

THE DISTRIBUTION AND ABUNDANCE OF THE ROOT
WEEVIL, HYLOBIUS WARRENI WOOD IN RELATION TO
LODGEPOLE PINE STAND CONDITIONS IN ALBERTA

by

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ABSTRACT

The distribution, population ecology, behavior and host interactions of the root weevil, Hylobius warreni Wood were investigated in lodgepole pine forests in Alberta. Highest incidence of the weevil occurs in the Lower Foothills Section of the Boreal Forest Region, between 2,500 and 4,000 feet in elevation. In even-aged forests weevil numbers are distributed according to stand maturity, stand density, tree size and duff depth. Interactions between these variables modify the patterns of abundance in different stands.

Attack incidence upon the host varies, being highest in the collar zone and least on lateral roots. As tree size increases the ratio of weevils on roots tends to increase. During normal stand development initial weevils on collar invasion of weevils occurs at age 6-10 years, and persists with successive attacks throughout the life of the stand. Weevil populations are highly aggregated in mature stands; "k" values of the negative binomial varied from 0.09 to 0.68, while Taylor's power law gave an aggregation index "b" value of 1.92.

Estimates of weevil populations indicated that low levels are characteristic of this species and are maintained, mostly within the range 200-1200 weevils per acre. Estimates of absolute numbers indicate similar levels of abundance occur in young and old stands alike, while population intensity values increase with stand maturity. The highest rate of increase of attack density per tree appears to occur during the ages of 30-45 years.

The structure of weevil populations was described and mortality factors were identified and measured for larval, pupal and teneral stages.

The main mortality factor of these stages appeared to be from excess moisture in the larval gallery and pupal cell. Only the first 3 larval instars are definable by head capsule width measurement.

The feeding behavior of larvae varies with its maturity. In the early instars the feeding pattern relates to bark thickness, but damage is insignificant. Damage of late instars may consist of decorticated gallery lengths up to 24 cm. Larval and pupal habitats are described to indicate the special adaptations for survival.

Adults live at least 3 years but lay their eggs during the second and third summers of adulthood. Their seasonal peak of activity occurs in June and early July. Dispersion in the forest tends to be random, commencing about 2 hours after sunset and when temperatures exceed 36-40 °F. Host trees are located partly by vision, the pattern of selection being related to host size. Maximum fecundity per female per season may be 36 or more eggs, but in the field the actual number may not exceed 12.0. Most eggs are deposited singly in niches excavated by the female in the root-collar bark, and are subsequently covered over with excreta. The egg requires a moist environment maintained for up to 42 days for successful hatch.

During stand development up to 100 percent of trees may sustain larval feeding damage accumulated to various degrees of intensity. Young trees up to 30 years of age show less resistance to girdling damage than older trees, and reasons are given for this. Estimates of mean height losses of 20-25-year old tree stems sustaining 50 percent girdling were 11.5 and 10.9 percent over 2- and 3-year periods respectively. The total impact of the weevil in the stand as a whole appears to hasten successional changes

during stand development.

A method of regulation of weevil abundance is postulated and takes into account the behavior of the female during oviposition, host selection, larval feeding habits, cumulative damage and host interactions. Overall numerical restraint and stability of numbers are considered to be effected largely through the inherent behavior of adults.

Several weevil control measures are suggested through forest management. Clearcutting of mature timber in alternate strips reduced a weevil population by an estimated 67 percent, but some larvae developed to adults in the cut stumps one and two years after tree removal. The effect of cutting resulted in a concentration of weevils ^{on} adjacent trees along stand peripheries, 3-5 years after cutting.

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INTRODUCTION

The root weevil, Hylobius warreni Wood is an indigenous pest to forests in Canada and the eastern United States (Warren 1956c; Finnegan 1962b; Warner 1966). It feeds upon various coniferous hosts in a wide range of ecological situations (Reid 1952; Ross 1955; Stark 1959b; Warren and Parrott 1965; Grant 1966). During its larval stage this insect mines the phloem and cambial tissues, causing large open wounds at the root collar and roots of its host trees (Reid 1952; Warren 1956b). Trees are susceptible to attack at ages from a few years to maturity, but ^{injury} is most severe in the more vigorous trees in the dominant, co-dominant and intermediate classes (Reid 1952). Unlike most other bark-cambium feeders the weevil requires no apparent pre-weakening of its host for successful attack. The susceptibility of trees in nearly all age categories indicate a wide range of tolerances in the weevil's selection of habitat.

In Alberta reports of tree mortality from weevil feeding over the past 15 years have been frequent, but included trees less than three inches in diameter almost exclusively. The weevil, however, has never been reported in such abundance as to be termed epidemic, except perhaps in pine plantations (Davialt 1949; Finnegan 1962b; Warren 1956c; Warren and Parrott 1965). These facts pose two essential ecological questions which are of immediate concern to forest management. The first question is what factors are responsible for the weevil's spatial variability in abundance in forested areas? The second question is what factors are responsible for the weevil's apparent overall numerical restraint and stability?

In this thesis essentially four main aspects are studied to provide answers to these questions. The first aspect is the geographical distribution of H. warreni within the natural range of its host species. A second aspect is concerned with annual weevil abundance and population structure within a variety of stand conditions. A third aspect is concerned with the behavior of the life stages of the weevil. This information increases the understanding of the weevil in relation to its host tree and to other factors of its environment. The fourth aspect is concerned with the impact of weevil feeding upon the host tree, and how this may ultimately affect the stand as a whole.

1. Historical Review

The first collections of adult H. warreni in western Canada were probably made during the 1930's, but concern for its damage to forest trees did not develop until about 1950. This was largely due to the insidious nature of the weevil and to the fact that forest insect surveys became intensified only after the mid-1940's. Insects attacking roots of trees were often overlooked. Widespread occurrence of the weevil was noted in Quebec (identified as Hypomolyx piceus) by Daviault (1949) and later in Manitoba by Warren and Whitney (1951), and by Reid (1952) in Alberta. These reports indicated a wide distribution pattern extending across most of Canada, and showed that several commercially important coniferous species were involved.

The weevil's extensive distribution, its preferred hosts and feeding damage characteristics demonstrated the need for investigations on

the biology of the weevil, and an ecological and economic evaluation of its damage potential. This need was intensified when it was discovered that Hylobius wounds provide an important avenue of infection for root rotting and staining fungi in spruce (Warren and Whitney 1951; Whitney 1952; Whitney 1961). Whitney (1962) also showed that the wounds were a significant factor in the development of stand-opening disease of spruce.

Intensive studies initiated by Warren on H. warreni in Manitoba and Saskatchewan provided basic information on life history, morphology and site factors associated with weevil populations (Warren 1956b, 1956d, 1958, 1960a, 1960b). The studies of Reid (1952) and Stark (1959b) in Alberta are complementary to those of Warren. Warren (1956b, 1956c) first drew attention to an important aspect of weevil damage to trees which he described as cumulative with each successive attack. He developed a damage appraisal system to survey stands on the basis of an accumulative "Damage Index". This appraisal system, however, has certain limitations for use in biological evaluation in that it deals indirectly with weevil populations. Essentially no studies were undertaken to follow weevil populations from year to year and thereby gain an insight into factors which may limit population increase. Estimates of weevil numbers per tree were made in lodgepole pine stands by Stark (1959b) but little attempt was made to relate pine forest conditions to levels of weevil abundance.

The studies of Warren in Manitoba were carried out primarily in white spruce, Picea glauca (Moench) Voss and in jack pine, Pinus banksiana Lamb. while those of Reid (1952) and Stark (1959b) in Alberta apply mostly to lodgepole pine, Pinus contorta Dougl. var. latifolia Engelm. The latter

two authors observed that H. warreni showed distinct preference for lodgepole pine over white spruce, where the two species were growing together naturally. In a stand 95 percent of the pine component had weevil scars (Reid 1952) and appeared to support nearly all of the weevil population. These facts open up the possibility that information gathered in spruce habitats may not wholly apply in lodgepole pine stands.

Coincident with the increased usage of lodgepole pine as a primary pulpwood species in Alberta and British Columbia is the need for an understanding of the silvical and economic effects of weevil damage to this host. This need parallels the increased emphasis placed upon forest protection. In the biological sense it is of interest to ascertain the intrinsic and extrinsic factors which affect the weevil's abundance since this allows predictions to be made in "new" forest situations. Few comprehensive studies of Hylobius populations are known in North America, Europe and Asia (Nordic Forest Entomologists' Research Group 1962; Millers 1965; Matsuzawa, et. al. 1963).

These studies of H. warreni were conducted by the author during the period 1961 to 1966 inclusive. They are of a research project with the Forest Research Branch of Canada Department of Forestry and Rural Development, being carried out in the foothills region of the Rocky Mountains in Alberta.

MATERIALS AND METHODS

1. The Study Insect

The experimental animal used throughout this study was Hylobius warreni. Its taxonomic description, life habits and known hosts are briefly reviewed and comparative information is given on a closely related species, H. pinicola. The similarities and differences between the two species are pointed out because of taxonomic problems encountered by previous authors (Wood 1957).

1.1 Taxonomy: The root weevil, H. warreni is the largest and perhaps most widespread of seven species of the genus in North America, all of which are coniferous feeders (Warner 1966). Prior to 1957 there was uncertainty about the correct taxonomic status of H. warreni. The initial studies of Warren in Manitoba revealed two adult forms. One was distinguished by well developed metathoracic wings, the other by a vestigial form of hind wing. These two forms were first believed to be a dimorphism of the same species and were identified as Hypomolyx piceus (De Geer), after the Eurasian species. Both forms were collected from essentially the same spruce habitats and only minor differences in external morphology were observed. Wood (1957), however, invalidated the genus Hypomolyx of Leconte and separated the Eurasian species, Hylobius piceus, from the Hylobius "complex" of Warren. Wood showed that two distinct species were present in Warren's material. The form with well-developed hind wings was Hylobius pinicola Couper while the vestigial winged-form was designated a new species, Hylobius warreni Wood. In a later comprehensive study Warren (1960b) presented a detailed

description of the external morphology of H. pinicola and H. warreni. Manna and Smith (1959) provided strong cytological evidence that these two species also differed in chromosomal counts.

Taxonomic keys for North American species of Hylobius adults have been provided by Wood (1957), Finnegan (1961), Millers, et al. (1963) and Warner (1966). No key is yet available to separate the immature stages of H. warreni from H. pinicola.

A search of the literature suggests that relatively few species are represented in the genus Hylobius throughout the northern hemisphere; seven in North America (Warner 1966), four in Europe (Scherf 1964) and several in Asia, including Japan (Manna and Smith 1959, Morimoto 1962, Takenouchi 1963).

1.2 Life Stages and Habits: This description of the life stages of H. warreni is summarized from the reports of Reid (1952), Warren (1956b) and Stark (1956b) and pertain to conditions in the Alberta foothills. The life history of the weevil is not completely understood, being complicated by an overlap of generations. The period from egg to adult extends approximately two years. Oviposition occurs from June to September and eggs are deposited in the root-collar zone of the host tree. When freshly laid the eggs are pearly white and ellipsoidal. They appear to hatch by September and overwinter in the larval stage. The number of instars is uncertain but seven were recorded from artificial rearings (Warren 1960a). On the basis of head capsule width measurements Stark (1959b) determined six.

The larvae feed upon the phloem and cambial tissues in the root-collar zone, causing continuous resinosis. Development of larvae terminates between mid-June and mid-July after a feeding period of about two years. At

this time the mature larva constructs a special chamber from resin and bark frass in which it transforms to a prepupal, pupal and teneral stages. Larvae remain on the same tree throughout their development. Transformation to the pupal stage takes about two weeks, lasts three to four weeks and ends with adult eclosion, usually in August. Similar observations were noted by Daviault (1949) in southern Quebec for the same weevil. The resinous chamber serves to protect the prepupa, pupa and young adult until the time of emergence during the latter part of August and early September. The studies of Stark (1959a) suggested that the weevil may overwinter in all stages of the life cycle.

The adult at maturity is robust in form, ranging in length from 11.7 to 15.1 mm. (Wood 1957); its beak is moderately elongated. It is reddish black in color and flightless, with greatly reduced metathoracic wings and wing supporting structures. The adult stage may extend one or more years including at least two overwintering periods. New adults are added to the population pool annually. This results in variation of age distribution from one year to the next. Egg laying may extend over one or more summers for individual females. The adults are mostly nocturnal in habit. At night they disperse laterally between trees and ascend tree trunks. They return to the forest litter before sunrise where they generally remain throughout the day.

1.3 Host Species and Geographical Distribution: Collections of adult H. warreni and H. pinicola indicate that they are distributed in a similar pattern in North America but may be separated largely by host and habitat preference. H. pinicola has been found predominantly in moist swampy habitats on the hosts, tamarack, Larix laricina (Du Roi) K. Koch, black spruce, Picea mariana (Mill.) BSP., white spruce (Warren 1956b; Wood 1957; Grant 1966) and balsam

fir, Abies balsamea (L.) Mill. (Smerlis 1957, 1961).

The primary hosts of H. warreni include lodgepole pine, jack pine, white spruce and western white pine, Pinus monticola Dougl. (Reid 1952; Ross 1955; Warren 1956b; 1960b; Grant 1966). Additional hosts include black spruce, red pine (Pinus resinosa Ait.) and Scots pine (P. sylvestris L.). Plantations of the latter two pine species in Newfoundland and southern Quebec were found particularly susceptible to H. warreni attack (Daviault 1949; Finnegan 1962b; Warren and Parrott 1965).

The geographical distributions of H. warreni and H. pinicola are described for north western America to indicate their spatial overlap, and to define potential forest problem areas. Collections of adult weevils were used for the preparation of distribution maps. All areas lying within the natural range of lodgepole pine in western Canada and the United States were considered, including some adjacent areas in Alberta and the Northwest Territories. In addition to specimens collected in Alberta, information on distribution records was requested from museums and forest research laboratories in western Canada and the U.S.

2. Studies of Hylobius Populations

The general problem underlying the weevil studies had three aspects. The first was to ascertain population patterns of abundance, their change with time and their correlation with stand conditions. The second was to ascertain the nature and extent of casualty factors operating on different stages in the life cycle of the insect. The third was to ascertain the effects of weevil injury on the host trees.

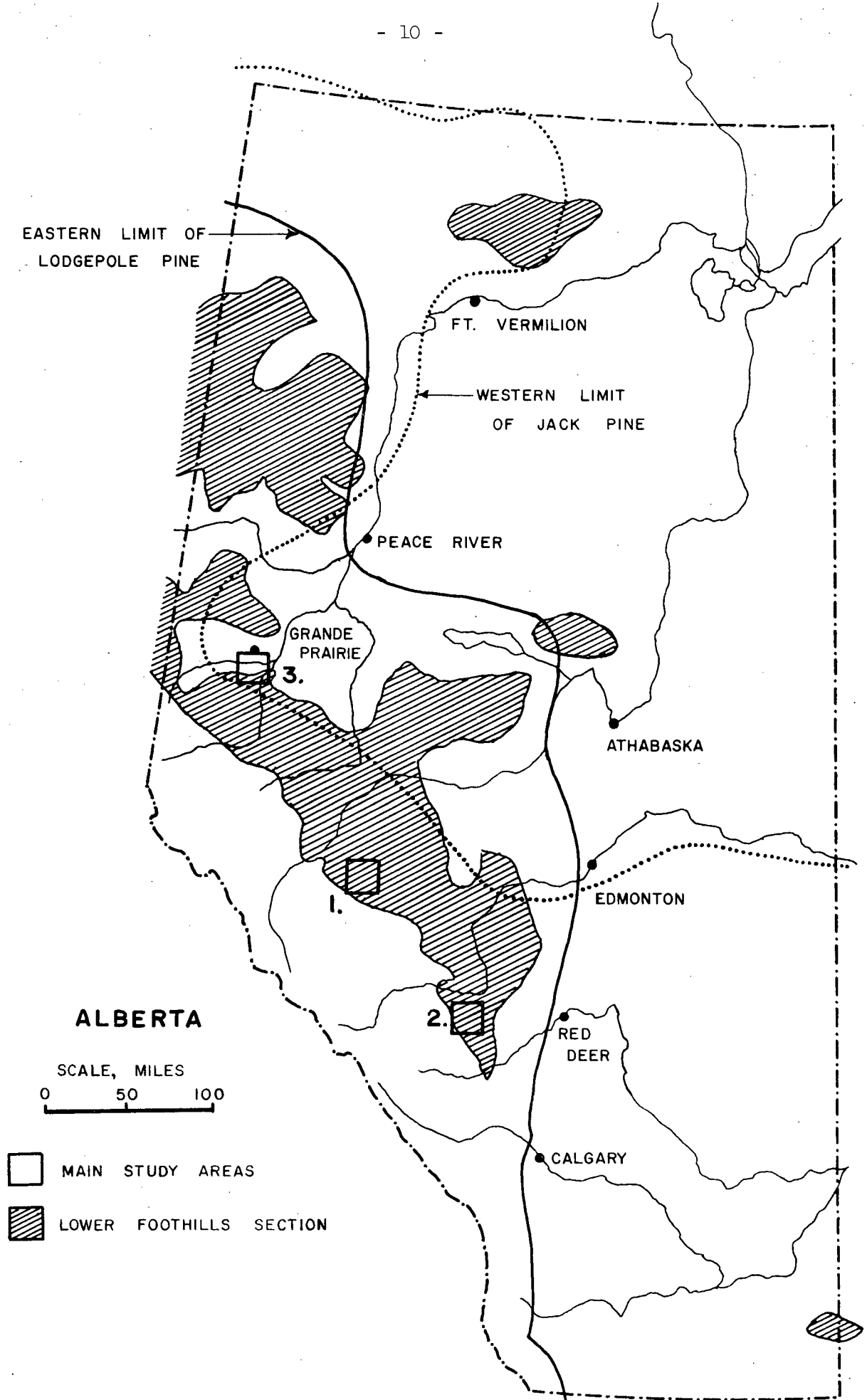
Population patterns were considered to be most likely related to

stand maturity, harvesting practices, tree size, stand density and duff thickness. The age of the stand was considered important since most areas of lodgepole pine have regenerated in an even-age condition. It was therefore necessary to determine the age of young stands when initial weevil invasion occurs, and to follow the subsequent changes in population patterns through to stand maturity. This necessitated sampling for weevil populations in a variety of even-aged pine stands. The method of clearcutting is most widely used in the harvest of lodgepole pine and this practice was incorporated into the overall design of a sampling plan. Tree size, tree density and duff depth are measurable variables which help to define the physical structure of the weevil habitat. The term "duff" as used here is defined as the living and dead organic matter measured to the depth of mineral soil.

