Studies on the biology of the mountain pine beetle, Dendroctonus monticolae Hopkins (Coleoptera: Scolytidae)
by Robert William Reid

A THESIS Submitted to the Graduate Faculty in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Entomology
Montana State University

Abstract:
The biology of the mountain pine beetle, Dendroctonus monticolae , Hopkins, was investigated from 1955 to 1959 in southern British Columbia.

The numbers of flights each year and the period during which the flight occurred depended upon seasonal weather, which varied considerably in different years. The vigour of the host tree determined whether or not the attacking beetles were able successfully to establish their broods. The length of the egg gallery and the number of eggs laid was related directly to the moisture content of the inner bark and outer sapwood. Gallery excavation and egg laying ceased when inner bark and/or outer sapwood moisture content dropped below 105% and 6o% respectively (oven dry might), and if temperatures were high the bark beetle left that tree and flew to attack another. Successfully attacked trees dried rapidly and later in the season heavy brood mortality occurred due to lack of sufficient moisture. Favourable weather and an abundance of host trees in a susceptible condition are prerequisites to outbreaks of the mountain pine beetle. The population in the experimental area declined in 1959 because those two conditions were not satisfied:.

STUDIES ON THE BIOLOGY OF THE MOUNTAIN PINE BEETLE

DENDROCTONUS MONTICOLAE HOPKINS (COLEOPTERA:SCOLYTIDAE)

by

R.W. REID

A THESIS

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in

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ABSTRACT

The biology of the mountain pine beetle, Dendroctonus monticolae Hopkins, was investigated from 1955 to 1959 in southern British Columbia. The numbers of flights each year and the period during which the flight occurred depended upon seasonal weather, which varied considerably in different years. The vigour of the host tree determined whether or not the attacking beetles were able successfully to establish their broods. The length of the egg gallery and the number of eggs laid was related directly to the moisture content of the inner bark and outer sapwood. Gallery excavation and egg laying ceased when inner bark and/or outer sapwood moisture content dropped below 105% and 60% respectively (oven dry weight), and if temperatures were high the bark beetle left that tree and flew to attack another. Successfully attacked trees dried rapidly and later in the season heavy brood mortality occurred due to lack of sufficient moisture. Favourable weather and an abundance of host trees in a susceptible condition are prerequisites to outbreaks of the mountain pine beetle. The population in the experimental area declined in 1959 because those two conditions were not satisfied.

INTRODUCTION

A challenging problem in forest biology in western North America concerns the role of the mountain pine beetle, Dendroctonus monticolae Hopkins (Scolytidae:Coleoptera), in the development and survival of lodgepole, white, and sugar pine (Pinus contorta Douglas, P. monticola Douglas, and P. lambertiana Douglas). An answer to this problem is important to an understanding of population biology, forest ecology, and forest management.

The mountain pine beetle is distributed throughout southern British Columbia, Idaho, Montana, Wyoming, Oregon, Washington and California. Within this area the size of the populations and the damage caused vary from place to place and from year to year. Some localities are affected more frequently than others.

The taxonomic description of the mountain pine beetle was made by Hopkins (1905) and the morphology of the adult described by Richmond (1935). A brief outline of its habits was published by Hopkins (1909). De Leon et al., 1934; Struble, 1934, 1935; Richmond, 1936; Evenden et al., 1943; Hopping and Mathers, 1945; and Brown, 1956, contributed further data on the life cycle and behaviour of this insect.

The main flight of the mountain pine beetle generally occurs in midsummer when young adults reach maturity, leave their brood trees, and fly to green uninfested trees. During the flight they are reported sometimes to cover distances as great as fifteen to twenty miles but it is not established whether they do this by their own flying ability or through the assistance of air currents (Evenden et al., 1943). The flight period lasts two to three weeks. When a tree is attacked, the female bores through the outer

bark and commences to construct her egg gallery within the region of the inner bark and outer sapwood (Pl. III, Fig. 1). About this time the female loses her ability to fly. The male enters the gallery soon after the female has made the entry hole and mating then occurs. During the early periods of gallery construction, the resin flow from disrupted resin canals (Pl. III, Figs. 3-5) interferes with the activities of the insects and may prevent them from becoming established in the tree. Soon after mating, and if the pitch flow is not too heavy and continuous, the female elongates her egg gallery in an upward direction for a length up to fifteen inches (Pl. I, Fig. 4). In this she deposits small white oval eggs (0.5 x one mm.) in egg niches along the sides (Pl. I, Fig. 1). The eggs hatch in about ten days and the larvae mine out into the inner bark at right angles to the axis of the main gallery (Pl. I, Fig. 5). The larva has a brown, heavily sclerotized head and the remainder of the body is white to greyish (Pl. I, Figs. 2, 6). Larvae from adjacent galleries intermingle (Pl. II, Fig. 1), and they require several months to develop to the prepupal stage. The insects generally overwinter in the larval stage. In the following spring and early summer the mature larvae cut small pupal chambers within the inner bark and outer sapwood region and pupate therein. At first the pupae are white, but on nearing maturity, two weeks later, they change to pale brown (Pl. I, Fig. 3). The young adults (tenerals) are initially pale brown but gradually become darker, and at maturity are black and heavily sclerotized (Pl. I, Fig. 3).

The same parents may establish two broods during one season, the second approximately three weeks after the first.

The life cycle as described above refers to populations in the more northern extension (British Columbia) of the insect's range. In southern

regions, the life cycle is more complicated. Three periods of attack have been reported to occur: in the spring, midsummer, and late summer. Broods from these overwinter as young adults, pupae or larvae and emerge in that sequence the following year. In addition, parent adult beetles may establish up to three separate broods which overwinter as larvae, pupae, or young adults respectively.

Favourable weather conditions and host abundance are prerequisites for outbreaks of many species of the Scolytidae (Felt, 1914; Swaine, 1918; Blackman, 1931; Chamberlin, 1939; Keen, 1958. Richmond (1936) and Hopping and Mathers (1945) suggested that weather affected the abundance of the mountain pine beetle. Hopping and Mathers found a relationship to exist between a period of prolonged drought and reduced tree vigour. They suggested that reduced tree vigour results in a condition favourable for an increase in the bark beetle populations.

An opportunity to study the mountain pine beetle in the northern portion of its range was afforded from 1955 to 1959 by outbreaks on lodgepole pine in British Columbia. A general study of the biology was undertaken, the objective being to determine the major limiting factors in the buildup and decline of large populations. When these factors are known critical studies can be undertaken to assess their individual importance.

Except for the brief period when the adults are in flight, a small portion of the host tree comprises the entire microenvironment of the insect. While the earlier work on the mountain pine beetle is of value, it does not explain sufficiently the relationships which exist between the insect and the tree.

The life history of the mountain pine beetle can be considered in two parts: a very short period (a matter of a few days) while the adult is flying to new hosts; and a very long period (the remainder of the year), spent entirely within the tree. The flight activities were investigated in relation to season and certain weather factors. Events within the tree may be further subdivided into those which are the direct result of the beetles themselves (i.e. gnawing into the tree, gallery formation and oviposition, fecundity, sex ratio, larval feeding and tunneling, pupation, structural changes within the parent beetle) and those which are imposed by the environment (i.e. host resistance, moisture levels and drying out, time available for brood development, temperatures, predators and parasites). Each of these events were investigated, some in greater detail than others.

The experimental area was in the Francis Creek valley and on the lower slopes of the adjacent mountain (Steamboat), about fifteen miles north of Invermere (elevation 2,800 feet) in the East Kootenay region of British Columbia. The forests in the experimental area were a mixture of lodgepole pine and Douglas fir (Pseudotsuga menziesii (Mirb.) Franco). At the lower end of the Francis Creek valley, the stands were open grown with patches of pine intermixed with the Douglas fir (Pl. IV, Fig. 3). At the upper end of the valley, stands were generally more dense and the pine more extensive (Pl. IV, Fig. 4). The age of the pines varied somewhat but most were between seventy-five and ninety-five years old and were of small diameter, the majority being under ten inches (diameter four and one-half feet from the ground).

MATERIALS AND METHODS

For the studies of the life cycle, behaviour, and mortality-survival, green uninfested logs were placed in cages (Pl. V, Figs. 5, 6) and experimentally infested with beetles, while green uninfested logs set up in the woods (Pl. VI, Fig. 4)were allowed to become infested by the wild population. Infested trees within plots (Pl. VI, Fig. 7) were also used. The time when beetles attacked this material was recorded and the trees and logs were later debarked at different intervals and the condition of the brood recorded. The parent adults, when present, were dissected and the condition of the internal organs i.e. wing muscles, fat body, reproductive and digestive systems noted. Daily temperatures were recorded with a hygrothermograph (Pl. V, Fig. 1).

The daily and seasonal data on emergence and flight were obtained by several techniques. Butt logs (Pl. VI, Fig. 3) from trees infested the previous year were placed in cages prior to the time of the main flight and inspected daily. The beetles which emerged were counted and sexed, using the method described by Chapman (1955) and Reid (1958). Fresh green logs in the woods and standing uninfested trees within plots were frequently examined for signs of attack.

The moisture content of the inner bark of infested and noninfested trees was studied in 1958 and 1959. For this, sample blocks one-fourth inch thick and one and one-half inches square were collected from the North, South, East and West sides of standing trees by using a one and one-half inch wood chisel. Each sample was wrapped immediately in aluminum foil and placed in a small waterproof can. To minimize evaporation the samples were unwrapped in a saturated atmosphere and prepared for weighing. The outer bark was discarded and the inner bark and sapwood weighed separately and then placed for four to six hours

in a desiccator from which the air was then exhausted by means of a water tap attachment (Hill, 1958). Sufficient water to float the samples was then admitted and the vacuum was maintained for an additional twenty-four to forty-eight hours. Additional soaking, up to 144 hours, did not appreciably increase the amount of water absorbed. The procedures described above are illustrated in Plates V (Figs. 2-4) and VII (Figs. 1-6). After saturation was reached, samples were removed, weighed, oven-dried for twenty-four hours at 105°C., and the percentage saturation calculated by the method described by Chalk and Biggs (1955):

$$\frac{\text{wet weight - dry weight}}{\text{saturation weight - dry weight}} \times 100$$

The percentage moisture content on an oven dry weight (o.d.w.) basis was calculated by the standard method as follows:

$$\frac{\text{wet weight - dry weight}}{\text{Dry weight}} \times 100$$

Moisture content calculated on a percent saturation basis elminates wood density as a variable, when moisture content of trees having different growth rates is compared. Wood infected with blue stain organisms is difficult to saturate, hence moisture content in these was determined by the oven dry weight method. As a check, both methods were used when possible. When density of the wood in the samples being compared was approximately equal, difference in moisture content was more apparent using the oven dry weight method.

By these methods the vertical distribution of moisture in the outer sapwood of five uninfested trees was determined. These trees were felled and outer sapwood samples were taken from four sides, at the base, at the five foot level, and at ten foot intervals from then on to the forty-five foot level.

Transverse discs cut from two uninfrested trees were used to determine the horizontal distribution of moisture. A series of samples was taken on the periphery and along a diameter of each disc.

The moisture variation in the outer sapwood and inner bark throughout the twenty-four hour day (diurnal march) was studied in four uninfested trees from samples $\frac{1}{2} \times \frac{3}{4} \times \frac{1}{4}$ inches deep secured with a special tool (Pl. VII, Fig. 1).

The seasonal moisture march was studied in a number of uninfested trees. In 1959, ten trees in the upper Francis Creek area were selected and sampled on four sides on May 30, June 26, July 24, August 25, and September 9. Five new trees were added at each sampling date, except the last, to test whether previous sampling had interfered with the current sample. Throughout the season, moisture measurements were made upon infested trees and these measurements were compared to those obtained from uninfested trees.

A laboratory technique was developed whereby moisture and temperature could be altered and controlled in the immediate environment of the insect. Short logs were cut from the upper region on the stem of green trees and brought into the laboratory where a strip of bark, two by twelve inches, was peeled along the main axis (Pl. VIII, Fig. 1). A notch one-eighth inch wide and one-half inch long was made in one end of the strip (Pl. VIII, Fig. 2). The bark strip was then placed between two pieces of one-eighth inch clear plastic and the sides taped with waterproof plastic tape to prevent loss of moisture (Pl. VIII, Fig.4). The completed unit is referred to as an observation plate.

The moisture content of the inner bark was determined at the time the plate was constructed (Pl. VIII, Fig. 5).

A strip of bark adjacent to the one used in the observation plate, was obtained at the same time, wrapped in aluminum foil, sealed with waterproof tape (Pl. VIII, Fig. 6), and stored at room temperature (unless otherwise stated) as was the corresponding plate. A small drop in moisture content occurred in the bark of most observation plates and stored samples even though they were sealed. The moisture loss may have been due to metabolic activity in the fresh bark.

To prevent moisture loss from bark during construction of the plate, a special room in which the air was kept saturated was designed (Pl. IV, Fig. 1). It consisted of a small area enclosed by two mm. plastic sheeting, with a door at one end.

The observation plates were placed in an upright position with the elongated notch at the bottom. A pair of beetles in the flying condition was introduced into each plate, via the elongated notch (Pl. VIII, Fig. 7), the female first. The beetles were observed through the plastic plate during their gallery construction (Pl. VIII, Fig. 8).

The female was allowed to construct egg galleries six, eight, or ten inches long. A section of bark immediately above the selected distance was removed by slitting the tape on both sides of the plate and pulling the bark out through the slit. This was replaced by one of the strips of bark wrapped in aluminum foil at the time of plate construction. The moisture content of the latter bark was lowered by removing the foil and exposing the bark to the ambient air prior to the exchange. The lower edge of the inserted bark was covered by a waterproof tape to prevent absorption from the lower bark. In the substitute bark a narrow opening, directly in line with the egg gallery below, was left free of tape. The method of exchanging bark is illustrated in Plate IX,

Figs. 1-4. In order to determine the exact moisture content of the replacement bark, one-half inch sections were removed and the moisture content determined.

For determination of moisture content of bark within the plates samples were removed through small "windows" cut in the plastic by use of a hand drill with dental burrs. The plastic windows were replaced and sealed with clear tape. Adults were removed for testing, and replaced, in the same manner (Pl. IX, Figs. 5-8).

Bark beetles freely entered the slit in the replacement bark when they reached the top of the original bark. Their actions then were determined by the moisture conditions in the replacement bark.

A second series of experiments was conducted to test further the effect of moisture on the behaviour of the female adult. Two logs, five feet in length, were obtained from two trees which were similar in appearance, bark characteristics, growth rate, and diameter. The logs were cut into ten pieces twelve inches long, and most of the outer bark on the upper six inches of each section was removed with a wood rasp. The remaining outer bark on the upper six inches, constituting a thin corky layer around the stem, was broken through in many places by the action of the rasp and inner bark was exposed in those areas. Five sections were waxed at both ends and placed in close fitting plastic envelopes while the remaining five sections were waxed only on the bottom and were not enclosed in plastic envelopes. In each twelve inch section were drilled four holes on the upper face close to the outer periphery of the sapwood. The holes were four inches deep and one inch in diameter. The purpose of the holes was to increase the rate of moisture loss from the sapwood in those sections which were not protected by plastic. Five evenly placed entrance holes were made

at the bottom of each twelve inch section and a female and male were placed together in each hole. Each section was covered with cotton mesh to prevent emerging adults from escaping. The appearance of the experiment is illustrated in Pl. IV, Fig. 2. Ten days later the logs were examined. In all sections, inner bark remained moist, despite the fact that much of the outer bark had been removed from the upper six inches of each section. The outer sapwood also remained moist, except in the upper six inch portion of the five exposed sections.

LIFE CYCLE AND BEHAVIOUR OF THE MOUNTAIN PINE BEETLE

First emergence and flight

Daily emergence and effect of temperature and light: The numbers of beetles which emerged at half hour intervals through the day were determined during four days in August, 1955. Although the daily period of emergence varied from six hours to nine hours, most of the insects appeared from 1:00 to 4:00 P.M. The emergence for one day is illustrated in Figure 1.

Most of the emergence occurred during the warm part of the day. Emergence in the morning began at 58° F. and ceased in the afternoon at about the same temperature. These morning temperatures were recorded near 8:00 A.M and evening temperatures near 6:00 p.m. The temperature and emergence data illustrated in Figure 1 indicate a typical relationship; but on several days, emergence was recorded at a slightly lower temperature than is suggested in that figure. The magnitude of daily emergence is directly related to temperature (Appendices I-IV).

When adults emerge from infested trees and logs they orient positively to light. Those emerging from caged logs collect on the walls of the cages and are most numerous in the areas where the light is most intense. Under natural conditions, emergence appears to occur most commonly during the daylight hours (Fig.1).

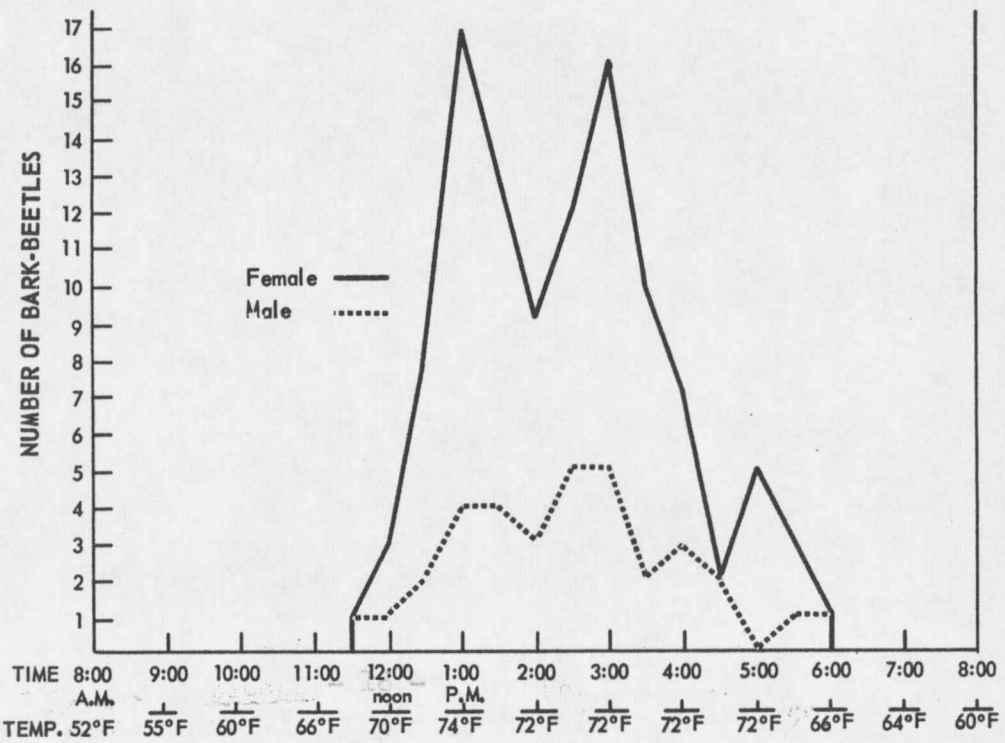

Fig. 1. Emergence of D. monticolae on the half hour, Aug. 4, 1955. Butt logs from trees infested the previous year placed in cages prior to commencement of emergence.

To determine if mountain pine beetles fly at night, as indicated by Spencer (1950), an experiment was conducted indoors from 11:00 p.m. to midnight, August 17, 1959, under clear sky conditions and bright moonlight. One hundred insects in the flying condition were released ten feet from a large window. The air temperature in the room was 82° F. Fifteen of the insects flew directly to the window, while fifty-two flew towards the window but dropped to the floor before reaching it. The remaining thirty-three dropped directly to the floor from the point of release.

Adults placed in cages in the daylight usually ignored fresh logs and collected on the sides of the cages. Such beetles placed manually into crevices of the bark would begin boring. Towards the evening, when light became less intense, the beetles moved throughout the cage and attacked the logs. Such phototropic reactions may influence the beetles to fly towards a point - source of light in the weak illumination of a dense forest.

Since beetles fly in poor light (moonlight) at high temperatures (82° F.), but not in good light (8:00 a.m.) at low temperatures (58° F.), temperature seems to exert a greater influence upon initiation of flight than does light.

Adults in the nonflying condition avoid light. The reactions of these insects were tested in large glass vials. The bottom half of each of the vials was enclosed in heavy black paper. A six inch strip of dampened cheesecloth was placed in the vial to allow sufficient footing for the insects. The vials were corked and placed on their sides, with the bottom cheesecloth acting as a carpet (Pl. IV, Fig. 5).

Eighty beetles were tested: forty flyers and forty nonflyers. Ten insects of each type were placed in the dark end of a vial and were offered, thereby, a choice of two light intensities. The numbers of insects which had

moved into and remained in the light end of each vial were counted after ten, fifteen, thirty, and forty-five minutes. The flying adults were attracted to the light, whereas those in the nonflying condition remained in the darkened end (Table I).

Seasonal emergence and influence of temperature: The period of emergence varied each year. In 1955, the midpoint in the total number of emergents was August 5; for 1956 - July 11; for 1957 - July 12; for 1958 - July 5; for 1959 - August 5. May and June temperatures in 1955 and 1959, the years of latest flight, were cooler than those which occurred during the intervening years (Fig. 2). The lower temperatures are believed to have reduced the rate of brood development.

Flight periods were always preceded by warm dry weather, but no definite relationship could be established between the duration of such periods and emergence.

The daily emergence each year from 1955 to 1959 is illustrated, together with daily maximum temperatures, in Appendices I-V, and the data are summarized in Table II.

Second emergence and flight

Many species of Dendroctonus have been reported to abandon their first gallery and establish another later in the season. Watson (1928) reported the spruce bark beetle, D. piceaperda Hopkins, established two galleries in one season. Simpson (1929) found that the eastern larch beetle, D. simplex Le Conte, cut three egg galleries per season. Bedard (1933) wrote that the Douglas fir beetle, D. pseudotsugae Hopkins, established two egg galleries in one season.

Table I. Correlation between flying capacity and positive phototropism.

Vial Number	Number of Insects		Treatment	Number of insects in light end after 10 min.	after 15 min.	after 30 min.	after 45 min.
1	10	Nonflyers	All placed in dark end of vial	1	1	1	2
2	10		"	0	0	0	1
3	10		"	0	0	1	1
4	10		"	0	0	0	1
5	10	Flyers	"	8	9	8	9
6	10		"	5	7	5	8
7	10		"	5	6	10	9
8	10		"	5	7	7	8

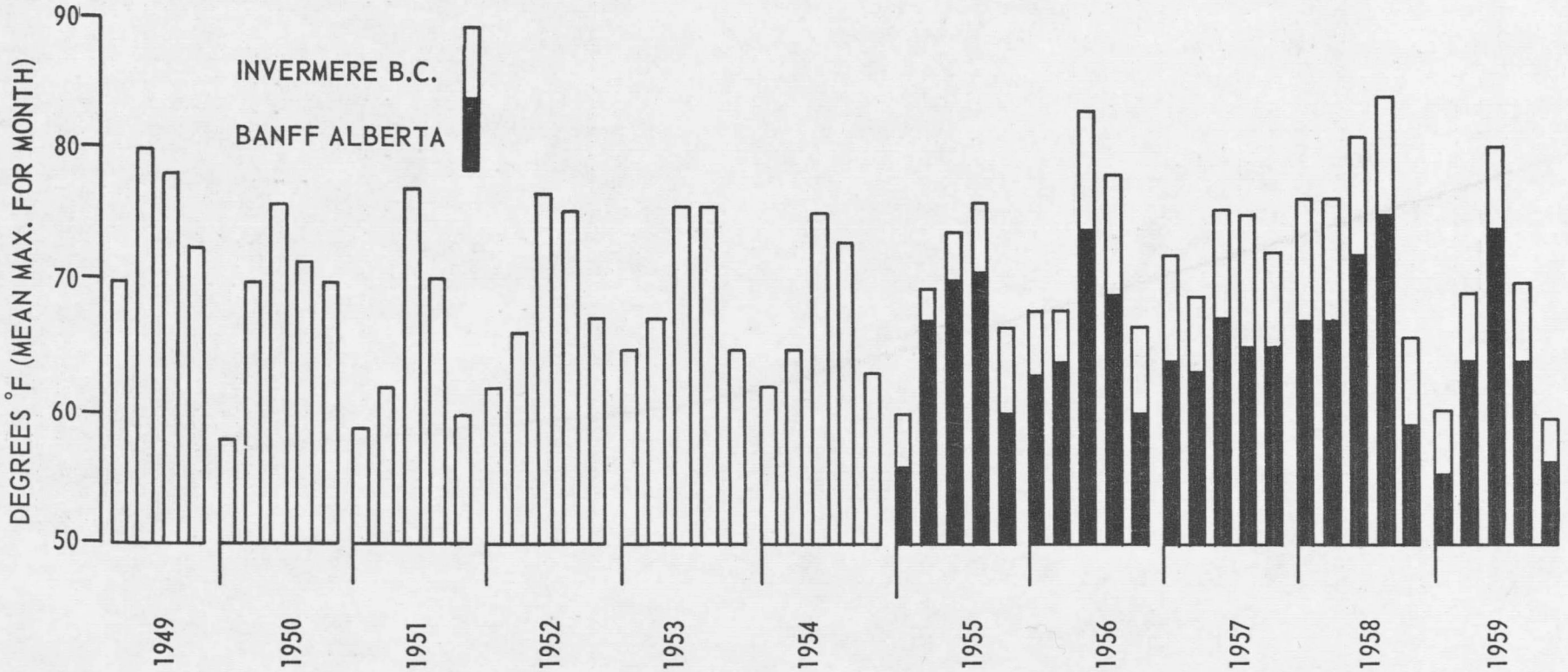

Fig. 2. Mean monthly maximum temperatures, May to September, Invermere, B.C., 1949-1959, and Banff, Alberta, 1955-1959.

DeLeon et al. (1934) confirmed earlier reports that the mountain pine beetle, D. monticolae, may establish more than one egg gallery per season; later workers were in general agreement (Struble, 1935; Evenden et al., 1943; Hopping, 1945).

A fall bark beetle survey in the experimental area was carried out in 1954 by the writer. Some trees appeared to have been infested late in that summer, which suggested a second flight. In 1955, when the present study was initiated, a single flight was observed. Since the procedure for detecting the occurrence of two flights had not been worked out, a small, second flight could have gone unnoticed. As was found later, however, the second flight could be forecast by examining parent females from their first egg galleries. In addition most parent adults had left first flight egg galleries in those years when second flights occurred.

In 1956 the first flight occurred earlier than in 1955 and was followed by a second flight in August. The initiation of the second flight was influenced by the temperatures in July and August which were warmer than in 1955 (Appendix VI). During the summer of 1957, temperatures were generally lower (Appendix VII) and only a first flight was detected. In 1958, a warmer year than 1957 (Appendix VIII), two flights occurred. The summer of 1959 was cool and wet (Figs. 2, 3 and Appendix IX) and there was only one flight, much later than in 1958.

A second flight appears to depend upon the weather. Parent adults establish two egg galleries in those years when the weather is warm and dry; whereas only a single egg gallery is established when cool wet weather prevails (Table II). The effect of tree moisture upon initiation of the second flight will be discussed in a later section.

Table II. Seasonal temperatures and midpoint of flight period, 1955-1959.

Year	Seasonal Weather	Peak of I Flight	Peak of II Flight
1955	cool	Aug. 5	none
1956	warm	July 11	Aug. 6
1957	cool	July 12	none
1958	warm	July 5	Aug. 14
1959	cool	Aug. 5	none

Behaviour of the insect under the bark

Gallery excavation: Females construct entry holes into the region of the inner bark. At about the time the female has excavated one inch, the male enters the gallery. Males did not initiate galleries unless caged on green logs without females.

The greatest difficulty encountered by the female during excavation was the flow of resin within the gallery from severed resin canals. Resin, i.e. pitch, frequently collected outside the entry hole and formed pitch tubes (Pl. VI, Fig. 6) varying in size depending upon the vigour of the tree. The term vigour, used in this manuscript, describes the ability of the tree to produce pitch.

Descriptions of egg gallery construction have been published by Hopkins (1909), and Evenden et al. (1943). Summary of a more extensive treatment given by Reid (1958) follows: The female elongates the gallery by biting off small particles of inner bark and outer sapwood. These bits constitute the boring dust which continually collects around the female and is kicked behind her. When a quantity of boring dust accumulates, she pushes it down the gallery until stopped by the male. She then moves forward and continues working at the upper end. If the male is close to the entry hole he pushes the boring dust out of the gallery. When beetles are some distance from the entry hole, the boring dust is compacted in the gallery by the male; or, if he is not present, this is done by the female. Before the female has completed the egg gallery, the males frequently leave, either by the original entrance or by boring their own exit hole. Unmated females construct short winding galleries which are kept unobstructed for much of their length. The beetles usually keep six to eight inches of gallery at the upper end free of boring dust (Pl. I, Fig. 4). Egg galleries are engraved into the inner bark and outer sapwood to a depth of one to five annual rings (Pl. III, Figs. 1, 2). The number of annual rings penetrated depends upon ring width, thickness of the inner bark, and size of the beetle.

