre la presion osmotique des Conifères et leur attaque par les Scolytidae. *Rev. Pathol. Vegetale* 38:215-233.
- Cleary, B. D. 1971. The effect of plant moisture stress on the physiology and establishment of planted Douglas-fir and Ponderosa pine. Ph. D. Thesis. Corvallis, Oregon State University. 85 numbered leaves.
- Craighead, F. C. 1925. Bark beetle epidemics and rainfall deficiency. *Journal of Economic Entomology* 18:577-86.

- Daterman, G. E., J. A. Rudinsky and W. P. Nagel. 1965. Flight patterns of bark and timber beetles associated with coniferous forests of Western Oregon. Corvallis, Oregon State University, Agriculture Experiment Station. Technical Bulletin 87, 46p.
- Dethier, V. G. 1953. Chemoreception. In: insect physiology. Roeder, K. ed., Willey & Sons, New York, 1100p. 544-76.
- Dixon, H. H. 1914. Transpiration and the ascent of sap in plants. The MacMillan Company, New York. 177p.
- Echols, H. W. 1967. Unpublished research in files at the Department of Entomology, Oregon State University, Corvallis.
- Francia, F. C. and K. Graham. 1967. Aspects of orientation behavior in ambrosia beetle *Trypodendron lineatum* (Olivier). Canadian Journal of Zoology 45:874-1002.
- Fry, K. E. 1965. A study of transpiration and photosynthesis in relation to stomatal resistance and internal water potential in Douglas-fir. Ph. D. Thesis. Seattle, University of Washington. 192 numbered leaves.
- Furniss, R. L. 1936. Bark beetle activity following the Tillamook fire. Timberman 37:21-22.
- Furniss, M. M. and P. W. Orr. 1970. Douglas-fir beetle. USDA Forest Service, Forest Pest Leaflets, 4p.
- Gara, R. I. 1963. Studies on the flight behavior of *Ips confusus* (Lec.) (Coleoptera:Scolytidae) in response to attractive material. Contribution from Boyce Thompson Institute 22:51-66.
- Gara, R. I. and J. P. Vité. 1962. Studies on the flight patterns of bark beetles (Coleoptera:Scolytidae) in second growth Ponderosa pine forests. Contribution from Boyce Thompson Institute 21:275-290.
- Gara, R. I., J. P. Vité and H. H. Cramer. 1965. Manipulation of *Dendroctonus frontalis* by use of a population aggregating pheromone. Contribution from Boyce Thompson Institute 23:55-66.
- Goeden, R. D. and D. M. Norris, Jr. 1965. Some biological and ecological aspects of ovipositional attack in *Carya* spp. by *Scolytus quadrispinosus* (Coleoptera:Scolytidae). Annals of the Entomological Society of America 58:771-777.

- Graham, K. A. 1959. Release by flight exercise of a chemotrophic response from photopositive domination in a scolytid beetle. *Nature*, London 184:283-284.
- Graham, K. A. 1968. Anaerobic induction of primary chemical attractancy for ambrosia beetles. *Canadian Journal of Zoology* 46:905-8.
- Graham, K. A. and A. E. Werner. 1956. Chemical aspects of log selection by ambrosia beetles. Bimonthly Progress Report, Canadian Department of Agriculture, Forest Biology Division 12:3-4.
- Heikkinen, H. J. and B. E. Hrutfiord. 1965. *Dendroctonus pseudotsugae*: A hypothesis regarding its primary attractant. *Science* 150:1457-1459.
- Hopping, R. 1928. Annual report of the Forest Insect Laboratory, Vernon, British Columbia, unpublished.
- Jantz, O. K. and J. A. Rudinsky. 1966. Olfactory behavior of the Douglas-fir beetle. Technical Bulletin No. 94. Agriculture Experiment Station, Oregon State University, 38p.
- Johnson, N. E. 1964. Effects of different drying rates and two insecticides on beetle attacks in felled Douglas-fir and Western hemlock. Weyerhaeuser Company Forestry Research Note No. 58.
- Johnson, N. E. and P. G. Belluschi. 1969. Host-finding behavior of the Douglas-fir beetle. *Journal of Forestry* 67:290-295.
- Johnson, N. E. and J. G. Zingg. 1969. Transpirational drying of Douglas-fir: Effect on log moisture content and insect attack. *Journal of Forestry* 67:816-819.
- Klepper, B. 1968. Diurnal pattern of water potential in woody plants. *Plant Physiology* 43:1931-1934.
- Kraemer, G. D. 1949. Die Brutbaumdisposition bei Borkenkäferbefall. *Anzeiger für Schädlingkunde* 22:49-51.
- Kraemer, G. D. 1950. Der grosse Tanenborkenkäfer, unter Berücksichtigung seiner beiden Verwandten und der Brutbaumdisposition. *Zeitschrift für Angewandte Entomologie* 31:349-430.
- Kraemer, G. D. 1953. Die Kritischen Grenzen der Brutbaum Disposition für Borkenkäferbefall an Fichte. *Zeitschrift für Angewandte Entomologie* 34:463-512.