To ascertain population patterns of abundance it was necessary to choose suitable areas to represent the desired stand conditions, to design a sampling plan, to choose techniques of observations and to apply appropriate statistical methods of analysis. Weevil populations as used in the context of this thesis refers to numbers of weevils per plot area or total numbers of weevils on all trees within specified plot areas.

2.1. Study Areas: Weevil studies were concentrated in two main areas of Alberta. These were (1) Robb study area and (2) Rocky Mountain House study area (Fig. 1). Both areas lie within the Lower Foothills Section of the Boreal Forest Region (Rowe 1959). The reasons for the choice of the Lower Foothills were several. Collections made prior to 1960 indicated that H. warreni occurred more commonly in pine stands at lower elevations of the Alberta foothills than at higher elevations. Other reasons relate to the

Fig. 1. Map of Alberta showing main study areas, Lower Foothills Section and the distributions of jack and lodgepole pine. The overlap of distributions of the two pine species in west central Alberta was defined as a hybridization zone (Moss 1953). Study areas 1, 2 and 3 are Robb, Rocky Mountain House and Grande Prairie respectively.



natural distribution of lodgepole pine (Fig. 1), and to its commercial values within the Lower Foothills Section. The following description summarizes the general aspects of the Lower Foothills which are considered pertinent to the studies of H. warreni.

2.1.1. Description of Lower Foothills Section: The criteria defining the Lower Foothills Section ~~were~~ outlined by Rowe (1959) and includes 54 percent of the total lodgepole pine forested area in Alberta (Smithers 1962). The importance of this area is indicated by the existence of one pulp mill currently in operation and three more planned for future development; all will provide management of pine forests within the Lower Foothills Section. Nearly all studies of the weevil were carried out within this section.

The distinctive tree species in the Lower Foothills is lodgepole pine which occurs in pure stands and in admixture with other species. According to Horton (1956), aspen, Populus tremuloides Michx., and to a lesser extent, balsam poplar, P. balsamifera L. compete with lodgepole pine as post-fire pioneers. In older stands white and black spruce are common constituents while alpine fir, Abies lasiocarpa (Hook.) Nutt. is comparatively rare. Scattered throughout this section are pockets of bog areas which support black spruce and tamarack. In Alberta lodgepole pine has been broadly termed the dominant subclimax species (Rowe 1959), and Bloomberg (1950) and Cormack (1953) have indicated that during secondary forest succession there is a general trend on the east slope of the Rockies from lodgepole pine, following fire, to a spruce-fir climax. Farther to the north and east where mixedwood components provide a more complex situation, a successional trend from pine and aspen to spruce is still recognizable (Moss 1953). However, throughout

the Lower Foothills immature pine and aspen stands predominate today, and stands over 100 years of age are rare (Horton 1956). According to Horton fire has been the major historic factor which has determined forest composition and succession. Climax forests are rarely attained and therefore succession has little significance in determining tree composition. Factors other than fire, especially logging, have been of secondary and localized importance, and only in the Lower Foothills Section. Historically there has been a large demand for pine ties and poles. These have generally been selectively harvested from accessible mixedwood stands, leaving behind partially cut stands of varying densities. This form of stand opening has often initiated "two-aged" pine stands or encouraged invasion of aspen.

The pattern of pine forests in the Alberta foothills is likely to change considerably in future years with expansion of the pulpwood economy. Indications at present point to a fairly intensive management of lodgepole forests in even age stands with a rotational period of about 80 years or less.

Forest fires have been of varying intensities, ranging from intense ground fires where all vegetation is killed, to light ground fires where considerable plant life has survived. Fires of the latter have been described as very common in the Lower Foothills (Smithers 1962), and have given rise to many "two-aged" stands. Often pockets of unburned timber as well as individual trees remain unharmed in burned over areas. These undoubtedly have provided "reservoirs" for surviving Hylobius populations.

The topography of the Lower Foothills Section consists of low hills and plateaux between 3000 and 4000 feet in elevation in the south and down to 2500 feet farther north. Throughout this section lodgepole pine has been found to be a highly adaptable species, occupying all soil sites from wet to

extremely dry. Horton (1958) noted that the wide adaptability of this species' rooting system was largely responsible for its successful establishment.

The major river systems flow eastward and valleys are often broad. Glacial drift of variable composition occurs most commonly and greywooded or related podzolic types characterize the soil profile development (Rowe 1959). During the growing months of May to August inclusive the average total precipitation has been determined as 9.1 inches, while the average annual precipitation is 17.7 inches (Smithers 1962).

Included with the Lower Foothills Section in Alberta are four out-lying regions; Pelican Mts., Caribou Mts., Clear Hills and Cypress Hills. These are defined by the same or similar characteristic features. In addition to the prevalent mixedwood types and elevation range, certain ground floral species were considered as important indicators of the Lower Foothills, namely Vaccinium myrtilloides, Maianthemum canadense and Aralia nudicaulis (Horton 1956).

(i) Robb Study Area: Investigations of the weevil were most intense near Robb because this area provided a range of stand conditions in respect to ages from current year seedlings to 65-70-year old stands. All plots established here were within a radius of 10 miles and were situated in essentially even-aged pine stands. All stands are within the boundary of a pulp lease under management by North Western Pulp and Power Limited at Hinton, Alberta. In addition, clearcutting operations in the vicinity provided the opportunity to determine the effects of tree removal upon the survival of weevil populations, and hence, to evaluate clearcutting as a

method of weevil control.

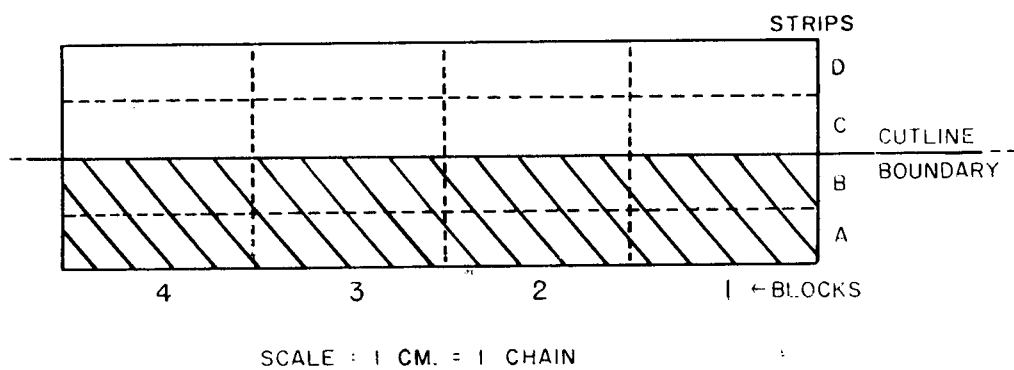
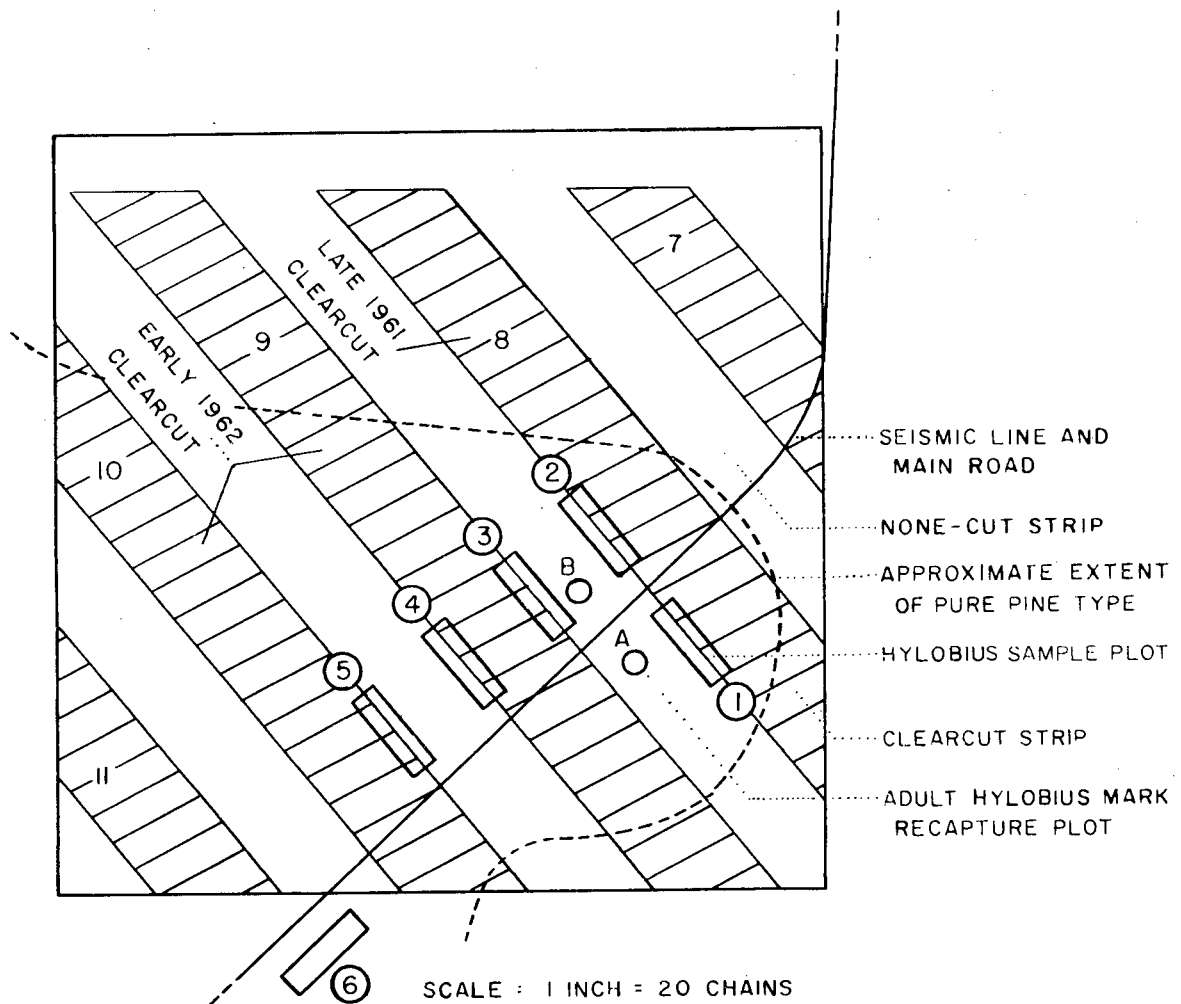
Root weevils were first reported relatively abundant in the Robb area in 1955-56, and in 1957 an area was set aside for studying Hylobius populations. This area, shown in Figure 2 consists of a 65-70-year old stand which was surveyed for the clearcut removal of pulpwood in an alternate strip pattern. Because of its intensive coverage, age and apparent uniformity of site, it was chosen for the major population studies. Sampling plots 1 to 6 were located within its boundaries.

The area enclosing plots 1 to 5 is a plateau which slopes gently to the southeast and extends for about one mile. Its altitude is 3500 feet above sea level. The forest cover type consists of a uniform stand of essentially pure pine with a scattered intermixture of white and black spruce, a Salix species and small isolated pockets of aspen. All intermixed species except aspen are well below the pine canopy level. The present stand is of fire origin and a few remnant pine 90+ years of age were found. These suggest that fire had been intense in both crown and ground levels.

Further observations were made to describe the weevil habitat in greater detail. This information is supplementary to that given for the Lower Foothills Section. Increment borings were made to determine stand age. Total counts of living pine trees within plot areas provided estimates of stand density. Felled trees cut during pulpwood removal were measured for average stand height. The tree diameters and frequency distributions of diameters were recorded for 800 randomly chosen trees. In all cases, diameter measurements were made at the 10-inch stump height (=d.s.h.).

Five soil pits, one located within each of plots 1 to 5 were

Fig. 2. Cut layout map showing H. warreni sample plots 1 to 6 and mark-recapture plots A and B in the 65-70-year old pine stand near Robb, Alberta. Lower figure illustrates the division of each 3-acre plot into 4 longitudinal strips, each subdivided into 4 blocks. Shaded areas indicate clearcut portions.



ENLARGEMENT OF HYLOBIUS SAMPLING PLOTS 1-7

excavated to measure and describe the soil profile characterizing the present pine stand. The profiles also served as an indicator of site and soil drainage patterns. The five profiles were combined for an average description of the stand. Horizon descriptions and soil profile classification were adapted from terminology of the report of the Meeting of the National Soil Survey Committee of Canada (1960). Color descriptions were made according to a Munsell Book of Color.

Near the center of the stand were located four circular plots, each 10 feet in diameter. These were examined for the total floral species complex growing within them. The species are considered representative of the stand. They were identified and an estimate of the relative abundance of each was made according to four categories. These were judged according to their presence or absence in all four plots. The categories were: V.A. = very abundant; C. = common; F.C. = fairly common; S. = scattered or scarce. Using the most abundant plant species, various canopy strata were recognized and described to indicate the three-dimensional aspect of the weevil habitat. The percentage of ground surface coverage was estimated for three dominant plant groups.

The degree of forest floor levelness was evaluated because of its influence upon conditions in the weevil habitat which relate to surface runoff, adult weevil movement, and in providing niches for predators. Surface levelness was evaluated by extending a cord parallel to the ground surface. Vertical measurements of distances between the cord and the bottom of all depressions were made as well as measurements of all horizontal distances between the centers of depressions. An average of these two sets of measurements provided estimates of the degree of undulation.

All stands sampled for H. warreni populations in the Robb area are recorded below according to plot numbers and brief descriptions are included.

Plots 1-6: Plots 1 to 5 sampled in 1961, 1962, 1963 and 1965; plot 6 sampled in 1961, 1962, and 1963.

Plot 7: Stand age, composition and origin similar to the area of plots 1 to 6; located 10 miles west of plots 1 to 6; sampled in 1962 and 1963.

Plot 8: Located one mile north of plots 1 to 6; stand origin, age and composition similar to area of plots 1 to 6. During the tree harvesting operation of 1957-58 this stand was clearcut except for regularly spaced seed blocks (each block measured about 130 ft.²) in which no trees were removed. Scarification treatment was applied to the cut over portions in July, 1960, and moderate stocking of pine followed. Two seed blocks separated by a distance of 600 ft. were sampled for weevil populations in 1963. The seed blocks were clearcut during the winter of 1963-64.

Plot 9: Located in 65-70-year old pine adjacent to plot 1; sampled in 1966.

Regeneration Plot Series I, II, III and IV: Plot series I and II were located in the clearcut area surrounding plot 8. The pine was 3-8 years old in 1966 and originated from natural seeding following scarification. The forest extending from the boundary consisted of 65-70-year old pine with a prominent understory of black spruce; weevil incidence was common.

Series III and IV were located near plots 1 to 6 in an area clearcut in an alternate strip pattern in 1959. The cut areas were scarified in 1960. Good stocking of pine followed and the trees were 2-6 years old in 1966. The residual strips still stand and consist of 65-70-year old pine with a light to heavy understory of black spruce.

Regeneration Plots V and VI: These were delineated and sampled in 1966 within the same clearcut area as plots I and II. Plot V extends from the stand periphery and was established to follow weevil incidence over a period of years; only attacked trees have been tallied so far. Plot VI was located farther within.