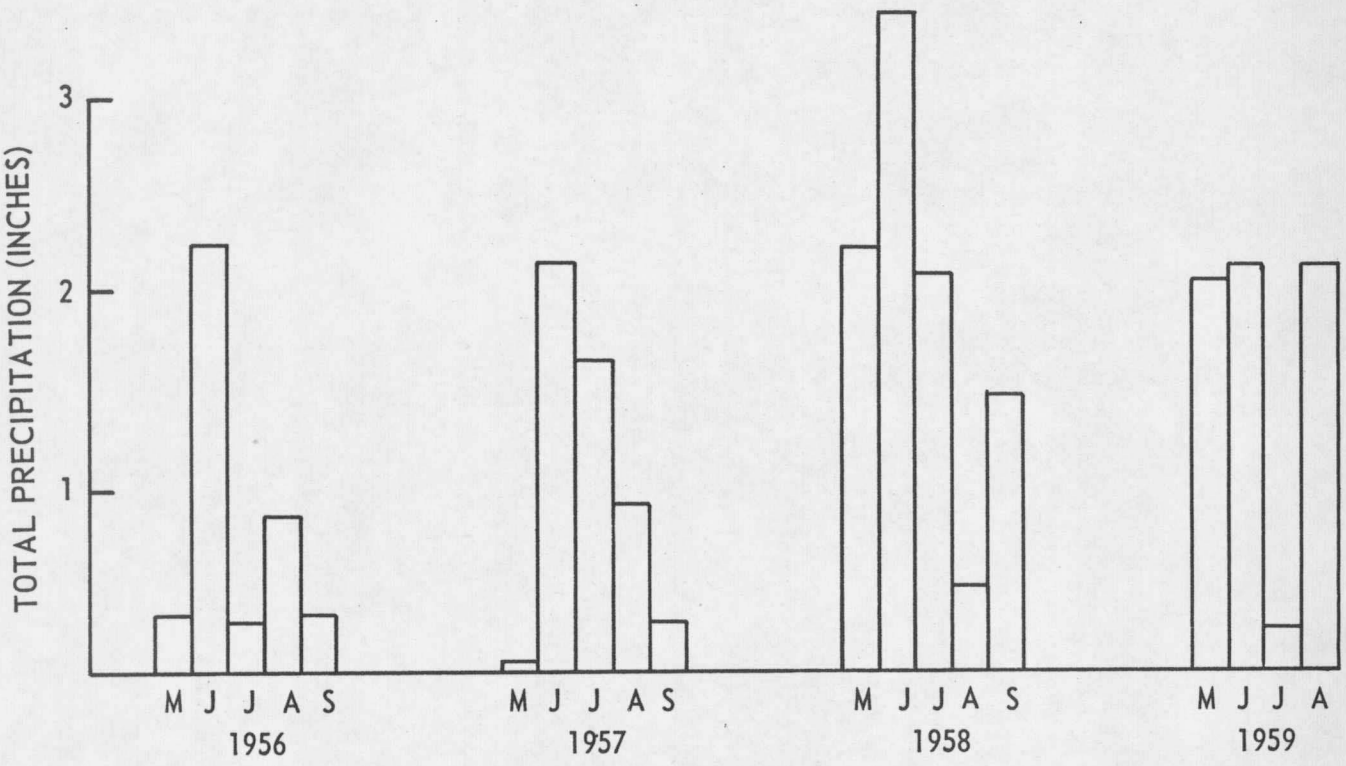

Fig. 3. Precipitation in inches, May to September, Invermere, B.C., 1956-1959.

Oviposition: Mating occurs only in the egg gallery. A single mating is sufficient for the life of the female even though she established a second gallery. Nevertheless, frequent matings occur when the male remains in the gallery with the female. Egg laying commences three or four days after the first mating. Each egg is deposited within an egg niche (Pl. I, Fig. 1) excavated at the extreme upper end of the gallery. The female goes through a specific sequence of movements before oviposition. After excavating an egg niche, she backs down to a wide spot in the gallery and turns around; she backs to the upper end and deposits an egg in the niche; then she returns to the wide spot, turns around, and moves up the gallery head first. She continues to elongate the gallery and in the process packs boring dust around the most recently laid egg. The female always maintains her position ahead of the male. In some cases when the male obstructs the gallery the female must force her way to a turn around place.

Egg distribution: The linear pattern along three galleries, seven, twelve, and eighteen inches long, is illustrated in Figure 4. Figure 5 illustrates the number of eggs laid each successive inch in a twenty-nine inch gallery. The female was still extending this gallery at the time the observations were made.

Examination of sixty-three egg galleries showed equal numbers of eggs were laid on both sides of the gallery. Few eggs, if any, were laid in the first inch; but the numbers increased rapidly thereafter. In galleries of the seven inch class, the maximum number of eggs per inch occurred at the four to five inch interval. The number of eggs laid per inch of gallery decreased rapidly from the fifth to sixth inch interval. No eggs were laid in the last inch of the gallery. Longer galleries had considerable differences in numbers of egg per inch. The fluctuations suggest the egg laying is intermittent.

To compare the number of eggs laid per inch in galleries of different lengths, eighty-four completed galleries were grouped into thirteen categories, based on their total length. The number of eggs laid per gallery was determined and that number was divided into the total length of the gallery. The long galleries contain more eggs per inch than the short galleries (Table III). The reduced number of eggs laid at the beginning and at the end of egg galleries resulted in a lower average figure per inch in short galleries than in long ones. The over all weighted average number of eggs laid per inch of gallery was 4.2.

The effect on the adult of changes in the moisture content of the bark:

Watching the behaviour of a female in an observation plate, when she was confronted with bark of several different moisture contents showed that when inner bark moisture content was above 133 percent (o.d.w.), insects mated and females constructed egg galleries; and when moisture content was 105 percent and below egg gallery construction ceased (Table IV). When egg laying ceased the females changed to the flying condition and flew when subjected to the toss test (Chapman, 1955).

Five of the females which had ceased egg laying due to dry bark and had changed to the flying condition, were placed in new observation plates containing inner bark of high moisture content. They all constructed egg galleries and without mating again, laid viable eggs. When bark moisture was reduced, they once more ceased egg laying and changed to the flying condition.

In experiments where the moisture content was altered in twelve inch logs, (see methods), female beetles in the moist plastic-protected sections constructed galleries to the top of the log and most of them emerged. Those in the

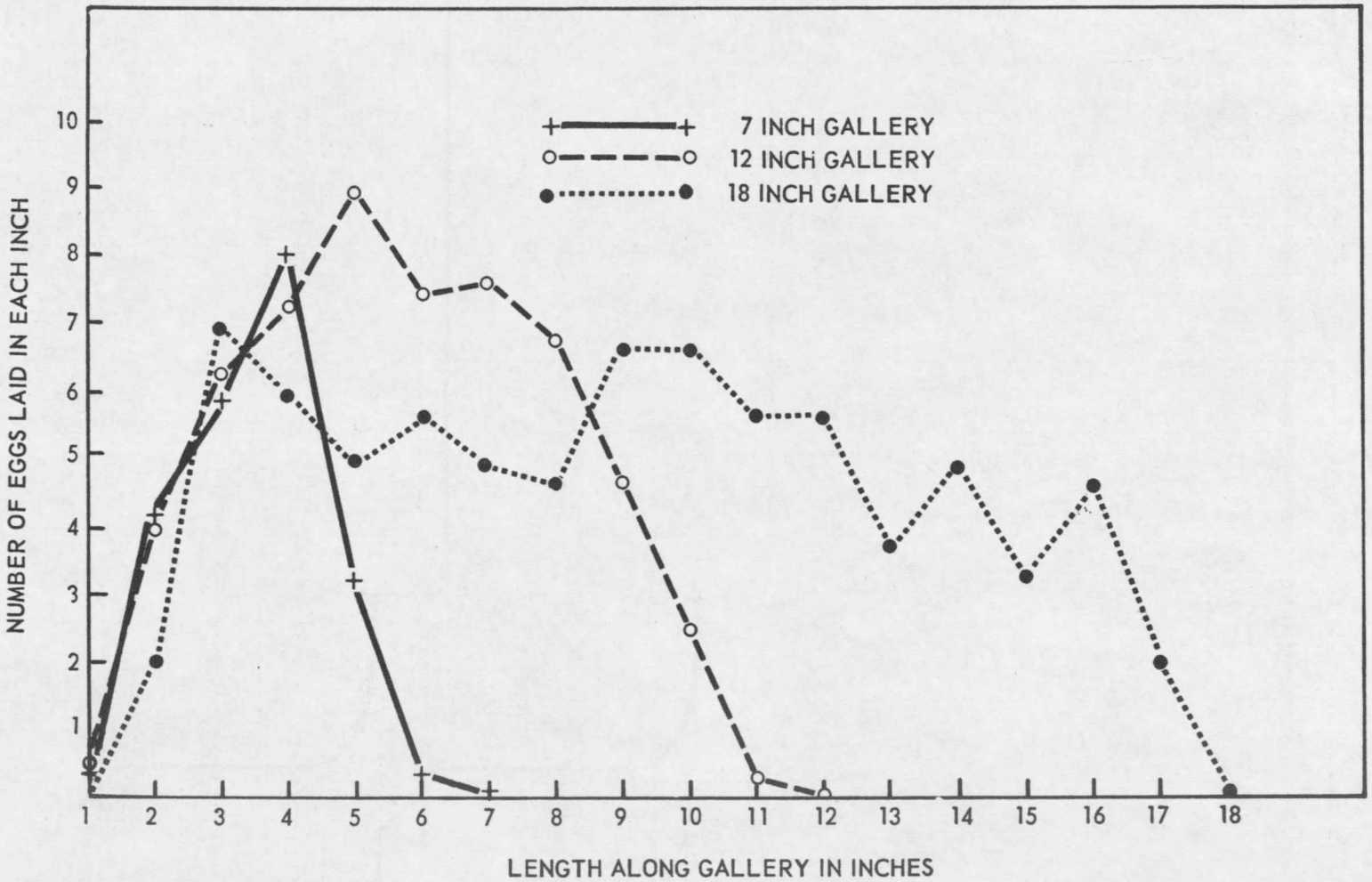

Fig. 4. Eggs laid each successive inch of completed gallery. Three galleries illustrated.

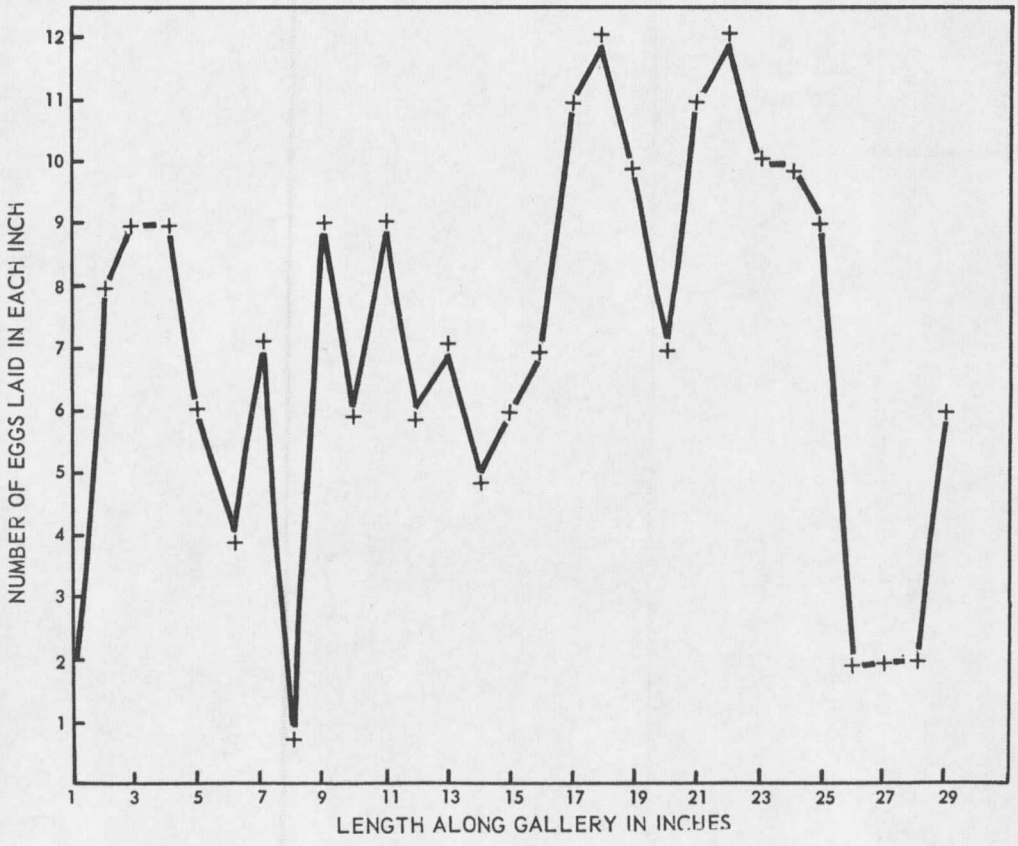

Fig. 5. Eggs laid each successive inch of gallery. Female still extending the gallery at time of examination.

Table III. Gallery length and eggs laid per inch.

Length of gallery (in.)	Number of galleries	Total length	Total eggs	Eggs/gallery	Eggs/in. of gallery
0 - 2	2	3	5	2.5	2.5
2.1 - 4	6	18	49	8.2	2.7
4.1 - 6	8	40	136	17.0	3.4
6.1 - 8	12	84	251	20.9	3.0
8.1 - 10	14	126	486	34.7	3.9
10.1 - 12	16	176	774	48.4	4.4
12.1 - 14	11	143	673	61.2	4.7
14.1 - 16	6	60	375	62.5	4.2
16.1 - 18	2	34	150	75.0	4.4
18.1 - 20	4	76	344	86.0	4.5
20.1 - 22	1	21	87	87.0	4.2
22.1 - 24	0	-	-	-	-
24.1 - 26	2	50	178	89.0	3.6

Average number of eggs per inch of gallery = 4.2, S.D. = 0.9

unprotected sections constructed galleries about six inches long (from the bottom to the midline) and emerged (Table V).

The above results, supported by those described earlier for the observation plates, indicate that when bark becomes too dry, females cease egg laying, change to the flying condition, and leave that egg gallery.

Females were allowed to establish galleries in a fresh four feet plastic covered log at the same time the experiment with the twelve inch logs was being carried out. Examination one month later found that the inner bark and outer sapwood of the longer log remained moist and the females were still extending galleries which now averaged thirty-four inches in length (Table V).

In 1958 studies on moisture content and insect behaviour in the field were carried out concurrently with the laboratory experiments. Moisture of samples from two infested trees was determined when the female beetles were leaving for their second flight. The egg galleries in these trees were not crowded nor did they interfere with each other at the upper level where the adults were working. The bark surrounding the upper end of the galleries was fresh, white, and moist in appearance. The lower five feet of the one tree had sixty attacks, while the other tree had forty-nine. There was little pitch flow. The moisture content of the trees, in percent oven dry weight, was 124 percent and 126 percent for the inner bark, and 62 percent and 60 percent for the outer sapwood. The moisture content of the inner bark at the time the parent adults left the trees was higher than that recorded for cessation of egg laying in observation plates. From these data it appears that moisture content of the sapwood was more influential than bark moisture. It was noted in the log experiments carried out in the laboratory that females left the logs when sapwood moisture was low, even though bark moisture was relatively high. Only inner bark was used in the observation plates.

Table IV. Effects of moisture on egg laying behaviour in observation plates.

Observation Plate Number	Initial Moisture Content Percent o.d.w.	Remarks	Final Moisture Content Percent o.d.w.	Remarks
1	187	Quickly established egg gallery	155	Egg laying continued into dryer bark
2	202	"	135	"
3	197	"	125	"
4	165	"	108	"
5	143	"	105	Egg laying ceased in dryer bark. Female altered to flying condition.
6	189	"	100	"
7	202	"	100	"
8	133	"	99	"
9	154	"	93	"
10	180	"	90	"
11	147	"	90	"
12	202	"	80	"

A minimum moisture content in the outer sapwood and inner bark within infested trees may be responsible for the second flight. This second flight, as will be demonstrated in a later section, had a high survival value to the population as a whole in the experimental area. When logs retained their moisture and temperatures were sufficiently high the females remained in their galleries and extended them from four to five feet in one season.

Average gallery lengths between trees frequently varied significantly (Table XVII). Successfully attacked trees, i.e. trees in which broods were able to develop, dried out at different rates due to differences in their degree of exposure, their normal moisture content (Fig. 17), and the density of the insect attack. The rate at which the infested trees dry determines the time available to the female beetle for gallery extension, and hence effects the average gallery length and numbers of eggs laid.

The effect on the adult of changes in the temperature in the bark: Of ten observation plates, containing females which were slowing down their rate of oviposition due to dry bark, five were placed in low temperatures (59°F. ±6°) and five were placed in high temperatures (75° ± 10°). When these adults were tested later for flight, all flew; but eventually three of the adults kept at the lower temperature did not fly when tested.

In the wild population in 1957 females remained in their original egg galleries throughout the season. They ceased egg laying by August, because the inner bark was too dry but they did not attempt a second flight because of cool weather (Figs. 2, 3). They broadened the ends of their egg galleries but did not increase the length appreciably. This was deviation from the characteristic straight gallery constructed during the process of oviposition. The laboratory experiments and these field observations seem to represent homologous events.

Table V. Effects of moisture on egg laying behaviour in logs.

Log No.	Log Length (in.)	Dia. in.	Upper half Dry	Upper half Moist	Total Number Galleries	Av. Lgth. of Gallery in.	Av. Lgth. of Gallery Upper half	Av. Lgth. of Gallery Lower half	Moisture content at end of study % oven dry weight Wood Upper half	Bark Upper half
1	12	6	*		5	8.6	0	8.6	47	154
2	12	6	*		3	6.8	1.8	5.0	46	227
3	12	6	*		4	9.0	0	9.0	41	127
4	12	6	*		2	6.3	0	6.3	67	242
5	12	6	*		5	5.9	0	5.8	50	171
6	12	6		*	5	10.6	5.1	5.5	124	307
7	12	6		*	4	14.0	8.8	5.2	129	264
8	12	6		*	6	8.0	3.8	5.1	118	309
9	12	6		*	7	11.4	5.3	6.1	114	284
10	12	6		*	6	8.1	5.5	2.6	100	278
11	48	6			4	34	24	10	125	258

* Indicates dry or moist condition.

Females in their second egg galleries sometimes continue to oviposit late into the fall if trees are sufficiently moist. To test the possible effects of low temperature on oviposition, fifteen observation plates containing moist bark and egg laying adults were acclimatized as follows: two days at 65°F., two days at 55°F., two days at 45°F., and two days at 35°F. Five of the plates were then placed at temperatures of 55°F., five more at 45°F., and the remaining five at 35°F. Egg gallery construction and oviposition occurred at 55°F. It was noted, however, that, whereas egg gallery construction ceased among females at 45°F., the females in the 35°F. temperature continued (very slowly) to construct egg galleries (Table VI).

A possible explanation for this lies in the fact that when the plates were originally set up at room temperature the five females which were ultimately placed in the 35°F. temperature had elongated their egg galleries much more rapidly than the others. By the time their acclimatization was completed, most had galleries nine to ten inches in length. Because there was less room left on those observation plates, they were placed in the lowest temperature. The inherent vigour of those insects still allowed them to be active at the low temperature. The less vigourous females in the other plates ceased activity at 45°F., but were active at 55°F. (Table VII). All fifteen remained in the egg laying condition during the full three weeks of the experiment. Perhaps a short period of below zero temperature was needed to cause in adults an internal change from the egg laying condition to a condition associated with quiescence.

Internal changes: Dissections were made of newly emerged female beetles, females in various stages of egg gallery establishment, mated and unmated females before, during, and after egg gallery construction, and females prior to overwintering and after overwintering. Examinations were made of the wing

Table VI. Egg laying activities of females at 3 different temperatures.

Observation Plate Number	Total Elongation of egg gallery in mm. after 7 days	after 14 days	after 21 days	Remarks
Temp. 54°F.:				
1	125	201		
2	115	191	reached top	
3	115	300	of observation	no egg hatch
4	101	171	plate	
5	119	195		
Temp. 44°F.:				
6	0	0	0	
7	1	1	0	No egg hatch
8	2	2	0	Females still
9	0	0	0	in egg laying
10	0	0	0	condition
Temp. 34°F.:				
11	2	6		No egg hatch
12	5	6	* Placed at	Females in
13	5	5	28°F.	egg laying
14	6	12		condition
15	0	5		after 14 days

* Two females changed internally to condition associated with quiescent (over-winter) stage: i.e. reduced reproductive system; enlarged fat body; reduced wing muscles.

Table VII. Internal changes in the female beetle associated with behavioural stages.

Stage of Female	Wing Muscles Enlarged (E) Reduced (R)	Fat Body Enlarged (E) Reduced (R)	Ovarioles Expanded (E) Reduced (R)	Corpora Luteum Present	Spermathecia with sperm	Ventriculus Expanded (E) Reduced (R)
Newly Emerged	E	E	R	No	No	R
Egg Laying	R	R	E	Yes	Yes	E
Second Emergence	E	E	R	Yes	Yes	R
*Unmated in egg gallery	R	R	E	Yes	No	E
Overwintering	R	E	R	Yes	Yes	R
**Quiescent in egg gallery	R	R	R	Yes	Yes	E

* After several weeks, when males were prevented from entering the gallery to mate with the female

** As occurred in 1957 when egg laying ceased in midsummer due to unpalatable bark but temperatures were too low to encourage flight development.

muscle condition, size of the fat body, condition of the digestive and reproductive systems. Observations reported by Reid (1958) and additional ones made since agree in many respects with a report by Chapman (1955) concerning internal changes in the ambrosia beetle, Trypodendron lineatum (Olivier). Each stage of the behaviour is associated with a characteristic condition of the internal organs (Table VII). These conditions, e.g. enlarged wing muscles and enlarged reproductive system do not occur at the same time. Plate X, Figures 1, 2, shows the internal differences which existed between females in the flying condition and in the egg laying condition.

To illustrate the relationship between moisture content, egg gallery construction, and internal condition of the beetle, there follows a description of a young female which has just established a gallery. She possesses massive flying muscles, a greatly expanded fat body, an empty digestive tract and a reduced reproductive system. Although by the next day the beetle has excavated one inch of gallery, the wing muscles, fat body, and reproductive organs have not been visibly altered but the digestive system begins to fill. She is now ready to mate. After mating, internal changes are accelerated. There occurs a reduction in size of flying muscles and of fat body, an increase in the size of the digestive system, particularly the ventriculus, a rapid enlargement of the reproductive system, especially the ovarioles. The female begins to lay eggs and increases the rate of elongating the gallery and deposits more eggs per inch of gallery as the ovarioles increase their output. Egg production reaches a peak by the time the gallery is four inches long. Size of the ovarioles now diminishes and egg production declines as the gallery is lengthened. In the meantime, the moisture content of the tree is rapidly declining due to activity of the insects in the tree and blue stain growth into the sapwood. By the time the gallery is five or

six inches long, the low moisture level of the inner sapwood causes a cessation of egg laying, and the reproductive organs are reduced in size. By the seven inch level the insect is once more in the flying condition. She then mines to the outside, emerges, and attacks a fresh tree. Internal changes in this sequence are illustrated in Figure 6.

The possibility of parthenogenic reproduction was investigated. Twenty-five virgin females were allowed to establish egg galleries. None of the eggs laid by these females hatched. These results were in agreement with those of Gibson (1927).

Causes of variation in production of viable eggs: A comparison of the width of the prothorax of egg laying females to the average number of eggs laid per day by each, indicated that rate of egg laying varied directly with the size of the beetle (Table VIII).

In long egg galleries, which characteristically do contain more eggs (Table III), both male and female beetles are often present. This suggests that the presence of the male has some effect upon length of the gallery. To test this hypothesis, debarking data collected in 1955 and 1956 were divided into three classes of gallery based upon beetle occupancy: those which contained no male or female, only a female, and a male and a female. There were 124 galleries in the first class, 117 in the second, and fifty-six in the third. The mean gallery length in inches and standard deviation (in brackets) in each class was 9.9 (5.6), 12.2 (6.8), 18.2 (6.4) respectively, and the differences were significant at the five percent level. Thus longer galleries were constructed when the males remained with the female.

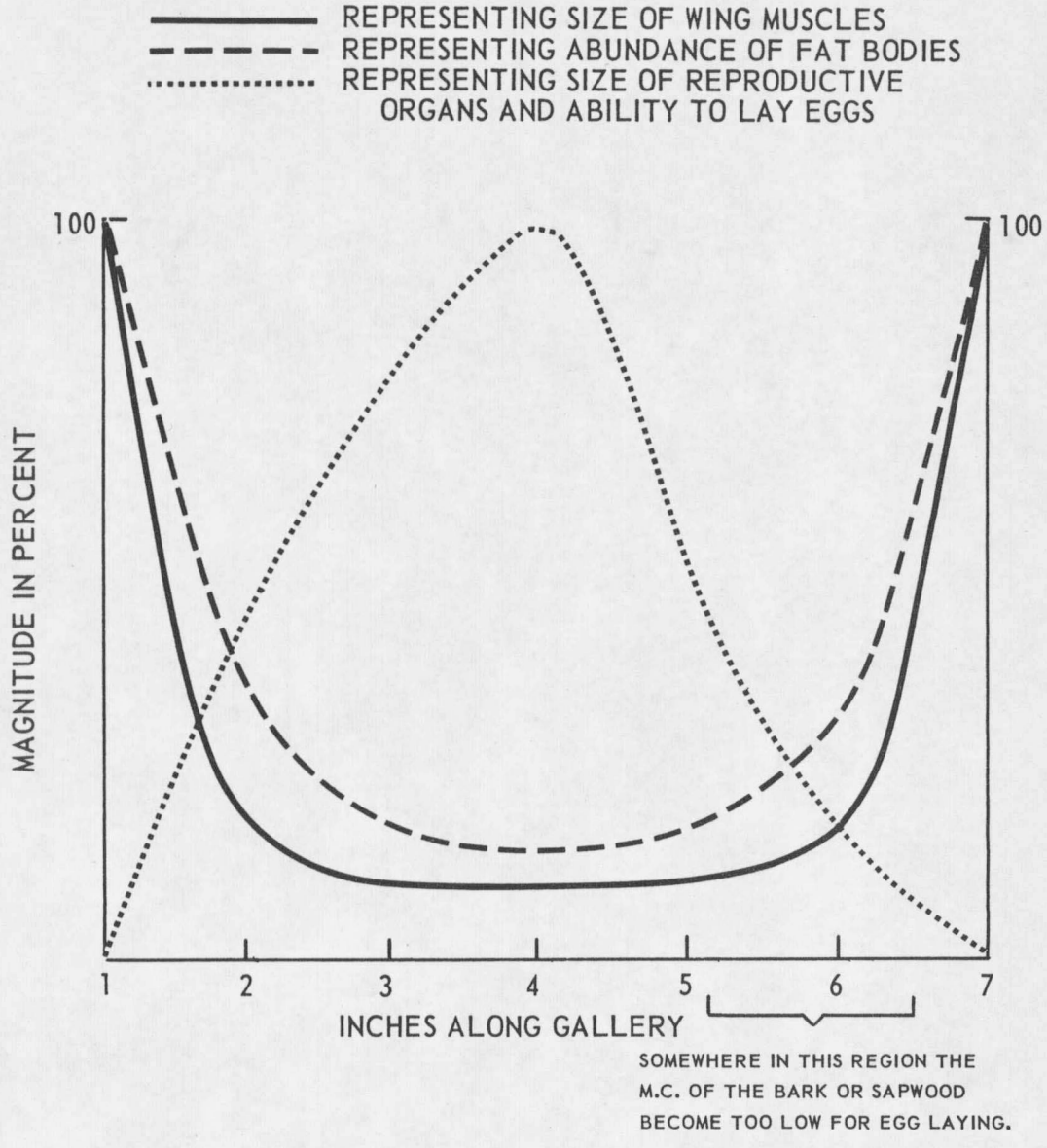

Fig. 6. Internal changes in the female associated with gallery excavation and egg laying.

Table VIII. Size of female related to number of eggs laid per day.

*Size of female as represented by width of prothorax (mm.)	Number of galleries and number of females measured.	Average number of eggs laid per gallery per day
1.694	2	1.94
1.848	16	1.87
2.002	20	2.19
2.156	16	2.21
2.310	20	3.04
2.464	10	3.60
2.618	2	3.35
2.772	1	1.20

* Size determined with binocular microscope and gridded eyepiece. Divisions on grid changed to mm.

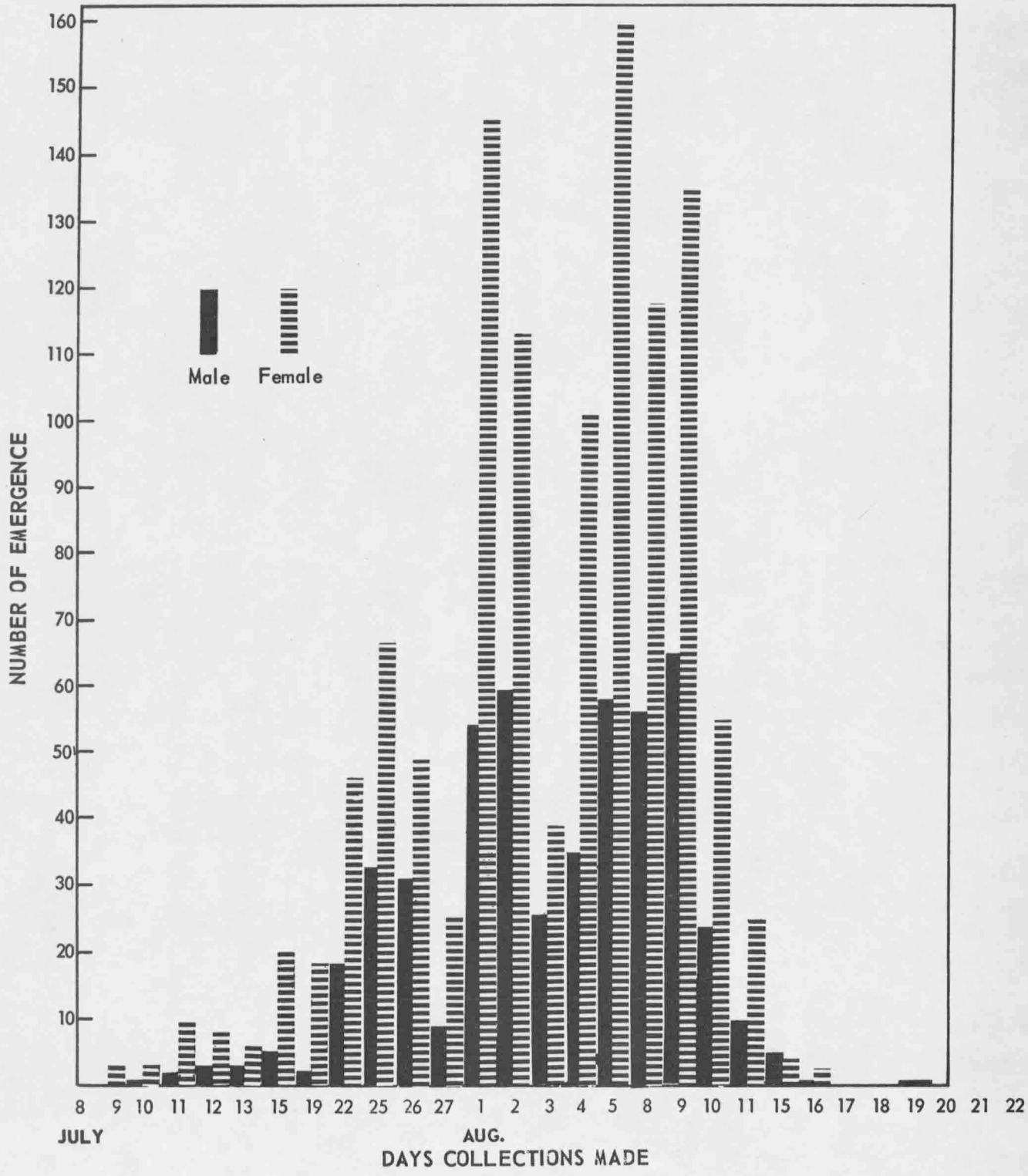

Fig. 7. Emergence of male and female beetles, 1955. Butt logs from trees infested the previous year placed in cages prior to commencement of emergence.