- Kramer, P. J. 1969. Plant and soil water relationships: A Modern Synthesis. McGraw-Hill, New York, 482p.
- Kramer, P. J. and T. T. Kozłowski. 1960. Physiology of Trees. McGraw-Hill, New York, 642p.
- LeConte. 1859. Additions to the Coleopterous fauna of Northern California and Oregon. Proceeding of the Academy of Natural Sciences of Philadelphia, 281-292p.
- Lopushinsky, W. 1969. Stomatal closure in conifer seedlings in response to moisture stress. Botanical Gazette 130:258-263.
- McCowan, V. F. and J. A. Rudinsky. 1954. Biological studies on the Douglas-fir bark beetle; Millicoma Forest, Coos Bay, Oregon. Weyerhaeuser Company Forestry Research Note No. 11, 21p.
- McMullen, L. H. and M. D. Atkins. 1962. On the flight and host selection of the Douglas-fir beetle, *Dendroctonus pseudotsugae*, Hopkins (Coleoptera:Scolytidae). Canadian Entomologist 94:1309-1325.
- Merker, E. 1953. Lockstoffe and Nährstoffe in Wirtzpflanzen einiger Waldschädlinge. Allgemeine Forst-Und Jagdzeitung 124:136-144.
- Merker, E. 1956. Der Widerstand von Fichten gegen Borkenkäferfrass. Allgemeine Forst-Und Jagdzeitung 127:129-145, 168-187.
- Merker, E. 1960. Der Einfluss des Baumzustandes auf die Überfermehung einiger Waldschädlinge. Zeitschrift für Angewandte Entomologie 46:432-44.
- Meyer, H. J. and D. M. Norris. 1967. Behavioral responses by *Scolytus multistriatus* (Coleoptera:Scolytidae) to host-(*Ulmus*) and beetle-associated chemotactic stimuli. Annals of the Entomological Society of America 60:642-647.
- Miller, J. M. and F. B. Keen. 1960. Biology and control of the Western pine beetle. A summary of the first 50 years of research. U.S. Department of Agriculture, Forest Service Miscellaneous Publ. 800, 381p.
- Moeck, H. A. 1970. Ethanol as the primary attractant in the ambrosia beetle *Trypodendron lineatum* (Olivier) (Coleoptera: Scolytidae). Canadian Entomologist 102:984-995.
- Norris, D. M. and J. E. Baker. 1969a. Feeding responses of the beetle *Scolytus multistriatus* to chemical stimuli in the bark of *Ulmus*. Journal of Insect Physiology 13:955-962.