Regeneration Plot Series VII, VIII, and IX: These plot series were located in a 20-25-year old pine stand surrounded by a 60-90-year old stand. The stand lies about 10 miles west of plots 1 to 6. The stand origin is from a fire which burned over approximately 1000 acres in 1941; the area has since been termed the Robb Burn. This area has regenerated by natural means to almost pure pine within a period of about seven years since the fire (Baranyay and Stevenson 1964). In recent years the development of a black spruce understory has become noticeable in many regions and aspen is scattered throughout. A brief description of the physiographic features of the area has been given by Baranyay and Stevenson (1964) who studied the distribution and abundance of pathogenic diseases and other damaging agents affecting the pine. From a series of seven permanent plots scattered throughout the burn these authors have examined the root systems of a large number of dead and dying pine. They reported almost negative incidence of H. warreni in all plots except one which is located near the edge of the stand.

The surrounding forest is composed of lodgepole pine with a fairly prominent intermixture of black spruce and aspen. Light infestations of H. warreni appear to be present at most points around the burn periphery. A wide variety of habitats is represented within the burn, ranging from very dry to near bog conditions; pine trees survive on all but extreme moist sites. A representative sample of floral species growing on average site conditions

were identified. An estimate of the relative abundance of each species is given; the categories used were the same as for plants collected near plots 1 to 6.

In 1965 three locations in the Robb Burn were chosen at the periphery where a fairly sharp boundary occurred between the young regeneration and the adjacent mature forest. Each location represented a different habitat type. These were identified as plot series VII, VIII and IX. Plot series VII was located on the south edge of the burn on a north facing gentle slope. The ground cover consisted of a 4-5 inch thickness of moss. Fairly moist conditions were a characteristic feature. Plot series VIII and IX were located on level aspects on the north side of the burn. Duff depth was 1-2 inches in series VIII and 1-3 inches in series IX. Plot series VIII represented dry conditions while series IX was intermediate.

(ii) Rocky Mountain House Study Area: Plot 10 (Strachan area) was located in a stand of 95-100-year old pine with a scattered understory of black and white spruce. A description of this stand by Crossley (1955) indicated that the number of pine stems per acre was 642 with an average diameter (d.b.h.) of 6.1 inches in 1952. The 1966 study revealed 610 stems per acre and an average diameter of only 6.4 inches (d.b.h.). The stand appeared to be in a general state of decadence as the crowns were very thin and dead snags were evident in most diameter classes.

Regeneration Plot Series X: This stand was about 15 years old in 1966 and originated from a fire in about 1943. Its location is 20 miles south of plot 10. A mature pine forest of variable composition surrounds this burn. Trees in plot series X were sampled in 1966.

All plots (1 to 10 and I to X) were used to determine weevil

population patterns of abundance, and to correlate weevil numbers with stand conditions. Plots 1 to 5 were followed intensively from 1961 to 1965 (except 1964) to establish patterns of population change with time, and in relation to clearcutting. Plots 6 and 7 also served to show population change with time.

The regeneration plots served to establish the age at which stands become initially invaded, and to show the rate of subsequent weevil spread into the stand.

2.2 Design of Plots and Sampling Procedure

2.2.1. Plots in Mature Pine: Prior to 1961 a one-square mile area of land had been surveyed by staff of the pulp company concerned into parallel strips one-eighth mile wide. A clearcut pattern of pulpwood removal was later carried out on alternate strips (Fig. 2). Plots 1 to 5 were delineated prior to any cutting in such a manner that the surveyed lines bisected each plot lengthwise. After tree removal the cutline boundary divided each plot into clearcut and non-cut halves. Plot 6 was located outside the cutting area to permit weevil population sampling to be done independently of cutting. The boundaries of all plots remained fixed throughout the 1961 to 1965 sampling period.

Plots 1 to 6 were each three acres in area and were of equal dimensions (198 x 660 ft.). As shown in the enlarged view of a plot in Figure 2, each was further subdivided into four equal longitudinal strips (designated A, B, C and D) and each strip into four equal blocks. The block constituted a minimum-sized sampling area in which 10 living pine were randomly chosen using a table of random numbers. Two numbers were used to

locate each tree, one representing breadth, the other length of the block in average sized paces. The two values were paced off and the nearest tree from the point of intersection was tagged for subsequent examination. Each tree was considered the basic sampling unit from which a variety of observations and measurements were recorded. This included stem diameter and average duff depth around the tree base. Three measurements of duff depth were taken around each tree base and an average was calculated to the nearest inch. The root collar and root bases of each tree were thoroughly examined and all weevils found were recorded and removed from the tree. Their position upon the host, extent of damage and the stage of weevil development were also noted.

A total of 160 trees were examined in each of plots 1 to 6 in 1961. Immediately following this sample all trees in the A and B strips of plots 1 to 5 were clearcut, while plot 6 remained undisturbed. In 1962 80 living trees were sampled in the C and D strips, while 80 cut stumps were examined in the A and B strips of plots 1 to 5. This procedure was repeated for the 1963 sample. Plot 6 was sampled in 1962 and in 1963 following the same procedure as in 1961.

A fourth sample was obtained in the C and D strips of plots 1 to 5 in 1965 but only 200 trees were randomly selected for sampling. In this case 20 blocks were selected randomly from the total possible of 40 with representation in all C and D strips. Ten trees were examined in each block.

Plot 7 was delineated with the same dimensions as plots 1 to 6 and sampling was carried out in 1962 and 1963. The method of tree location and sampling procedure was identical to that in plots 1 to 6.

During the 1961-1965 sampling period no one tree was sampled more

than once. Each three-acre plot was sufficiently large to contain an estimated 40-50 percent of unsampled trees at the end of the fourth annual sample.

The removal of weevils from the sampled trees might be regarded as an introduction of error to the sampling system by lowering the population level for subsequent samples. However, this was compensated somewhat by removing the duff layer around each sampled tree to discourage immediate re-attack, and thus impede further dilution of the population. Warren (1956b) described this procedure as an effective means of mechanical control of Hylobius.

The layout and sampling procedure in plots 8, 9 and 10 were treated differently from that described for plots 1 to 7. In plot 8 a total of 80 trees were used. Forty trees were randomly chosen in each of two seed blocks and the results were combined. Plots 9 and 10 were each one-fifth-acre circular plots with a radial dimension of 51.4 ft. The location of each plot was selected as representing average site conditions. All living pine within each plot area were sampled.

2.2.2. Plots in Regeneration Pine: Plot series I, II, III and IV each consisted of 15 one-mil-acre plots (each was 6.6 x 6.6 ft.) arranged serially without spacing. Each series extended at right angles from a cutline boundary into a clearcut area. The mil-acre plots were numbered consecutively from the stand edge. All conifer seedlings in the four plot series were examined for evidence of weevil damage in 1963, and again in 1965. Seedling ages and a representative sample of heights were measured in 1965.

The dimensions of plot VI measured 30 x 70 ft. All pine within it were measured for height and examined for weevils in 1966.

Each of plot series VII, VIII, IX and X extended at right angles from the peripheral edge of the stand into young regeneration pine. Each series consisted of 20-foot diameter circular plots spaced at 30-foot intervals. The number of plots established was 11, 8, 10 and 10 for series VII to X respectively. All trees within each circular plot were examined for the presence of weevils and its damage characteristics were noted. Trees were measured for height and diameter (d.s.h.) in series VII, VIII and IX, and only heights were measured in series X. Total counts of trees in each circular plot provided a measure of density.

2.3 Techniques of Population Analysis:

2.3.1. Treatment of Sample Trees: Sampled trees in plots 1 to 10 were summarized by strip and plot for each year using four statistics. These were mean tree diameter (\bar{x}), diameter range (R), standard deviation of diameters (s) and coefficient of variation of diameters (C.V.). The procedures of calculation were as outlined in Steel and Torrie (1960). The C.V. values express sample standard deviation as a percentage of the sample mean and are therefore a relative measure of variation. This statistic permits direct comparison between strips, plots, areas and years.

2.3.2. Weevil Numbers and Population Structure: Weevil populations in plots 1 to 10 were expressed in two ways; as absolute numbers or numbers per block or per acre, and as numbers per tree. The latter expression is a measure of population intensity and is useful in showing weevil-tree size relationships within and between stands. However, population intensity values may be affected by changes in stand density and in tree size. Weevil numbers on a fixed scale of measurement such as the block or acre allows reliable comparisons

to be made between sites, between stands and between years. Since only a portion of the trees were sampled in plots 1 to 7 each year, weevil population estimates are based on counts of total numbers of trees per plot.

Weevil numbers were compiled from total counts of live larvae, pupae and teneral adults removed from the root-collar portion of the tree. Egg counts were excluded since they were rarely observed in the field, and it was not always possible to distinguish living from dead material. Mature adults were also excluded since they were few in number, represented a non-stationary phase of the life cycle and therefore, do not represent absolute values. The sampling period each year generally extended from May to early August. In plots 1 to 6, sampling began with plot 1 and progressed to plot 6 each year.

Plot comparisons of weevil abundance were made using the statistics: mean weevils per tree (\bar{x}); range in numbers found on sampled trees (R); standard deviation of weevils per tree (s) and the coefficient of variation of weevils per tree (C.V.).

The structure of weevil populations in plots 1 to 10 has been described in a variety of ways. The percentage of larvae pupating each year served to estimate the proportion of the population transforming to new adults. Larval head capsules were measured dorsally at their maximum width to determine the annual distribution of size groups and instars. The frequency distribution of weevil numbers per tree conformed to the negative binomial distribution. Two parameters describe this distribution; mean (\bar{x}) and an exponent "k". As described by Southwood (1966) the "k" value provides a measure of the degree of dispersion in a population, and is a useful characteristic for comparing different populations of the same insect or populations from different habitats and years, providing that a standard

sampling unit has been adhered to. The use of the tree as the basic sampling unit in plots 1 to 10 was adequate for this stipulation. All "k" values of plots 1 to 10 were calculated by the iterative solution in the following formula as outlined by Southwood (1966).

$$\log \frac{N}{n_0} = k \log \frac{1 + \bar{x}}{k}$$

where N = numbers of trees sampled,

n_0 = number of trees with zero weevils,

\bar{x} = mean number of weevils per tree

and "k" = measure of population dispersion.

Populations of root weevils were further described using Taylor's power law. Taylor (1961) showed that when the mean (\bar{x}) and variance (s^2) of a series of samples are plotted they tend to increase together and to obey a power law as expressed by the following formula:

$$s^2 = a\bar{x}^b$$

The parameters "a" and "b" are constants, where "a" is largely a sampling factor and "b" is said to represent a true "index of aggregation" characteristic of and constant for the species (Southwood 1966). In this respect it describes an intrinsic property of H. warreni. To obtain estimates of these parameters plots 1 to 10 (except 9) were used. The plots were first divided into five groups of infestation levels as given below. Group I had the highest infestation level, Group V had the lowest. Within each group, 15 sampled

Group I: Plot 8 (1963) + plots 1-5 CD (1965)

Group II: Plots 1-5 ABCD (1961) + plots 1-5 CD (1962) + plots 1-5
CD (1963)

Group III: Plot 6 (1961-1963) + plot 7 (1962-1963)

Group IV: Plot 10 (1966)

Group V: Plots 1-5 AB (1963)

trees were randomly drawn with replacement for each sample. Fifteen such samples were taken from each group, making a total of 75 samples. The mean (\bar{x}) and variance (s^2) were calculated for total weevil counts from each sample of 15 trees, and these values were then plotted on log-log paper.

The constant "b" value may be used to establish an appropriate transformation which, when applied to population values, establishes independence between variance and mean (Southwood 1966). The transformation is determined by solving the following equation.

$$P = 1 - \frac{1}{2}b$$

If $P = 0$, a log transformation should be used, and if $P = 0.5$, a square root transformation is applicable.

2.3.3. Weevil Distribution Patterns in the Forest and on the Host: A variety of methods was required to analyse weevil numbers in relation to tree size, tree density and duff depth. In stands represented by plots 1 to 10 tree diameter classes of one-inch intervals were used; in plots VII, VIII and IX diameters were taken to the nearest half-inch. Weevil numbers in relation to tree size were analysed by strip, year and by arbitrarily defined population classes (Groups I to IV). Appropriate transformation scales were used in order to subject the data to graphical and statistical presentation. Weevil numbers per tree were transformed to a log scale while a square root transformation was used for tree diameter. Because of low counts of weevils in young stands the log of percentage trees attacked was used instead of weevil numbers. Straight lines were fitted to the transformed data by the least squares method of the weighted regression (Steel and Torrie 1960).

This gave equal weight to the trees represented in each diameter class. A t-test (LeClerc et. al. 1962) was applied to the correlation coefficient (r) values in each graph to test the null hypothesis that r differs significantly from zero.

The 1961 data from plots 1 to 6 were used to analyse weevil numbers in relation to tree density. Total weevils per block area were estimated from total tree counts and from the 10 sampled trees in each block. Each block was 0.1875 acres. Tree attack incidence was used to describe the density relations in young stands.

Data from plots 1 to 7 were used to analyse weevil numbers in relation to duff depth around the bases of 4, 8, 10 and 12 inch diameter trees. Weevils found on main lateral roots were recorded separately from those found on the collar region. The two tallies were compared with respect to duff depths of different tree diameter groups. Numbers of weevils on roots and collar regions were compared to determine whether the distribution pattern of weevils remained constant on all host tree sizes. All living trees sampled from 1961 to 1965 in plots 1 to 5 were used for this analysis. The data were graphically presented and a straight line was fitted by the least squares method (LeClerc et. al. 1962). Weevil numbers in plots VII, VIII and IX were related to different sites; each site was characterized by a mean duff depth.

2.3.4. Weevil Attack Patterns: Several techniques were devised to describe weevil attack patterns in young and old stands.

Plot series I to X were established to determine the age when initial weevil invasion occurs, the pattern of tree attack and the rate of weevil spread. In plots VI to X weevil attack patterns were determined with respect and VII to tree size distributions. Each of plot series I to IV, to X commenced at a

cutline boundary where an abrupt transition occurred between regeneration and mature pine. These areas provided the conditions necessary to follow the pattern of weevil emigration from the residual mature trees where "reservoir" populations existed. Percentage trees attacked were related to distance from the stand edge.

The patterns of current attacks in young and old stands were analysed to establish a relationship between percentage of trees with current attacks and weevil numbers. This relationship was further explored as a sampling tool for survey purposes. The percentages of trees attacked, old and current attacks combined, in a variety of young to old stands were broadly related to tree density and stand age. This was to establish the cumulative attack pattern during normal stand development.

Trees in the 65-70-year old stand near plots 1 to 5 were examined to determine the nature and history of attack since the time of initial invasion. Three groups of tree sizes were selected and these were designated Small, Medium and Large. Trees within each group were selected for uniformity of size and the weevil damage characteristics of each group were considered near average for the stand.

A total of 31 tree stems were cut transversely at a level on the stump which was visually judged to represent the region of maximum weevil feeding damage (Fig. 3). Each stump was smoothed with a rotary sander to clarify annual increment boundaries and old weevil scars. The latter were dated according to approximate year of attack and an estimate was made of the total number of attacks. These were tallied by consecutive five-year intervals for each stump, and then a series of averages were obtained for each of the three groups. In addition, radial growth measurements were taken at about the

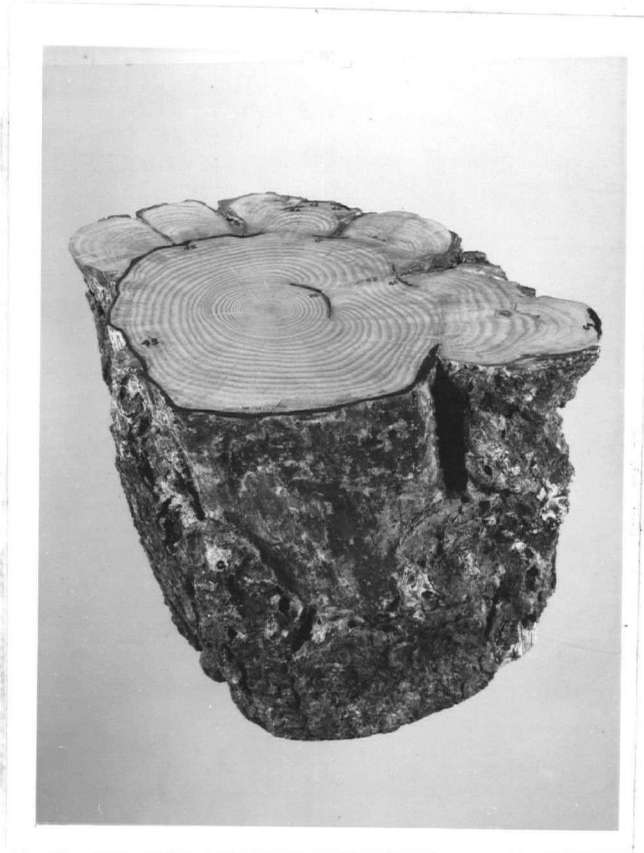


Fig. 3. Cross-section through a 66-year old pine stump at root collar level where maximum damage was observed. Weevil scars are accentuated with black ink and numbers indicate approximate years of attack. Note large patch of dead phloem and cambial tissue which occurred at the age of 43-45 years.