Sex ratio in mountain pine beetle populations varies between regions. Reid (1958) pointed out that first flight adults in the experimental area were close to one male to two females in every year from 1955 to 1958. In addition, that ratio was apparent in the daily emergence (Fig. 1) and the seasonal emergence (Fig. 7). It was suggested that the uneven sex ratio was due to the greater mortality that occurred among male teneral adults than among female teneral adults under the normal crowded conditions of brood galleries prior to emergence.

Five different sex ratios were compared to determine their effect upon the fertilization of the females. For each ratio a caged log (Pl. V, Fig. 5) was populated with thirty females and a specific number of males: nine, fifteen, twenty-one, twenty-seven, and thirty-three respectively. The beetles were released in the cages in the experimental area during the first week of July, 1957, and the logs were examined at the end of September. Each female established only one egg gallery and remained in this gallery all summer. Approximately equal number of egg galleries were established at each ratio and all contained viable eggs. It appears that even when the number of males is reduced to a ratio of near 1:3 (males to females), all the females were mated.

It was mentioned that males were frequently blocked out once the female started to elongate the egg gallery. In contrast, unmated females did not plug their galleries with boring dust and newly emerged males could readily enter these open galleries and mate with the virgin females. Thus the polygamous habits of the male overcomes the unequal sex ratio.

Under natural conditions, female beetles lay only a small fraction of the eggs they were capable of producing. Egg galleries are short in most infested trees (Table XVII) and contain fewer than seventy-five eggs. Under maintained

favourable conditions of moisture and temperature and without crowding, females excavate galleries forty to fifty-five inches in length. In a gallery fifty-two inches long, the female had laid 263 viable eggs and was still ovipositing at the time the gallery was examined.

Brood development and effect of temperature

The time required for egg hatching in the experimental area in 1956 was estimated by removing newly laid eggs and placing them on moist, bleached, blotting paper within Petri dishes. The time required for egg hatch in mid-July was six days. Eggs laid after August 22 failed to hatch in the laboratory at field temperatures, nor was there any evidence of hatch in the field after that date. Late August and early September temperatures (mean maximum 67°F.) were apparently too low for embryo development. However, eggs laid during that period and in October hatched when reared at 85°F. In 1957, egg hatch in the field was retarded by cool weather (Appendix VII), none was observed until three weeks to a month after galleries were established. In 1959, few eggs hatched in infested trees, and low August temperatures (Appendix IX) were considered responsible. Because wide variations have been observed in the success and time required for egg hatch, further work on this aspect of the life cycle is necessary.

Broods generally spend most of their time in the larval stages. Larvae of the mountain pine beetle pass through four instars (Table IX) as do other species of Dendroctonus (D. simplex - Prebble, 1933; D. pseudotsuga - McMullen and Walters, 1956).

In 1955, by recording the first appearance of each instar during examination of broods established on known dates, the length of each larvae stadium was

Table IX. Larval head capsule width and number of instars.

Instar	No. of larvae	Mean width of head capsules - mm.	S.D.	C.L. t.05
I	265	0.479	0.041	.0049
II	107	0.648	0.021	.0038
III	62	0.848	0.050	.0127
IV	221	1.159	0.081	.0107

estimated. The number of degrees above 60°F. each hour in the day was tabulated from the hygrothermograph records of that season. By this method there was some consistency in the total day-degree-hours above 60°F. necessary for development to fourth instar, pupal, and teneral stages (Appendix X), but little consistency was indicated in time required for development of earlier stages.

In 1956, prepupal larvae (late fourth instar) were removed from infested logs and placed upon moist bleached blotting paper in Petri dishes. The stadium between the moult to the pupal stage and the moult to the teneral stage required eleven days in late June, five to six days in mid August, and ten to eleven days in mid September. The mean maximum temperature for each period was 68°, 87°, and 76°F.

No comparable data were collected on teneral adults as the change from late teneral to early adult can not be determined exactly. Under optimal conditions in the laboratory, tenerals developed to young flying adults within ten days.

The rate of brood development of populations in two regions having different seasonal temperatures was studied in 1955. In the warmer region (experimental area), a number of logs was infested at known dates. When the broods were well established, half of the logs were removed to the cooler region (Eisenhower Field Station in Banff National Park). The rate of development in each region was determined by examining the broods at intervals. Daily temperatures were recorded at both sites. Brood development was more rapid in the warmer region than in the cooler region. In the warmer region, broods reached maturity, established galleries and laid eggs. In contrast, brood development in the cooler region did not advance beyond the fourth instar. If these broods had been established initially in the cool region rather than in the warm region, they probably would not have reached the fourth instar. The difference in rate

of brood development (Fig. 8) may be attributed to temperature differences illustrated in Figure 9. These results are not in agreement with those reported by Struble (1933) where differences of ten to fifteen degrees (at higher temperatures) were found to have little effect on the rate of brood development.

In mid July of 1956, mature beetles from the experimental area were allowed to establish egg galleries in caged logs in the region of lower temperatures. The logs in which the broods developed were kept shaded and the sapwood remained moist even though the inner bark region was thoroughly chewed. The broods developed only to third and fourth instar larvae by fall despite the unusually warm season for that region. Teneral adults appeared under the bark in August of 1957 but no emergence occurred until July of 1958, indicating that the low temperatures in this region caused the insect to extend its life cycle from the usual one year to a two year cycle. Evenden et al. (1943) reported that a two year cycle may occur.

An outbreak of the mountain pine beetle with a one year life cycle was recorded in Banff, the cooler region, from 1939 to 1943 (Hopping, 1945), but the insect has not been observed there since. During years in which the outbreak persisted, mean monthly temperatures for July-August (Fig. 10) were slightly higher than occurred at the time of the present experimentation. Low temperatures may therefore be largely responsible for the scarcity of the mountain pine beetle in this region since 1943. In Figure 2, temperatures for this cooler region are superimposed, in part, over the temperature records from the experimental area where the insect has persisted for many years. The differences are consistent and in agreement with Henson (1959).

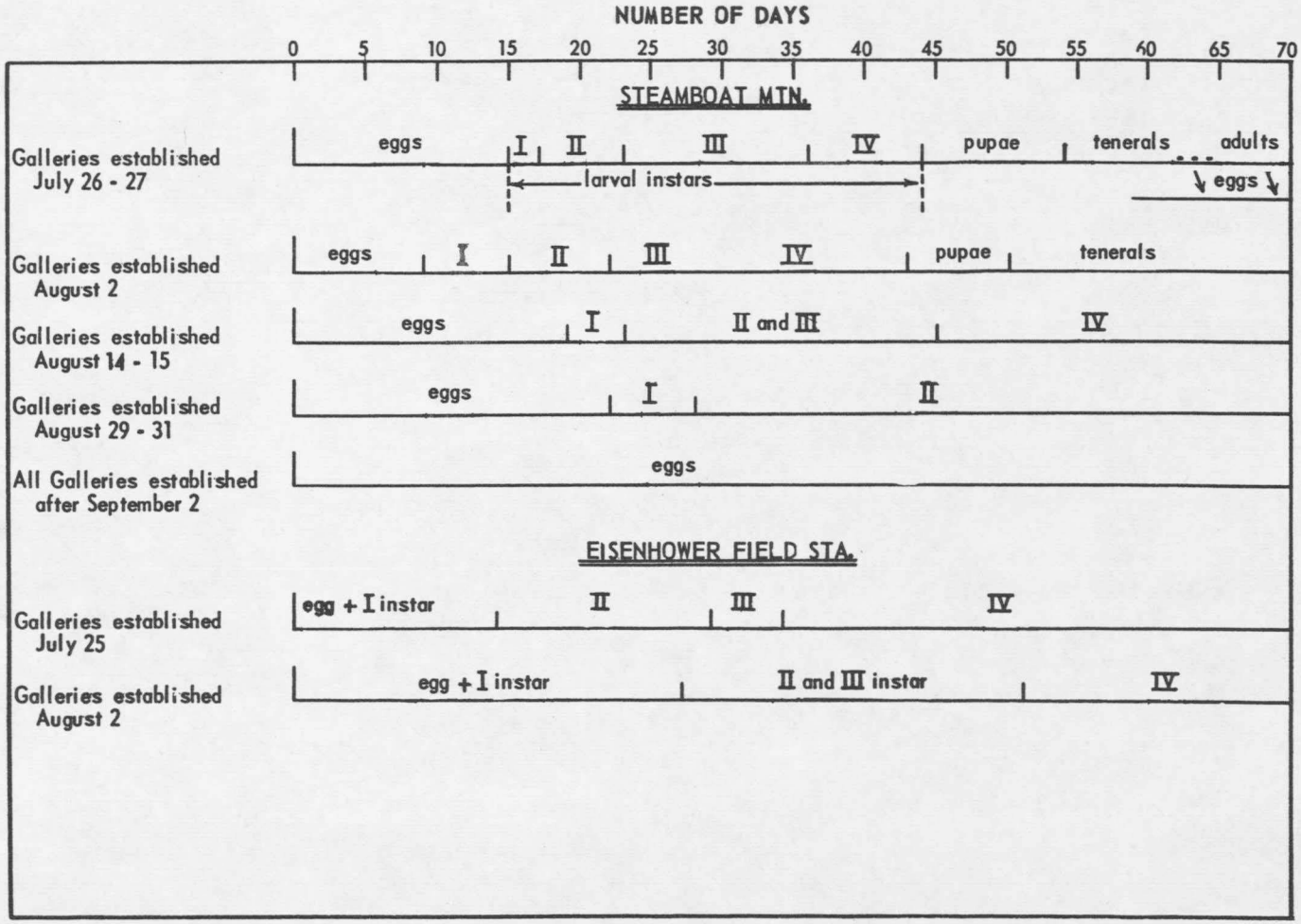

Fig. 8. Brood development in caged logs at two sites, 1955.

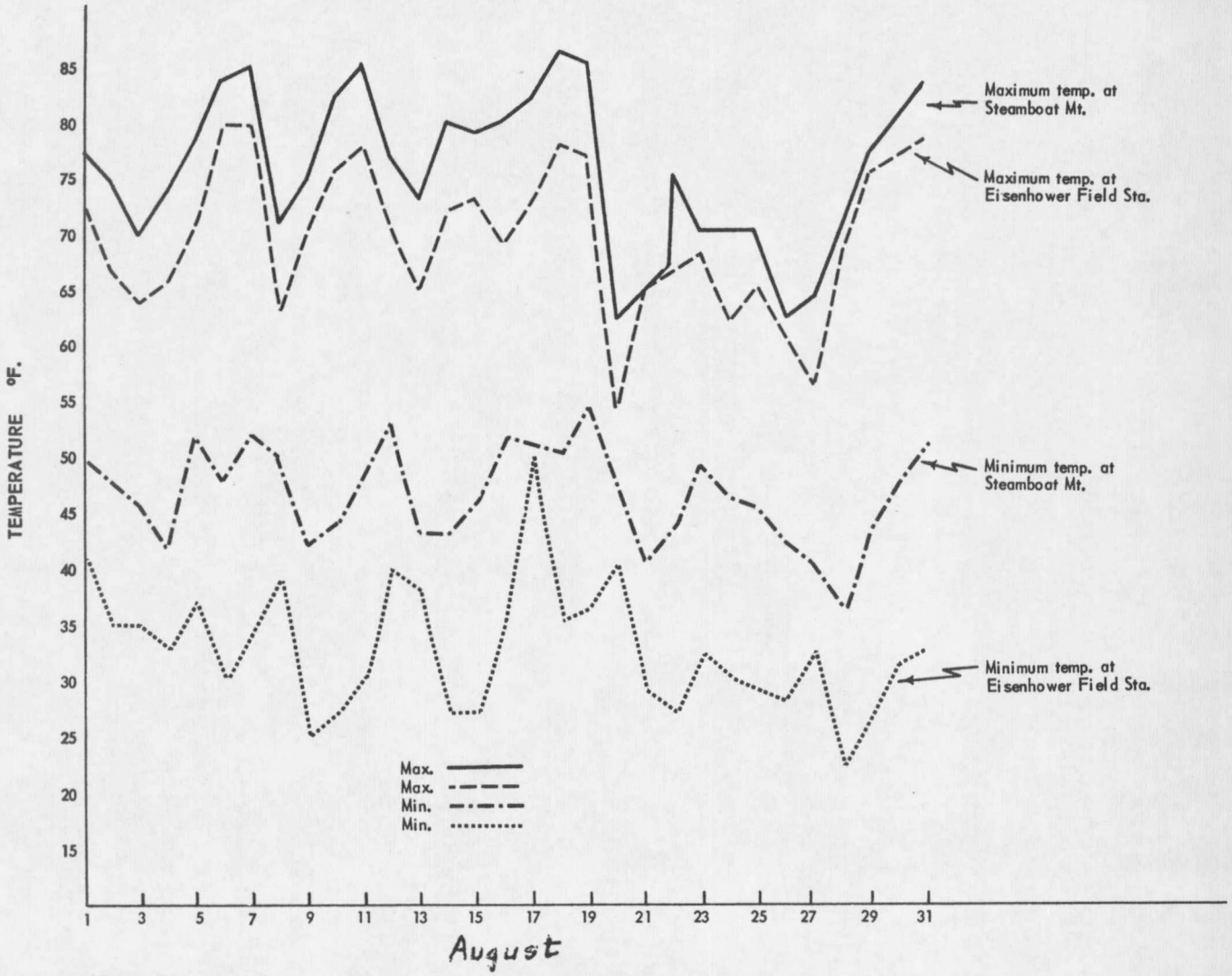

Fig. 9. Maximum and minimum temperatures at two sites, 1955.

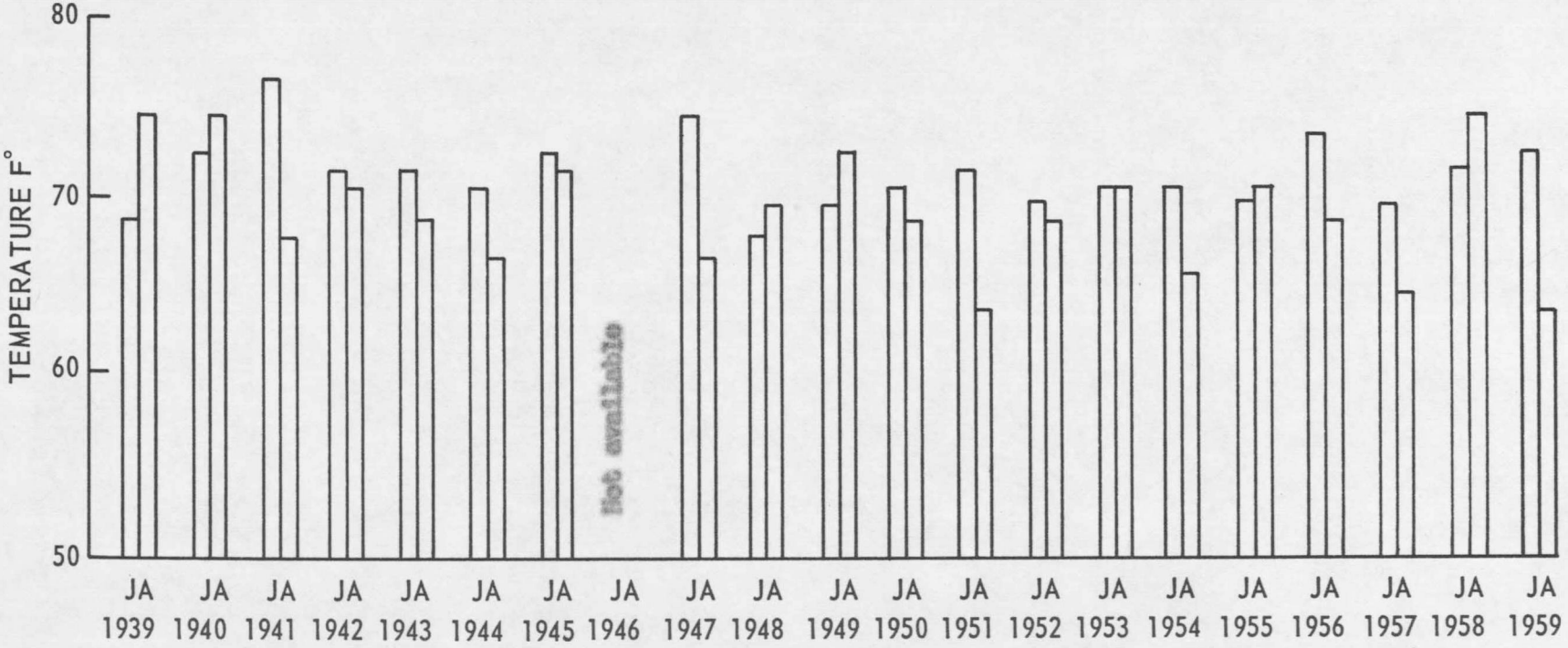

Fig. 10. Mean monthly maximum temperature, July-August, Banff, Alberta, 1939-1959.

Populations in caged logs behaved differently from the wild population in the years when two flights occurred (1956 and 1958). Broods established in caged logs at the same time as the first flight broods in the field, emerged in mass as adults in May and early June of the following year but there was no comparable flight by the wild population. Broods established in caged logs at the time of the wild population's second flight in 1956 and 1958 emerged at the same time as the wild population in 1957 and 1959.

The rate of brood development in any one season depends upon the time they were established and upon the temperatures prevailing during their development. In the experimental area, the maximum rate of brood development occurred during the two warm years (1956, 1958), when broods established by the first flight reached the teneral and early adult stages by fall. Survival was so low in those broods however, that the emergence in the fall and the following spring was too low to be important. (The limiting factor here mainly concerns the condition of the host tree and this aspect is discussed in a later section). During cool wet years, the first (and only) flight broods advanced by fall to the late larval stages. Therefore, under the most optimal conditions, which prevailed from 1955 to 1959, a single and a partial second generation occurred. Otherwise, broods required one season and part of the following summer to reach maturity.

The development and life cycle of broods from 1955 to 1959 in the experimental area are summarized in Fig. 11.

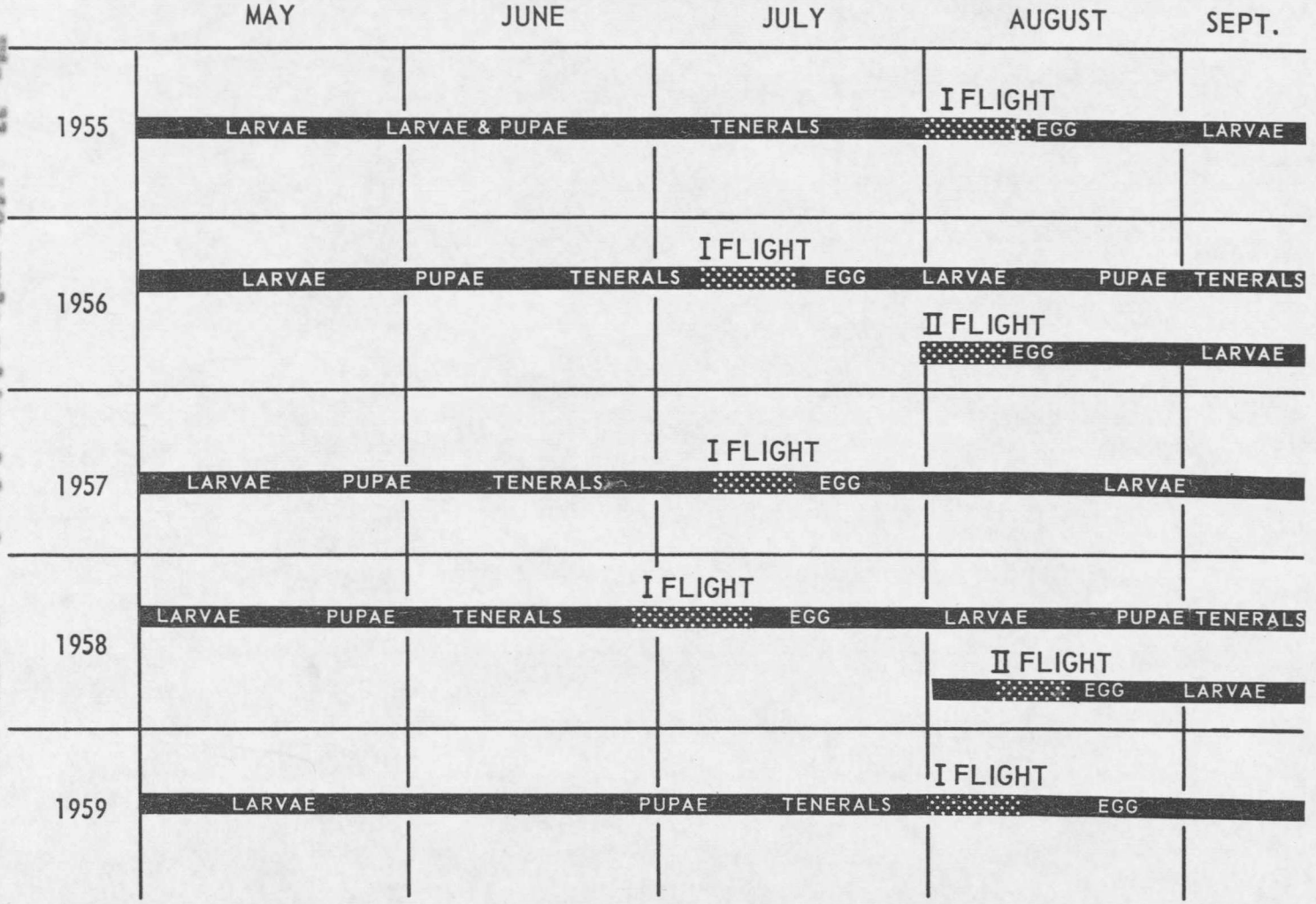

Fig. 11. Life cycle and brood development, 1955-1959. Experimental area.

MORTALITY FACTORS

Parasites and predators: The behaviour of the larval parasite, Coeloides dendroctoni Cushman (Braconidae: Hymenoptera) in oviposition and upon hatching have been described by De Leon (1935). In the experimental area, the life cycle of Coeloides generally coincided with that of the host, as indicated by emergence data and debarking studies. In 1957 however, when beetle eggs did not hatch until three weeks to a month after galleries were established, the adult Coeloides emerging at the time or shortly after the parent adult beetle, had no larval stages to attack. Whatever effect the parasite may have had would be reduced in such a situation.

De Leon (1935) found this parasite to be of little importance. Several considerations may have had a bearing on the apparent ineffectiveness. First, thick bark may have prevented the ovipositor from reaching the host. Secondly, there may be a question as to the validity of the criterion measuring parasitism by associating fourth instar larval head capsules with parasite cocoons, as done by Bedard (1933). Bark beetle larvae younger than the fourth instar may also be attacked but are too small to support the parasitic larvae to maturity. Under these conditions, the host and the parasite die. In short, Coeloides may destroy more bark beetle larvae than indicated by the presence of cocoons.

The common insect predators within mountain pine beetle broods each year were Medeterus aldrichii Wheeler (Dolichopodidae: Diptera)and Enoclerus sphegaus Fabricius (Cleridae:Coleoptera). The ovipositing behaviour of these predators and the activity of their larvae have been described by De Leon (1935) and Reid (1957). These predacious larvae move easily under the bark attacking all stages of the host from early instar to young tenerals. They remove the body fluids of the host. In a short time these empty "skins" become discolored and their presence is difficult to determine.

In 1956 specific data on brood mortality caused by parasites and predators were obtained from two naturally infested logs, on which Coeloides and Medeterus were actively ovipositing. When the logs were debarked two to three weeks later each gallery was sectioned into one inch lengths and the number of eggs laid in each inch and the number of larvae destroyed by predators or parasites was determined. Egg and larval mortality was grouped. Mortality data from twelve separate seven inch galleries are summarized in Figure 12. Since no parasitic or predacious insects other than Medeterus and Coeloides were detected it was assumed that the greatest amount of mortality was caused by them.

An extensive nematode complex is associated with mountain pine beetle broods. A list of the species and their location within the gallery (Table X) were obtained in 1955 and 1956. Although little is known of the biology of these nematodes or their effect on the mountain pine beetle, observations indicate only a few species were directly parasitic. These were found in the body of the adult stage only.

The most important of these nemic parasites, Sphaerularia bastata Khan (Allantonematidae: Nematoda) frequently heavily infested the beetles. Infested beetles were characteristically lethargic and made no attempt to escape when removed from the gallery; when placed on their backs, they made no effort to right themselves; there was frequently a noticeable tremor in the antennae and legs. Several adults displaying those symptoms were observed closely. All died within four days. Immediately following death, many Sphaerularia larvae and adults left the host by forcing their way through sutures between sclerotized portions of the abdomen. They moved into the surrounding boring dust and frass of the gallery where they were available for reinfestation of adult beetles.

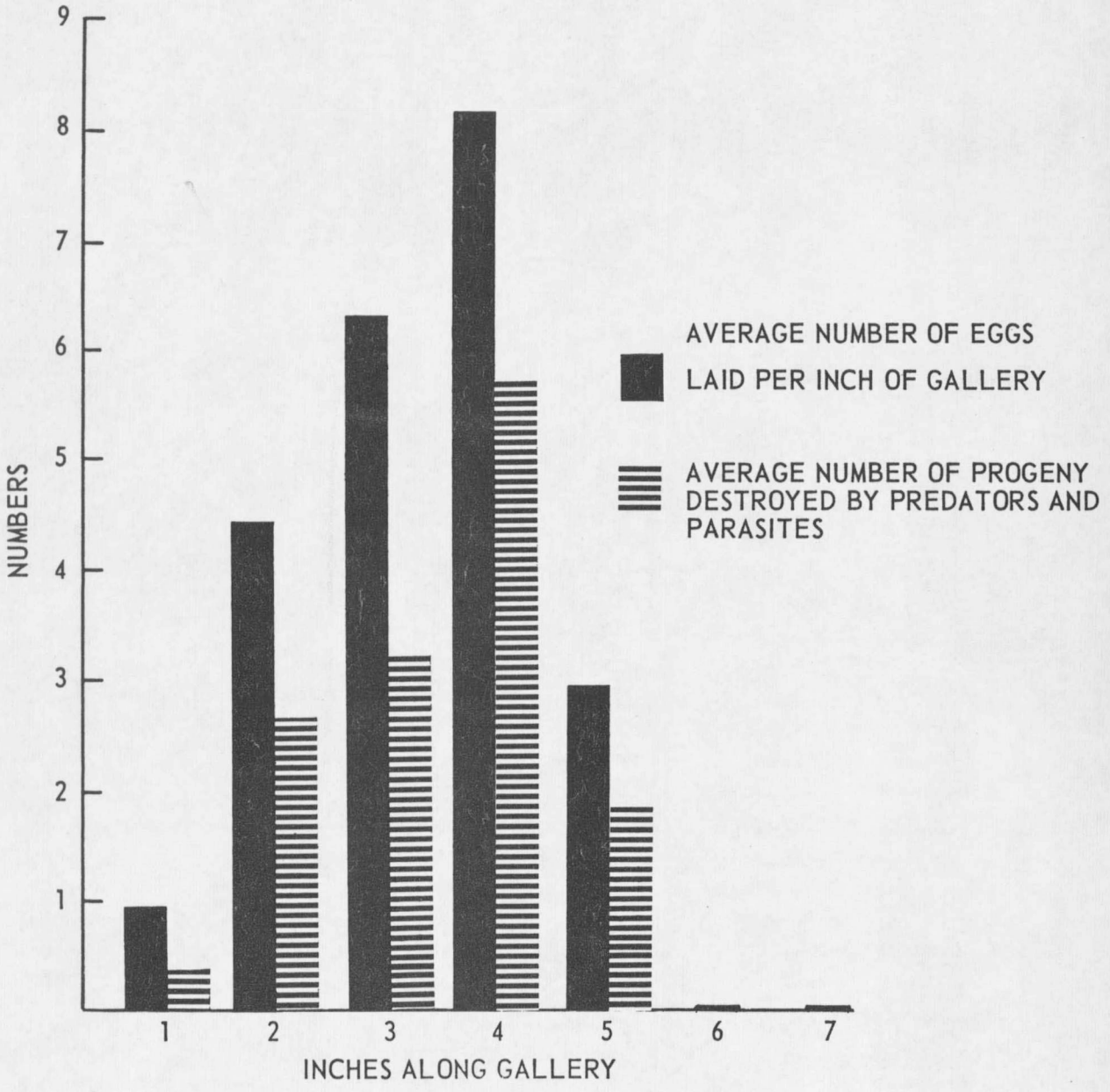

Fig. 12. Effect of predators and parasites on broods established in logs examined after 3 weeks.