- Norris, D. M. and J. E. Baker. 1969b. Nutrition of *Xyleborus ferrugineus*. I. Ethanol in diets as a tunneling (feeding) stimulant. *Annals of the Entomological Society of America* 62:592.
- Person, H. L. 1931. Theory in explanation of the selection of certain trees by the Western pine beetle. *Journal of Forestry* 29:696-699.
- Perttunen, V. 1957. Reactions of two bark beetle species, *Hylurgops palliatus* Gyll. and *Hylastes ater* Payk (Coleoptera:Scolytidae) to the Terpene α -Pinene. *Annales Entomol. Fennica* 23:101-110.
- Philip, J. R. 1966. Plant water relations: Some physical aspects. *Annual Review of Plant Physiology* 17:245-268.
- Pitman, G. B. 1966. Studies on the pheromone of *Ips confusus* (LeConte), III. The influence of host material on pheromone production. *Contributions from Boyce Thompson Institute* 23:147-158.
- Reid, R. W. 1963. Biology of the mountain pine beetle, *Dendroctonus monticolae* Hopkins, in the East Kootenay Region of British Columbia, III. Interaction between the beetle and its host, with emphasis on brood mortality and survival. *Canadian Entomologist* 95:225-38.
- Reid, R. W. and H. Gates. 1970. Effect of temperature and resin on hatch of eggs of the mountain beetle (*Dendroctonus ponderosae* Hopkins). *Canadian Entomologist* 102:617-622.
- Rudinsky, J. A. 1962. Ecology of Scolytidae. *Annual Review of Entomology* 7:327-48.
- Rudinsky, J. A. 1963. Response of *Dendroctonus pseudotsugae* Hopkins to volatile attractants. *Contribution from Boyce Thompson Institute* 22:23-38.
- Rudinsky, J. A. 1966a. Scolytid beetles associated with Douglas-fir response to Terpenes. *Science* 152:218-219.
- Rudinsky, J. A. 1966b. Host selection and invasion by the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, in coastal Douglas-fir forests. *Canadian Entomologist* 98:98-111.
- Rudinsky, J. A. and G. E. Daterman. 1964. Field studies on flight patterns and olfactory responses of ambrosia beetles in Douglas-fir forests of Western Oregon. *Canadian Entomologist* 96:1339-52.

- Rudinsky, J. A. and J. P. Vité. 1956. Effects of temperature upon the activity and the behavior of the Douglas-fir beetle. *Forest Science* 2:258-267.
- Rudinsky, J. A., G. W. Kinzer, A. F. Fentiman, Jr. and R. L. Foltz. 1972. Trans-verbenol isolated from Douglas-fir beetle: Laboratory and field bioassays in Oregon. *Environmental Entomology* 1:485-488.
- Samaniego, A. and R. I. Gara. 1970. Estudios Sobre la Actividad de Vuelo y Selección de Huespedes por *Xyleborus* spp. y *Platypus* spp. (Coleoptera:Scolytidae y Platypodidae). *Separado de Turrialba* 20:471-477.
- Schimitschek, E. and E. Wienke. 1963. Untersuchungen über die Befallsbereitschaft von Baumarten für Secundärschädlinge, I Teil. *Zeitschrift für Angewandte Entomologie* 51:219-257.
- Schimitschek, E. and E. Wienke. 1966. Untersuchungen über die Befallsbereitschaft von Baumarten für Secundärschädlinge, Teil II. *Zeitschrift für Angewandte Entomologie* 57:73-139.
- Scholander, P. F., H. T. Hammel, E. P. Bradstreet and E. A. Hemmingsen. 1965. Sap pressure in vascular plants. *Science* 148:339-346.
- Shepherd, R. F. 1966. Factors influencing the orientation and rates of activity of *Dendroctonus ponderosae* Hopkins (Coleoptera:Scolytidae). *Canadian Entomologist* 98:507-517.
- Schoonhoven, L. M. 1968. Chemosensory bases of host plant selection. *Annual Review of Entomology* 13:115-136.
- Silverstein, R. M., J. O. Rodin and D. L. Wood. 1966. Sex attractants in frass produced by male *Ips confusus* in Ponderosa pine. *Science* 154:509-510.
- Silverstein, R. M., R. G. Brownlee, T. E. Bellas, D. L. Wood and L. E. Browne. 1968. Brevicomín principal sex attractant in frass of the female Western pine beetle. *Science* 159:889-891.
- Smith, R. H. 1961. The fumigant toxicity of three pine resins to *Dendroctonus brevicomis* and *D. jeffreyi*. *Journal of Economic Entomology* 54:365-369.
- Smith, R. H. 1966. Resin quality as a factor in the resistance of pines to bark beetles. In H. D. Gerhold, E. J. Schreiner, R. E. McDermott, and J. A. Wisniewski, Eds. *Breeding Pest Resistant Trees*. Pergamon Press, New York pp. 189-196.