10-inch stump level of each tree. Each series of measurements for each tree was in turn an average of four sets of measurements taken at right angle transects upon the stump in order to reduce the error resulting from asymmetrical growth. The values for all trees within each size group were then averaged to obtain one curve for each tree group. The frequency distribution of weevil attacks for each tree group was summarized on the basis of numbers of scars per stump.

3. Studies of the Life Stages of *H. warreni*

Biological factors in distribution and abundance were considered to concern microhabitat conditions for the larvae, pupae, adults and eggs, as well as natural enemies of these stages.

3.1. Larval Stage: Observations of larvae were made to determine the number of instars, pattern of gallery initiation, feeding patterns and time of development, characteristics of bark in the larval feeding universe and mortality factors. Larval instars were determined from head capsule width measurements recorded through a stereo microscope with a micrometer eyepiece. The definition of instars by capsule measurement was used in identifying stages of development throughout the summer, in rearing experiments and in relating larval size to conditions within its feeding universe. Mature larvae extracted from pupal chambers were readily recognized as prepupae and measurements of their capsules served to indicate range of size undergoing pupation.

The survival of newly hatched larvae was tested in a moist environment within a vial in which no food was added. The larvae were

examined after five days to determine their general condition. Other first instar larvae were observed under experimental conditions to determine the manner of initial excavation into the bark tissue, and their pattern of gallery formation. The larvae were placed upon fresh pine bark sections kept moist in petri dishes. Daily observations were made for seven days when the larvae were removed and their head capsules measured.

The depth of feeding within live bark tissue may be an important aspect in successful establishment and survival of young larvae, and has implications in making estimates of its damage potential. This aspect of larval size and feeding depth was examined on 20-25-year old pine trees. Bark sections containing the galleries of early instar larvae were removed from trees, and the average depth of penetration by each larva was measured as well as total bark thickness. Head capsule widths of the corresponding larvae were recorded.

Other observations were made of gallery orientation and feeding patterns on young and old trees. Measurements of the total gallery length scored through to xylem tissue of four mature larval wounds indicated the total amount of feeding required per larva, and was an estimate of the girdling damage potential.

Field observations of larval sizes and egg rearing studies (Cerezke 1967) provided information on the general rate and period of larval development.

Two aspects of bark morphology considered important to the well being of larvae were thickness of living phloem and the presence of resin cavities formed within the phloem of the root-collar zone. Bark thickness serves both nutritive and protective roles while resin cavities are at least partly protective. The distribution of bark thickness and the distribution,

size and relative abundance of resin cavities were described on 20-25-year old pine trees. Three trees were selected from an area characterized with a moss covering of 3-5 inches. The trees were excavated intact and discs were cut from the main stem at two-inch intervals up to a height of 18 inches, thereafter at six-inch intervals to a height of four feet. The first disc was taken at the collar base. Discs were also removed, one from each of the main lateral roots at a distance of one inch from the stem axis. The bark thickness of each disc was obtained from an average of four measurements. Counts of the total number of bark resin cavities were made from the transverse cut of the bark on each disc; measurements were made using a micrometer eyepiece. The shape of the resin cavities varied from spherical to ellipsoidal and two measurements were taken of each cavity to derive an average value of the diameter. Thirty cavities were measured from each disc and the diameters were summed to obtain an overall estimate of mean cavity diameter. This value was used to estimate the total cross-sectional area of the transverse bark section occupied by resin cavities. The same procedure was applied to each disc. The total cross sectional area of the bark of each disc was calculated by treating the bark as a narrow rectangle since bark thickness and circumference can be measured directly. The length of the rectangle was an average of inside and outside bark circumference measurements. It was recognized that, although the techniques for calculating resin cavity statistics had some inaccuracies, the data appeared adequate to show the general patterns. Bark thickness and resin cavity measurements were related to distance up the stem and on the lateral roots.

Larval habitat temperatures were determined in a clearcut area and in an adjacent pine stand 65-70-years old. Soil temperatures were

recorded at four cut stumps in the open and at four tree bases in the forest using a potentiometer and thermocouple wires. The wires were inserted on the north and south aspects, and at two- and four-inch depths at each cut and non-cut stump. Readings were taken at two-hour intervals from 5:00 a.m. to 5:00 p.m. during an average sunny day in July. For comparison, air temperatures were recorded at the same time intervals. Soil temperature differences between cut and non-cut areas were related to pupae collections made in the two habitats.

3.2. Pupal Stage: Observations were made of the microhabitat conditions of pupae within its chamber. These relate to the construction of the chamber, its placement with respect to the host tree and to duff surface and to orientation of the chamber. Data from sampling and rearing provided information on time of initiation of the pupal stage and its duration. Because of their fragility most pupae were reared in moistened vials after wrapping them individually in soft tissue.

3.3 Mortality Factors of all Stages: Natural mortality factors of all stages of the life cycle were observed during field collections in all sample plots. These included internal and external parasites, predators, fungal disease and mortality due to other factors. When insect larval parasites were obtained an attempt was made to rear them through to adults. Samples of each unknown parasite and predator were submitted to taxonomic specialists for species identification. A collection of 46 shrews (Sorex cinereus cinereus Kerr.) was made from pit-fall traps located in the region of plots 1 to 5 during 1963 and 1965. Their stomach contents were examined for sclerital remains of the adult weevil.

3.4. Adult and Egg Stages: Large numbers of adult weevils were required for behavior and field experimental studies. For this purpose all adults were obtained from the Robb area. Studies of the behavior of adults were undertaken to identify and describe crucial periods during its daily and seasonal existence in the natural habitat. These periods can occur during adult dispersion in the forest and during feeding, mating and oviposition. The timing and pattern of these events need to be described to interpret survival and population changes.

Techniques were devised to describe: the distribution of adults in the forest in relation to tree size; rate and direction of adult dispersion; sequential changes in adult activity or changes in numbers during the summer period; longevity of adults; egg laying; mating and feeding. Experiments were conducted to describe adult activity hourly and daily, and in relation to light and temperature. Egg laying and mating activity were studied in the field, in the laboratory and from dissections of adults collected at intervals during the summer.

3.4.1. Collecting Methods, Adult Numbers and Sex Ratios: The task of collecting adults was tedious and time consuming. This difficulty was partly overcome with the adoption of several collecting methods. Virgin adults were reared from pupae and teneral adults collected within pupal chambers. Some mature adults were collected in the duff at tree bases during the population sampling. A third method of collection was by trapping, which made use of the trap design illustrated in Figure 4. The trap is a modification of a design used by Embree (1965) to collect winter moths. It consists of a half-gallon sized, wax-coated cardboard container with a two inch hole cut in the bottom. The top rim of a paper cup was inverted over the hole inside the

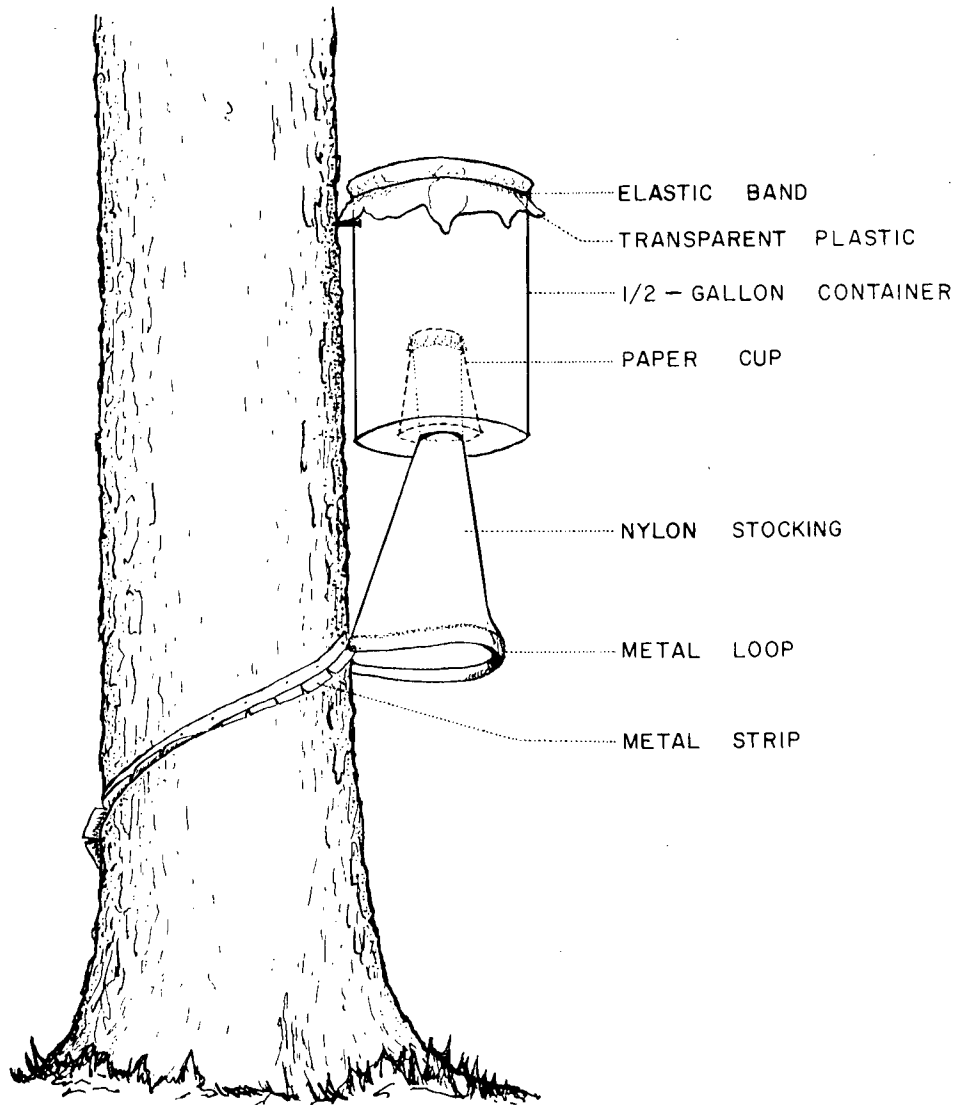


Fig. 4. Trap design used for live trapping adult H. warreni during mark-recapture studies in plots A, B, C and D.

container and glued. The bottom of the cup was also removed. A portion of a nylon stocking was passed through the bottom of the container, through the inside of the cup and glued to its outside rim. The lower end of the nylon cone thus formed was fastened to a loop on a metal strip which passed around the tree trunk. The container was fixed to the tree with a small staple directly above the metal loop. Each metal strip was cut $1\frac{1}{2}$ inches by 4 feet in length from thin galvanized sheeting. The strip was bent at right angles along its midlength to form a three-quarter inch flange when nailed around the tree trunk. The design of the trap took advantage of the entire tree circumference as a collecting surface, and of the adult habit of ascending trees during hours of darkness to feed in the upper canopy (Reid 1952). The adults were live trapped as they ascended trees. The metal flange was oriented at an oblique angle with the stem axis to act as a guide in directing the weevil to the nylon cone, and thence to the inside of the container. A small pine branch tip was placed at the bottom of the container as a food source and to attract the adult until morning. The original tops of the container were replaced with transparent plastic and fixed with an elastic band. This prevented escape of the weevils and prevented moisture from entering. In addition, the transparency appeared to be less disturbing to a weevil entering the bottom of the container since it did not shut out light from above.

Sex ratios of adults were determined from a variety of adult collections. These included living and dead adults collected at tree bases, from pupal rearings and from traps located within plot areas. In 1965 the trap method was tested on 60 trees, 30 were on ~~border~~ border trees of a clearcut strip and 30 were on trees approximately 50 feet within the same stand. Care

was taken to match the two trap tree groups by diameter size prior to the setting of traps. In 1966 traps were placed on an additional 43 trees at the border of a cut strip and all captured adults were sexed.

3.4.2. Dispersal Patterns of Adults: The patterns of terrestrial movement of adults were studied in the 65-70-year old pine stand of plots 1-5 using a capture-mark-release-recapture technique. Two circular plots, each one-fifth of an acre and 105 feet in diameter, were established as plots A and B (Fig. 2). Plot A was established in 1964; plot B in the following year. Neither plot had physical boundaries so that dispersal movement to and from the plots was unrestricted. Collecting traps as described earlier were placed, one on each living pine in the two plots and these were checked each morning. All adults present were sexed and individually coded with "Glow-color" fluorescent paint of different colors. This paint was chosen for its fast-drying, long-lasting and low toxicity qualities, and in addition, had good adhesive properties. The marking of individuals was carried out using a combination of one, two and three paint spots of the same color applied in one, two or three of six different positions on the elytral surface. These positions were designated anterior, median and posterior on each elytron. This procedure permitted the identification of a total of 41 individuals with one color combination. A different color was used to segregate the sexes. The weevils were released at the same tree base after being marked.

The position of each tree within the fifth-acre plots was measured to scale on large sheets of paper in order that the path of subsequent recaptures of marked weevils could be plotted. The trapping system was not carried out continuously throughout the summer but at varying lengths,

ranging from four to 13 days in June, July and August. Data were collected during 1964, 1965 and 1966 in plot A and during 1965 and 1966 in plot B.

A similar trapping experiment was conducted in 20-25-year old pine of the Robb Burn. During the fall of 1964 two circular plots, each 20 feet in diameter were delineated side-by-side on a weevil-free site. Each plot was enclosed with a six-inch plywood fence, on the inside surface of which a thin band of "Tree Tanglefoot" was applied. This material prevented the escape of the adults since they showed some repellency toward it. No weevils were ever found stuck within it. One application of the material each spring appeared to be adequate.

The plot arenas were designated C and D and contained 47 trees with an average d.s.h. of 2.1 inches and 49 trees with an average d.s.h. of 2.1 inches respectively. The position of each tree was plotted to scale as in plots A and B. Fifty newly emerged adults (including 30 virgin females and 20 males) were placed in each arena during the fall of 1964 after each had been coded with paint for individual recognition. Traps were placed on 20 of the largest trees in each plot in the spring of 1965 and trapping was followed at intervals during the summers of 1965 and 1966, as described for plots A and B. Fresh pine tips were added to the traps every few days. A hygrothermograph enclosed in a Stevenson's screen was positioned immediately adjacent to plots C and D to record temperature and humidity at ground level.

The data from the four plots were analyzed in various ways. Absolute numbers of adults could not be determined in plots A and B but relative numbers were obtained by the mark-recapture method. The weevils were expressed as mean numbers captured per day during three and four sequential periods of the summer. For plot and year comparisons adults were expressed as numbers of adult captures per day per trapping day. The mark-

recapture data from plots C and D were analysed similarly.

The adults captured and recaptured during 1964, 1965 and 1966 in plots A and B were analysed to describe rate of dispersion in the forest. Linear distances between trap trees where the same weevils were captured, and the time in number of days between recaptures were used as a measure of dispersion. These distances were measured from the scale drawings of plot areas. The average rate of linear travel during any one night by an adult was related to the average distance between trees, and to the average distance from each tree to its nearest neighbor. Average distance between trees was estimated by dividing the total area (ft.²) by the number of trees. This estimate of the mean area occupied per tree was converted to a square, the length of the side of which provided a measure of the average distance between trees. In the case of nearest tree neighbor, the distance from each tree in the plots to its nearest neighbor tree was measured and an average obtained for all trees.

The data from plots A and B were analysed separately for directional movement of adults. Only those trees were considered where the same individual weevil was recaptured on two consecutive mornings. In each case the tree with the first capture was considered as the origin and from it the direction of the second tree was measured as a deviation in degrees from cardinal north. The observations were then totalled into eight 45-degree quadrants. A chi square test was performed for a 1:1:1:1:1:1:1:1 ratio of males and females separately in each plot.

3.4.3. Weevil Reproduction: Several field and laboratory experiments were established for making observations on a variety of aspects of weevil reproduction. These studies are identified under separate experiments below.

Experiment 1: The pattern of oviposition was observed from tree base examinations in plots C and D at the end of the summers of 1965 and 1966. Total larvae, total eggs and their positions on the host were observed. In order to test the effect of duff depth upon egg laying behavior a layer of fresh sphagnum mosses was placed around each tree base in plot C in the spring of 1966 (Fig. 5). The duff depth was thereby increased to 4-5 inches. Plot D remained as a control with no addition of moss, and had a duff thickness of 1-2 inches. The number of eggs plus larvae per tree in 1966 was analysed with respect to tree diameter. The least squares method of a weighted regression was used to fit lines. Standard errors of the mean ($S_{\bar{x}}$) were calculated for total eggs and larvae collected in each tree diameter class. Correlation coefficient (r) values were computed for each plot.