Table X. Nematodes associated with the mountain pine beetle.

Species	Where Found
Sphaerularia hastata Khan	Digestive tract of adults Body cavity of adults Reproductive organs of adults Egg niches
Sphaerularia sp. (Juvenile stages)	Frass in main galleries
Aphelenchoides tenuidens Thorne 1935	Egg niches *Frass in larval galleries Frass in main galleries
Aphelenchoides latus Thorne 1935	Frass in main galleries
Aphelenchoides talonus Thorne 1935	Egg niches Frass from main galleries Frass in larval galleries
Panagrodontus dentatus Thorne 1935	Egg niches Frass in main galleries
Diplogaster pinicola Thorne 1935	Frass in main galleries

* Accumulated boring dust and excreta

The life cycle of Sphaerularia is postulated as follows. After entering the body cavity of the bark beetle, the nematodes mate and the female nematodes produce large numbers of eggs which hatch in the body of the host. The increased parasitism then begins to affect the normal functioning of the host. In time, the build-up of nematodes is so extensive that the host dies. The nematodes force their way out of the carcass to infest other adults.

In one selected group of fifteen female beetles which were dissected, seven were heavily infested with nematodes, three were lightly infested, and five had none. All the beetles were of the same age but some were establishing a second gallery while others were still in their first. In the heavily infested females reproductive organs were reduced and contained no mature ova. The digestive tract of the heavily infested adults was partially to completely empty. The data from these dissections are summarized in Appendix XI.

Observations of lightly infested ovipositing females showed that nematodes were ejected from the female with the egg. Dissection of a female beetle which had just laid an egg having nematodes upon it showed that the reproductive system contained nematodes. Nematode larvae and eggs were found within the vagina, and larvae were found appressed to the walls of the median oviduct, with the largest number occurring in the bursa copulatrix. Within the latter organ, they were in sufficient numbers to give a turgid appearance to the structure. Thus, the nematodes had many opportunities to attach themselves to the egg before it was ejected. The nematodes may also interfere with normal reproductive functioning. Their presence in large numbers in the bursa would interfere with movement of the sperm and prevent fertilization of the egg. Eggs from non-fertilized female beetles are known to collapse soon after oviposition. Since collapsed eggs are present in nematode infested galleries, the nematodes may be indirectly responsible for them.

Total egg production of infested females was approximately thirty-three percent less than egg production by non-infested females (the difference was significant at the one percent level). Perhaps the lower egg production was the result of the parasitism. These findings agree with Fuchs (Van Zwelumenburg, 1928) who studied nematode parasites associated with Ips typographus (L) and Hylobius abietus (L), and by Massey (1956) who reported on the effects of nematode parasites in the Engelmann spruce beetle (D. engelmanni Hopkins).

The importance of insect parasites and predators in the wild population is difficult to assess for several reasons. The most important being the difficulty in recognizing that type of mortality, particularly in mature broods (Pl.II, Fig.1). In addition, the action of the parasites and predators in reducing host density would, to a degree, improve conditions for the remaining individuals in the bark beetle brood (see crowding).

Despite the apparent importance of insect parasites and predators, as indicated by earlier discussion, they were not considered to have played a crucial role in control of the wild bark beetle population in the experimental area. This agrees, in part, with Miller and Keen (1960) who summarized records on the westem pine beetle (D. brevicomis Lec.) and concluded as follows: "The records accumulated over a period of thirty years fail to indicate that parasitism plays an important part in natural control of the western pine beetle."

Woodpeckers are sometimes considered important in the control of bark beetles (Chamberlin, 1939; Knight, 1958). Woodpeckers were active in the experimental area but their role was not assessed. They almost invariably removed some broods as well as bark from every successfully infested tree, ie. trees in which broods were able to develop (Pl. VI, Fig. 3). Most of the predation by woodpeckers was believed to occur in the late fall and in the spring. Bark on the lower part of

the stem was frequently too thick for the woodpeckers, and broods in that region were less subject to predation by these birds. The thin bark on the upper portions of the stem did not afford much protection. Regardless of woodpecker predation, that region did not produce mountain pine beetle broods as it usually dried out too fast. In addition, most of the mortality to the first flight broods had occurred before the woodpeckers became active on the infested trees.

Lethal temperatures: Mortality due to lethal temperatures has been reported to occur in broods of different scolytids (Graham, 1924; Patterson, 1930; Blackman, 1931; Miller, 1931; Beal, 1933; Chamberlin, 1939). In exposed locations, temperatures within galleries of Ips pini in lodgepole pine reached 140°F. when the ambient air temperature was 70°F. (Reid, 1957). Ambient air temperatures above 70°F. were frequently recorded in the experimental area, and it is likely that some mortality due to high lethal temperatures occurred in broods.

To test the effect of low temperatures in the experimental area in 1955, four logs five feet long were arranged vertically so that two would be covered by snow and the other two would be above the anticipated snow line. One log in each place contained broods from the first flight, the second had second flight broods. A fifth log, containing first flight broods was placed above snow line in an area where recorded winter temperatures were even lower (Eisenhower Field Station). The overwintering insects were mostly third and fourth instar larvae and their parents. In the following spring, soon after the snow melted, all were examined.

While mortality of adults was greater in exposed logs than in snow-covered logs, there was no appreciable difference in larval mortality within logs kept above the snow and below the snow (Fig. 13).

At the colder site, broods which overwintered in the log above the snow suffered complete mortality. The minimum temperatures which were from fifteen to twenty degrees lower than in the experimental area (Table XI) were probably responsible for the high brood mortality.

Crowding: In experiments to determine possible effect of competition within the broods for food and living space during 1956 and 1959, four fresh logs were placed in a large cage and infested with bark beetles. The logs, each approximately ten inches in diameter and four feet in height, were cut from the lower eight feet of two trees selected for their similarity. Top and bottom ends of the logs were waxed to prevent excessive drying. Two of the logs were removed from the cage after approximately twenty-five galleries had been established in each. The other two logs remained in the cage until they contained over 100 galleries. Each log was then kept in a separate cage. The broods established in 1956 were allowed to develop to maturity and the adults were counted when they emerged from the logs. The broods established in 1959 were allowed to develop until mid September of that year, when the logs were debarked and surviving larvae, pupae and young adults were counted.

In the 1956 experiment, emergents per gallery from the heavily infested logs were 5.0, and from the lightly infested logs, 10.6 (Table XII). Among the emergents the ratio of male to female beetles was approximately 1:1 and was much more equal than the wild population ratios which always showed a greater number of females than males (Fig. 7). The reason for the difference was not determined. The size of more than 300 adults, as determined by the width of the prothorax, did not appear to be affected by the crowded conditions.

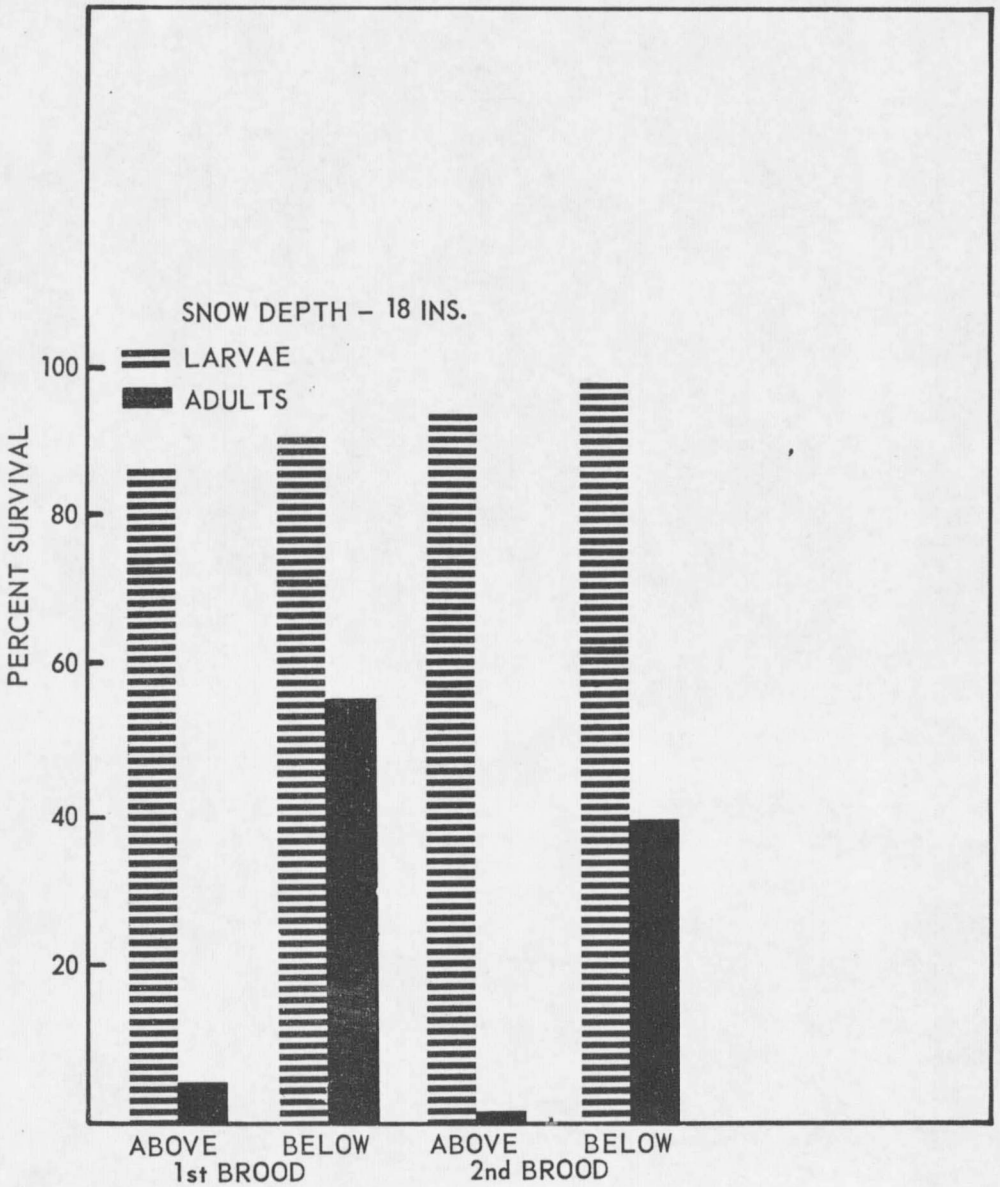

Fig. 13. Survival of larvae and adults above and below the snowline.

Table XI. Maximum and minimum mean temperatures (F.°) October to March, 1955-1956, Invermere, B.C., and Banff, Alberta.

		Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
Invermere	High	64	43	40	42	40	52
	Low	16	-12	-14	-14	-15	- 4
	Mean	43	18	16	19	17	31
Banff	High	67	43	33	40	37	58
	Low	20	-28	-34	-28	-33	-19
	Mean	39	12	9	12	12	26

The 1959 study confirmed the 1956 results. Galleries in lightly infested logs were long, the females laid more eggs, and survival was high compared to the heavily infested logs (Table XIII).

Mortality from over crowding occurring between progeny in the same gallery and between progeny in adjacent galleries could result from two conditions: (1) direct contact between individuals in which the weaker succumbed; and (2) inner bark so thoroughly depleted that smaller or weaker individuals did not obtain proper food. The greater the degree of crowding, the more rapid the immediate environment of the broods deteriorated and the rate of mortality increased.

The host: Trees showed a considerable range of resistance to bark beetle attack. The vigour or thriftiness of the host tree must determine to a great extent whether or not broods are successful. A relationship between tree vigour and resistance to attack has been indicated by past investigations (Felt, 1914; Person, 1931; Struble, 1935; Keen, 1936; Chamberlin, 1939; Hopping, 1945). To obtain an understanding of this relationship studies were carried out on tree moisture (see Materials and Methods section), resin flow, and blue stain fungal infection.

During drought conditions the "hydrature" of trees is affected (Walters, 1955), but those with superior root systems, and/or on better sites, would be subjected to a water deficit of less magnitude and duration. Respiration and photosynthesis would eventually be influenced as the hydrature was reduced, and the "health" of the tree would be affected. For this reason several aspects of tree moisture were studied in relation to the micro-habitat of the beetle, i.e. the inner bark and outer sapwood. The objectives were to determine (1) what the moisture distribution was within the tree and whether there were significant differences between different parts of the stem and between trees, (2) if diurnal and seasonal moisture changes occurred in the tree, (3) if there was any correlation between the moisture content

Table XII. Effects of density of galleries on brood survival, 1956.

	Log No.	No. of galleries per log	Average Gallery length (in.)	Total emergencies		Average emergencies per gallery
				Male	Female	Both sexes
Lightly infested 3.1 galleries per sq. ft.	1 2	27 38	10.5 10.4	311	380)	10.6
Heavily infested 11.2 galleries per sq. ft.	3 4	117 118	8.8 7.0	503	672	5.0

Table XIII. Effects of density of galleries on brood survival, 1959.

	Log. No.	Length in feet	Diameter in in.	Total sq.ft.	Total number galleries	Av. length gallery in in.	In. of gallery per sq. ft.	Total survival	Survival per sq.ft. bark	Survival per in. gallery
Heavily Infested	1	4	8.3	8.7	90	9.6	98.9	1292	199	1.50
	2	4	8.3	8.7	96	10.6	116.6	1019	126	1.10
Lightly infested	3	4	8.5	8.9	22	20.8	51.4	1000	124	2.20
	4	4	8.0	8.4	31	16.0	58.9	1152	137.1	2.30

of the inner bark and outer sapwood and resistance to mountain pine beetle attacks, and (4) the effect of successful bark beetle attacks on moisture content of the tree.

The methods used have been explained in a previous section. The moisture determinations taken at various levels on the uninfested tree suggest that there was no consistent variation in the moisture content of the outer sapwood from the base up the stem (Fig. 14). This contrasts with Caird's (1935) report of a slight moisture gradient in southern yellow pine, decreasing towards the top.

Moisture determinations taken horizontally through the stem of an uninfested tree indicated a steep gradient from a high in the outer sapwood to a low in the heartwood, and a slight rise again in the core (Fig. 15).

Moisture contents were compared for different aspects on the same tree and for the same aspects on different trees. Four uninfested trees were sampled in this study, and an analysis of variance indicated intra-tree difference in moisture content as well as inter-tree differences (both differences were significant to the one percent level). The moisture content in the same aspect, i.e. N, S, E, or W, of different trees, were not related.

Moisture changes in uninfested trees throughout the day showed a gradual rise during the night and early morning followed by a gradual decline during the afternoon (Fig. 16). This was more evident on an oven dry weight basis than on a percentage saturation basis. The evidence of a diurnal change agrees with Kramer (1956).

There were small changes in the moisture content of the inner bark and outer sapwood of uninfested trees during the season (Figs. 17,18). The moisture content rose in May and declined slightly in September. No examinations were made from October to April. Chalk and Biggs (1955) recorded somewhat similar data from

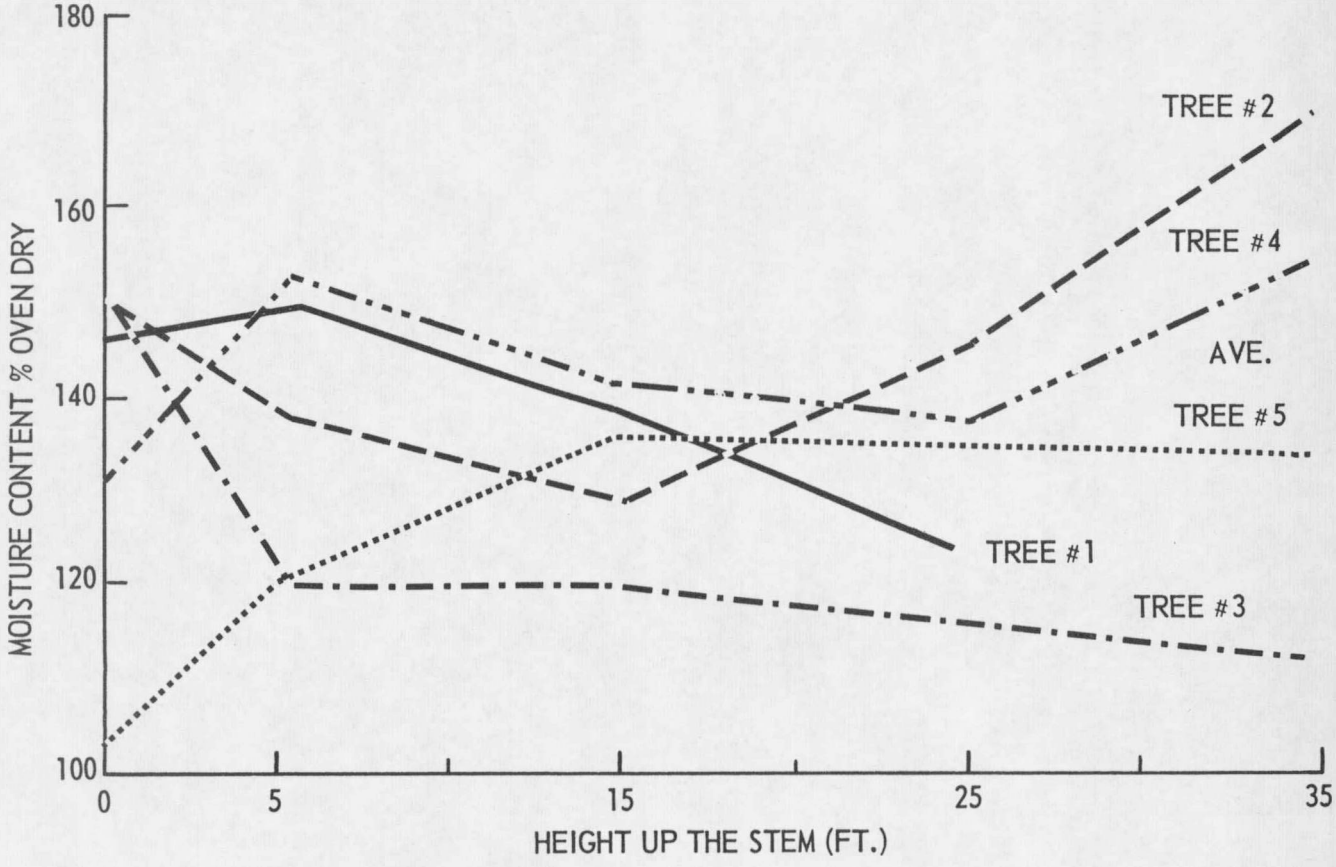

Fig. 14. Vertical distribution of moisture in the outer $\frac{1}{4}$" of sapwood.

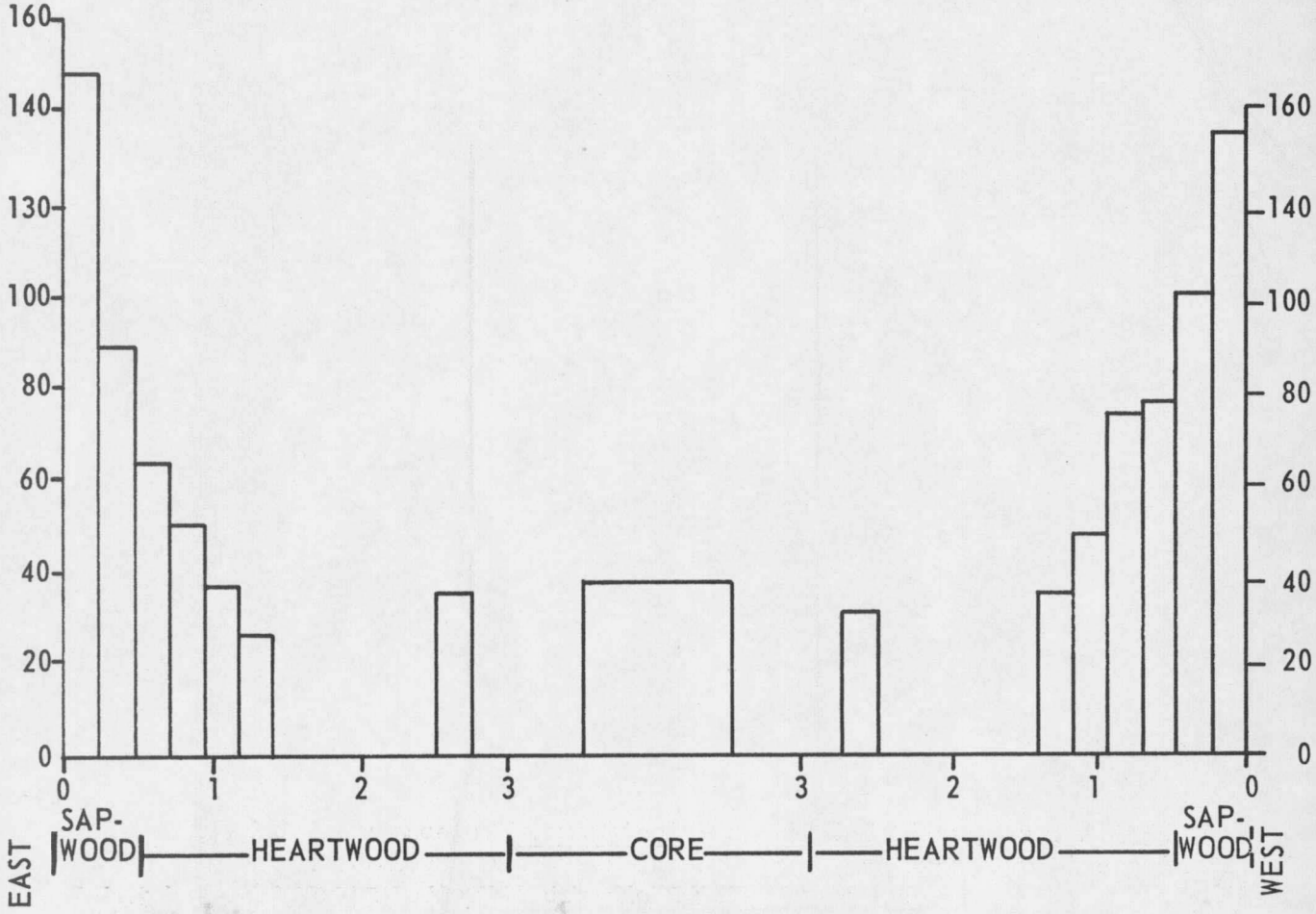

Fig. 15. Distribution of moisture horizontally through the base of a tree stem.

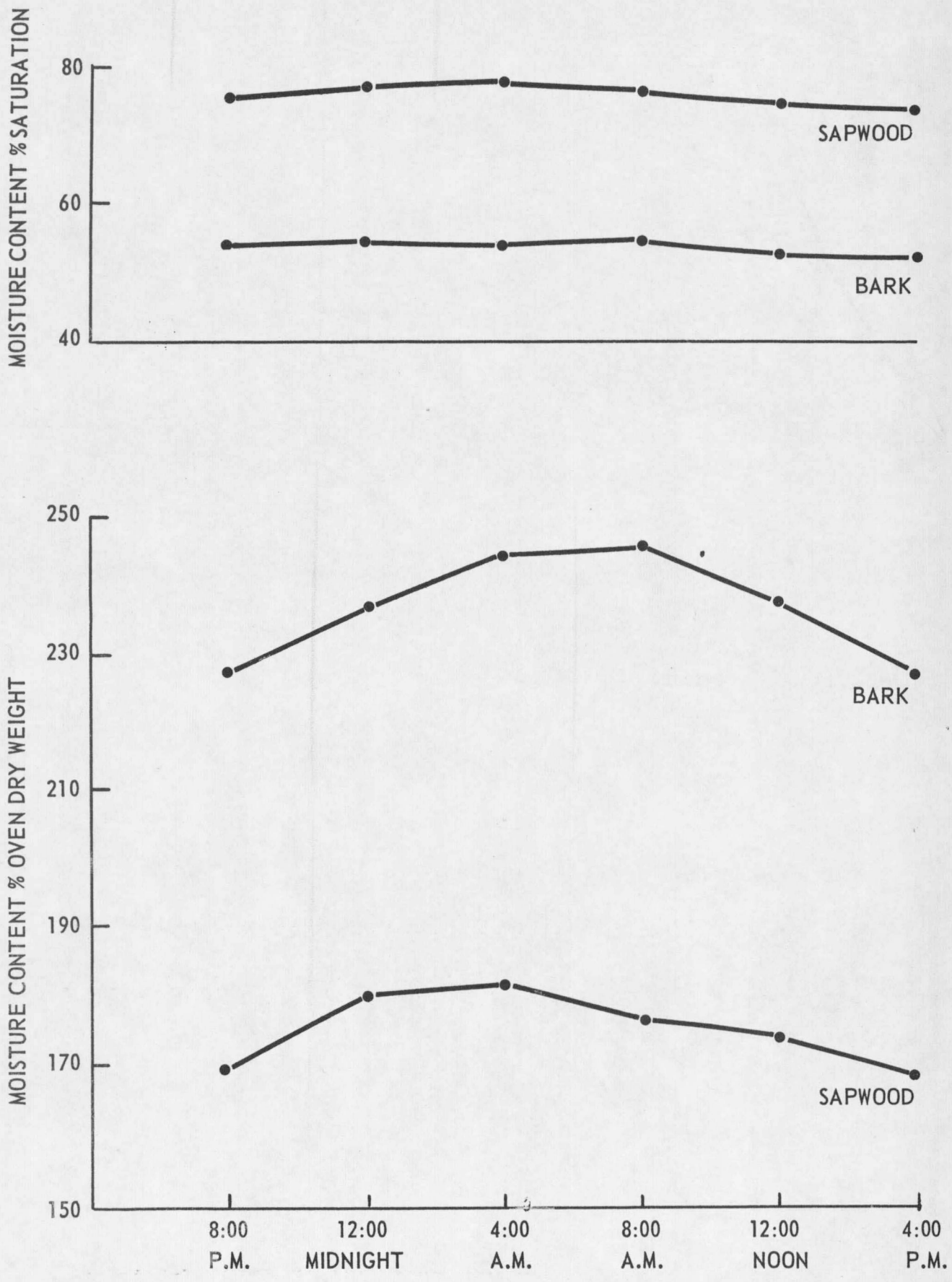

Fig. 16. Daily moisture march in a tree stem - outer $\frac{1}{4}$" sapwood. 1959. (Average of 4 trees).