- Southwood, T. R. E. 1962. Migration of terrestrial Arthropods in relation to habitat. *Biological Review* 37:171-214.
- Stark, R. W. 1965. Recent trends in forest entomology. *Annual Review of Entomology* 10:303-324.
- Stark, R. W., P. R. Miller, F. W. Cobb, Jr., D. L. Wood and J. R. Parmeter, Jr. 1968. Photochemical oxidant injury and bark beetle (Coleoptera:Scolytidae) infestation of Ponderosa pine. I. Incidence of bark beetle infestation in injured trees. *Hilgardia* 39:121-126.
- Stark, R. W. and F. W. Cobb, Jr. 1969. Smog injury, root diseases and bark beetle damage in Ponderosa pine. *California Agriculture* 23:13-15.
- Stoszek, K. J. and J. A. Rudinsky. 1967. Injury of Douglas-fir trees by maturation feeding of the Douglas-fir Hylesinus, *Pseudohylesinus nebulosus* (LeConte) (Coleoptera:Scolytidae). *Canadian Entomologist* 99:310-311.
- Swaine, Y. M. 1918. Canadian bark beetles, Part II. Canadian Department of Agriculture, Entomology Branch Bulletin 14, p. 75.
- Taylor, L. R. 1963. Analysis of the effect of temperature on insects in flight. *Journal of Animal Ecology* 32:99-112.
- Thorsteinson, A. J. 1960. Host selection in Phytophagous insects. *Annual Review of Entomology* 5:193-218.
- Vité, J. P. 1961. The influence of water supply on oleoresin exudation pressure and resistance to bark beetle attack in *Pinus ponderosa*. *Contributions from Boyce Thompson Institute* 21:37-66.
- Vité, J. P. 1962. Volatile attractants from Ponderosa pine attacked by bark beetles (Coleoptera:Scolytidae). *Contribution from Boyce Thompson Institute* 21:251-274.
- Vité, J. P. and J. A. A. Renwick. 1968. Insect and host factors in the aggregation of the Southern pine beetle. *Contributions from Boyce Thompson Institute* 24:61-63.
- Vité, J. P. and J. A. Rudinsky. 1960. Untersuchungen über die Anwendbarkeit von Harzdruckmessungen zur Bestimmung des physiologischen Zustandes von Coniferen im Rahmen der Borkenkäferforschung. *Forstwissenschaftliche Centralblatt* 79:162-169.

- Vité, J. P. and J. A. Rudinsky. 1962. Investigations on the resistance of conifers to bark beetle infestation. Eleventh International Congress of Entomology Vienna. 1960. Proceedings 2:219-225.
- Vité, J. P. and D. L. Wood. 1961. A study on the applicability of the measurement of oleoresin exudation pressure in determining susceptibility of second growth Ponderosa pine to bark beetle infestation. Contributions from Boyce Thompson Institute 21:67-78.
- Vité, J. P., R. A. Gara and R. A. Kliefoth. 1964. Collection and bioassay of a volatile fraction attractive to *Ips confusus* (LeConte) (Coleoptera:Scolytidae). Contribution from Boyce Thompson Institute 22:461-470.
- Walters, J. and L. H. McMullen. 1956. *Pseudohylesinus nebulosus* - life history and habits in the interior of British Columbia. Canadian Entomologist 88:197-202.
- Waring, R. H. 1970. Die Messung des Waterpotentials mit der Scholander - Methode und ihre Bedeutung für die Forstwissenschaft. Forstwissenschaftliche Central Blatt 4:195-200.
- Waring, R. H. and B. D. Cleary. 1967. Plant Moisture Stress: Evaluation by Pressure Bomb. Science 155:1248-1254.
- Werner, A. E. and K. A. Graham. 1957. Volatile wood constituents in relation to ambrosia beetles. Canadian Department of Agriculture, Forest Biology Division, Bimonthly Progress Report, 13:3.
- Wigglesworth, V. B. 1950. The principles of insect physiology. Methuen and Company, Ltd., London, 544p.
- Wood, D. L. 1962. The attraction created by males of a bark beetle *Ips confusus* (LeConte) attacking Ponderosa pine. Pan-Pacific Entomologist 38:141-145.
- Wood, D. L. 1963. Studies on host selection by *Ips confusus* (LeConte) (Coleoptera:Scolytidae) with special reference to Hopkins' host selection principle. University of California Publications in Entomology 27:241-282.