Experiment 2: The patterns of oviposition and egg hatch were observed after paired adults were enclosed in transparent plastic cups. These were inverted and held firmly with wire on the outer bark surface of tree bases. All cups were positioned immediately above the duff layer for ease of observation and were shaded from direct sunlight. A fresh pine branch tip was supplied regularly as food. Twenty weevil pairs were thus prepared in July, 1964 and were left for a period of about three weeks. The cups were then removed and the position of each egg was marked with a pin. The eggs were checked for hatching throughout the fall of 1964 and again in the spring of 1965.

Experiment 3: The fecundity and laying frequency were determined during the period from June 1 to August 23, 1964. Twenty-four pairs of adults



Fig. 5. Circular-shaped plot C located in the Robb Burn showing trap attachment to the main stems of the largest trees. Note layer of *Sphagnum* mosses placed around each tree base and a band of "Tree Tanglefoot" on the inside surface of the arena wall.

were enclosed in paper cups inverted over fresh pine bark sections which were kept moist in petri dishes. The top of each cup was covered with screen mesh to prevent escape of the adults. This allowed the female minimal contact with the outer bark surface. A fresh pine branch tip was added frequently as food. Daily checks were made of oviposition and a record was maintained of total eggs laid by each female. All eggs were transferred to moistened paper and stored in petri dishes for hatching.

The average egg productivity was expressed as the number of eggs laid per female per day. Maximum fecundity per female during the total summer period was estimated by multiplying the average number of eggs laid per female per day by 103 days. This value of 103 was considered a reasonable estimate of the total egg laying period, extending from May 20 to August 31.

The periodicity of oviposition was analysed by using the eggs laid in 10-day intervals consecutively throughout the summer. For each 10-day period egg production was expressed as the average number of eggs laid per female per day.

Experiment 4: Egg viability and period of embryonic development were studied from 39 paired weevils reared in 70 ml. vials during the summer of 1965. A small amount of moss with a few drops of water added periodically to each vial kept the environment moist. Fresh pine tips were added regularly as food. The vials were stored in a ventilated box submerged a few inches in the ground within the Robb Burn. The rearing period extended from July 1 to the first week of September, and eggs were collected at about 10-day intervals. These were transferred to sealed vials, maintained in an atmosphere saturated with moisture and stored in the ventilated box until hatching was complete. The average period of embryonic development and

percentage hatch were calculated for each group of eggs from a 10-day period.

Experiment 5: Some effects of temperature upon oviposition and early development of progeny were observed in specially constructed plastic cages (Cerezke 1967). Thirty pairs of adults were enclosed, one pair per cage, during June, July and August of 1966. Two cages were fastened to a pine stump which sat in a pan of moist moss, and 15 pine stumps were thus prepared. Cages 1 to 10 were maintained at normal day-night light and temperature conditions. Cages 11 to 20 and 21 to 30 were stored in cabinets maintained at constant 60° F and 50° F respectively. Temperature fluctuations in each cabinet were of the order $\pm 1.5^\circ$ F. A light intensity of about four candle power was supplied to the two cabinets. The fluorescent lights were controlled with a timer to provide light during the hours from 5:00 a.m. to 8:30 p.m.; the remainder of the day was in darkness. Weevil rearing was terminated after 50 days when the contents of all cages were carefully examined for numbers of eggs and larvae. The position of all eggs and larvae was noted. Egg productivity for each caged group of 10 females was expressed as numbers of eggs laid per female per day. Total counts of eggs included all larvae observed.

Experiment 6: The development and gross changes in the fat body and reproductive structures were observed from 36 dissected females collected at different periods during the summers of 1964 and 1965. The fat bodies and ovaries were given relative ratings of size; small, medium and large. The criteria of ovary size was based upon counts of oocytes per four ovarioles present in each female as follows: small = 12-24 oocytes; medium = 25-36 oocytes and large = 36+ oocytes. Lengths of the germarium portions of

ovarioles were measured to determine changes in size as a result of maturation. Also, lengths of spermathecal glands were measured to provide an index of mating and the egg laying condition. Spermathecae were examined for the presence of spermatozoa and the vaginal pouch was checked for presence of spermatophores. These two characteristics helped to separate virgin from mated females.

3.4.4. Light and Temperature Response and Orientation of Adults: A series of experiments were conducted to describe the daily activity patterns of adult weevils within their natural habitat. Activity was assessed in relation to temperature, time of day and orientation within the forest.

Experiment 1: The influence of night temperatures upon weevil movement up tree stems was analysed from captured adults collected daily in the traps of plots C and D. Only the data collected during June, 1965 and 1966 were used. During the first stage of the analysis total daily captures were correlated with temperatures recorded during the previous night at hourly intervals from 8:00 p.m. until 1:00 a.m. A correlation coefficient value (r) was calculated for each set of temperatures. These were plotted over time to indicate the hour of maximum correlation. The temperatures were extracted from hygrothermograph charts. In the second phase of analysis weevil numbers were plotted over temperatures recorded at this r-maximum hour. A linear regression was fitted to the data.

Experiment 2: This experiment was established to observe the time of emergence of adult weevils from the duff during the evening, and the pattern of orientation above the duff surface. The experimental site was in a clearing of approximately one acre within the Robb Burn. A patch of ground

was smoothed near the center of the clearing and a small circular arena, 90 cm. in diameter was constructed. Transparent acetate plastic, 10-mil in thickness and about 10 cm. high was used as the arena wall. A narrow band of "Tree Tanglefoot" was placed around the inside wall to discourage escape of adults. Ten-degree intervals were marked on the wall to facilitate the plotting of adult directional movement. A sapling sized pine tree and a post were positioned upright outside the arena at a distance of about two meters from the center of the arena. Weevils were placed in the center of the arena and covered with moss in the early evening. Their time of appearance from the moss and path of movement were noted. Ground surface temperatures and light intensity were recorded at 15-minute intervals. Observations were made on June 15, 21, 23, 27 and July 6, 1966. The pattern of directional movement was tallied into 20-degree quadrants to determine whether the tree or post served as visual cues in guiding lateral movement over the forest floor.

Experiment 3: This experiment was conducted to observe behavior of male and female adults confined to a small arena. An oval shaped arena was constructed using plywood and Tree Tanglefoot as described previously, and enclosed two trees in the 65-70-year old stand. The smaller tree was four inches and the larger was 12 inches (d.s.h.). A scaffold was constructed around the trees to observe weevil behavior up the trees to a height of 21.5 feet (Fig. 6) where a ring of Tree Tanglefoot was placed around the main stem axes. Ten weevils of each sex were coded with paint and placed in the arena on July 16, 1963. Hourly checks were made for the next three days. General behavior patterns were described for each sex.



Fig. 6. Arena and scaffold enclosing two pine trees in the 65-70 year old stand used for adult weevil behavior studies. White markers on the tree stem measure one-foot intervals.

3.4.5. Adult Feeding Pattern

Experiment 1: Two small arenas, six and seven feet in diameter respectively were constructed in the Robb Burn to observe feeding behavior of adult weevils. Each arena surrounded one co-dominant tree. A small number of adults was placed in each arena and left throughout the summer. Counts were made at the end of the summer of the number of feeding scars on each branch at each internode level, and an average value was calculated for each internode up the tree. The distance out on the branch from the main stem of each feeding scar was also measured and whether it occurred on the upper or lower surfaces of the branch stock.

Experiment 2: Observations of adult feeding were made on terminal shoots of 6-8-year old pine and on seedlings 1-2 inches high. In the latter case four two-foot square arenas which enclosed several seedlings each were constructed. A few adult weevils were placed in each arena and daily checks were made of the seedlings for evidence of feeding. The experiment was terminated after two weeks.

4. Studies of the Effects of Weevil Damage to Trees

The main objective of these studies was to assess the impact of weevil injury upon its host tree, and determine how the damage may effect the stand as a whole. Larval feeding was considered to have an effect upon the host's defense mechanisms against foreign injury, upon tree mortality and growth reduction and upon changes in stand structure. These effects in turn have implications in short and long term influences upon weevil survival and abundance.

The effect of weevils on trees was studied by measurements of shoots,

needles and ring increments. Observations were made of changes in the resin duct system and tracheid infiltration, and of wound repair patterns.

4.1 Anatomical Effects: The root-collar zone of a variety of sizes and ages of pine were examined for effects of weevil damage. Cross-sections of main stems and of lateral roots and taproots were made adjacent to larval feeding sites. The freshly cut sections were soaked in 70 percent ethanol for a few days to fix intracellular starch and to dissolve excess resin. Vertical resin ducts were differentiated with a starch-reacting stain of iodine, consisting of 0.4 gms. I_2 + 1.8 gms. KI per 100 ml. water (Reid, personal communication). After they were dry the discs were sanded smooth with a rotary sander to clarify ring boundaries and old weevil scars. Cellular details in the xylem were made more visible with an application of several coats of a clear laquer such as "Urethane". Discs prepared in this manner could be examined under magnification of at least 50 times.

4.2. Growth Loss Effects: Some effects of weevil girdling damage to trees were studied in two young pine stands to estimate growth loss in stem terminals, upper branch whorls, needles and of radial increment. Twenty pine trees in the dominant to co-dominant category in the Robb Burn stand and 21 similar sized trees seven miles south of Grande Prairie (Fig. 1, area 3) were selected for growth measurements. The pine stand near Grande Prairie was several acres in extent, 20-25-years old and probably originated from fire and natural seeding. The area lies immediately outside the Lower Foothills Section. In the two areas, 1 and 3 respectively (Fig. 1), 10 and 11 trees were located which had current or very recent weevil damage amounting to about 50 percent girdling of the root collar circumference. The remainder 10 trees in each

area were selected as controls and had no attacks. Care was taken to locate these trees as near as possible to the attacked trees and having characteristics of size, crown shape and competitive aspects similar to the attacked group. The measurements were made during June and July, 1965 in the Robb Burn and in September, 1966 in the stand near Grande Prairie.

All trees were excavated with most of the roots intact to allow careful examination of the root and collar regions for hidden weevil wounds. Tree age was determined at about the one-inch stump level. The extent of the collar girdled to xylem tissue on each attacked tree was accurately measured after all bark was removed from the root collar zone. This was expressed as a percentage of the inside bark circumference. The periods of weevil damage were dated from discs removed immediately above the level of wounding. The earliest ring showing traumatic resin duct formation was recorded as the year of initial attack. An average year of attack was then calculated for each group of attacked trees. Terminal branch lengths of the 1963 and 1964 growths were measured on trees from the Robb Burn. Also, the lengths of all 1964 laterals of the top whorl and all 1963 laterals of the second top whorl were measured. The lengths at each whorl were averaged for each tree and an overall average was calculated for each tree group. In addition, 25 needles were removed from near mid-length of all 1964 and 1963 laterals; their lengths were determined and an overall average per year per tree group was calculated. Overall averages of the 1963 and 1964 terminal lengths were similarly determined.

On trees from the Grande Prairie area measurements were made of the 1966, 1965 and 1964 terminal lengths, and of the 1966, 1965 and 1964

lateral branch lengths of the top, second-top and third-top whorls respectively. Their lengths were averaged similarly as in the Robb Burn group. No measurements were made of needle lengths.

The effects of weevil damage on stem growth increment were analysed by using the three-dimensional growth patterns defined by Duff and Nolan (1953) for Pinus resinosa. The procedure used was similar to that of Mott et. al. (1957) and Stark and Cook (1957) who applied the Duff and Nolan growth sequence patterns to the analysis of insect defoliation damage on lodgepole pine, balsam fir and eastern larch. For the terminology, definition and theory of the three growth measurement sequences as they relate to insect-caused damage, the author refers to Graham (1963). Only the essential characteristics of each sequence are given below.

Type 1, or oblique sequence is a series of ring thickness measurements taken at each internode from the top to the base of each annual conical shell of wood. The values in each series of measurements characteristically rise to a maximum in the first few internodes, then gradually decline toward the base of the stem. The pattern is claimed to be due to nutritional gradients in the stem. The influence of extrinsic and intrinsic factors on growth may appear as a shift in the average level of line which defines the inherent physiological gradient of values at the internodes.

Type 2, or horizontal sequence is a series of measurements of ring widths in a transverse section across a chosen internode. Increment values rise to a maximum in the first few rings and gradually decline towards the periphery in a similar manner as in the oblique sequence. The strong pattern

in the first few rings is derived from the type 1 sequence and is also due to nutritional gradients since each ring is produced by progressively older cambia. Thus the decline towards the periphery, as well as the systematic intrinsic variations, tend to mask the effects of random extrinsic factors.

Type 3, or vertical sequence is a series of measurements made downward at successive internodes on rings produced by cambium of similar cambial age. It is thus free from effects of nutritional gradient or cambium age and is theoretically the best suited of the three sequences to portray the influence of extrinsic factors on radial growth in different years.

In preparing the trees for growth measurement sequences, discs of wood were removed near the lower third of at least the top 10 internodes of the axis and a bottom disc at the 10-inch stump level. Ring widths were measured in four radii at right angles on each disc and an average was calculated for each year's growth on each disc down the stem of each tree. Ring width measurements were made under a dissecting microscope to a tenth of a mm.

For the oblique sequence measurements of the Robb Burn trees, five annual increments were used; 1958, 1959, 1962, 1963 and 1964. The first two years represent the pre-attack period for most attacked trees while the last three increments represent the post-attack period of some trees. Attacked trees from the Grande Prairie area were treated similarly; i.e., 1960 and 1961 increments represent the pre-attack period for most trees while 1962, 1963, 1964, 1965 and 1966 increments cover the period during and after attack.

All annual increments from the pith to the stem periphery at the 10-inch stump level were used for the horizontal sequence measurements. In

the vertical sequence the second ring from the pith was measured at each internode of all trees.

For the final analysis the data for each group of 10 and 11 trees were grouped to give a combined average of each year's growth at each internode level. The data have been plotted separately according to attacked vs. non-attacked tree groups, separately for each area and separately by growth sequence.

RESULTS

1. Distribution of Hylobius Warreni

The distributions of H. warreni and H. pinicola in western Canada and the United States are illustrated in Figure 7. They coincide approximately with the Boreal Forest Region. Although the patterns of the species overlap considerably the data indicate that H. pinicola occupies a more northerly pattern. Adults of H. warreni were found as far north as 50 miles beyond the northern Alberta boundary and in the Cypress Hills in the southeastern extremity of the province. Several isolated populations of H. warreni exist on islands off coastal British Columbia and southern Alaska, as well as in the Cypress Hills. No collections of either species have been reported south of the Alberta and British Columbia boundaries.

The known distribution of H. warreni in Alberta is indicated in Figure 8. Although the northern half of the province has not been adequately covered by surveys, most adult collections were from lodgepole pine forests along the foothills of the Rocky Mountains. Within the range of lodgepole

Fig. 7. Known distribution of Hylobius warreni and H. pinicola in western Canada and Alaska. Points in British Columbia and the Yukon Territory were taken from Grant (1966).