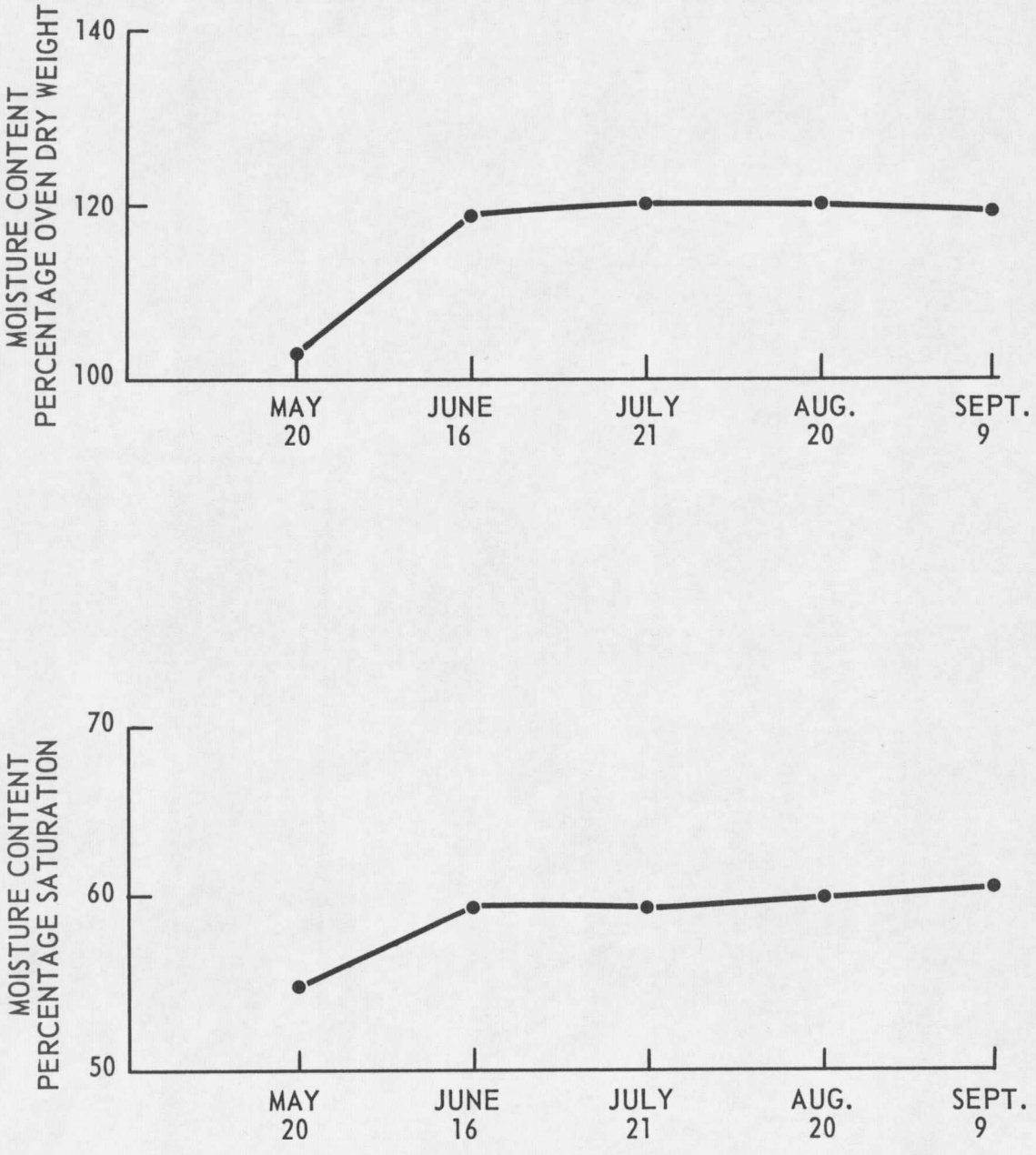

Fig. 17. Seasonal moisture march in tree stem - outer $\frac{1}{4}$" sapwood. 1959. (Average from 25 Trees)

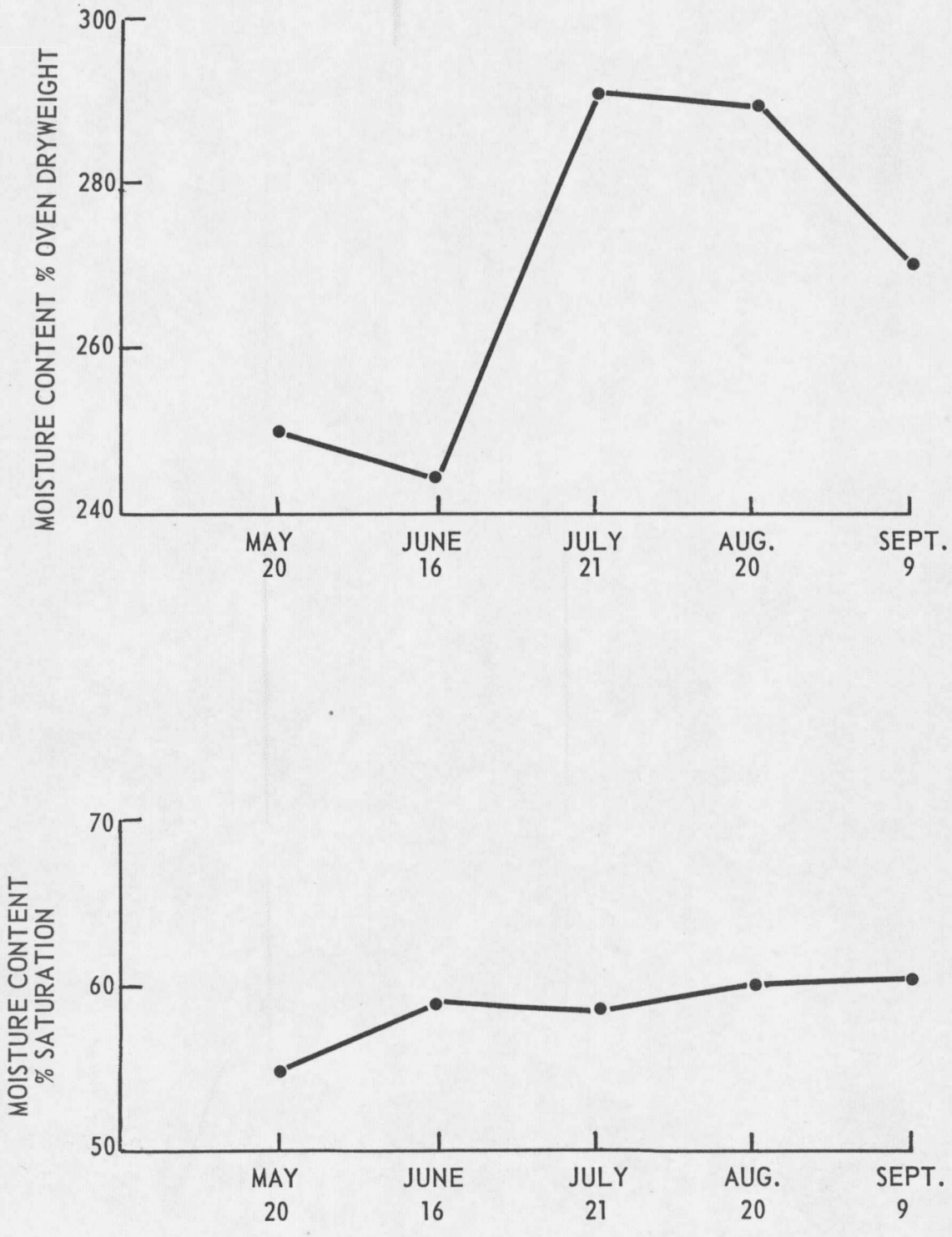

Fig. 18. Seasonal moisture march in tree stem - inner bark, 1959. (Average from 25 trees).

Sitka spruce, Picea sitchensis (Bong.) Carr. Coniferous trees, as opposed to deciduous, do not generally exhibit large seasonal changes in moisture content (Gibbs, 1958).

The relationship of tree moisture to the success or failure of bark beetle attacks was determined by caging small groups of adults on trees of varying moisture content. Under natural conditions trees of low moisture content were farily easy to locate, but the low population of bark beetles resulted in low probability of the trees being attacked. Instead, seven trees, each having different moisture contents, were located within a small area, and ten pairs of adults were caged on the base of each tree. The trees were examined after a month and a half. In trees having a low moisture content, egg galleries up to seventeen inches were constructed and the eggs hatched; whereas, trees having a high moisture content also had strong pitch flow and contained short galleries less than six inches long and no egg hatch. (Table XIV).

In the field, only one tree having a low moisture content (85 percent o.d.w.) was detected before being attacked. The attack was successful and there was only a small amount of pitch flow. Many trees were examined soon after attack by bark beetles, and all showing complete resistance, i.e. no brood development, also retained a high moisture content (Fig. 19). Moisture content in successfully attacked trees dropped so fast it was not possible to estimate their original moisture content unless measurements were made within several days of the initial attack.

Trees in which beetles were unable to establish broods were those with abundant pitch (resin) flow. Heavy pitch flow was evidenced by the presence of large pitch tubes. Available evidence, while not complete, indicates that resin flow is reduced in trees having a low moisture content.

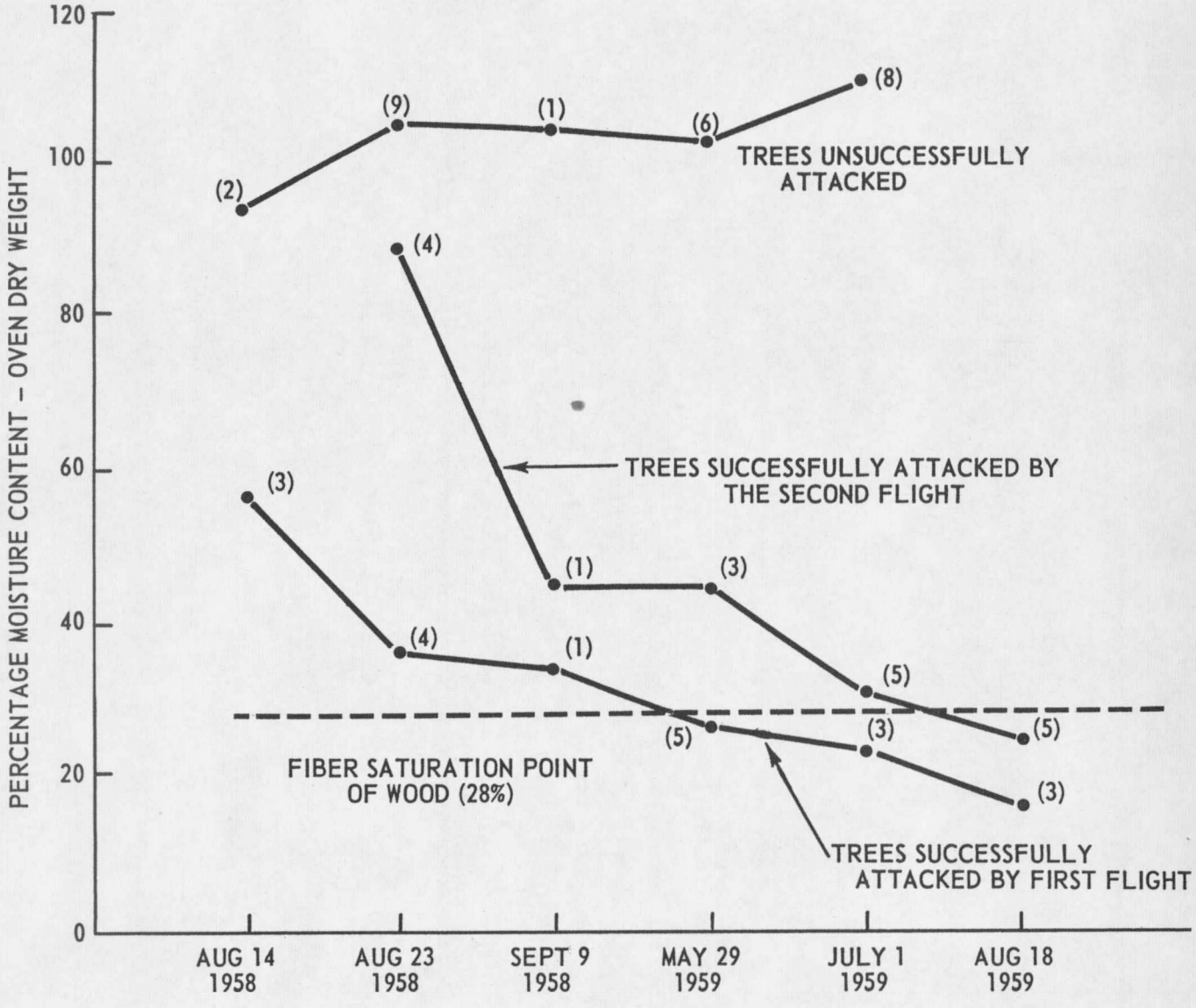

Fig. 19. Moisture content in outer $\frac{1}{4}$" of sapwood of infested trees, 1958, 1959. (Number of trees sampled in brackets.)

The rate at which infested trees dry is important to the survival of the broods. The moisture content of the inner bark and outer sapwood of infested trees was measured at intervals following the attack. The percentage moisture saturation was difficult to determine accurately when the sapwood became heavily impregnated with the blue stain, a condition which always occurred in successfully attacked trees. The percentage moisture content on the oven dry weight basis gave a more accurate measurement than percentage saturation.

The moisture content in three groups of infested trees was studied: Trees successfully attacked, i.e. galleries were established and broods developed, during the first flight (in July); trees successfully attacked during the second flight (in August); and trees unsuccessfully attacked, i.e. short galleries were constructed but broods did not develop, during both flights. At times, it was necessary to change the categories in which trees were placed, i.e. successful or unsuccessful, as it was not possible in all instances to detect this factor externally.

Trees which did not succumb to the bark beetle attacks retained a high moisture content. Some of these trees had up to fifty attacks on the bottom five feet of the stem but the broods were not able to become established.

Trees in which the broods were able to develop successfully lost moisture rapidly. Mortality in all stages from larvae to young adults, resulted when the tree moisture dropped to low levels. Larvae which had died from this cause were shriveled and brown in color, a condition noted also by Blackman (1931). Thus, there is a race between development of the broods and drying out of the tree, and not infrequently entire broods die when moisture drops below a minimum level.

The moisture conditions in the three categories of trees throughout the season are illustrated in Figure 19. Following the initial attacks, about two weeks elapsed before moisture measurements were started on "first flight" trees in the successful and unsuccessful categories depicted in Figure 19; but moisture measurements on the "second flight" trees were commenced within four days after the attacks. Trees in the first flight, successful category, had lost considerable moisture before measurements were started.

Trees successfully attacked during the first flight dried more rapidly than trees successfully attacked during the second flight. The second flight occurred later in the season when daily temperatures were on the average lower and drying conditions were less severe. These trees were still moist in the fall and brood survival (Fig. 21) was relatively high. Trees successfully attacked during the first flight, however, were dry by the fall and brood survival (Fig. 21) was very low. Few beetles emerged from these trees the next year (Table XVII). Therefore, the insects which compose the next year's first or main flight were contained within the moist "second flight" trees (Table XVII). However, by the time the first flight occurred in the following season, the "second flight trees" had dried to the point where it became necessary for the young adults to leave or succumb to the lack of moisture.

The protection afforded to broods by thick bark was observed in 1958. A large, thick barked thirty inch diameter tree, and numerous adjacent small six to ten inch diameter thin barked trees were infested in July, 1957. The low survival of the broods in the sixty-three smaller trees in July 1958 was due partly to hastened drying resulting from woodpecker removal of much of the bark from the upper portions of the stems, and partly to the high numbers of broods and the

long period of occupancy (July 1957 to July 1958). Few progeny managed to develop to young mature adults as determined by examination in the field and by emergence from the butt logs of caged infested trees. Emergence of adults was less than one per square foot of bark.

In the large tree, brood survival was high into July 1958. Woodpeckers had removed none of the bark from the heavily branched and shaded main stem. The inner bark region had been thoroughly macerated by the bark beetle broods. While no moisture measurements were taken, the appearance of the outer sapwood indicated a high moisture content. Prior to bark beetle emergence, that tree was felled and the lower eleven feet were removed and placed in a rearing cage. The more than 13,000 adults which emerged averaged 125 adults per square foot of bark. This was a great contrast to that one per square foot of bark which emerged from the smaller surrounding trees. Therefore, most of the adults which emerged in that area originated to a large extent within a single tree.

The amount of resin flow from the host tree has been recognized by many workers as an important factor in the success or failure of attacks by the mountain pine beetle (Hopkins, 1909; Büsgen and Münch, 1931; Callaham, 1955). Resins are considered to be the end products of tree metabolism and, once formed, are not used again but are secreted by the epithelial cells into the resin ducts (Mirov, 1958). Resin ducts are of two main types, longitudinal (Pl. III, Fig. 5) and transverse (Pl. III, Figs. 3,4). Longitudinal resin ducts exude far greater amounts of resin when severed than do transverse resin ducts. As adult bark beetles engrave the outer sapwood they continually sever many longitudinal resin ducts which, in vigourous trees, exude large amounts of pitch, frequently enough to prevent the insect from completing the gallery. Young larvae normally do not engrave deeply enough into the sapwood to disrupt longitudinal resin canals, only deeply enough to

Table XIV. Success of infestation, moisture content, and pitch flow. Fifteen females and 15 males caged at the base of each tree. Eggs laid in all galleries.

Tree No.	No. Strikes	Av. Length Gallery	Eggs Hatched	Moisture Content Sapwood % o.d.w.	
1	9	13.7	*	107	No pitch tubes
2	4	10.1	*	114	No pitch tubes
3	8	5.3		125	Medium pitch tubes
4	5	5.3		129	Pitch tubes
5	10	1.9		143	Pitch tubes
6	12	2.7		171	Pitch tubes

* Egg hatch

sever the transverse resin canals. If the tree was still capable of producing resin up to the time egg hatch occurred, large amounts of pitch were not generally produced by the larval feeding but sufficient was produced to cause extensive resinosus of the inner bark which in turn prevented further larval development. Furthermore, it was observed that when eggs in the niches became coated with resin a reduced number hatched.

It is important to the success of the beetle that tree resistance (resin flow) be reduced quickly following initiation of the gallery. Observations in the field suggested that blue staining fungi were in many cases important in reducing vigour to the extent that the insects could become established.

Van Schrenk (1903), and later Craighead (1928), suggested a symbiotic relationship between blue stain organisms and bark beetles. The latter suggested that the blue staining organisms introduced into the tree by the beetle might disrupt the normal water movement in the sapwood and hasten the death of the tree. Nelson and Read (1929) stated that the southern pine beetle was unable to kill trees by itself but the combination of the beetle and the blue stain organism complex caused tree mortality. They reported that moist trees were found to inhibit blue stain. Caird (1935) stated that within four days following attack by the southern pine beetle, the outer tree ring lost its ability to conduct water due to the blue stain. Within twenty-five to thirty days the moisture content of the tree had dropped about thirty percent (o.d.w.). Bramble and Holst (1940) found that within twenty-four hours following bark beetle attack some fungi had penetrated the sapwood to a depth of one millimeter. Within seven days, the sapwood was thirty percent infected and the blue staining organisms interfered with water conduction. Hetrick (1949), however, has reported that blue stain is not always apparent in trees successfully attacked by the southern pine beetle.

In the experimental area, examination of trees which were successfully attacked by bark beetles always revealed conspicuous blue stain in the sapwood (Pl. VI, Fig. 2). Conversely, no unsuccessfully attacked trees contained blue stain in any appreciable amount. Mycelia could be detected microscopically in the sapwood of bark beetle infested trees prior to the appearance of the characteristic blue color. Small pieces of sapwood with recent galleries of the mountain pine beetle on the surface were stored under aseptic conditions at room temperature. Within ten to fifteen days, all of these samples showed the typical blue color caused by the blue stain fungi. Control samples without galleries showed no color change. This suggested that the bark beetles introduced, or provided an entrance for, the blue stain and that the fungus developed for a considerable period before the blue color appeared.

In the laboratory, inoculations of a blue staining organism (Leptographium lundbiergii) were made on blocks of sapwood taken from the same tree. Seven moisture levels from thirty to 150 percent (o.d.w.), with a difference of twenty percent between levels, were represented. Five wood blocks were used at each level and the temperature was maintained at 65°F. Blue stain developed in blocks at all levels except the drier with only thirty percent moisture.

The results above indicate that this blue staining organism has a wide tolerance for moisture and that, in all likelihood, the high moisture content in trees was not itself likely responsible for resistance to infection. In vigourous trees, which in all observed instances had high moisture content, blue stain did not become actively established. Obviously something besides moisture was involved in the resistance. The fact that the blue staining organisms did not establish in wood samples having a moisture content of thirty percent may explain in part why the drier heartwood (Fig.15) in infested trees remains free from infection (Pl. VI, Figs. 1,2).

A relationship between tree diameter and bark beetle attack has been noted by many workers (Blackman, 1931; Keen, 1936; Hopping, 1948; Brown, 1956). During a mountain pine beetle outbreak approximately thirty miles from the present experimental area, Hopping (1948) reported that few trees below a diameter of seven inches were killed by the insect. Later, Brown (1956), studying an outbreak within the same general region, reported a somewhat similar diameter to attack relationship.

Measurement of the diameters of all trees attacked prior to 1958 within a large plot in the present experimental area showed that trees which had succumbed to the bark beetle attack had a larger average diameter (9.9 inches) than the trees which remained (7.6 inches). The difference in diameter was significant to the five percent level (Table XV). The diameters of trees attacked in 1958 were also measured (Table XVI) and it was found that the average diameter of the successfully attacked trees (9.0 inches) was larger than the diameter of the unsuccessfully attacked trees (8.1 inches). This difference was significant to a level just under five percent. From these data it appears tree diameter and success of the bark beetle attack are related but the reason was not established.

Overall brood mortality and survival: These studies were carried out to obtain a better appreciation of the mortality and survival in the wild population. From experience in the experimental area, the results are considered representative of the population as a whole.

Under natural conditions, specific mortality factors were frequently masked (Pl. II, Fig. 1), and with the data at hand it was not possible to quantitatively assess the effect of each factor. For this reason only total mortality was recorded.

Table XV. Diameter of trees successfully attacked prior to 1958 and diameter of remaining trees (within plot).

Diameter Class in.	Number Dead Trees	Number Living Trees
5	17	59
6	9	61
7	20	76
8	24	89
9	38	84
10	27	42
11	30	13
12	11	6
13	3	0
14	2	0
Average diameter	9.9 inches	7.6 inches
Total Trees	181	420

Table XVI. Diameter of trees attacked in 1958.

Diameter Class (in.)	*Group I Successfully Attacked	Group II Unsuccessfully Attacked	Group III Attacked with Partial Success
4	0	1	0
5	0	1	0
6	1	4	1
7	6	5	1
8	10	12	9
9	10	9	4
10	8	5	2
11	5	1	1
12	2	1	1
Average Diam.	9.0	8.1	8.6
Total trees	42	39	19

* First flight 37 trees
Second flight 5 trees
42

Logs in 1955 and 1956 and trees in 1957, 1958, and 1959 infested by the wild population, were examined at approximately two week intervals following the first and second attacks. The logs were five feet in length, nine to eleven inches in diameter, with thick bark, and located under partial shade (Pl. VI, Fig. 4).

When trees were used, they were felled and the lower five feet of the stem was debarked. In selecting trees for examination, the success of the brood and their chances for development to maturity were considered. This was necessary for several reasons. (1) On occasion, broods established in small trees (around six or seven inches in diameter) failed to develop past the early instar stages because the tree dried too rapidly. (2) In other instances long egg galleries were sometimes constructed within "pitchy" trees and the eggs failed to hatch. (3) Resinosus in the inner bark region occurred in some trees and the broods, while advancing to the larval stage, were unable to complete their development, due to the resin. Infested trees exhibiting these characteristics were not used in the study.

Seasonal mortality on an inch of gallery basis was better for comparison than average gallery length per tree (Table XVII). In all years except 1955, comparisons were made on that basis.

Results indicated that mortality each year was heavy and continuous within the broods from the time they were first established until mature adults appeared (Appendices XII to XV). In years with two flights brood survival was greater in trees infested during the second flight than during the first flight. The data for 1955 and 1958-59 are illustrated in Figures 20 and 21. These results agree with McMullen and Walters' (1956) report that survival was higher in second flight broods than in first flight broods of the Douglas fir beetle.

Table XVII. Trees infested 1958 and the 5-foot butt logs from each placed in separate cages in July 1959. Emergence recorded.

	Tree Number	Tree Diam. (in.)	Total Bark Surface 5' Butt Log in Sq. Feet	Total Number Galleries Butt Log	Average Length Galleries (in.)	Total Emergence from Butt Log	Average Emergence per Sq. Ft. Bark	Average Emergence per inch of Gallery
I Flight-unsuccessful	1376	8.5	11.1	115	6.3	0	0	0
	1225	9.0	11.7	89	8.8	0	0	0
	1230	9.5	12.4	155	7.3	(2)	0	0
	1257	11.0	14.3	205	10.8	(2)	0	0
II Flight-successful	1263	12.0	15.6	282	7.8	0	0	0
	1265	9.0	11.7	190	9.1	44	3.76	0.025
	1266	9.5	12.4	124	12.0	9	0.95	0.006
	1269	9.5	12.4	151	11.2	20	2.11	0.012
	1357	10.0	13.0	152	11.2	4	0.31	0.003
I Flight-successful	1352	11.0	14.3	232	10.3	105	7.34	0.044
	1252	8.0	10.4	85	10.1	85	8.09	0.099
	1451	8.0	10.4	43	9.8	80	7.69	0.189
	1373	8.5	11.1	117	8.3	114	10.27	0.117
II Flight-successful	1363	9.5	12.4	85	15.3	115	9.27	0.088
	1377	10.5	13.7	240	8.2	427	31.16	0.218

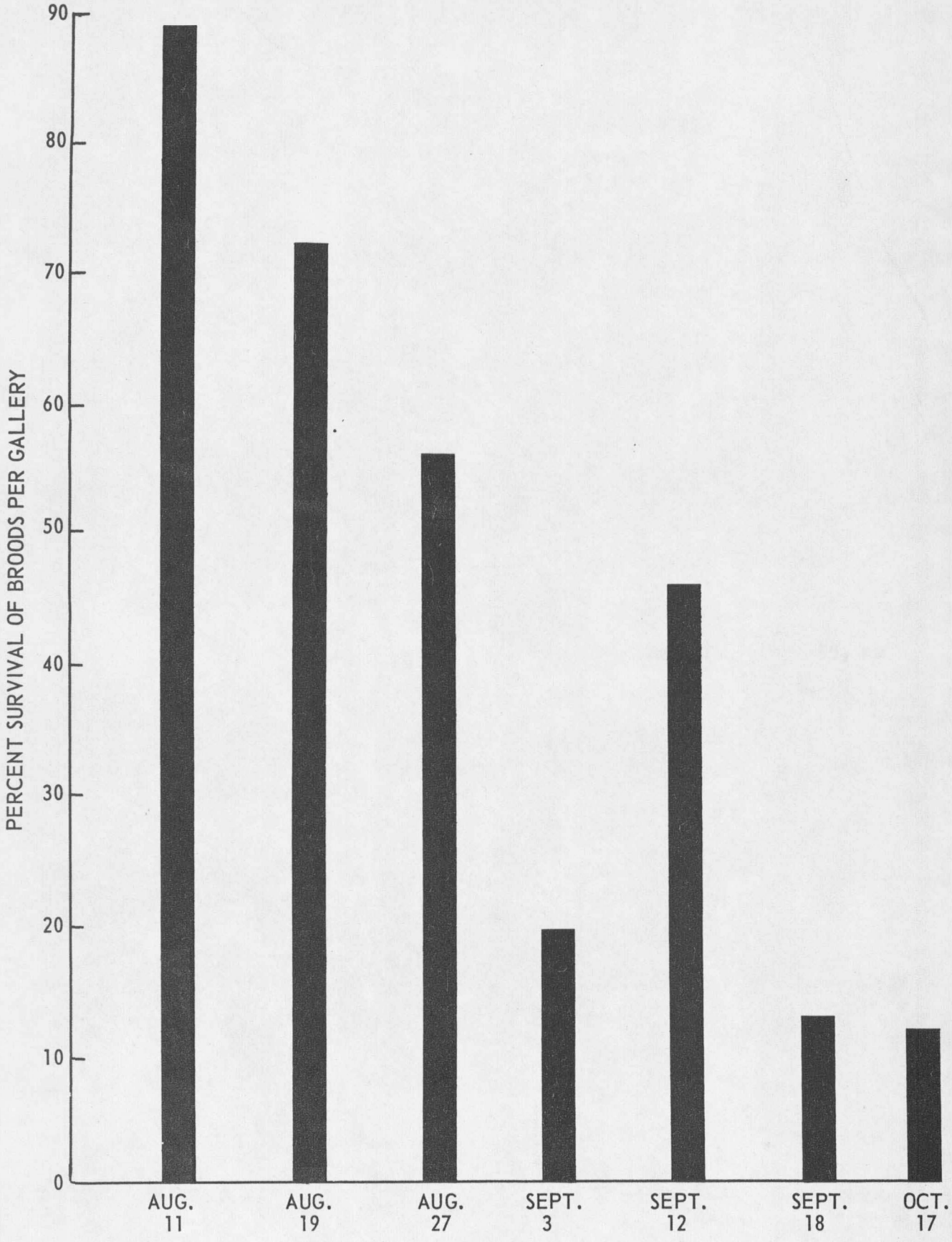

Fig. 20. Survival in broods, established by the first flight, 1955, as determined on different dates.

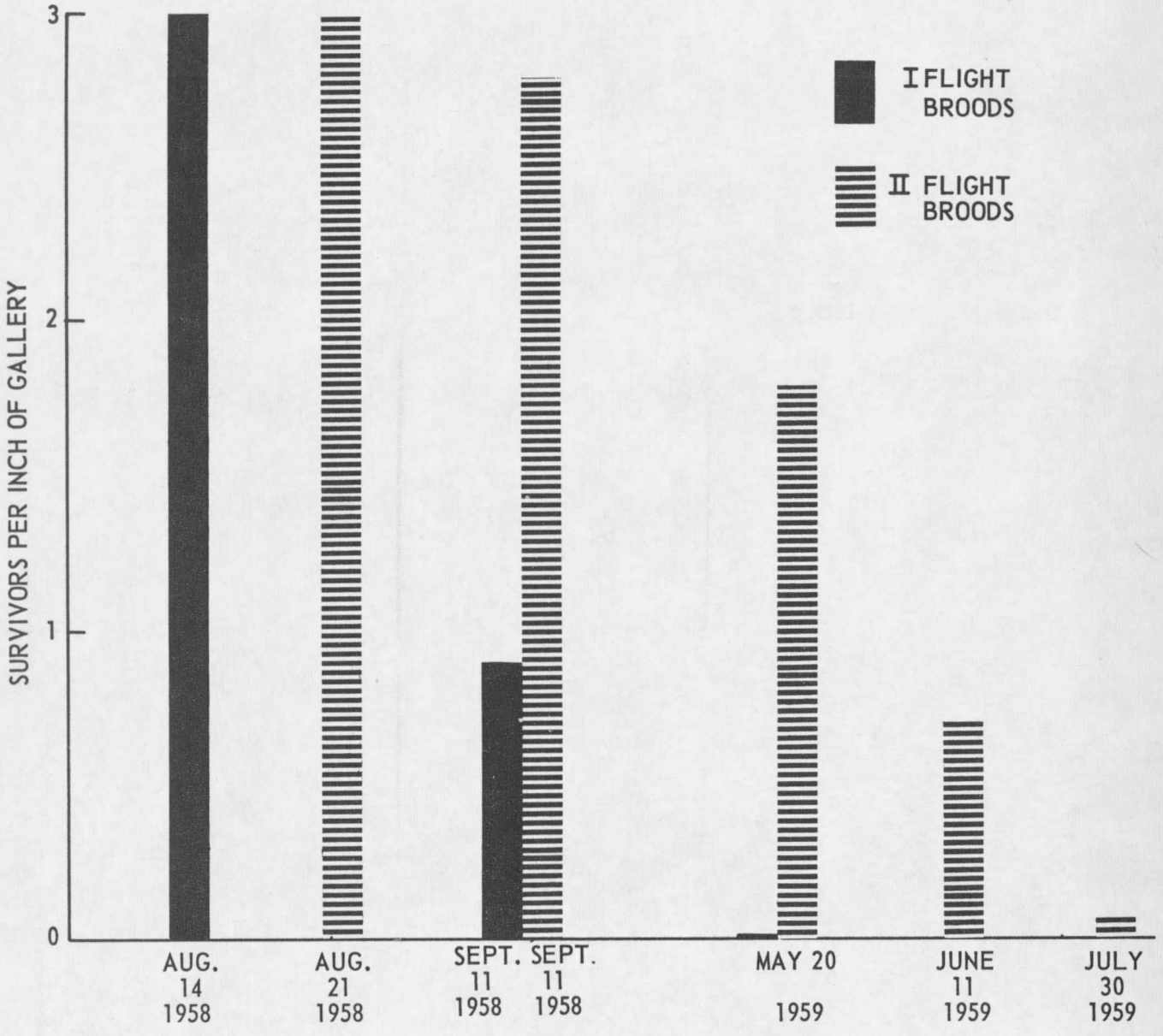

Fig. 21. Survival in broods, established by the first and second flights as determined on different dates.