- Wood, D. L. and J. P. Vité. 1961. Studies on the host selection behavior of *Ips confusus* (LeConte) (Coleoptera:Scolytidae) attacking *Pinus ponderosa*. Contributions from Boyce Thompson Institute 21:79-96.
- Wood, D. L., L. E. Browne, W. D. Bedard, P. E. Tilden, R. M. Silverstein and J. O. Rodin. 1968. Response of *Ips confusus* to synthetic sex pheromones in nature. Science 59:1373-1374.
- Wright, R. H. 1958. The olfactory guidance of flying insects. Canadian Entomologist 90:81-89.
- Wright, K. D. and P. A. Lauterbach. 1958. Ten-year study of mortality in a Douglas-fir saw-timber stand in Coos and Douglas counties, Oregon. Department of Agriculture, USFS, Pacific Northwest Forest and Range Experiment Station Research Paper 27, 12p.
- Zaerr, J. B. 1971. Moisture stress and stem diameter in young Douglas-fir. Science 17:466-469.
- Zavitkovski, J. and W. K. Ferrell. 1970. Effect of drought upon rates of photosynthesis, respiration, and transpiration of two ecotypes of Douglas-fir. II. Two-year-old seedlings. Photosynthetica 4:58-67.
- Zethner-Moller O. and J. A. Rudinsky. 1967. On the biology of *Hylastes nigrinus* (Coleoptera:Scolytidae) in Western Oregon. Canadian Entomologist 99:897-911.
- Zwölfer, W. 1957. Ein jahrzehnt Forstentomologischer Forschung 1946-1956 (Ruckschau und Ausblick). Zeitschrift für Angewandte Entomologie 40:422-432.

TABLE A. Response of sexually immature *Pseudohylesinus nebulosus* beetles to temperature and light intensity.

Beetles Tested (No.)	Part of Day	Surface Temperature (°C)	Light Intensity (f.c.)	Response (% of Tested <i>P. nebulosus</i>)					
				Phototropic		Thigmotactic		Flight	
				+	-	Yes	No	Attempt	Takeoff
15	A.M.	12.8	35		100	100			
15	A.M.	14.2	55		100	100			
15	A.M.	14.6 - 15.2	70	6	94	94	6	(6)	
45	A.M.	15.3 - 16.9	220 - 450	100				100	
15	P.M.	17.6	24	100				66	34
15	A.M.	17.8	420	100				94	6
60	A.M.	18.3 - 26.7	450 - 7500	100					100
15	P.M.	24.2	21	100					100
15	P.M.	22.2	19	40	60		60		40
15	P.M.	21.9	11.5	20	80		80		20
15	P.M.	21.3	4.5		100		100		

Date: July 30, 1967 In Shade; Slight Gust; RH 30%

APPENDIX

TABLE B. Response of sexually immature *Pseudohylesinus nebulosus* beetles to increasing temperature levels.

Beetles Tested (No.)	Surface Temp. (°C)	Response (% of Tested <i>P. nebulosus</i>)									
		Phototropic			Quiescent	Crawl	Flight Takeoff		Disorg. Crawl	Hyperact. Crawl	Instant Death
		+	-	None			Gradual	Instant			
20	> 13.3	-	-	-	100						
20	13.6 - 15.6	75	25	0	25	75					
20	16.1 - 21.1	95	5	0		100					
20	21.7 - 25.6	100	0	0		100					
20	26.1 - 27.8	100	0	0			100				
20	28.9	100	0	0			100				
25	30.6	84	16	0			100				
20	34.4	85	0	15				85	15		
20	34.4	15	15	70					100		
20	35.0	0	30	70					100		
20	35.6	0	0	100					100		
10	37.8	0	0	100						100	
20	38.9	0	0	100						100	
20	40.6 - 46.0	0	0	100				(Within 30 Seconds, Dead)			20
Date: August 3, 1967 Open; Light Int. 2400 f.c. - 9500 f.c.; Calm and Sunny; RH 30%											

TABLE C. Air temperature and flight occurrence of sexually mature
P. nebulosus early spring.

Air Temp. (°C)	Flight Occurrence					
	1966			1967		
	None	Yes	% Yes	None	Yes	% Yes
9.0	1	0	0	3	0	0
10.0	1	0	0	5	0	0
10.5	2	0	0	0	0	0
11.0	2	0	0	3	0	0
11.5	2	0	0	0	0	-
12.0	10	2	16	4	1	25
12.5	2	1	33	1	1	50
13.0	3	5	62	1	10	90
13.5	0	8	100	0	10	100
14.0	0	15	100	0	15	100
14.5	0	10	100	0	10	100
15.0	0	17	100	0	15	100
15.5	0	6	100	0	9	100
16.0	0	12	100	0	9	100
16.5	0	2	100	-	-	
17.0	0	8	100	-	-	

TABLE D. Moisture stress in Douglas-fir and initial colonization by *Pseudohylesinus nebulosus* (mature beetles).