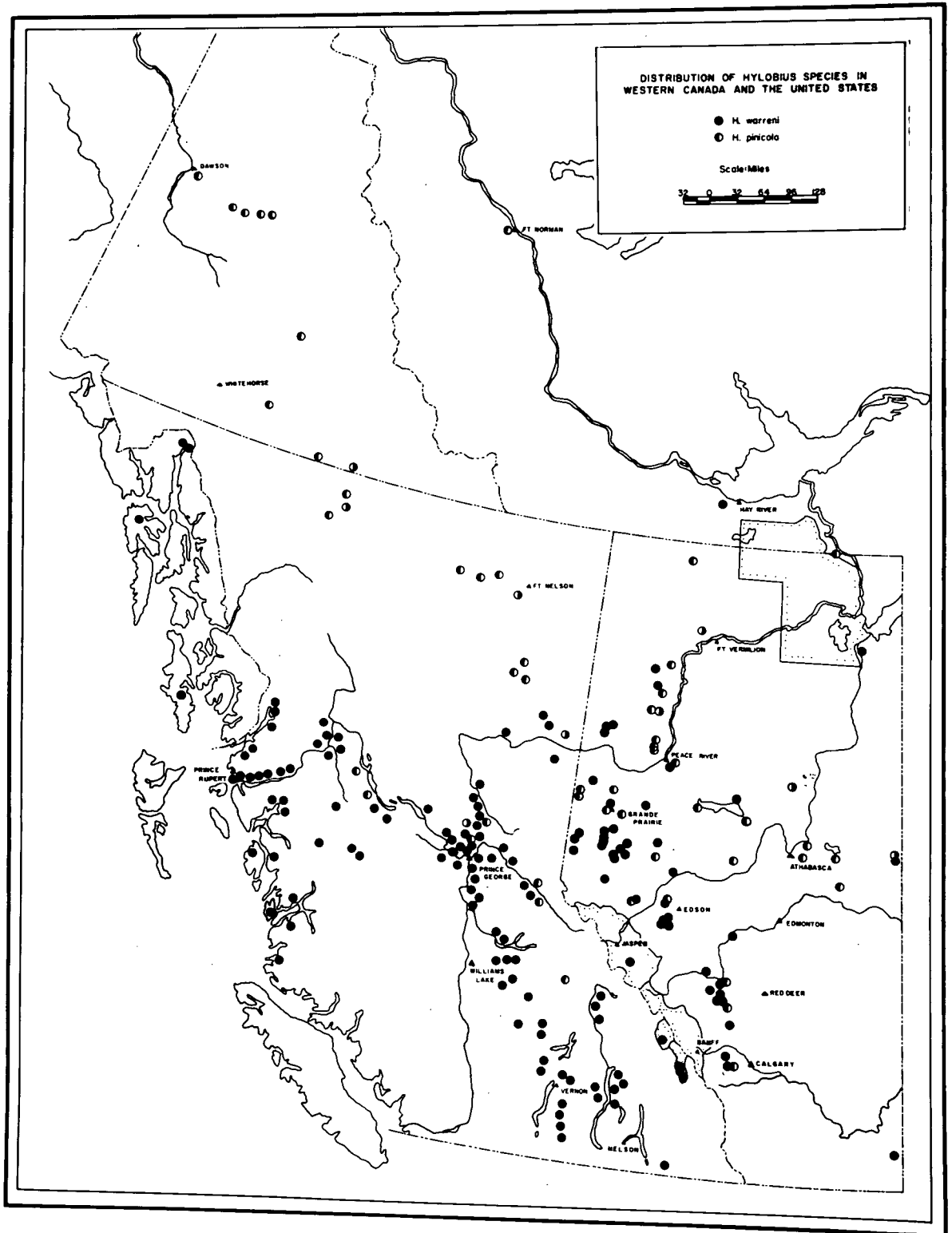
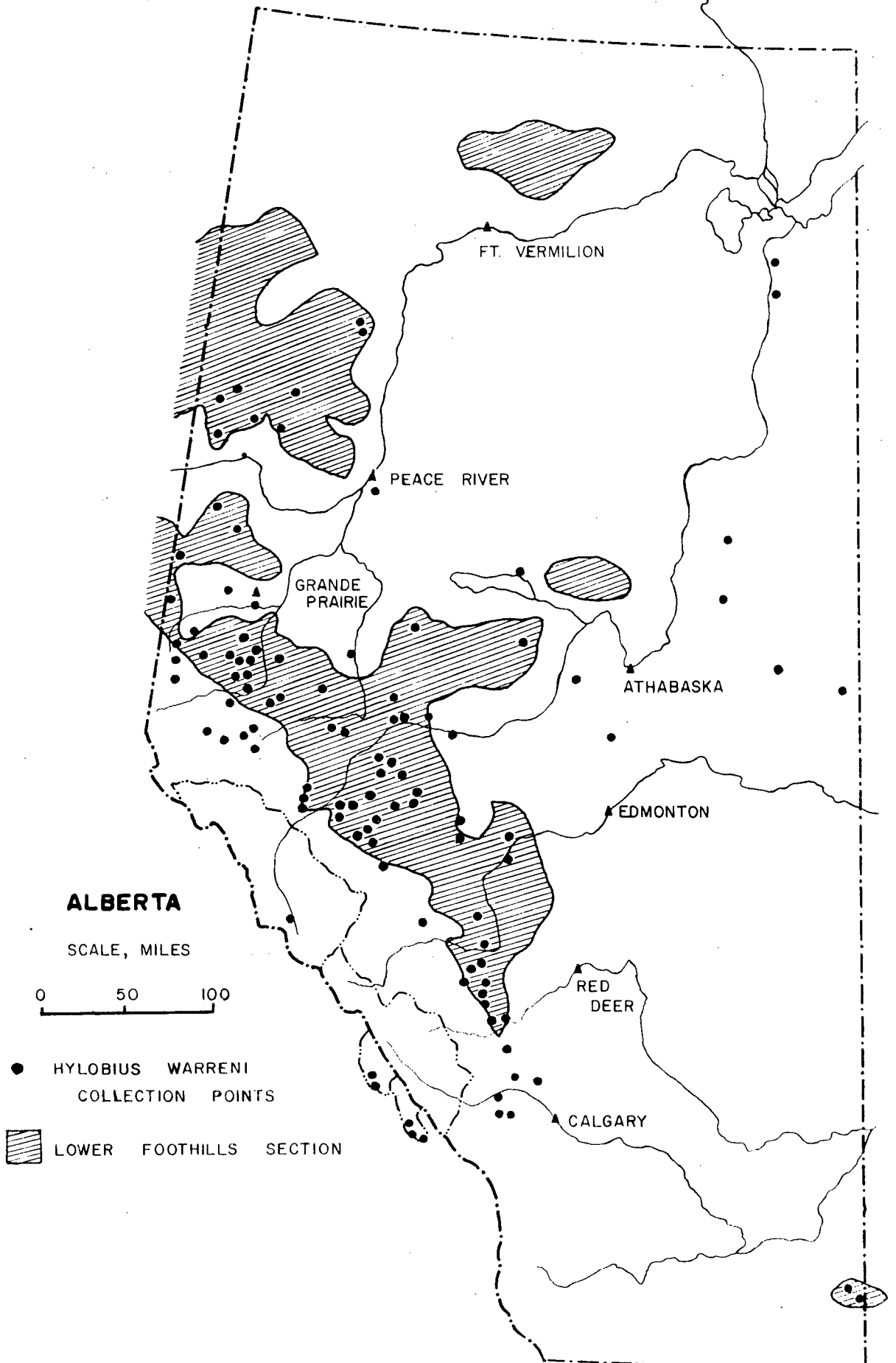


Fig. 8. Map of Alberta showing the distribution of H. warreni in relation to the Lower Foothills Section.



pine greatest continuity of the weevil occurs in the Lower Foothills Section, occupying an area roughly between Calgary and north of Grande Prairie.

Collections of the adult were also obtained in restricted localities at valley bottoms in Jasper, Yoho and Kootenay National Parks. No collections or evidence of damage were observed in forested areas south of Calgary.

Throughout Alberta collection points of H. warreni have ranged in altitude from 700 feet some 20 miles south of Lake Athabasca to near 5000 feet 40 miles west of Calgary. Along the foothills, within the range of lodgepole pine, collection points varied from 5000 feet west of Calgary to about 2500 feet in the Peace River district.

The distribution patterns of H. warreni and H. pinicola have been prepared from adult collections, but the host species involved have not always been a valid indicator of the preferred hosts. This is true except where larval feeding has been associated with the collection. For example, in Alberta mature adults of H. warreni and H. pinicola have been removed from a Populus species and a Salix species respectively. No adult H. pinicola specimens were found in the study areas of lodgepole pine.

2. General Characteristics of the Weevil Habitat

The distribution of tree stem frequencies of plots 1 to 5 is described in Figure 9; tree diameters varied from 3 to 16 inches (d.s.h.). Other stand statistics measured in 1965 are summarized below.

Mean tree diameter (d.s.h.)	-----9.0 ins.
Average age	----- 67 years
Average height	----- 60 ft.
Average density	----- 481 trees per acre

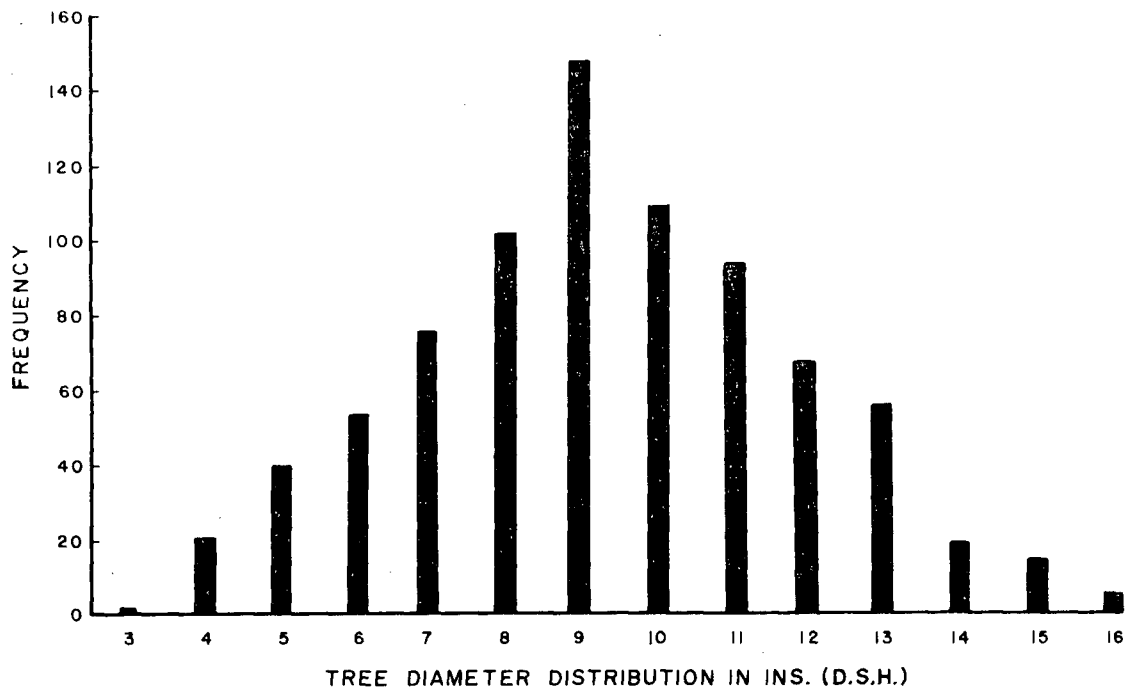


Fig. 9. Tree diameter frequency distribution of sampled trees in plots 1 to 5 during 1961. The number of trees used was 800.

The soil profile of the region of plots 1 to 5 can be described as a Textural Podzol which is considered as an intergrade between the Podzol and the Grey Wooded Soil Groups. Horizon descriptions are summarized as follows.

- L - H : $\frac{1}{2}$ - 1 inch; decomposing organic layer consisting of decaying pine needles, twig and litter of alder and other ground floral species; mostly black in color; abundant mycelia present; line of demarcation between L-H and Ae fairly sharp.
- Ae : 1 - $1\frac{1}{2}$ inches; medium greyish yellow-red yellow (10 YR 5/2); generally strongly eluviated; fine sandy-clay-loam; fine granular, loose and structureless to weakly platy; friable; thin AeB sometimes present or Ae may be weakly defined.
- Bft : 3 - 4 inches; fairly dark yellow-red-yellow (10 YR 4/4); layer is enriched with hydrated iron, some organic matter and silicate clay; silty-clay-loam to very fine sandy-clay-loam; fine granular to weakly blocky, sometimes platy; friable; few traces of carbon; gleying generally present with mottles often prominent in the lower B horizon.
- BtFC : 8 - 12 inches; medium dark reddish yellow (2.5 Y 5/4); a layer of variable thickness gradually intergrading into the C horizon; fine sandy clay; fine granular, weakly blocky to fragmental and weakly platy; friable to firm; gleying generally present; stones of variable size scattered throughout the B horizon.
- C : Begins 12 - 18 inches down; medium dark reddish yellow (2.5 Y 5/4); fine sandy to sandy clay; fine granular, fragmental to weakly blocky; firm; scattered stoniness throughout; gleying and mottling present.

TABLE I. LIST OF GROUND FLORAL SPECIES REPRESENTATIVE OF THE 65 - 70-YEAR OLD PINE STAND OF PLOTS 1 TO 5.

Species	Relative abundance	Species	Relative abundance
<u>Mosses</u>			
<i>Calliergonella schreberi</i>	V.A.	<i>Viola (nephrophila ?)</i>	C.
<i>Brachythecium</i> sp.	C.	<i>Aster conspicuus</i>	F.C.
<i>Hylocomium splendens</i>	C.	<i>Lycopodium annotinum</i>	F.C.
<i>Hypnum crista-castrensis</i>	C.	<i>Mitella nuda</i>	F.C.
<i>Polytrichum commune</i>	C.	<i>Equisetum sylvaticum</i>	S.
<i>Bryum</i> sp.	F.C.	<i>Gymnocarpium dryopteris</i>	S.
<i>Ditrichum</i> sp.	F.C.	<i>Lycopodium obscurum</i>	S.
<i>Polytrichum juniperinum</i>	F.C.	<i>Mertensia paniculata</i>	S.
<i>Timmia austriaca</i>	F.C.	<i>Pyrola secunda</i>	S.
		<i>Streptopus amplexifolius</i>	S.
<u>Herbs</u>			
* <i>Aralia nudicaulis</i>	C.	<u>Shrubs</u>	
<i>Arnica cordifolia</i>	C.	<i>Alnus crispa</i>	V.A.
<i>Calamagrostis canadensis</i>	C.	<i>Rosa acicularis</i>	C.
<i>Cornus canadensis</i>	C.	<i>Spiraea lucida</i>	C.
<i>Epilobium angustifolium</i>	C.	<i>Viburnum edule</i>	C.
<i>Linnaea borealis</i>	C.	<i>Rubus strigosus</i>	F.C.
* <i>Maianthemum canadense</i>		<i>Vaccinium caespitosum</i>	F.C.
var. <i>interius</i>	C.	<i>V. membranaceum</i>	F.C.
<i>Pyrola asarifolia</i> var.		<i>Ledum groenlandicum</i>	S.
asarifolia	C.	<i>Lonicera involucrata</i>	S.
<i>Rubus pubescens</i>	C.	<i>Ribes lacustre</i>	S.
		* <i>Vaccinium myrtilloides</i>	S.

V.A. = very abundant; C. = common; F.C. = fairly common; S. = scattered or scarce

* Denotes key indicator plants of the Lower Foothills Section.

Scientific names of plant species are according to Conard (1956) and Moss (1959).

TABLE II. LIST OF GROUND FLORAL SPECIES REPRESENTATIVE OF AVERAGE SITE CONDITIONS IN THE ROBB BURN.

Species	Relative abundance	Species	Relative abundance
<u>Mosses and Lichens</u>			
		<i>Fragaria virginiana</i>	
		var. <i>glauca</i>	F.C.
<i>Polytrichum commune</i>	C.	<i>Equisetum scirpoides</i>	F.C.
<i>Cladonia</i> sp.	F.C.	<i>Oryzopsis (pungens ?)</i>	F.C.
<i>Cladonia</i> sp.	F.C.	<i>Viola adunca</i>	F.C.
<i>Cladonia</i> sp.	F.C.	<i>Gentianella amarella</i>	
<i>Peltigera aphthosa</i>	F.C.	ssp. <i>acuta</i>	S.
<i>Peltigera canina</i>	F.C.	<i>Pedicularis labradorica</i>	S.
<u>Herbs</u>		<u>Shrubs</u>	
<i>Antennaria neglecta</i>	C.	<i>Vaccinium vitis-ideae</i>	V.A.
<i>A. parviflora</i>	C.	<i>Arctostaphylos uva-ursi</i>	C.
<i>Cornus canadensis</i>	C.	<i>Rosa acicularis</i>	C.
<i>Elymus innovatus</i>	C.	<i>Ledum groenlandicum</i>	F.C.
<i>Epilobium angustifolium</i>	C.	<i>Salix</i> sp.	F.C.
<i>Linnaea borealis</i>	C.	<i>Betula pumila</i> var.	
<i>Achillea millefolium</i>	F.C.	glandulifera	S.
<i>Aster ciliolatus</i>	F.C.	<i>Shepherdia canadensis</i>	S.
		* <i>Vaccinium myrtilloides</i>	S.

V.A. = very abundant; C. = common; F.C. = fairly common; S. = scattered or scarce.

* Denotes key indicator plant of the Lower Foothills Section.

Scientific names of plant species are according to Conard (1956) and Moss (1959).

A list of ground floral species characteristic of the 65-70-year old stand of plots 1 to 5 is given in Table I. For comparison, Table II shows the species representative of the Robb Burn. The relative abundance of each species is expressed as one of four categories. Only seven species were common to the two pine stands; the relative abundance rating of these were identical except for one species. Several species included in Table II, such as the lichens, Archtostaphylos uva-ursi and Antennaria spp. are indicative of a dry habitat. Key indicator plants of the Lower Foothills Section are indicated with an asterisk.

The various plant canopy layers and their approximate percentage cover of the forest floor in the 65-70-year old stand are described in Table III. Five distinct canopy strata were recognized at 2 ins., 4 ins., 12 ins.,

TABLE III. VEGETATIONAL CANOPY STRATA OF FOUR SMALL PLOTS IN THE 65 - 70-YEAR OLD PINE STAND.