To test the relationship between actual emergence data with the survival and mortality information obtained by debarking logs, a study on emergence was carried out in 1959 prior to the main flight. Fifteen trees infested in 1958 and all within the same plot were felled and the butt log from each was placed in a separate cage. Three categories, each with five infested trees, were represented as follows: (1) trees attacked successfully (i.e. broods develop) during the first flight, (2) trees attacked successfully during the second flight, and (3) trees which had been attacked with partial success during the first flight (i.e. broods developed only on one or two sides of the tree, or were unable to develop due to resinosus in the inner bark), but successfully attacked during the second flight. Trees in the latter category commenced to lose moisture after the first attack but less rapidly than trees in which the attacks were immediately successful. By the time of the second flight these trees were in a weakened and relatively dry condition but still retained sufficient moisture to be attractive to the second flight bark beetles.

The results from this study (Table XVII) supported those obtained from the debarking studies. No adults emerged from the trees which contained broods established during the first flight (July 1958). Few adults emerged from trees attacked with partial success during the first flight but successfully during the second flight. Most of the emergents came from the trees attacked successfully by the second flight in August, 1958, and even in several of those trees, fewer female beetles emerged as progeny than initially entered as parents. The trees attacked during the second flight maintained a more satisfactory moisture level (Fig. 19) during the period when the broods were developing. Therefore, in the study plot, the insects comprising the 1959 flight originated to a large degree within the second flight trees. The trees successfully attacked during the first flight, while more numerous (Table XVI) contributed few, if any, bark beetles.

DISCUSSION AND CONCLUSIONS

The number of flights by the mountain pine beetle, and the time when they occurred, varied in different years. The underlying causes for this are related to weather, which influences indirectly through the host the behaviour of the adult insects and also the rate of brood development.

Regional conditions (climate and size of host) shape the life cycle of the mountain pine beetle in the experimental area. This life cycle, while varying to a degree in different years, is still considerably different from the life cycles reported to occur in the more southerly portions of its range (Evenden et al., 1943). In the experimental area, no spring flight (May-June) was recorded whereas a flight during that period commonly occurs in the other regions. Within the experimental area, when a first and second flight occurs, there is a possibility a spring flight might also occur in the next year. The latter would be composed of surviving progeny from the first flight established during the preceding year. However, such a spring flight of mountain pine beetle was never observed in the area. The reason for this is the almost complete mortality of first flight broods in years when two flights occur. In contrast, when the first flight broods were caged and protected from excessive drying conditions and from predators and parasites, large numbers of progeny survived and emerged in the spring as young adults. Under natural conditions this would have constituted a spring flight. In the experimental area, lodgepole pine is of small diameter, generally less than ten inches, and the bark is thin. These trees dry rapidly following a successful attack. First flight and brood mortality is heavy. Second flight broods, however, established later in the season, are not subjected to as severe drying conditions and hence survival is always much greater. Survivors from the latter broods constitute the main or first flight in midsummer (July) of the following year.

The importance of the second flight varies in different regions, and depends upon the size and number of the susceptible trees and upon the weather. In regions where large trees are available and several generations of insects develop per year, survival from the broods established by the second flight augment the existing population but are not essential to its continuance. Within the experimental area, the trees are small (few are over twelve inches) and when these trees are struck early during a warm dry summer, few progeny survive. However, when a warm dry summer occurs, a second flight also occurs, three to four weeks after the first. While the number of trees successfully attacked by the second flight is always considerably less than in the first, broods in second flight trees exhibit a relatively high survival. This ensures the presence of a reproductive population the succeeding year.

During cold wet years, and providing a satisfactory flight occurs, brood survival is high up to the overwintering period. If the following spring (April, May, June) is warm and dry, heavy brood mortality results due to the increased rate of tree dessication and few progeny emerge as adults. The reproductive population for that year originates in large wolf trees, which have been able to maintain satisfactory moisture levels for brood development. The number of insects in that years flight depends therefore upon availability of the large trees, which in the experimental area are scarce.

A diapause condition reported to occur in the adult Douglas fir beetle (Vité and Rudinsky, 1957) has not been observed in the mountain pine beetle in the experimental area. Providing temperature and moisture conditions were adequate, many successive generations of bark-beetles were reared in cages with no complications due to diapause.

There is no indication that trees successfully infested in one year are ever reinfested the next year. Reinfestation is reported to occur frequently in large diameter sugar pine (twenty-two to eighty-four inches) which may take three or four years before they lose their attractiveness to the bark beetles (Struble, 1934). In the experimental area, within two or three weeks following successful infestation, the trees dry out to the extent where they no longer satisfy attacking beetles.

Trees obtain their resistance to bark beetles largely by an ability to produce resin in copious and continuous amounts, following the attack. The resin production is considered here to be a reflection of general "thriftiness" or vigour on the part of the tree. Keen (1958), in a review of the entire bark beetle problem, emphasized the importance of reduced tree vigour to the building up of large populations while Hall (1958) demonstrated statistically a close relationship between years of high temperatures, low precipitation, low soil moisture, and increased tree mortality from bark beetle attacks. Trees in the experimental area showed wide differences in their degree of resistance to bark beetle attack. In some cases, it is believed that the introduction of blue staining organisms into the sapwood reduced resin flow and allowed the insects to establish egg galleries and broods to develop.

Within successfully infested trees, immature broods are immobile in the sense that they are unable to move from the environment and when mortality factors are contained therein the broods die. Brood mortality factors include parasites and predators, crowding, lethal temperatures, resinosus within the inner bark, and drying-out of the inner bark and outer sapwood. Drying out is accelerated by the establishment of the blue stain fungi in the outer sapwood.

The general deterioration of conditions in the tree following a successful bark beetle attack is considered to be the most important single cause of brood mortality. This deterioration is brought about by moisture loss from the inner bark and outer sapwood and by high brood density, and results in conditions unfavorable to the developing broods. Infested trees vary in their rates of deterioration.

Only a small number of trees contributes insects to the succeeding years population. Those are trees in which brood survival has been high. Brood survival in the majority of trees is extremely low.

Brown (1956), referring to a specific outbreak, indicated that trees with a diameter less than twelve inches were not able to sustain mountain pine beetle populations in high numbers and, once the larger trees had been killed, the insect population declined. Results from studies in the experimental area are in agreement, although the critical diameter is considered to be near ten inches. A few large decadent trees scattered through the stand would be generally favourable to the insect population.

In regard to mountain pine beetle populations in the experimental area, it is believed there are two prerequisites to an increase in numbers: (1) abundance of host trees in a susceptible condition and a minimum diameter of ten inches, (2) several consecutive years of favourable weather with average July and August mean maximum temperatures near 80°F. or above. It is believed unlikely that populations will build up unless both are present.

Infested locations in the experimental area were confined mainly to small widely scattered patches. Demonstrably susceptible trees were not present in

high numbers over a wide area. The presence of infested areas in the lower end of the valley became less apparent after 1957. The insect was more in evidence at the upper end of the valley in 1958 and 1959. The population, throughout the whole experimental area, appeared to have collapsed by the fall of 1959 and cold wet August weather may have been the major factor. Little or no egg hatch occurred in the egg galleries established in 1959. Some hatch occurred in galleries established within trap logs at the lower end of the valley. Most of next year's population would have to come from the few parent adults which successfully overwintered. It is likely the population will be so reduced that several years of favourable weather will be required before it can build up to conspicuous numbers again. This, together with the scarcity of suitable trees, suggests that high populations will not occur for a number of years.

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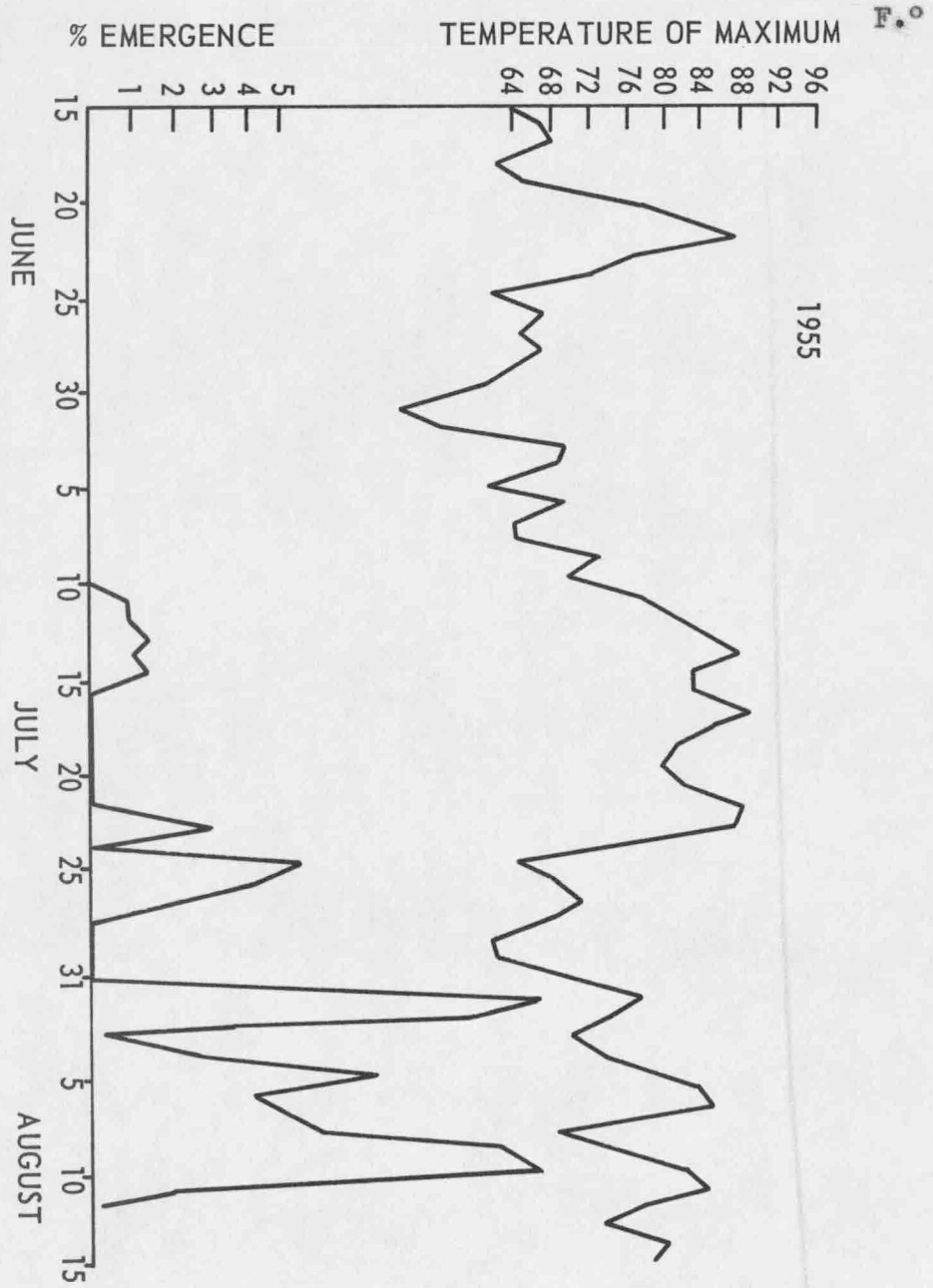
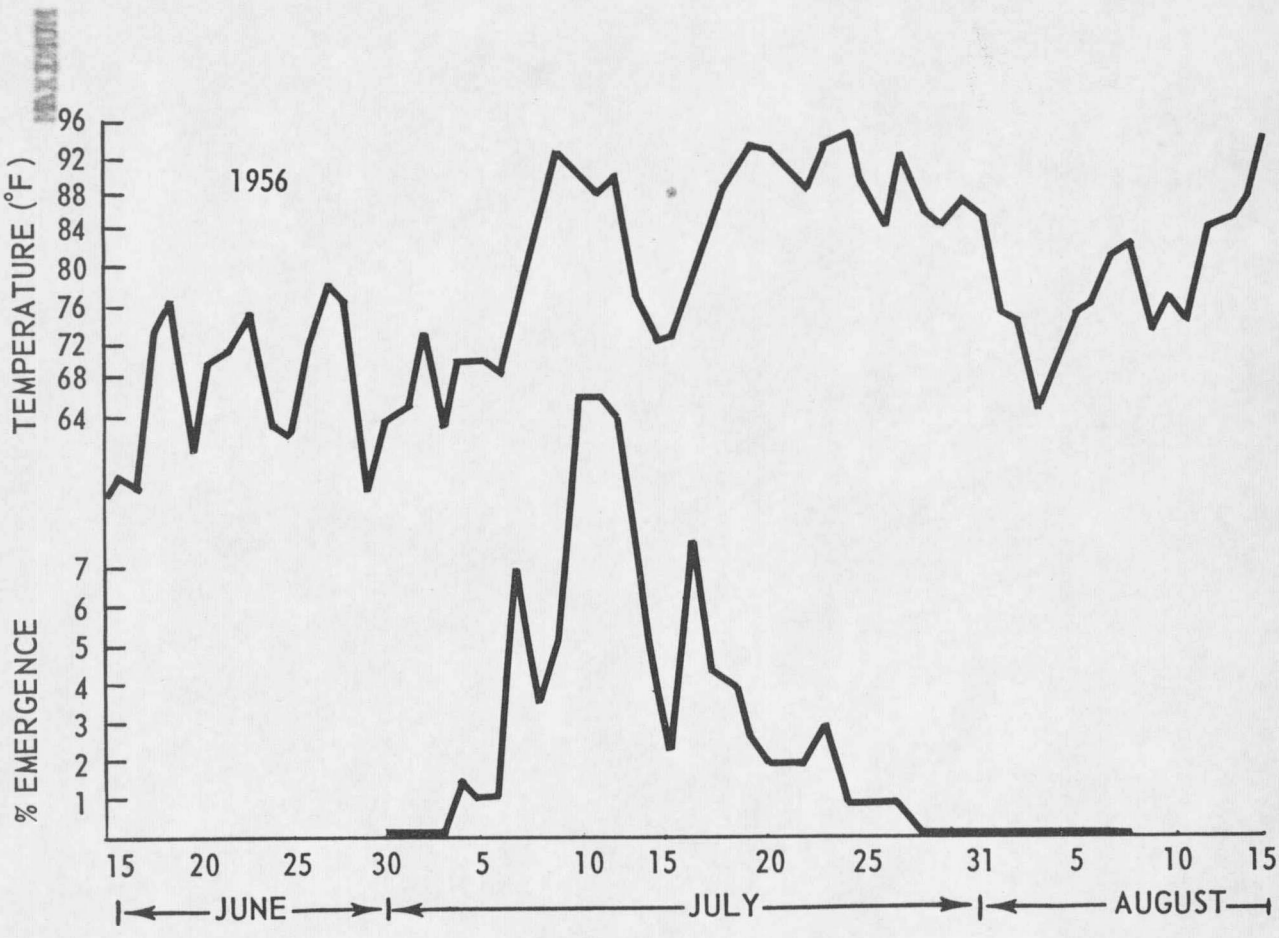
APPENDIX I



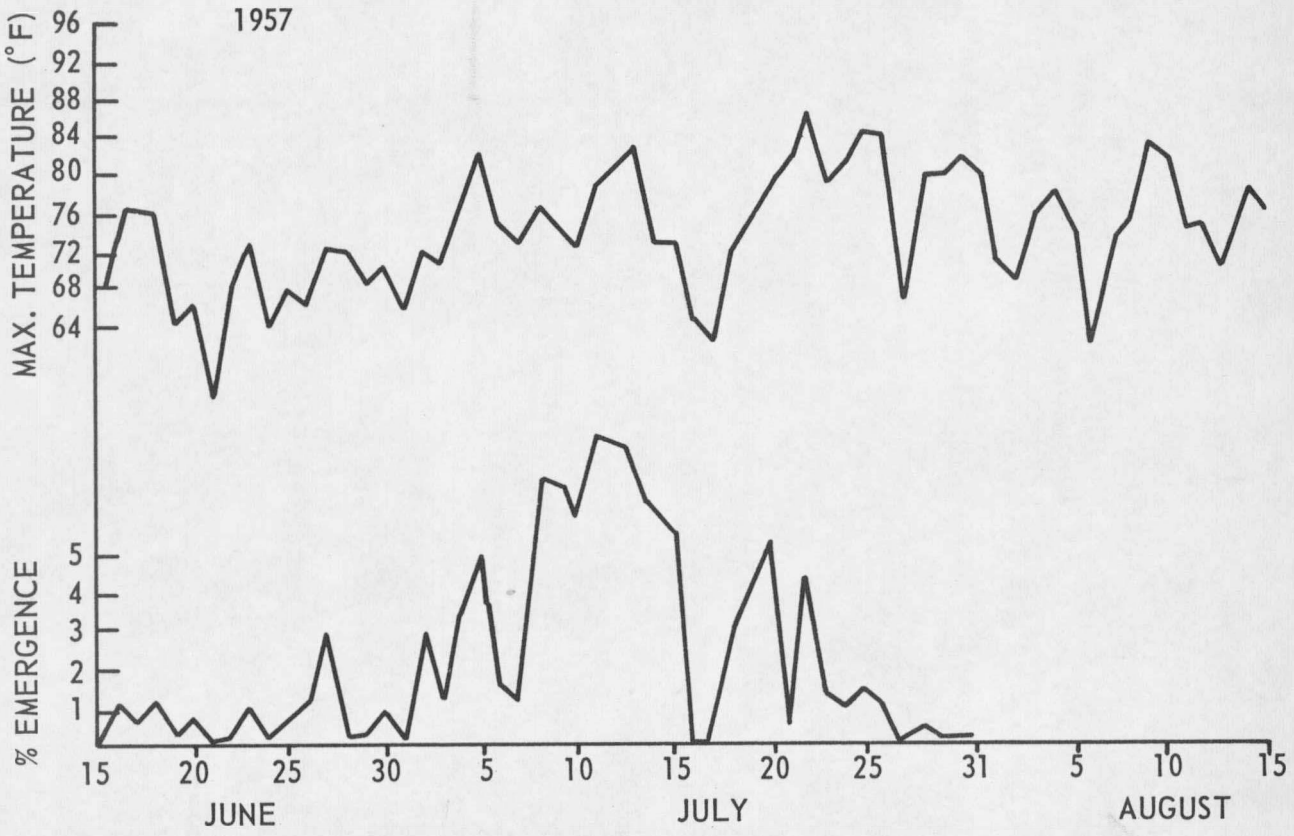
Mountain pine beetle emergence and maximum daily temperatures (F.°) - 1955.

APPENDIX II



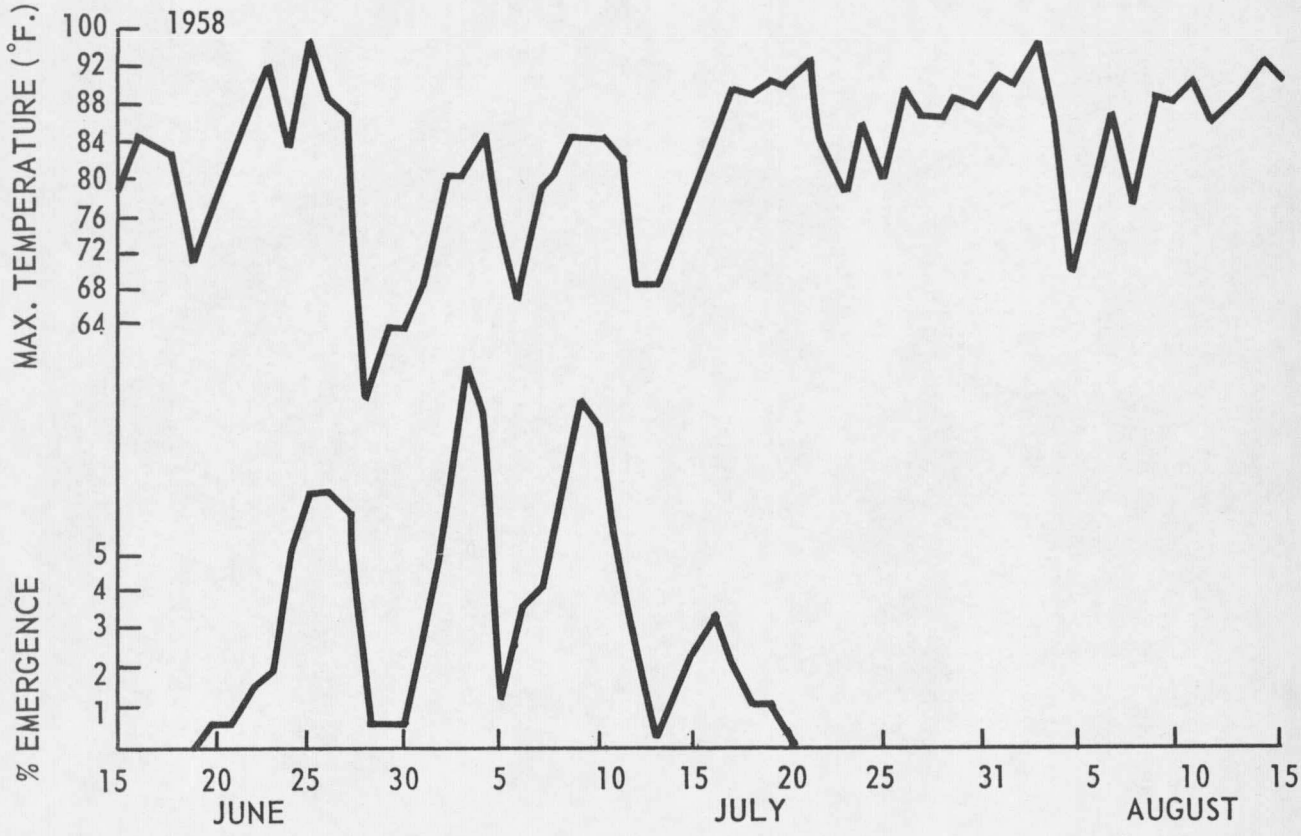
Mountain pine beetle emergence and maximum daily temperature (F.°) - 1956.

APPENDIX III



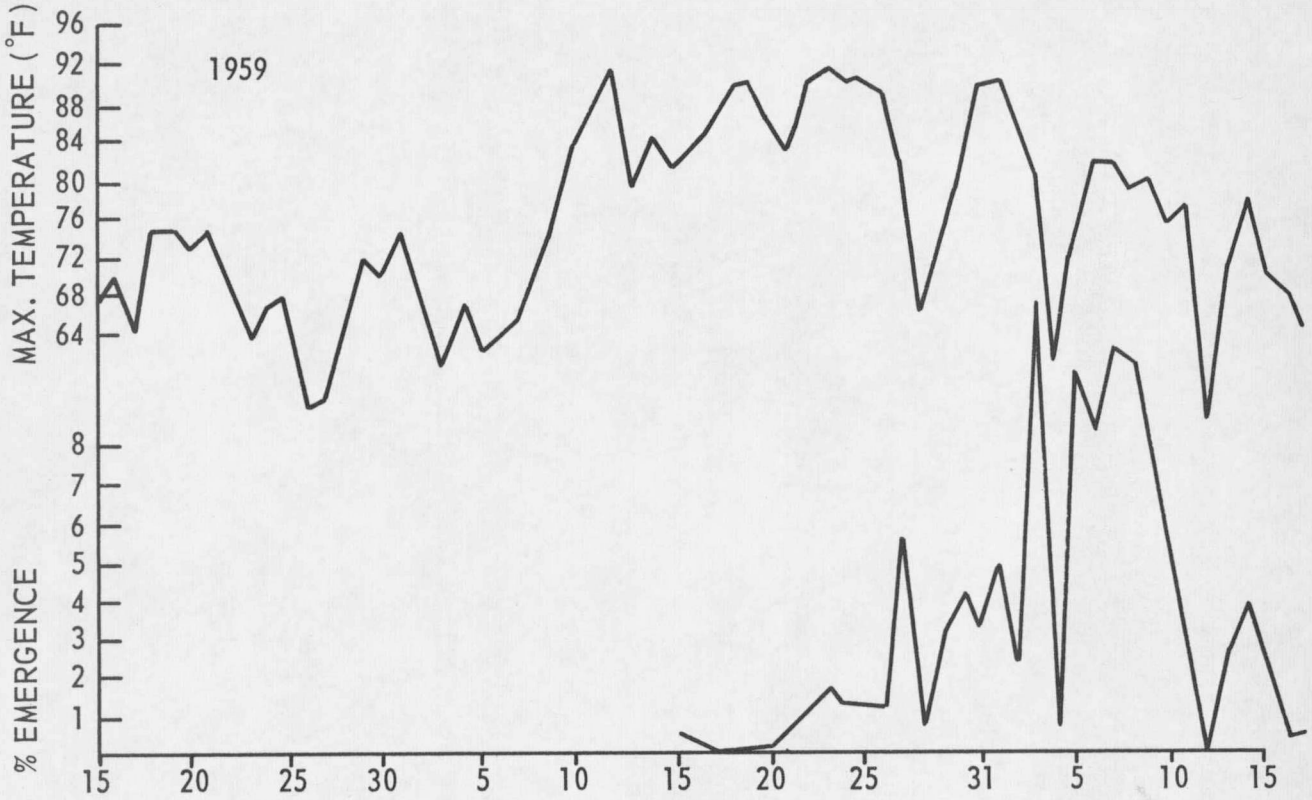
Mountain pine beetle emergence and maximum daily temperatures (F.°) - 1957.

APPENDIX IV



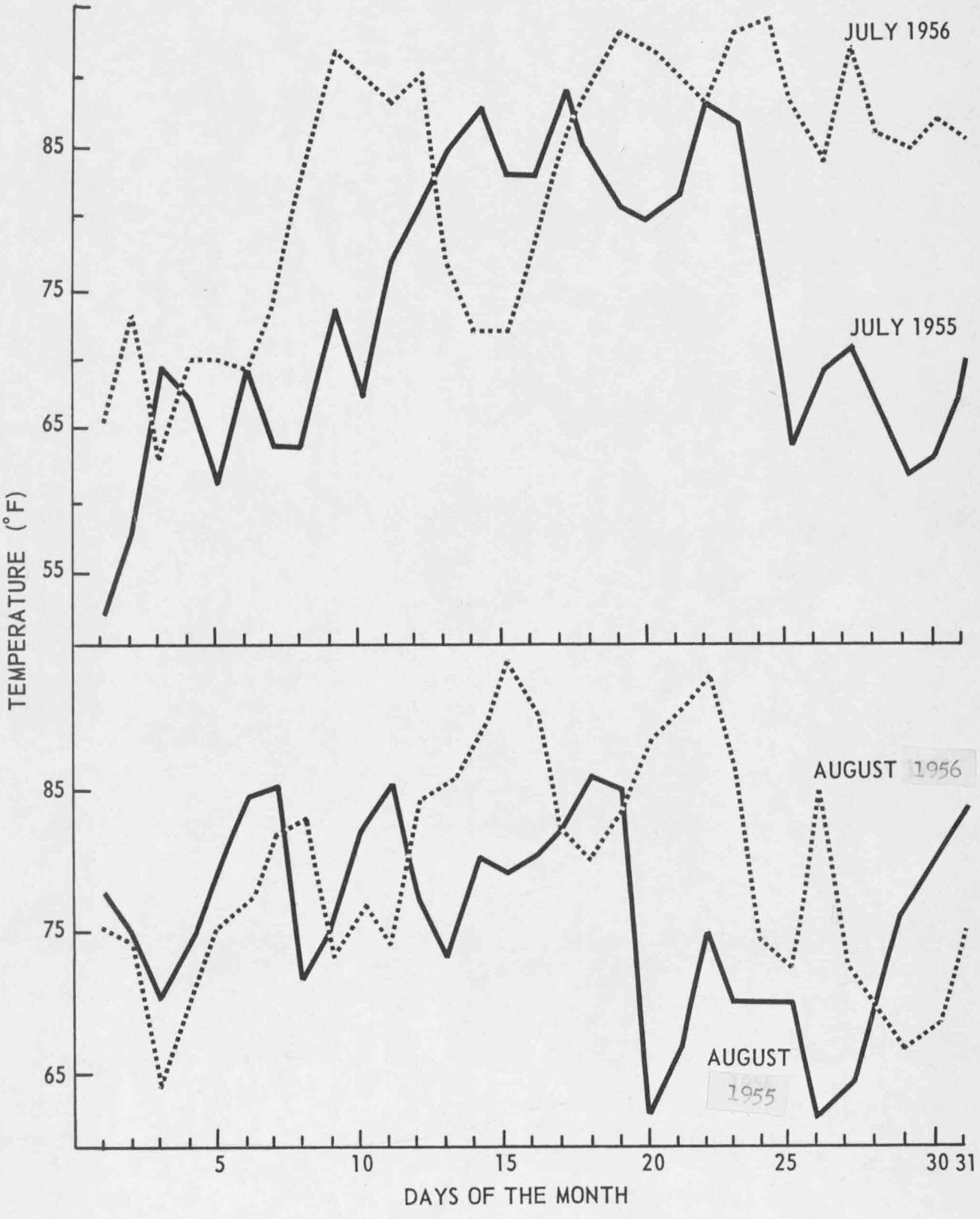
Mountain pine beetle emergence and maximum daily temperatures (F.°) - 1958.