PMS (atm.)	Number of Trees		% Infested
	Infested	Uninfested	
≤ 10.1	-	10	0
10.2-13.5	-	6	0
13.6-16.9	-	3	0
17.0-20.3	3	-	100
20.4 \leq	4	-	100
TOTAL:	7	19	-

TABLE E. Moisture stress in Douglas-fir and maturation feeding site colonization by *Pseudohylesinus nebulosus* (immature beetles).

PLANT MOISTURE STRESS

Group A < 7 atm.				Group B 14 - 20 atm.				Group C > 36 atm.			
Tree No.	Number of Feeding Sites			Tree No.	Number of Feeding Sites			Tree No.	Number of Feeding Sites		
	Active	Aborted	Total		Active	Aborted	Total		Active	Aborted	Total
August 17:											
4	3	0	3	1	2	0	2	2	4	0	4
7	3	0	3	5	3	0	3	3	1	0	1
9	2	0	2	8	0	0	0	6	2	0	2
12	4	0	4	10	2	0	2	11	3	0	3
16	1	1	2	13	5	0	5	14	2	0	2
18	1	1	2	15	3	0	3	17	0	0	0
22	4	0	4	19	1	0	1	20	1	0	1
23	1	0	1	24	2	0	2	21	3	1	4
25	1	0	1	26	1	0	1	29	2	0	2
28	2	0	2	27	0	0	0	30	3	0	3
-	22	2	24	-	19	0	19	-	21	1	22
		N.S.	N.S.			N.S.	N.S.			N.S.	N.S.
August 21:											
4	3	0	3	1	3	0	3	2	6	0	6
7	1	2	3	5	3	0	3	3	0	1	1
9	1	1	2	8	1	0	1	6	0	2	2
12	2	2	4	10	3	1	4	11	3	2	5
16	1	1	2	13	5	0	5	14	1	3	4
18	2	0	2	15	3	0	3	17	1	1	2
22	4	0	4	19	3	0	3	20	1	0	1
23	1	0	1	24	4	0	4	21	4	0	4
25	0	2	2	26	2	0	2	29	2	0	2
28	4	0	4	27	2	0	2	30	1	2	3
-	19	8	27	-	29	1*	30	-	19	11	30

TABLE F. Moisture stress in Douglas-fir and initial colonization
by *Dendroctonus pseudotsugae*.

PMS (atm.)	Number of Trees		% Infested
	Infested	Uninfested	
≤ 10.1	-	8	0
10.2-13.5	-	1	0
13.6-16.9	-	-	-
17.0-20.3	2	-	100
20.4 \leq	3	-	100
TOTAL:	5	9	-

TABLE G. *Dendroctonus pseudotsugae* colonization in relation to moisture stress in Douglas-fir.

PMS (atm.)	Number of Trees with <i>D. pseudotsugae</i> Colonization		% Aborted
	Aborted	Continuing	
8.4	1	-	100
8.5-10.2	-	-	-
10.3-13.6	-	-	-
13.7-17.0	-	2	0
17.1-20.4	-	1	0
20.5 \leq	-	4	0
TOTAL:	1	7	-

TABLE H. Moisture stress in Douglas-fir in relation to colonization
by larval Buprestidae.

PMS (atm.)	Number of Trees		% Infested
	Infested	Uninfested	
≤ 16.9	-	1	0
17.0-20.3	-	1	0
20.4-23.7	3	1	75
23.8-27.1	6	-	100
27.2 \leq	2	-	100
TOTAL:	11	3	-

TABLE I. Colonization by Buprestidae in relation to moisture stress
in Douglas-fir.

PMS (atm.)	Number of Trees with Colonization		% Aborted
	Aborted	Continuing	
≤ 10.1	1	-	100
10.2-13.5	1	-	100
13.6-16.9	1	2	33
17.0-20.3	1	2	33
20.4-23.7	-	-	-
23.8 \leq	-	2	0
TOTAL:	4	6	-