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

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A THESIS

Submitted to the Graduate Faculty

in

partial fulfillment of the requirements

for the degree of

Doctor of Philosophy in Entomology

at

Montana State College

Approved:

Head, Major Department

Chairman, Examining Committee

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Bozeman, Montana
June, 1960

ACKNOWLEDGEMENTS

I wish to thank Mr. G.R. Hopping, formerly Officer-in-Charge of the Forest Biology Laboratory, Calgary, Alberta, for his helpful attitude and assistance during the course of this study. Appreciation is expressed to Messrs. H. Cerezky, P. Barclay, and C. Cameron for assistance in the collection of field data, and P. Debnam for taking the photographs. I am indebted to Drs. J.H. Pepper, R.C. Froeschner, P.D. Skaar, and E.B. Harvey, Department of Entomology and Zoology, Montana State College, for their considerable aid in the preparation of the manuscript. Thanks are extended to Dr. M.L. Prebble, Director, Forest Biology Division, Canadian Department of Agriculture, Ottawa, Canada, for permission to use the data from this study, and to Dr. B.M. McGugan, Associate Director, for his review of the manuscript.

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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):

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

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

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

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 $\frac{1}{2}$ x $\frac{3}{4}$ x $\frac{1}{4}$ 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).

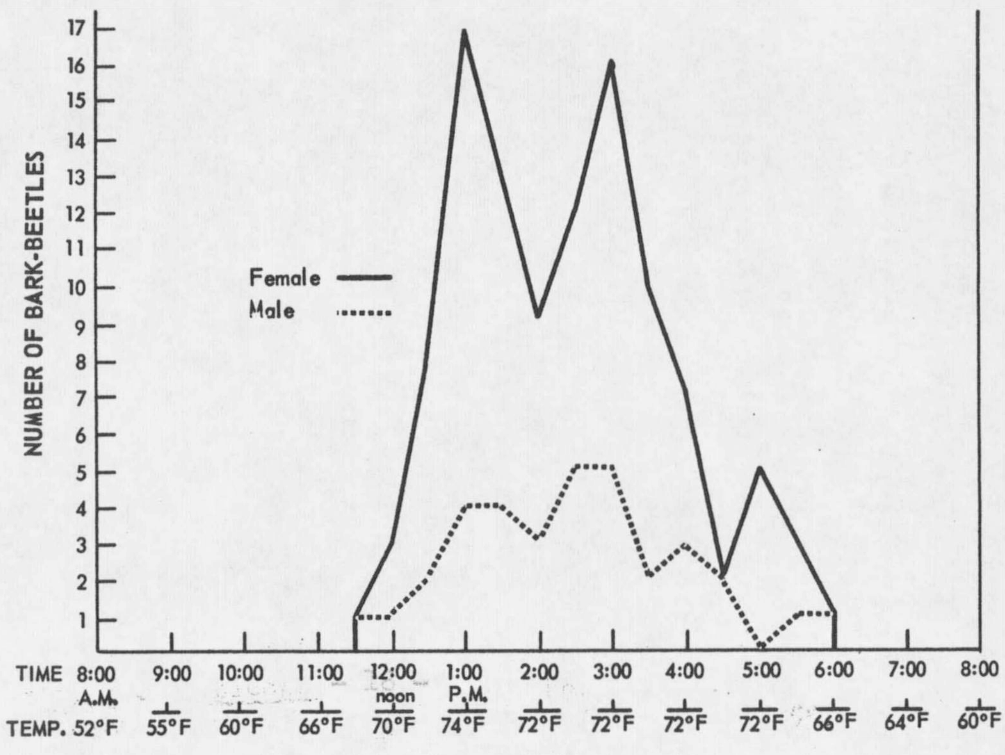

Fig. 1. Emergence of D. monticolae on the half hour, Aug. 4, 1955. Butt logs from trees infested the previous year placed in cages prior to commencement of emergence.