APPENDIX V

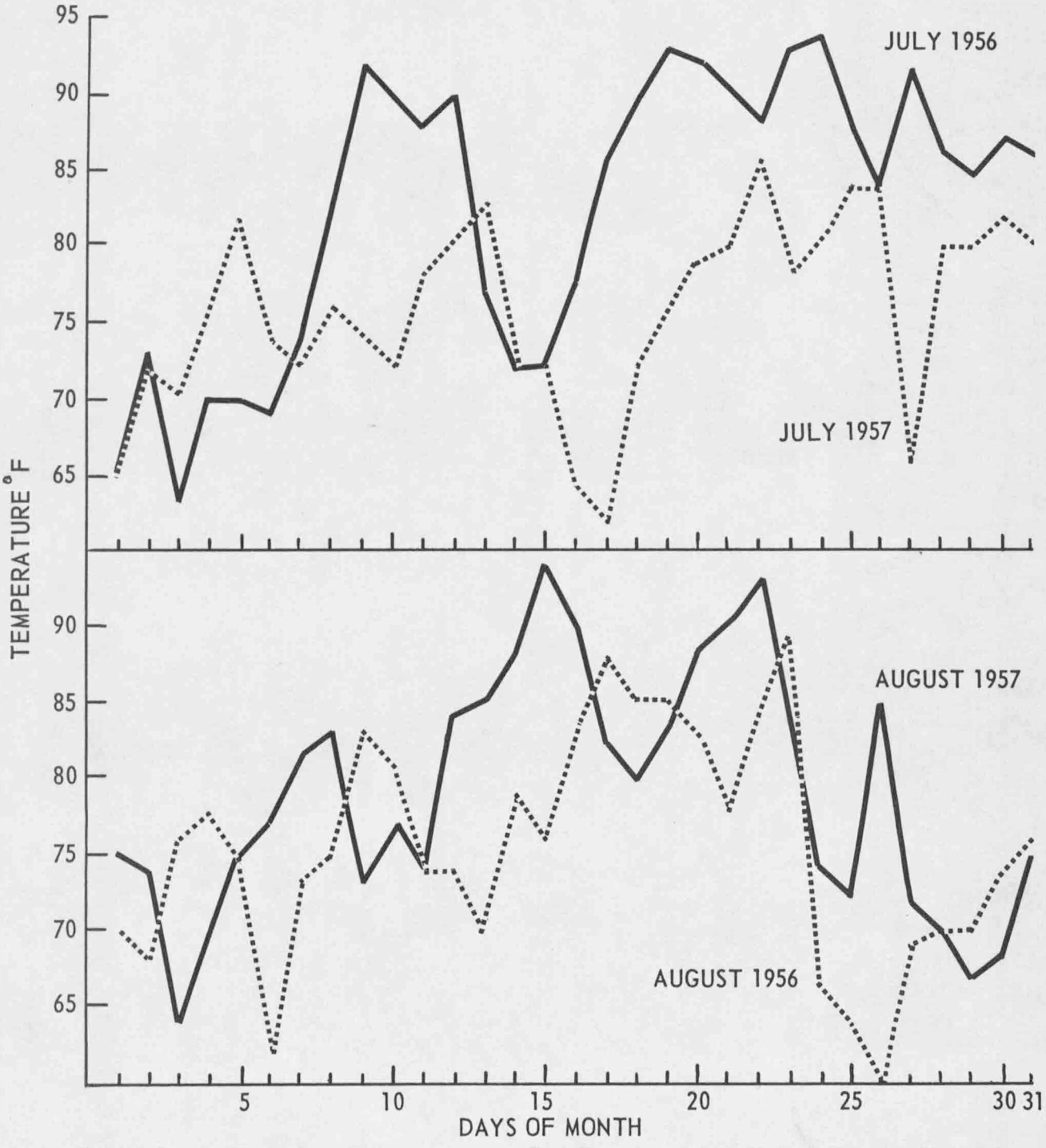


Mountain pine beetle emergence and maximum daily temperatures, (F.°). - 1959.

APPENDIX VI

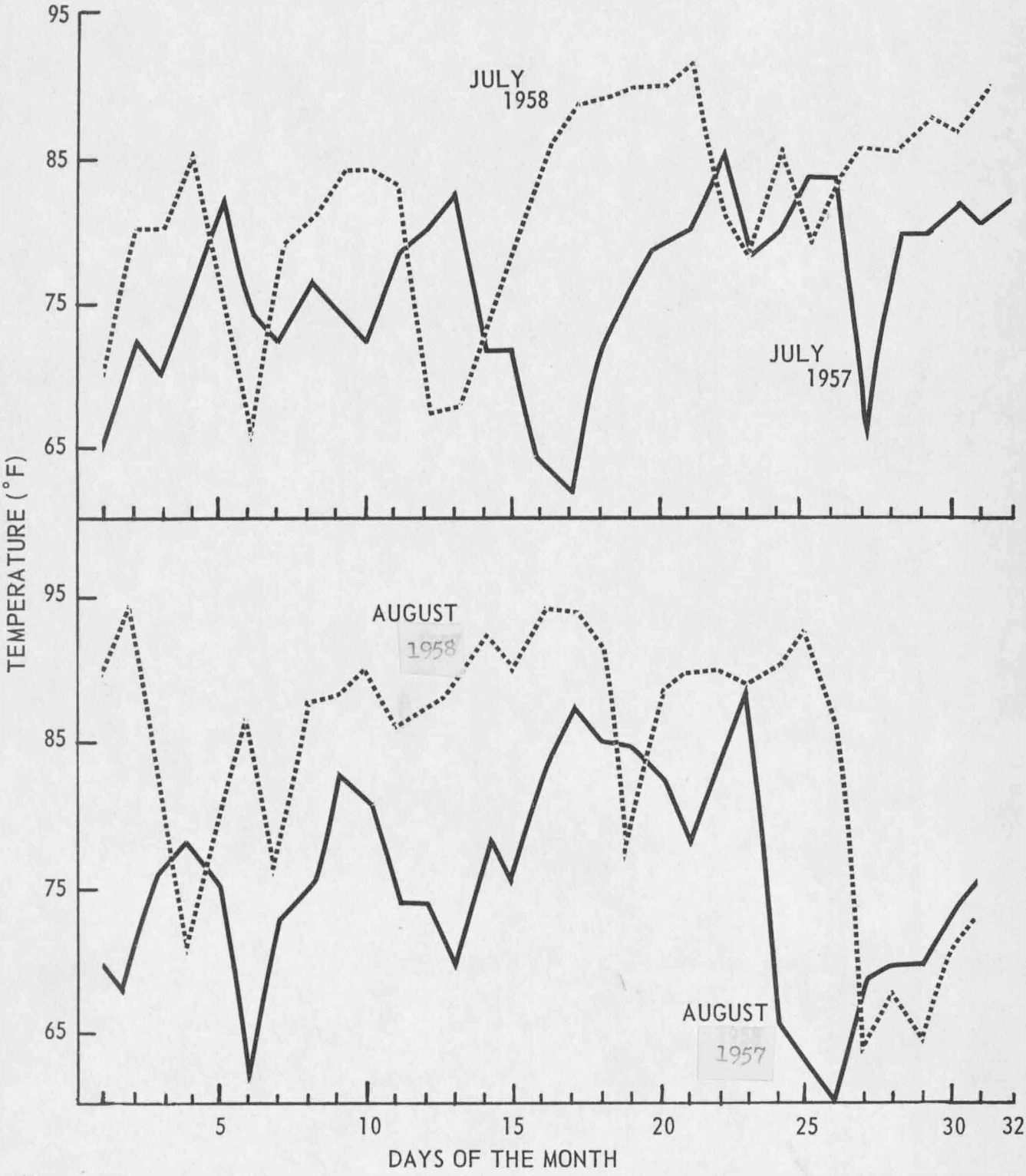


Comparison of maximum temperatures (F.°), July and August, 1955-56



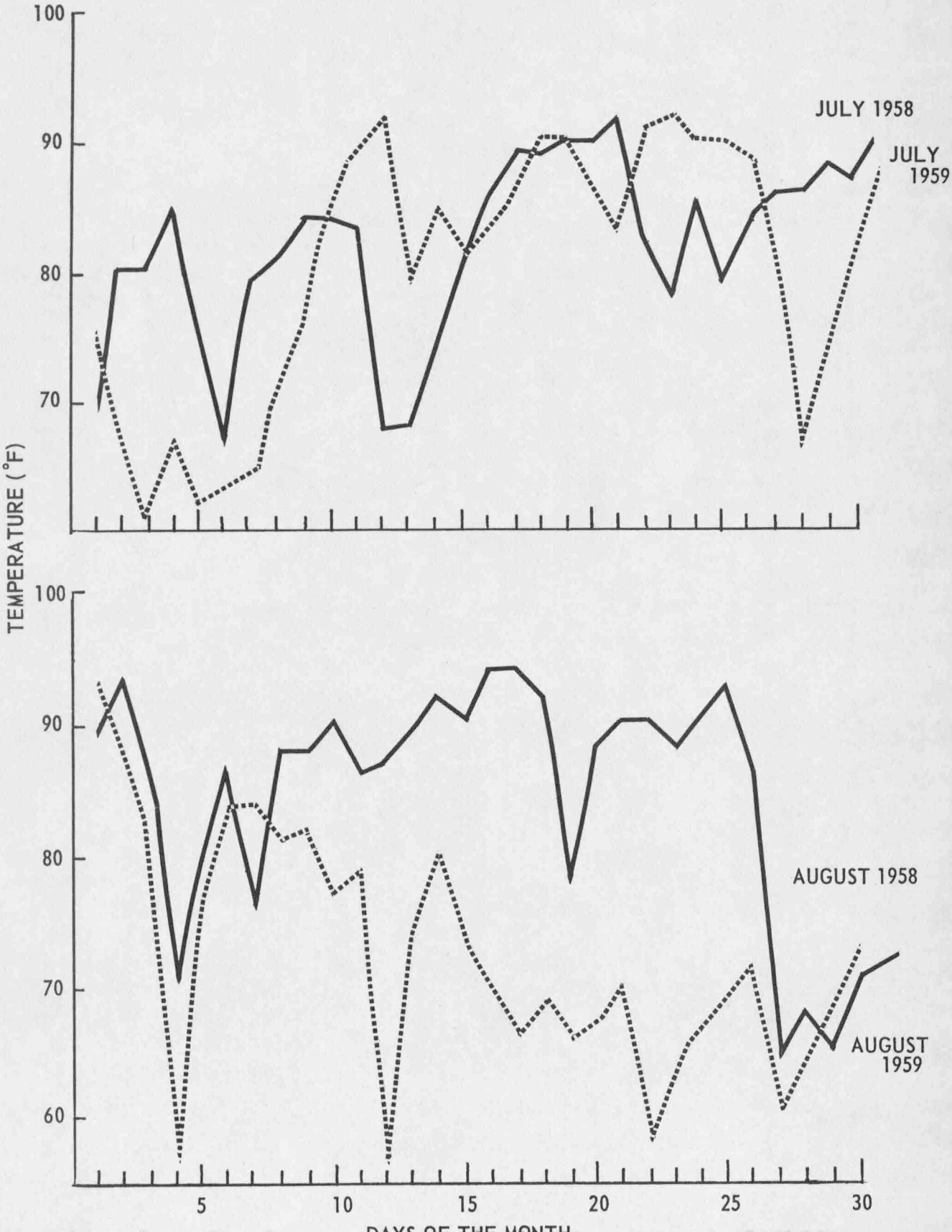
Comparison of maximum temperatures (F.°), July and August, 1956-57.

APPENDIX VIII



Comparison of maximum temperatures (F.°), July and August, 1957-1958.

APPENDIX IX



Comparison of maximum temperatures (°F), July and August, 1958-1959.

Appendix X

X. Brood development and degrees hours above 60°F.

Date galleries established	Stage of Development	Number of days from time gallery established to first appearance	Total degrees hours above 60° F.
July 26-27	I instar larvae	15	1064
	II instar larvae	17	1428
	III instar larvae	23	2117
	IV instar larvae	36	2960
	pupae	44	4144
	tenerals	54	4501
August 2	I instar larvae	8	838
	II instar larvae	15	1720
	III instar larvae	22	2420
	pupae	43	4240
	tenerals	50	4291
August 14	I instar larvae	18	1620
	II instar larvae	23	2367
	IV instar larvae	45	2983
August 29	I instar larvae	22	1729

XI. Dissections of nematode infested female beetles.

Date of attack	Date of debarking	Length of gallery (in.)	Egg production	Degree of infestation	Condition of reproductive organs	Condition of digestive organs	Gallery
July 7	Sept. 15	11	48	Heavy	R*(no mature ova)		1st
Aug. 2	Sept. 2	22	51	Heavy	R (no mature ova)	R partially empty	1st
Aug. 10	Aug. 24	6	35	Light	N**(mature ova)	N - full	2nd
July 22	Oct. 12	22	41	Heavy	R (no mature ova)	N - empty	1st
Aug. 10	Sept. 2	31	79	Heavy	R (no mature ova)	N - full	2nd
Aug. 15	Oct. 8	14	67	Light	N (mature ova)	N - full	2nd
Aug. 24	Oct. 13	11	54	Heavy	R (no mature ova)	some reduction	2nd
Aug. 15	Oct. 13	8	34	Heavy	R (no mature ova)	N - empty	2nd
Aug. 31	Sept. 2	2	6	Light	N (mature ova)	N - full	2nd
Aug. 15	Sept. 1	9	88	Light	N (mature ova)	N - full	2nd
Aug. 15	Sept. 23	12	85	none	N (mature ova)	N - full	2nd
Aug. 30	Oct. 9	15	73	None	N (mature ova)	N - full	2nd
Aug. 24	Oct. 14	23	72	None	N (mature ova)	N - full	2nd
Aug. 2	Sept. 16	18	60	None	N (mature ova)	N - full	1st
Aug. 2	Sept. 16	28	111	None	N (mature ova)	N - full	1st

APPENDIX XI

* R - reduced
** N - normal

APPENDIX XII

XII. Brood survival through the season - 1955.

Log Number	1	2	3	4	5	6	7
	Aug.	Aug.	Aug.	Sept.	Sept.	Sept.	Oct.
Date log debarked	11	19	27	3	12	18	17
Total galleries	32	38	17	18	27	31	11
Number of eggs/gallery at time of debarking	26.3	19.2	7.2	0.5	6.6	0.9	0
Egg hatch per gallery at time of debarking	15.6	36.5	32.9	33.8	33.5	51.1	42
Larval survival per gallery	13.9	26.4	18.5	6.6	15.1	6.8	4.9
% larval survival per gallery	89	72	56	20	46	13	12

APPENDIX XIII

XIII. Brood survival through the season - 1956.

	I Flight (midpoint-July 11)						II Flight (midpoint Aug.4)
Date when log debarked	July 25	Aug. 1	Aug. 9	Aug. 14	Aug. 23	Sept. 8	Sept. 6
Log Number	1	2	3	4	6	7	1
Total number of galleries	43	36	62	64	11	57	40
Average length of gallery (inches)	10.0	7.0	12.0	10.0	15.0	8.5	15.0
Average mort/inch of gallery - due known causes	0.8	1.9	0.3	0	0	0	
Average mort/inch of gallery due unknown causes	0	0.4	1.8	3.6	4.2	*	1.1
Average number of survivors per inch of gallery	2.3	1.1	2.3	1.7	0.2	0.2	1.9
% survival/gallery	73	33	52	32	5	*	69

* Region of inner bark too badly chewed to determine egg hatch, hence unable calculate mortality and percentage survivors.

APPENDIX XIV

XIV. Brood survival through the season (caged logs) - 1956.

Date when log debarked	I Flight broods		
	Aug. 20	Sept. 1	Sept. 6
Log number	1	2	3
Total number galleries	29	31	34
Average length gallery (inches)	11.0	11.0	9.0
Average mortality/inch of gallery - unknown causes	1.0	1.6	2.9
% survival per gallery	65	59	51

Brood survival through the season - 1957.

Date of debarking	Tree No.	Diam. in.	No. Strikes	Av. Gallery Length in.	Av. Larvae per in. of gallery
Aug. 27	#1	10	262	9	2.9
Oct. 6	#2	8	116	16	0.7

APPENDIX XV

XV. Brood survival through the season - first and second flight - 1958.

First flight	1958				1959
Date of debarking	July 23	July 31	Aug. 14	Sept. 11	May 20
Tree number	1003	1200	30	1250	1228
Tree diameter (in.)	8.5	6.0	7.0	6.0	8.5
Total number of galleries - lower 5 ft.	113	42	49	121	107
Average length of gallery (in.)	4.3	5.9	9.0	6.8	10.9
Average survival/inch of gallery	>*3.0	>3.0	>3.0	0.9	0.09
Percentage moisture content - outer $\frac{1}{4}$ sapwood	?	?	62	34	29
Percentage parent adults in gallery	100	100	30	0	0

* Eggs on July 23, still mainly eggs Aug. 14. More than 3 eggs per inch in each case.

Second flight	1958		1959	
Date of debarking	Aug. 21	Sept. 11	May 20	June 11
Tree number	1427	1429	1432	1353
Tree Dbh (in.)	8.5	7.0	8.0	8.5
Total No. galleries	63	70	188	125
Average length galleries (in.)	10.0	10.0	7.0	11.0
Average survival/inch of gallery	(eggs)	2.8	1.8	0.7
Moisture content outer sapwood	61%	44%	31%	30%

Plate I

Fig. 1. Eggs in egg gallery. Boring dust removed from gallery and egg niches.

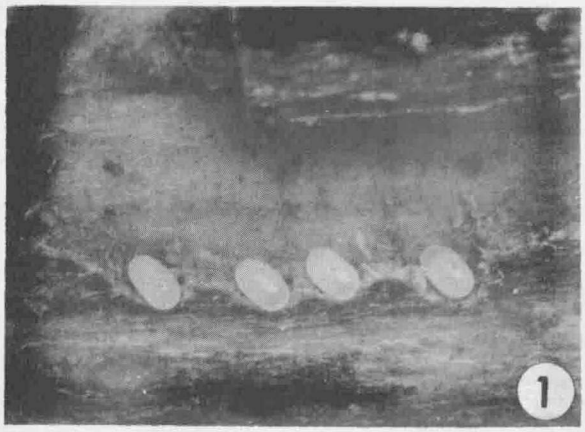
Fig. 2. The four larval instars.

Fig. 3. From the left, early and mature pupae, young teneral, 4 mature adults.

Fig. 4. Egg gallery, male and female at upper end. Note boring dust in lower part of gallery. Eggs in niches along sides of gallery have not yet hatched.

Fig. 5. Egg gallery after eggs have hatched, showing larval galleries extending laterally.

Fig. 6. Fourth instar larva in its gallery.



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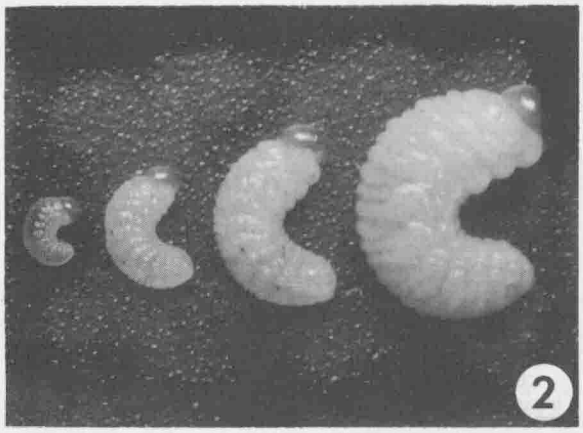

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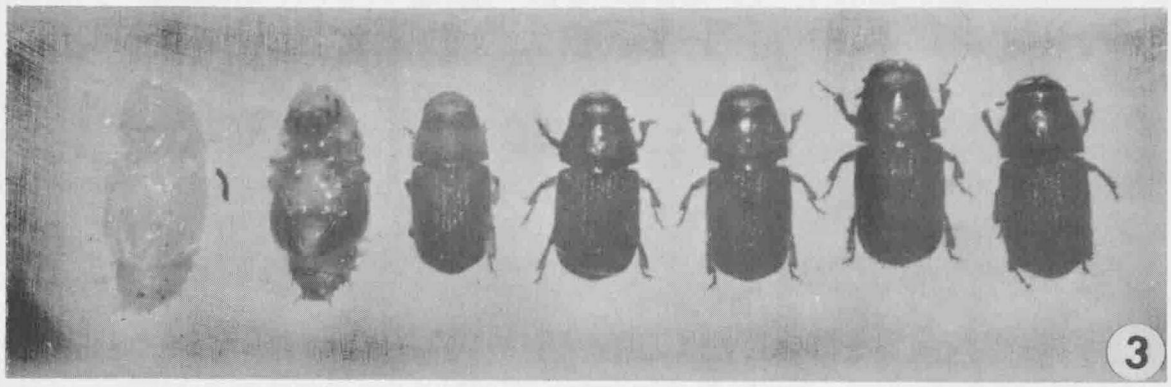

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PLATE II

Broods of the mountain pine beetle nearing maturity.

Plate III

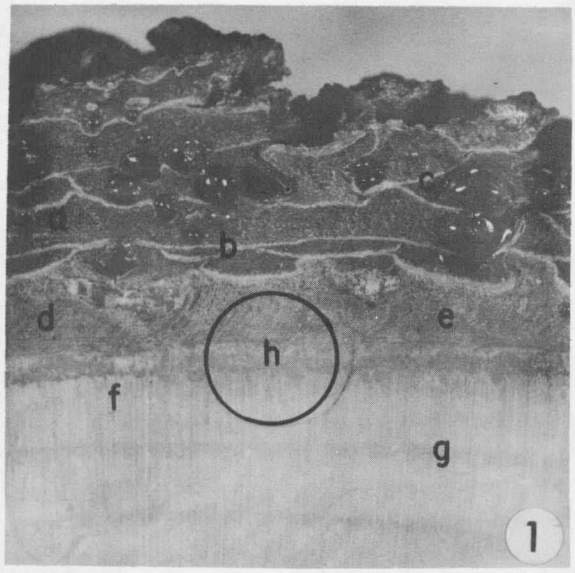
Fig. 1. Transverse section showing outer bark, inner bark and sapwood, and the region outlined where the bark beetle constructs the egg gallery.

Fig. 2. Cross section of sapwood (bark removed) and egg galleries, showing depth of penetration into sapwood. White flecks in the dark summer wood are cross sections of longitudinal resin canals.

Fig. 3. Tangential section through the sapwood showing cross section of transverse resin canal and epithelial cells.

Fig. 4. Radial section through the sapwood showing portion of transverse resin canal passing from summer wood to spring wood.

Fig. 5. Transverse section through sapwood showing cross section of longitudinal resin canal and epithelial cells.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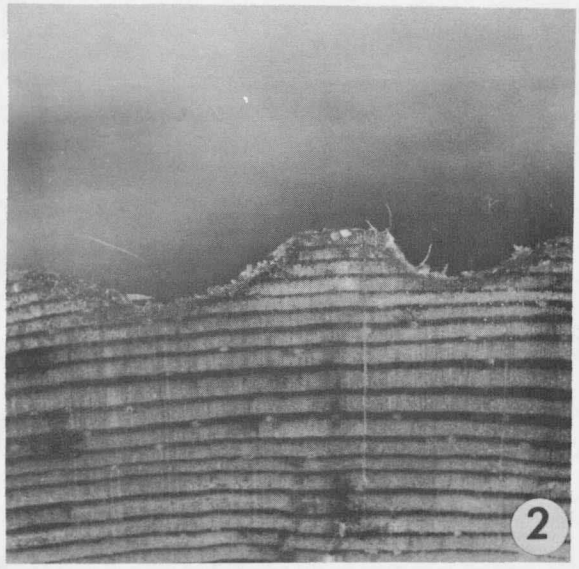
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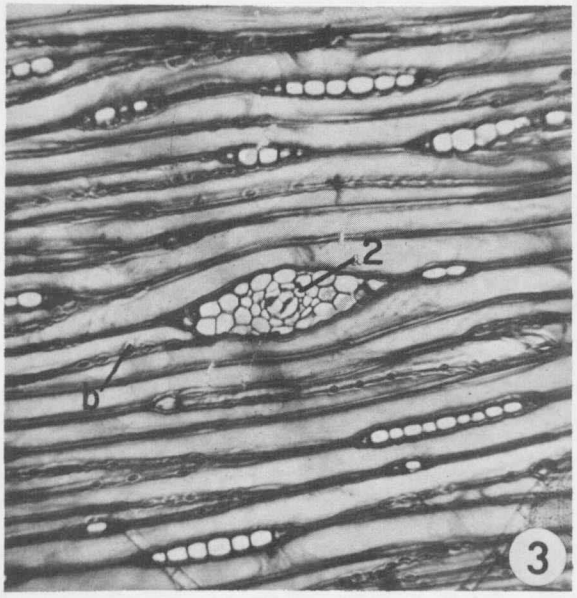
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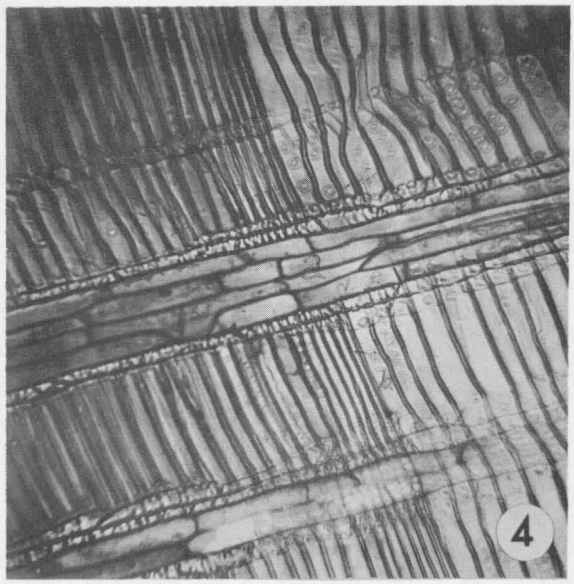
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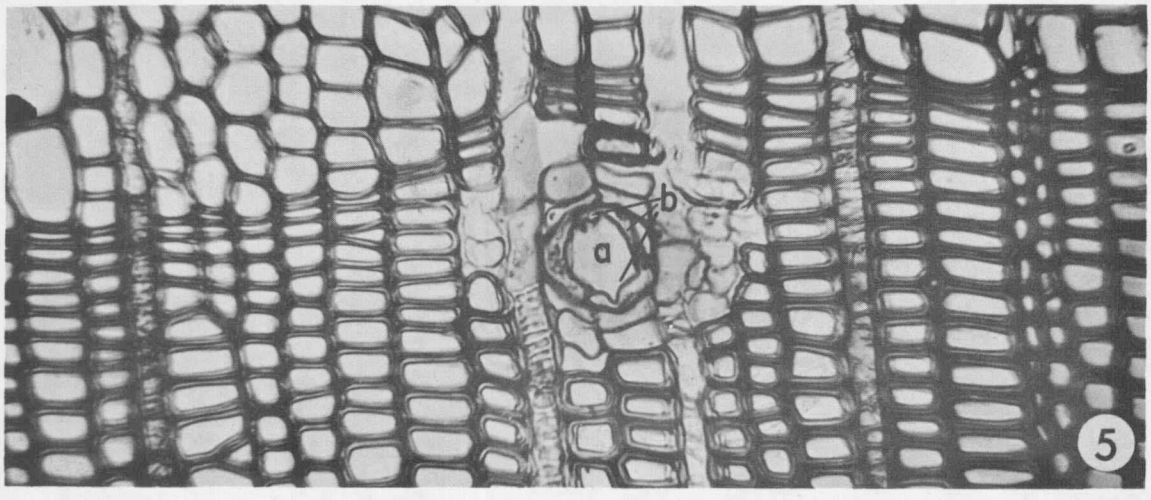
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Plate IV

Fig. 1. Polyethylene humidity chamber.

Fig. 2. Experimental set-up to determine the reaction of egg laying females when they encountered dry inner bark and outer sapwood.

Fig. 3. Mixed lodgepole pine and Douglas fir stand in lower end of Francis Creek Valley.

Fig. 4. Pure lodgepole pine stand in upper end of Francis Creek Valley.

Fig. 5. Glass tube used to determine reaction of bark beetles to light.


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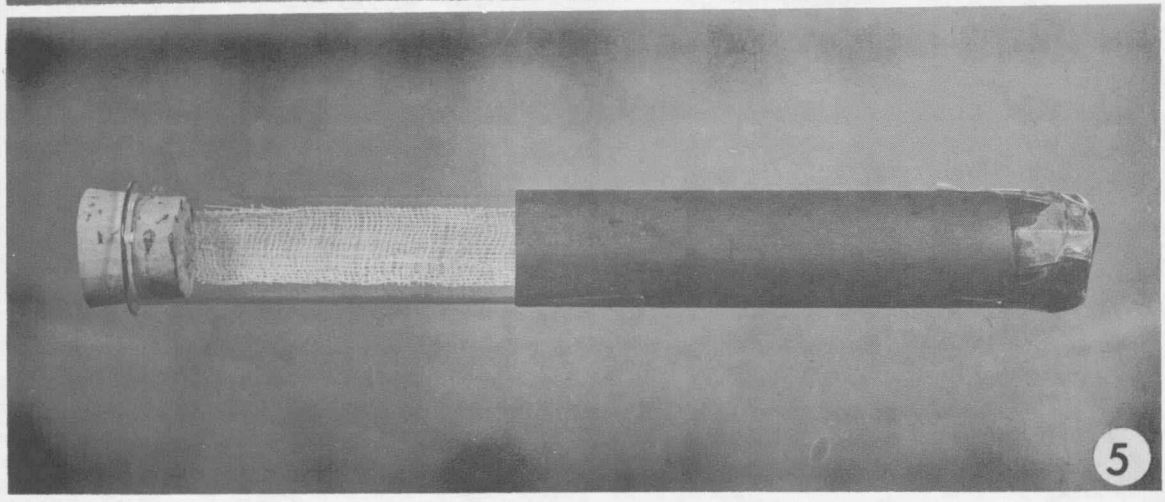
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Plate V

Fig. 1. Weather recording instruments. Hygrothermograph, maximum and minimum thermometers.