Canopy layers	Percentage ground surface coverage	Ave. height of dominant species forming distinct canopy layers
Moss species	82	2 inches
Herbs and low shrubs	65	
<u>Cornus canadensis</u>	-	4 inches
<u>Aralia nudicaulis</u>	-	12 inches
<u>Alnus crispa</u>	15	9 feet
<u>Pinus contorta</u> var. <u>latifolia</u>	-	60 feet

9 ft. and 60 ft.

Forest floor levelness in the 65-70-year old stand was found to undulate on the average of 5.9 inches in height every 4.7 feet horizontally. The main causes of this appeared to be from tree uprooting and from decaying logs. The latter were abundant in this stand and most were covered with a growth of moss species. Decaying logs and pitting of the ground surface were far less abundant in the Robb Burn. This reduction was partly the result of a sanitation harvest of the burnt snags, and partly because the stand was largely 40-50-years old at the time of the burn. In contrast, the stump diameters of some standing snags in the older stand were in excess of 15 inches.

3. Weevil Abundance, Their Change with Time and Attack Density

The sampled trees of plots 1 to 5 are summarized in Tables IV, V and VI, according to individual strips A, B, C and D for each plot and year. Table VII summarizes the tree characteristics of plots 6 to 10. The coefficient of variation values of tree diameter range between 19.4 and 34.6 percent. They indicate that the method of tree selection provided sufficient randomization. Tree density in plots 1 to 5 varied from 356 to 525 trees per acre as calculated from strip totals; densities in plots 6, 7, 9 and 10 were considerably higher.

Weevil numbers collected in plots 1 to 5 are summarized in Tables VIII, IX, and X, and in Table XI for plots 6 to 10. The 1965 data of plots 1 to 5 were combined for all C strips and all D strips (Table XI). In all cases the variance (s^2) is greater than the mean (\bar{x}), indicating that the weevil populations were contagious.

TABLE IV. SUMMARY OF STAND DENSITY AND TREE DIAMETER (D.S.H.) CHARACTERISTICS IN H. WARRENI SAMPLING PLOTS 1 TO 5 DURING 1961.

Plot and strip	trees/acre	N	\bar{Y}	R	S	C.V.
Plot 1: A	469	40	8.68	5-12	1.99	23.0
B	431	40	9.03	3-15	2.88	31.9
C	488	40	8.08	4-11	1.93	23.9
D	481	40	8.55	4-14	2.39	27.9
Plot 2: A	394	40	9.93	6-15	2.13	21.5
B	369	40	9.68	5-15	2.55	26.4
C	356	40	10.48	6-16	2.54	24.3
D	363	40	9.58	4-16	2.69	28.1
Plot 3: A	413	40	8.80	3-14	2.61	29.7
B	425	40	9.30	4-16	1.88	20.2
C	469	40	9.88	4-15	2.54	26.2
D	444	40	8.80	4-15	2.83	32.2
Plot 4: A	506	40	9.15	4-15	2.65	28.9
B	494	40	9.08	4-14	2.79	30.7
C	506	40	8.63	4-14	2.38	27.6
D	444	40	9.05	4-14	2.43	26.8
Plot 5: A	525	40	8.55	3-14	2.25	26.4
B	500	40	8.35	4-13	2.34	28.0
C	494	40	8.45	4-14	2.44	28.9
D	456	40	8.73	4-13	2.57	29.5

N = number of trees sampled,

\bar{Y} = mean tree diameter per 40 sampled trees in inches,

R = range of tree diameter (s. h.) in inches per 40 sampled trees,

S = standard deviation of the diameters of 40 sampled trees,

C.V. = coefficient of variation of the diameters of 40 sampled trees.

TABLE V. SUMMARY OF TREE DIAMETER CHARACTERISTICS IN H. WARRENI
SAMPLING PLOTS 1 TO 5 DURING 1962.

Plot and strip	N	\bar{Y}	R	S	C.V.
Plot 1: A	40	8.50	5-12	1.80	21.2
B	40	8.63	5-12	1.96	22.7
C	40	8.63	4-12	2.34	27.1
D	40	8.55	4-14	2.79	32.7
Plot 2: A	40	9.18	5-13	1.78	19.4
B	40	8.88	5-14	2.42	27.3
C	40	9.98	5-15	2.82	28.2
D	40	9.68	5-17	2.64	27.3
Plot 3: A	40	8.78	4-15	2.59	29.5
B	40	8.95	6-13	1.89	21.2
C	40	8.68	4-14	2.69	31.0
D	40	9.28	3-14	2.74	29.5
Plot 4: A	40	8.48	3-16	2.28	26.9
B	40	8.40	4-14	2.36	28.1
C	40	9.28	6-13	1.95	21.0
D	40	9.48	4-15	2.22	23.4
Plot 5: A	40	8.45	4-13	2.20	26.0
B	40	8.73	4-12	1.91	21.9
C	40	8.98	4-15	2.59	28.8
D	40	8.73	5-13	2.39	27.4

N = number of trees sampled,

\bar{Y} = mean tree diameter per 40 sampled trees in inches,

R = range of tree diameter at stump height in inches per 40 sampled trees,

S = standard deviation of the diameters of 40 sampled trees,

C.V. = coefficient of variation of the diameters of 40 sampled trees.

TABLE VI. SUMMARY OF TREE DIAMETER CHARACTERISTICS IN H. WARRENT
SAMPLING PLOTS 1 TO 5 DURING 1963.

Plot and strip	N	\bar{Y}	R	S	C.V.
Plot 1: A	40	8.3	4-12	1.97	23.7
B	40	8.0	4-12	2.06	25.8
C	40	8.1	3-14	2.66	32.9
D	40	9.0	4-15	2.39	26.5
Plot 2: A	40	8.1	4-12	2.12	26.2
B	40	8.3	4-13	2.42	29.2
C	40	9.6	4-16	2.15	22.4
D	40	10.0	5-15	2.24	22.4
Plot 3: A	40	8.5	4-12	2.39	28.1
B	40	8.6	4-13	2.21	25.7
C	40	9.5	3-13	2.12	22.4
D	40	9.4	4-16	2.52	26.8
Plot 4: A	40	8.6	4-15	2.53	29.4
B	40	8.8	5-13	2.27	25.8
C	40	9.5	5-15	2.45	25.8
D	40	9.3	4-13	2.26	24.3
Plot 5: A	40	7.7	3-12	2.20	28.6
B	40	8.0	4-12	2.06	25.8
C	40	8.1	4-14	2.80	34.6
D	40	8.3	3-13	2.55	30.8

N = number of trees sampled,

\bar{Y} = mean tree diameter per 40 sampled trees, in inches,

R = range of tree diameter at stump height per 40 sampled trees,

S = standard deviation of the diameters of 40 sampled trees,

C.V. = coefficient of variation of the diameters of 40 sampled trees.

TABLE VII. CHARACTERISTICS OF TREES SAMPLED FOR H. WARRENI POPULATIONS IN SEVERAL PLOT AREAS OF MATURE PINE.

Plot and year	No. of trees/acre	N	\bar{Y}	R	S	C.V.
Pts. 1-5: C, 1965	-	100	8.69	3-15	2.49	28.6
Pts. 1-5: D, 1965	-	100	8.73	5-15	2.35	27.0
Pt. 6, 1961	595	160	8.07	3-14	2.17	26.9
Pt. 6, 1962	-	160	8.28	3-15	2.33	28.1
Pt. 6, 1963	-	160	7.79	3-14	2.12	27.2
Pt. 7, 1962	545	160	8.58	5-14	1.95	22.7
Pt. 7, 1963	-	160	8.46	4-15	2.09	24.7
Pt. 8, 1963	-	80	10.52	5-15	2.39	22.7
Pt. 9, 1966	640	128	7.50	3-12	2.22	29.6
Pt. 10, 1966	610	122	7.50	4-12	1.81	24.1

N = number of trees sampled,

\bar{Y} = mean tree diameter in inches,

R = range of tree diameter at stump height in inches,

S = standard deviation of tree diameters,

C.V. = coefficient of variation of tree diameters.

TABLE VIII. THE 1961 H. WARRENI POPULATIONS TALLIED BY STRIP IN PLOTS 1 TO 5.

Plot and strip	N	\bar{X}	R	S	C.V.	Number of weevils per acre
Plot 1: A	40	1.00	0-5	1.28	128	469
B	76	1.90	0-10	3.67	193	819
C	70	1.75	0-8	2.23	127	853
D	45	1.13	0-6	1.84	164	541
Plot 2: A	91	2.28	0-15	3.54	155	896
B	42	1.05	0-6	1.45	138	387
C	60	1.50	0-13	2.42	161	534
D	54	1.35	0-8	2.09	155	489
Plot 3: A	56	1.40	0-8	1.93	138	578
B	98	2.45	0-19	3.76	154	1041
C	63	1.58	0-10	2.66	169	738
D	65	1.63	0-24	4.10	252	721
Plot 4: A	80	2.00	0-9	2.55	128	1013
B	74	1.85	0-10	2.73	148	913
C	41	1.03	0-8	1.87	183	519
D	97	2.43	0-17	3.63	150	1076
Plot 5: A	40	1.00	0-9	1.83	183	525
B	64	1.60	0-10	2.38	149	800
C	76	1.90	0-8	2.18	249	938
D	65	1.63	0-10	2.39	147	741

N = number of weevils (larvae + pupae + tenerals),

\bar{X} = mean number of weevils per tree,

R = range of number of weevils found on all sampled trees,

S = standard deviation of weevils per tree,

C.V. = coefficient of variation of weevils per tree.

TABLE IX. THE 1962 H. WARRENI POPULATIONS TALLIED BY STRIP IN PLOTS 1 TO 5.

Plot and strip	N	\bar{X}	R	S	C.V.	Number of weevils per acre
Plot 1: A	66	1.65	0-7	2.23	135	773
B	67	1.68	0-12	2.55	152	722
C	91	2.28	0-14	3.06	135	1109
D	75	1.88	0-15	3.28	175	902
Plot 2: A	53	1.33	0-9	1.98	149	522
B	44	1.10	0-8	1.96	178	406
C	70	1.75	0-8	2.45	140	623
D	98	2.45	0-14	3.41	139	888
Plot 3: A	82	2.05	0-7	2.28	111	846
B	92	2.30	0-14	3.35	146	978
C	53	1.33	0-9	1.75	132	621
D	97	2.43	0-20	4.12	170	1076
Plot 4: A	74	1.85	0-13	2.98	161	937
B	40	1.00	0-7	1.75	175	494
C	92	2.30	0-15	3.54	154	1164
D	85	2.13	0-14	2.75	129	943
Plot 5: A	59	1.48	0-8	1.97	134	774
B	70	1.75	0-11	2.70	154	875
C	69	1.73	0-12	2.77	160	852
D	52	1.30	0-8	1.98	152	593

N = number of weevils (larvae + pupae + teneral),

\bar{X} = mean number of weevils per tree,

R = range of number of weevils found on all sampled trees,

S = standard deviation of weevils per tree,

C.V. = coefficient of variation of weevils per tree.

TABLE X. THE 1963 H. WARRENI POPULATIONS TALLIED BY STRIP IN PLOTS 1 TO 5.

Plot and strip	N	\bar{X}	R	S	C.V.	Number of weevils per acre
Plot 1: A	12	0.30	0-4	0.94	313	141
B	17	0.43	0-3	0.81	191	183
C	56	1.40	0-8	2.15	153	683
D	100	2.50	0-11	2.91	116	1203
Plot 2: A	17	0.43	0-4	0.93	219	167
B	15	0.38	0-4	0.87	231	138
C	77	1.93	0-17	3.50	182	686
D	90	2.25	0-13	3.23	143	816
Plot 3: A	19	0.48	0-3	0.79	165	196
B	14	0.35	0-3	0.77	220	149
C	88	2.20	0-10	2.33	106	1031
D	63	1.58	0-7	3.90	247	699
Plot 4: A	24	0.60	0-4	0.98	164	304
B	19	0.48	0-5	0.93	196	235
C	86	2.15	0-12	2.73	127	1088
D	99	2.48	0-13	2.93	118	1098
Plot 5: A	20	0.50	0-3	0.85	170	263
B	14	0.35	0-3	0.70	200	175
C	71	1.78	0-12	2.57	145	876
D	74	1.85	0-15	3.01	163	844

\underline{N} = number of weevils (larvae + pupae + tenerals),

\underline{X} = mean number of weevils per tree,

\underline{R} = range of number of weevils found on all sampled trees,

\underline{S} = standard deviation of weevils per tree,

$\underline{C.V.}$ = coefficient of variation of weevils per tree.

TABLE XI. HYLOBIUS WARRENI POPULATIONS COLLECTED FROM SEVERAL PLOT AREAS OF MATURE PINE.

Plot and year	N	\bar{X}	R	S	C.V.	Number of weevils per acre
Pts. 1-5: C, 1965	381	3.81	0-29	5.43	143	1764
Pts. 1-5: D, 1965	255	2.55	0-31	4.42	173	1117
Pt. 6, 1961	153	0.96	0-14	1.97	206	569
Pt. 6, 1962	160	1.00	0-15	2.16	216	595
Pt. 6, 1963	108	0.68	0-10	1.54	228	402
Pt. 7, 1962	119	0.74	0-8	1.49	200	405
Pt. 7, 1963	110	0.69	0-17	1.68	244	375
Pt. 8, 1963	306	3.83	0-31	5.46	143	-
Pt. 9, 1966	169	1.32	0-9	1.98	150	845
Pt. 10, 1966	57	0.47	0-13	1.45	310	285

N = number of weevils (larvae + pupae + tenerals),

\bar{X} = mean number of weevils per tree,

R = range of number of weevils found on all sampled trees,

S = standard deviation of weevils per tree,

C.V. = coefficient of variation of weevils per tree.

In plots 1 to 5 most weevil population estimates fell into the range of 400 to 1000 weevils per acre. A substantial reduction in numbers occurred in the A and B strips in 1963 as a result of the clearcut treatment (Table X).

There was wide variation in the numbers of weevils found on any one tree. The highest number recorded was 31 in plots 1 to 5 (1965) and 31 in plot 8. This variability is described by the C.V. values which range from 106 to 313 percent for all 10 plots. In general the C.V. values are inversely related to weevil population estimates per acre (Tables VIII, IX, X and XI).

Although weevil numbers were highly variable it was possible to recognize different levels of abundance between different areas and stands. In Table XII the data from plots 1 to 10 (except 9) have been arbitrarily divided into five classes of abundance on the basis of average numbers of weevils per tree. The data show the pattern of change of infested tree frequencies with decreasing population densities. Changes in the percentage of trees having no weevils are especially notable. The percentage of trees with one weevil were similar for all groups. The pattern of Group V is not as clearly established as in Groups I to IV. This may reflect the clearcut treatment applied to strips A and B.

The weevil samples collected annually in plots 1 to 7 were compared to show trends in population density in time. In plot 6 the values for weevils per tree (Table XI) suggest a slight increase from 1961 to 1962, and a substantial reduction from 1962 to 1963. A similar trend occurred in plot 7. Plots 1 to 5 showed an overall yearly increase in weevil density from 1961 to 1965 (Fig. 10, graphs C and D).

Tables XIII, XIV, XV and XVI show the structure of weevil populations

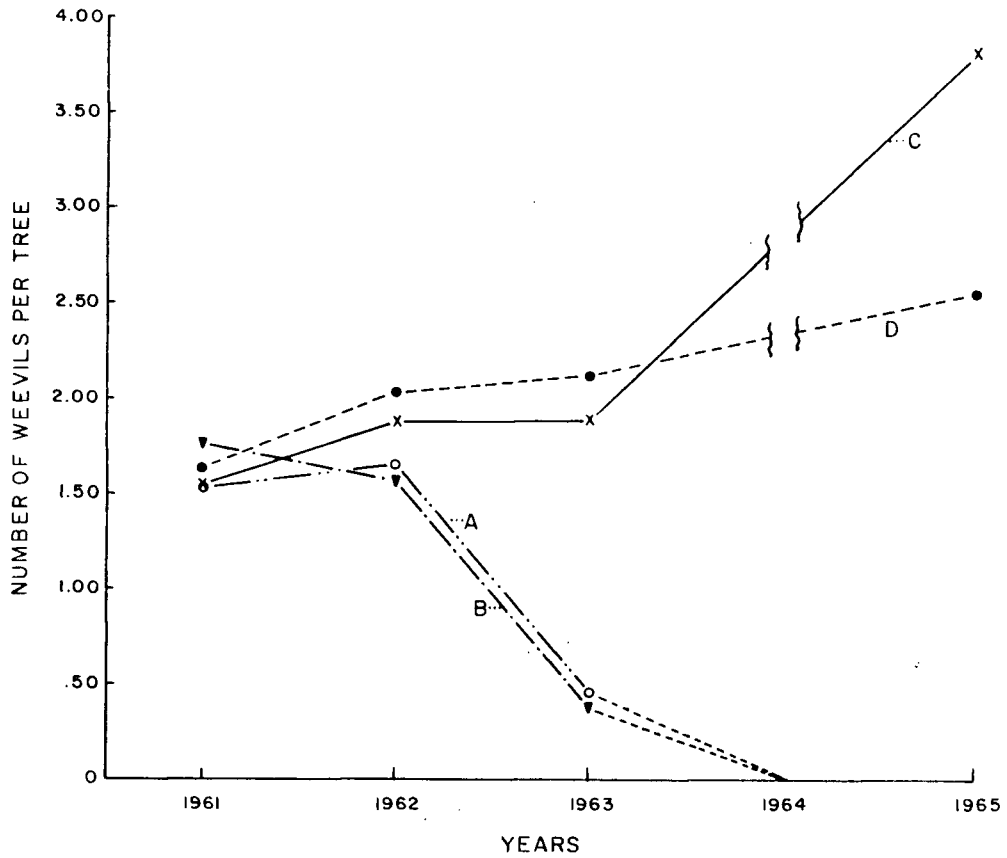


Fig. 10. *Hylobius warreni* population levels in different strips of plots 1 to 5 during 1961 to 1965. Strips A and B were clearcut after the 1961 sample was taken while strips C and D remained undisturbed.