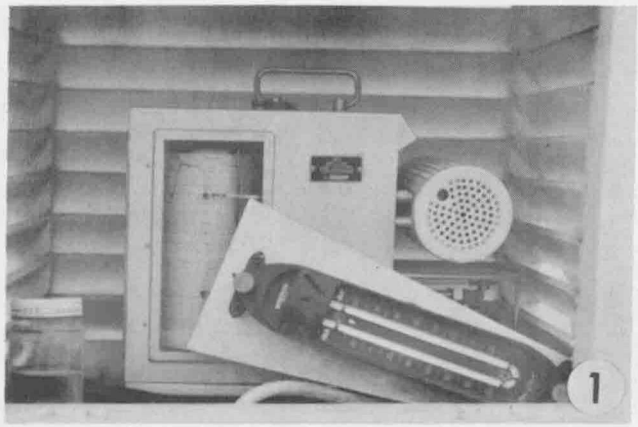
Fig. 2. Precision balance for weighing samples in moisture determinations.

Fig. 3. Moisture saturation apparatus.

Fig. 4. Samples for moisture determinations in drying oven.

Fig. 5. Sleeve cages used for brood studies.

Fig. 6. Cages used for rearing and emergence studies. Normally shaded with canvas fly.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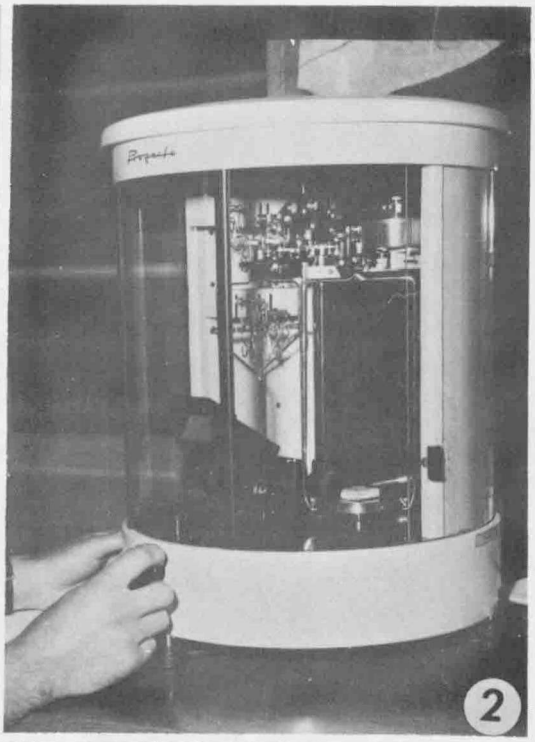
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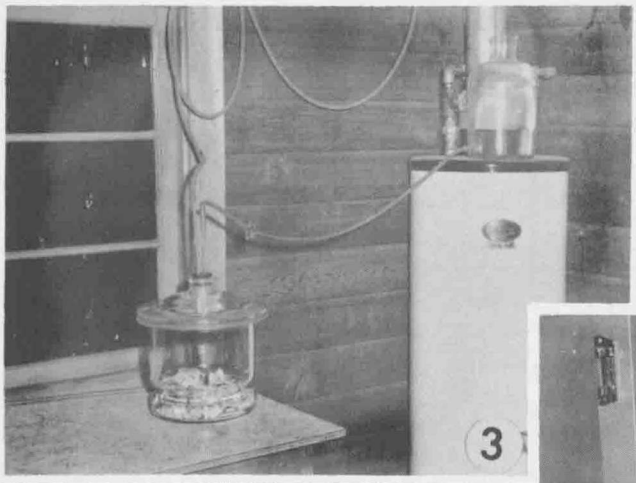
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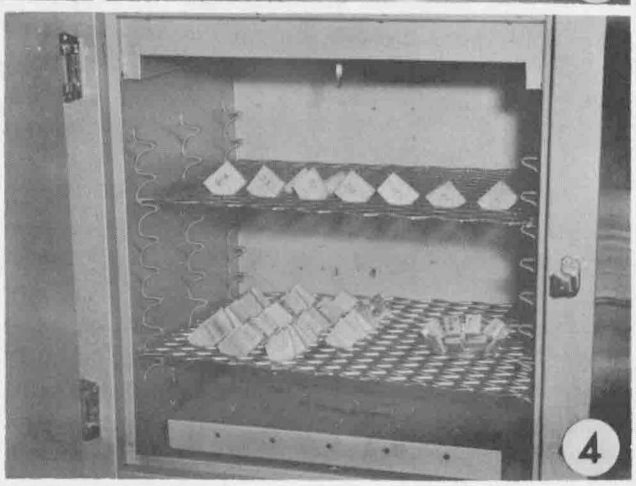
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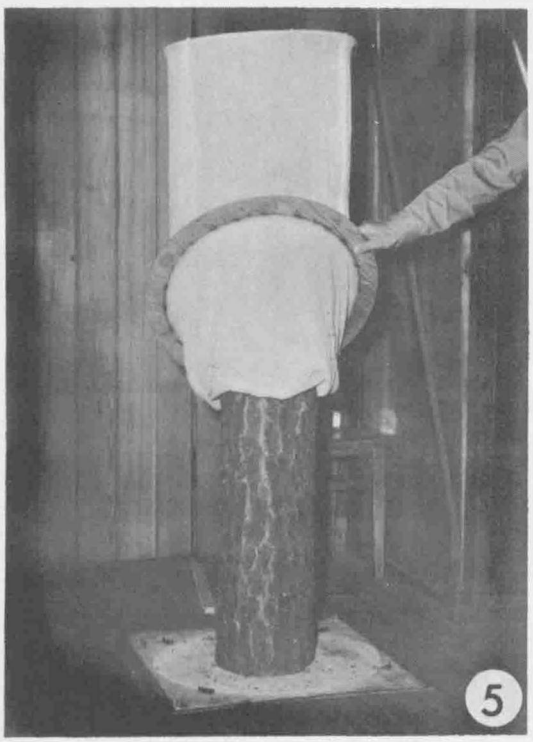
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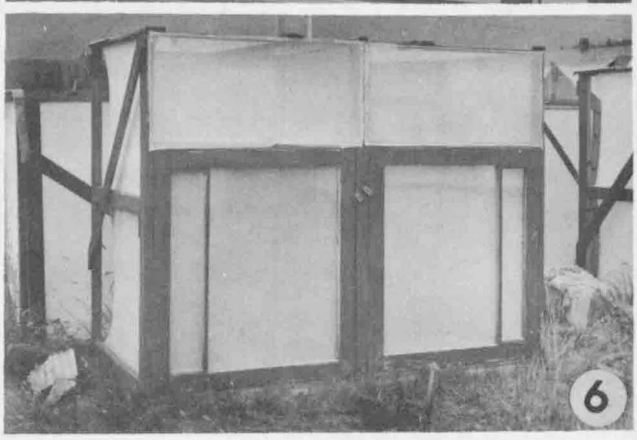
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Plate VI

Fig. 1. Three disks from the same tree. Pencil line shows division between heartwood and sapwood.

Fig. 2. Disk from an infested tree showing blue stain in sapwood.

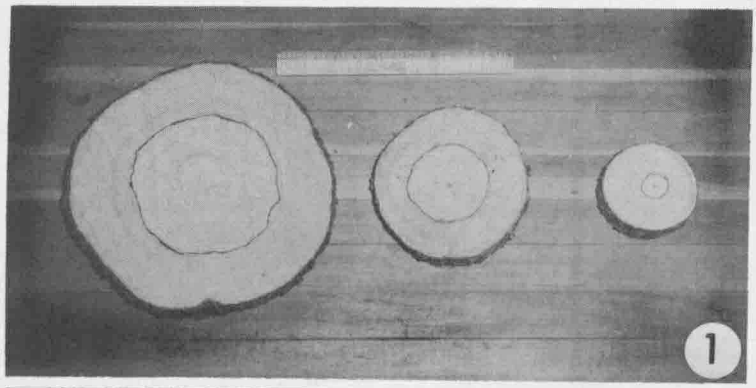
Fig. 3. Four butt logs from infested trees showing pitch tubes. Note woodpecker work in right hand log.

Fig. 4. Arrangement of logs to trap bark beetles.

Fig. 5. Section of a tree killed by the mountain pine beetle. Note main galleries roughly parallel.

Fig. 6. Section of trunk of a vigorous tree showing recent attack. Note large pitch tubes.

Fig. 7. Stand type. Note pitch tubes on attacked tree at left.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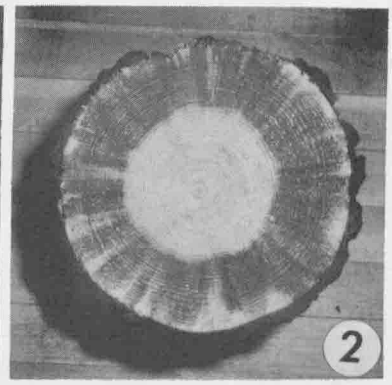
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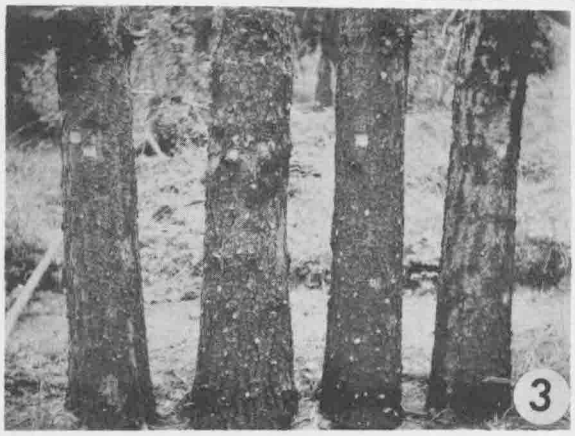
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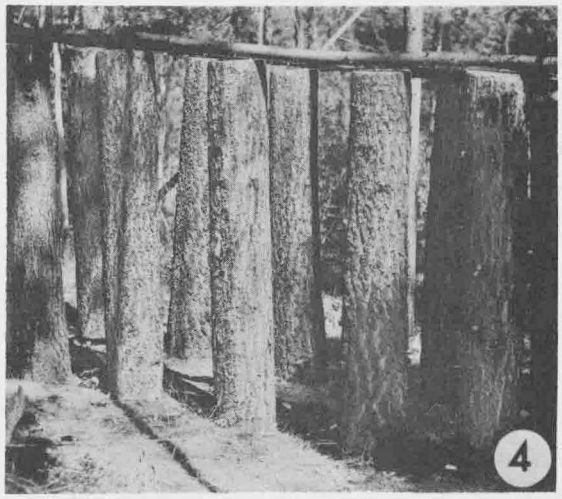
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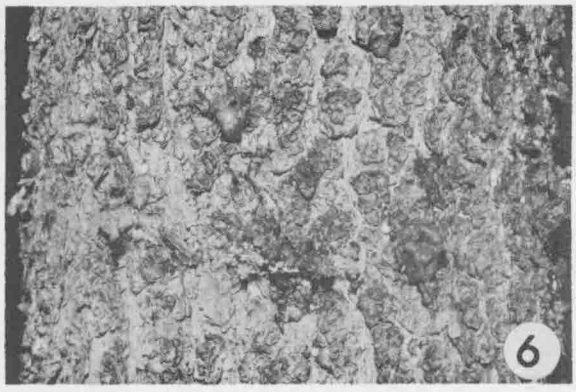
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Plate VII

Fig. 1. Tool for rapid removal of small samples for moisture determinations.

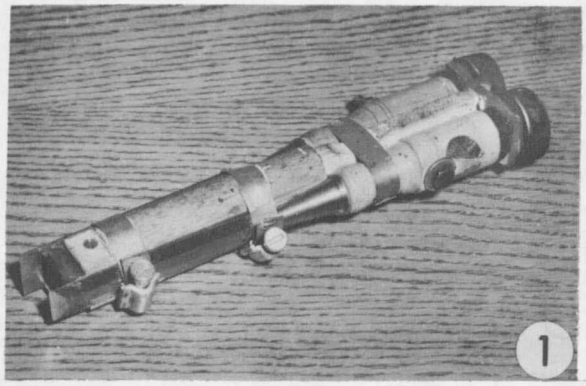
Fig. 2. Sampling tool in use.

Fig. 3. Removing samples and placing them in vials. The bark has been separated from the sapwood.

Fig. 4. Taking large samples with ordinary wood chisel.

Fig. 5. Aluminum foil ready to wrap sample.

Fig. 6. Marking data directly on large sample.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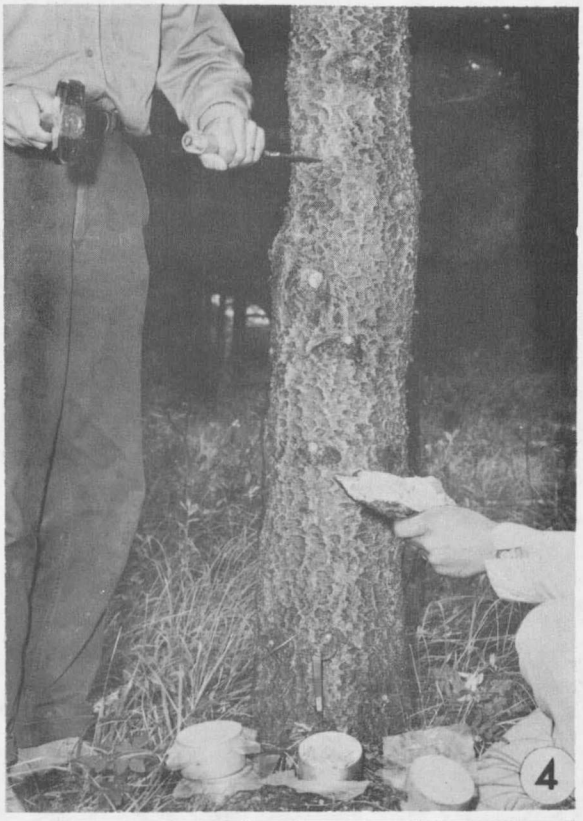
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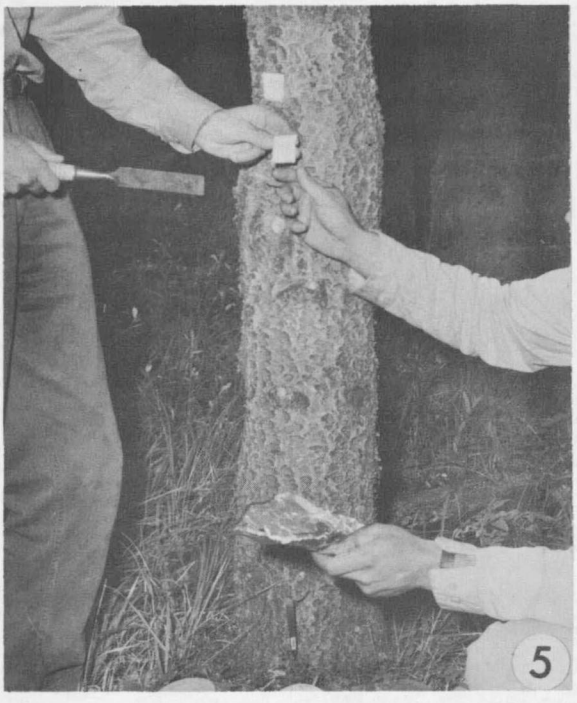
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Plate VIII

Preparation of plates for observation of activities of the mountain pine beetle during gallery construction and brood development.

Fig. 1. Removing fresh bark strip in humidity chamber.

Fig. 2. Placing strip between 1/8" thick plastic sheets, and constructing slot in bottom of bark strip.

Fig. 3. Dividing bark strip into sections.

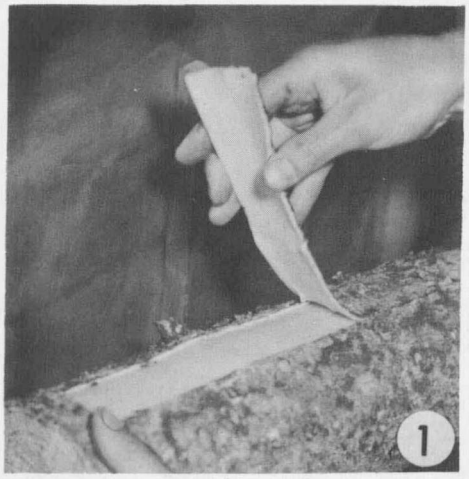
Fig. 4. Sealing the edges of the plastic covered bark with waterproof tape.

Fig. 5. Wrapping samples in aluminum foil for later moisture determinations.

Fig. 6. Wrapping strip of bark adjacent to original strip (Fig. 1) for later use to replace sections in plastic mount.

Fig. 7. Inserting male and female beetles into slot to start gallery.

Fig. 8. Observation plates kept in vertical position.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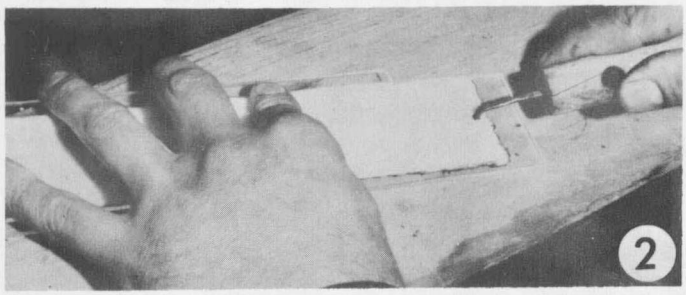
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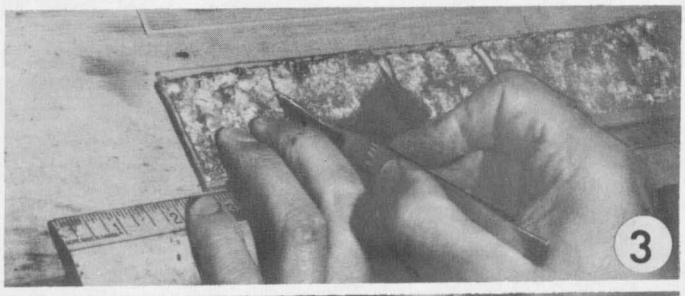
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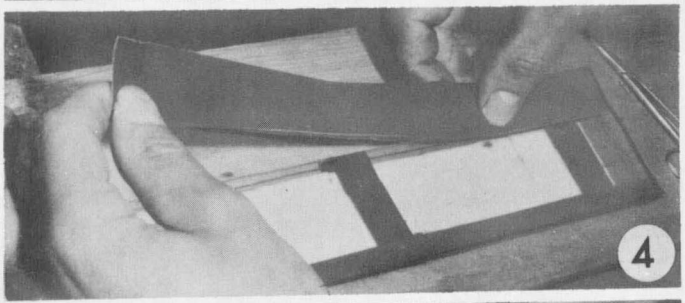
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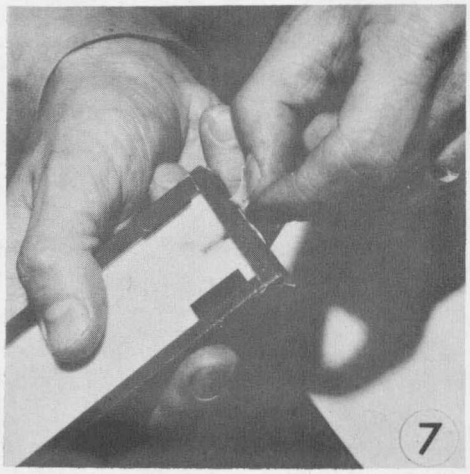
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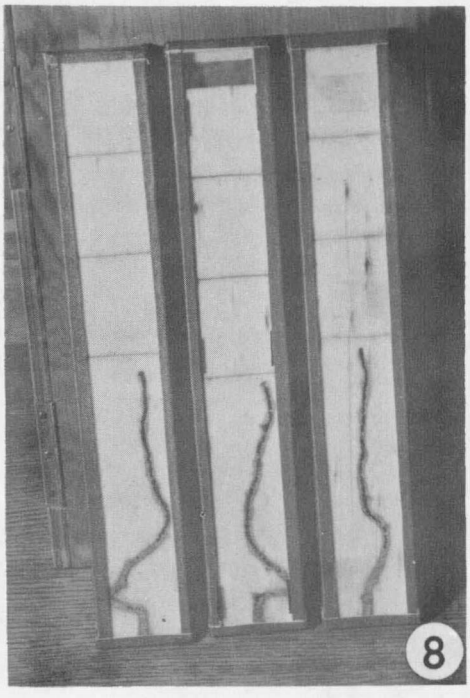
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Plate IX

Figs. 1-4. Replacing upper portions of bark.

Figs. 5-8. Cutting window in plastic with dental burr to remove bark for moisture determination and insects for testing.

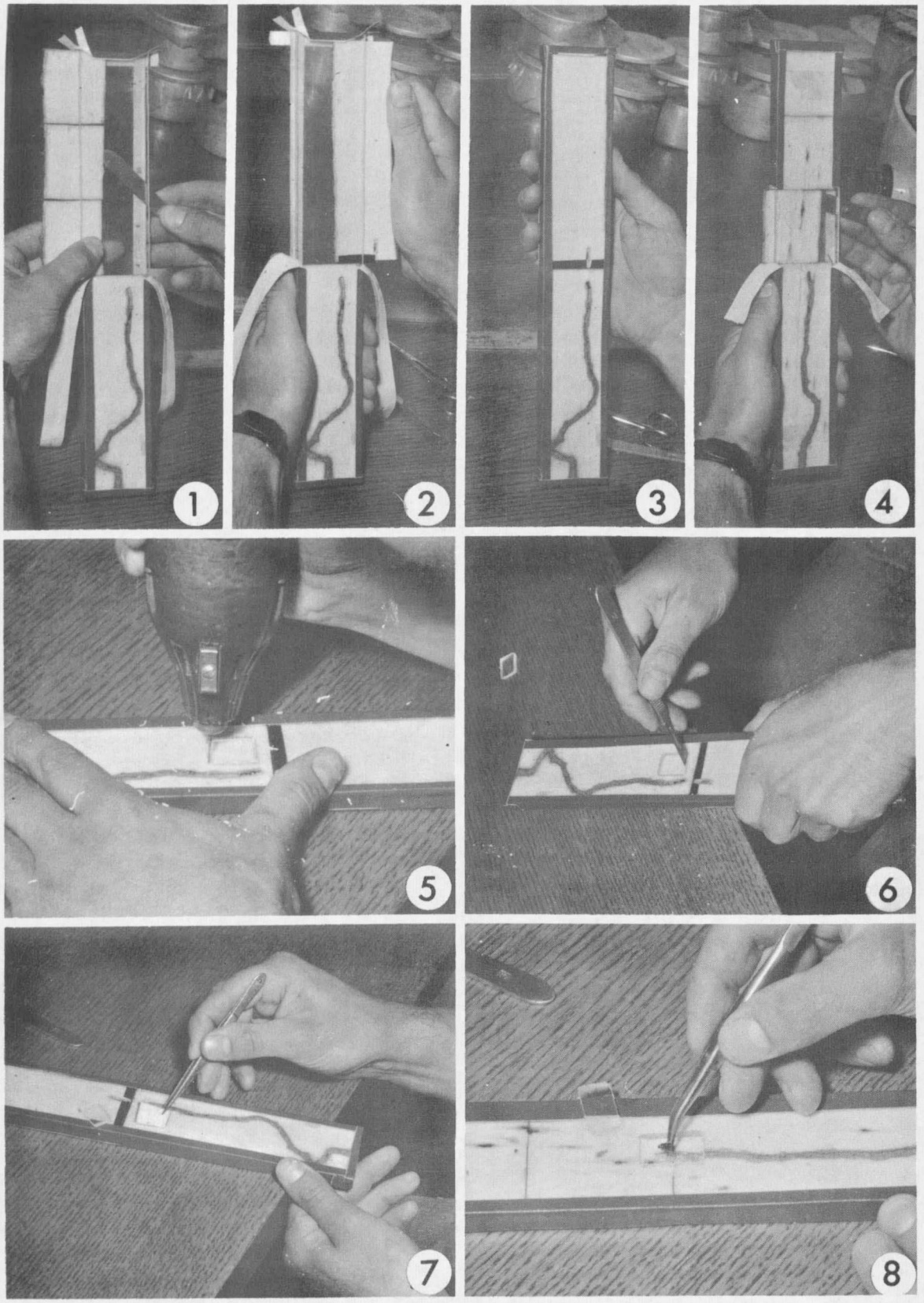
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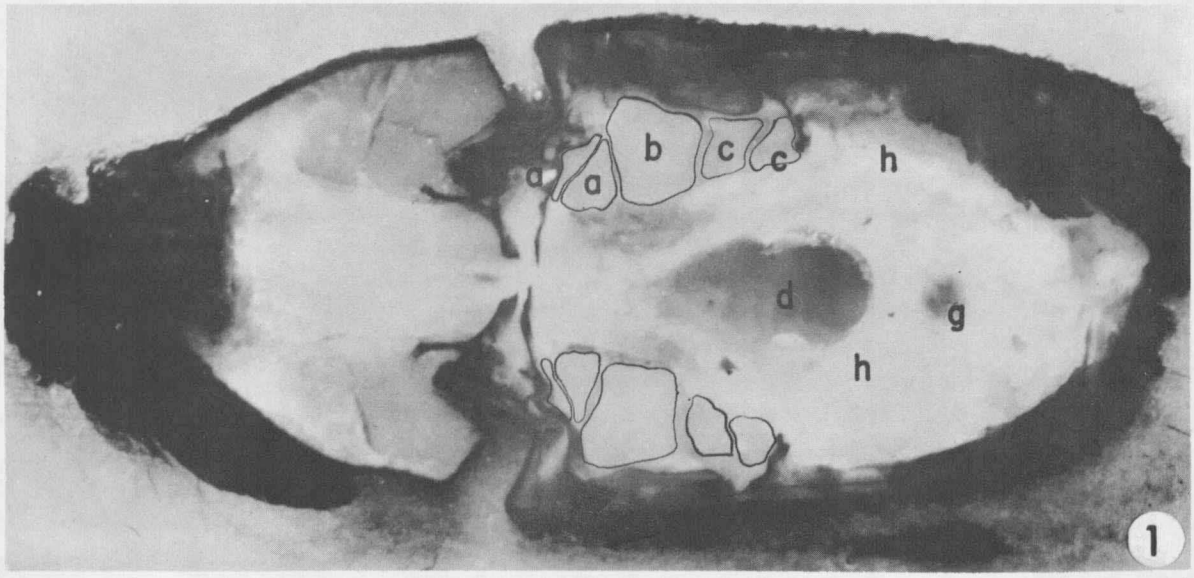
Plate X

Fig. 1. Frontal section through young female in condition for flight.

Fig. 2. Frontal section through a female in the egg laying condition.

a,b,c - Indirect flying muscles
d - Ventriculus
e - Proventriculus
f - Crop
g - Hind intestine
h - Fat body
i - Oöcyte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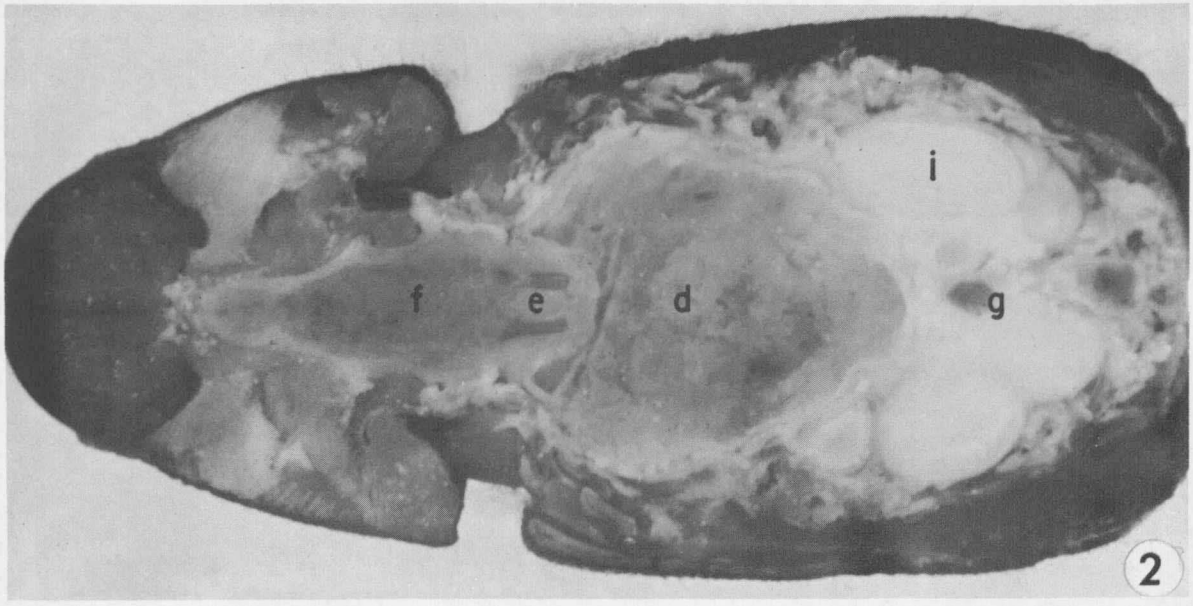
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