TABLE XII. COMPARISON OF SAMPLED TREE FREQUENCY DISTRIBUTIONS (IN PERCENT) BETWEEN PLOT GROUPS OF DIFFERENT WEEVIL INFESTATION LEVELS.

Number of weevils	Gr. I	Gr. II	Gr. III	Gr. IV	Gr. V
0	32.14	46.63	67.50	77.87	73.25
1	17.86	16.63	15.00	12.30	17.00
2	12.86	11.06	7.38	6.56	5.25
3	7.50	6.63	3.88	.82	3.00
4	3.93	5.25	1.88	-	1.25
5	6.79	4.88	1.13	.82	.25
6	3.21	2.44	1.13	.82	-
7	1.43	1.88	.63	-	-
8	3.21	1.44	.50	-	-
9	1.43	.75	.38	-	-
10	1.43	.63	.25	-	-
11	1.79	.31	-	-	-
12	.71	.50	-	-	-
13	1.43	.25	-	.82	-
14	.71	.19	.13	-	-
15	.36	.25	.13	-	-
16-20	1.07	.25	.13	-	-
21-25	.71	.06	-	-	-
26-30	.71	-	-	-	-
31-35	.71	-	-	-	-

Group I: Plot 8, 1963 + plots 1-5 CD, 1965,

Group II: Plots 1-5 ABCD, 1961 + plots 1-5 CD, 1962 + plots 1-5 CD, 1963,

Group III: Plot 6, 1961-1963 + plot 7, 1962-1963,

Group IV: Plot 10, 1966,

Group V: Plots 1-5 AB, 1963.

TABLE XIII. SUMMARY OF THE POPULATION STRUCTURE OF H. WARRENI COLLECTED IN PLOTS 1 TO 5 DURING 1961.

Year and strip	Life stage	Number of weevils					Plots 1 - 5		
		Pt. 1	Pt. 2	Pt. 3	Pt. 4	Pt. 5	Total weevils	Total pupal cells	Percent pupating
1961 - A	Larvae	40	90	55	77	37	299	45	14.7
	Pupae	0	0	1	3	3	7		
	Tenerals	0	1	0	0	0	1		
	Adults	0	3	1	1	0	5		
1961 - B	Larvae	76	41	98	65	63	343	32	9.0
	Pupae	0	0	0	9	2	11		
	Tenerals	0	1	0	0	0	1		
	Adults	0	6	3	6	2	17		
1961 - C	Larvae	70	60	63	38	73	304	33	10.6
	Pupae	0	0	0	3	3	6		
	Tenerals	0	0	0	0	0	0		
	Adults	1	5	1	2	1	10		
1961 - D	Larvae	45	54	65	88	58	310	40	12.3
	Pupae	0	0	0	9	7	16		
	Tenerals	0	0	0	0	0	0		
	Adults	1	0	1	2	1	5		
1961 - AB	Larvae	116	131	153	142	2100	642	77	11.6
	Pupae	0	0	1	12	5	18		
	Tenerals	0	2	0	0	0	2		
	Adults	0	9	4	7	2	22		
1961 - CD	Larvae	115	114	128	126	131	614	73	11.5
	Pupae	0	0	0	12	10	22		
	Tenerals	0	0	0	0	0	0		
	Adults	2	5	2	4	2	15		

TABLE XIV. SUMMARY OF THE POPULATION STRUCTURE OF H. WARRENI COLLECTED IN PLOTS 1 TO 5 DURING 1962.

Year and strip	Life stage	Number of weevils					Plots 1 - 5		
		Pt. 1	Pt. 2	Pt. 3	Pt. 4	Pt. 5	Total weevils	Total pupal cells	Percent pupating
1962 - A	Larvae	66	53	81	74	57	331	56	16.8
	Pupae	0	0	1	0	2	3		
	Tenerals	0	0	0	0	0	0		
	Adults	0	1	1	0	0	2		
1962 - B	Larvae	67	44	92	40	66	309	70	22.4
	Pupae	0	0	0	0	4	4		
	Tenerals	0	0	0	0	0	0		
	Adults	0	1	0	0	0	1		
1962 - C	Larvae	90	70	53	92	68	373	73	19.5
	Pupae	0	0	0	0	1	1		
	Tenerals	1	0	0	0	0	1		
	Adults	2	1	2	2	2	9		
1962 - D	Larvae	75	98	97	85	50	405	59	14.5
	Pupae	0	0	0	0	2	2		
	Tenerals	0	0	0	0	0	0		
	Adults	1	0	2	1	0	4		
1962 - AB	Larvae	133	97	173	114	123	640	126	19.5
	Pupae	0	0	1	0	6	7		
	Tenerals	0	0	0	0	0	0		
	Adults	0	2	1	0	0	3		
1962 - CD	Larvae	165	168	150	177	118	778	132	16.9
	Pupae	0	0	0	0	3	3		
	Tenerals	1	0	0	0	0	1		
	Adults	3	1	4	3	2	13		

TABLE XV. SUMMARY OF THE POPULATION STRUCTURE OF H. WARRENI COLLECTED IN PLOTS 1 TO 5 DURING 1963.

Year and strip	Life stage	Number of weevils					Plots 1 - 5		
		Pt. 1	Pt. 2	Pt. 3	Pt. 4	Pt. 5	Total weevils	Total pupal cells	Percent pupating
1963 - A	Larvae	11	15	19	13	3	61	60	65.2
	Pupae	0	2	0	11	16	29		
	Tenerals	1	0	0	0	1	2		
	Adults	0	0	0	0	0	0		
1963 - B	Larvae	17	15	14	9	8	63	41	51.9
	Pupae	0	0	0	10	6	16		
	Tenerals	0	0	0	0	0	0		
	Adults	0	0	0	0	0	0		
1963 - C	Larvae	56	77	88	81	58	360	49	13.0
	Pupae	0	0	0	5	13	18		
	Tenerals	0	0	0	0	0	0		
	Adults	4	3	2	4	2	15		
1963 - D	Larvae	98	90	63	98	67	416	28	6.6
	Pupae	0	0	0	1	7	8		
	Tenerals	2	0	0	0	0	2		
	Adults	2	2	1	1	3	9		
1963 - AB	Larvae	28	30	33	22	11	124	101	59.1
	Pupae	0	2	0	21	22	45		
	Tenerals	1	0	0	0	1	2		
	Adults	0	0	0	0	0	0		
1963 - CD	Larvae	154	167	151	179	125	776	77	9.6
	Pupae	0	0	0	6	20	26		
	Tenerals	2	0	0	0	0	2		
	Adults	6	5	3	5	5	24		

TABLE XVI. SUMMARY OF THE POPULATION STRUCTURE OF H. WARRENI COLLECTED IN SEVERAL PLOTS AND YEARS.

Life stage	Plots 1-5		Plot 6			Plot 7		Pt. 8	Pt. 9	Pt. 10
	1965-C	1965-D	1961	1962	1963	1962	1963	1963	1966	1966
Larvae	357	237	137	153	106	120	110	291	154	54
Pupae	20	15	13	7	2	0	0	15	15	3
Tenerals	2	2	0	0	0	1	0	0	0	0
Adults	2	5	2	2	0	2	6	2	0	1
Total weevils	381	259	152	162	108	123	116	308	169	58
Total pupal cells	22	17	16	23	3	27	14	16	16	8
Percentage pupating	5.8	6.7	10.7	14.4	2.8	22.3	12.7	5.2	9.5	14.0

collected in plots 1 to 10 during 1961 to 1966. Larvae of all sizes comprised the bulk of each population. Large variation occurred between the numbers of pupae and tenerals recorded in plots 1 to 5 during the same summer. Pupae did not appear until the second and third weeks of June. However, their chambers were easily recognized as early as mid-May. The percentage of the population pupating in plots 1 to 5 was lowest in 1965 and highest in 1962. The highest percentage in plots 6 and 7 also occurred in 1962. Adult collections agreed with this, being the highest in 1963 for the C and D strips of plots 1 to 5. The numbers of adults refer to those specimens which were found at tree bases during sampling. They ranged from zero to six for samples of 40 trees. Highest numbers of pupal cells were reported in plots 1 to 5, A and B, during 1963 (Table XV); i.e., 101 pupal cells compared to 77 in the C and D strips of the same plots.

The structure of the larval portion of the population from plots 1 to 5 and 9 are compared in Figure 11 for the years 1961, 1962, 1963, 1965 and 1966. Head capsule widths have been grouped into mm. categories. All distribution curves show a similar pattern but the greatest variation between samples occurred in the early and late instars; the largest proportion being in the late instars.

When the individual tree is used as the basic sampling unit for H. warreni populations the frequency distribution of numbers per tree (Table XII) appears to be adequately expressed by the negative binomial distribution. Mean numbers of weevils per tree (\bar{x}) and the corresponding "k" values are given for plots 1 to 10 (Table XVII). The values of "k" vary from 0.09 for the lowest population (except plots 1 to 5, AB, 1963) to 0.68 for the highest.

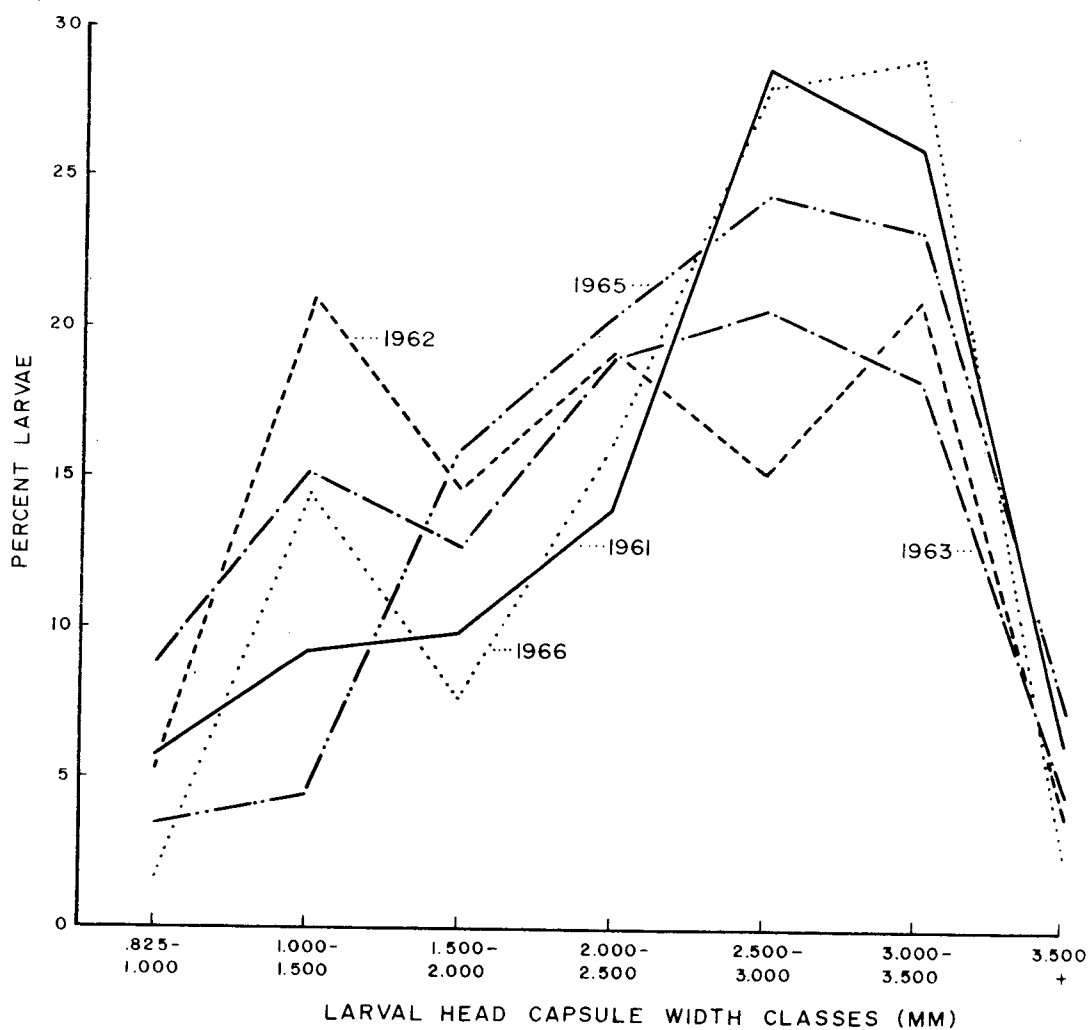


Fig. 11. Comparison of the structure of *H. warreni* larval populations between years for plots 1 to 5, 1961, 1962, 1963 and 1965 and plot 9, 1966.

TABLE XVII. CALCULATED "K" VALUES OF THE NEGATIVE BINOMIAL DISTRIBUTION USED AS A MEASURE OF THE DEGREE OF AGGREGATION OF DIFFERENT WEEVIL POPULATIONS AND HABITATS.

Plot descriptions	N	n ₀	\bar{X}	k
1961, Pts. 1 - 5: A	200	94	1.53	0.42
B	200	90	1.78	0.43
C	200	102	1.55	0.33
D	200	104	1.63	0.30
1962, Pts. 1 - 5: A	200	91	1.65	0.44
B	200	96	1.57	0.39
C	200	93	1.88	0.38
D	200	97	2.04	0.32
1963, Pts. 1 - 5: A	200	144	0.46	0.14
B	200	150	0.40	0.12
C	200	85	1.89	0.47
D	200	81	2.13	0.48
1965, Pts. 1 - 5: C	100	32	3.79	0.51
D	100	38	2.54	0.49
1961, Plot 6	160	103	0.94	0.19
1962, Plot 6	160	111	1.00	0.13
1963, Plot 6	160	113	0.68	0.15
1962, Plot 7	160	107	0.76	0.17
1963, Plot 7	160	106	0.69	0.18
1963, Plot 8	80	21	3.83	0.68
1966, Plot 9	128	71	1.32	0.28
1966, Plot 10	122	95	0.47	0.09

N = number of trees sampled,

n₀ = number of trees with zero weevils,

\bar{X} = mean number of weevils per tree (based upon total larvae + pupae + tenerals),

k = an index of aggregation or measure of dispersion in the population

The populations of the weevil obtained in all plots except 1 to 5, AB, 1963, are described in Figure 12 according to Taylor's power law. For H. warreni the parameters "a" and "b" were estimated as 2.80 and 1.92 respectively. When "p" is determined from the following equation, it has a value close to zero.

$$p = 1 - \frac{1}{2}b$$

This suggests that a logarithmic transformation should be applied to the raw sampled data for statistical evaluation.

Data from sampling in the regeneration plot series VII to X are summarized in Table XVIII. In the plot series VII, VIII and IX the calculated tree densities varied from 1854 to 4687 stems per acre, but the pattern of tree attack, based upon a percentage of total trees, appeared to be nearly constant for the three different sites; i.e., 13.7, 12.1 and 13.6 percent respectively. The percentage trees attacked in series X was only 2.82, while the calculated density was 5391 stems per acre. The averages of numbers of weevils per tree were all considerably lower than observed in plots 1 to 10. However, estimates of absolute numbers of weevils suggest a similarity between the 20-25-year old stand and the 65-70-year old stand. The estimated population for plot series VII is well within the range of estimates for the older stands.

The frequency distributions of weevil attack density in plot series VII to IX combined, and in plot series X are shown in Table XIX. Plots V and VI are added for comparison, although the values shown only indicate the number of trees with current attacks. Most attacked trees in the two burn areas each supported a weevil density of one per tree, and only one tree had three weevils. The tree heights of the infested trees of the burn and

Fig. 12. Variance plotted against the mean of H. warreni populations per 15 sampled trees, on a log-log scale to obtain the constant "a" and "b" values of Taylor's power law. Five different population levels and habitats are represented. The values beside the points indicate the number of points having the same coordinates. (Line sight-fitted).

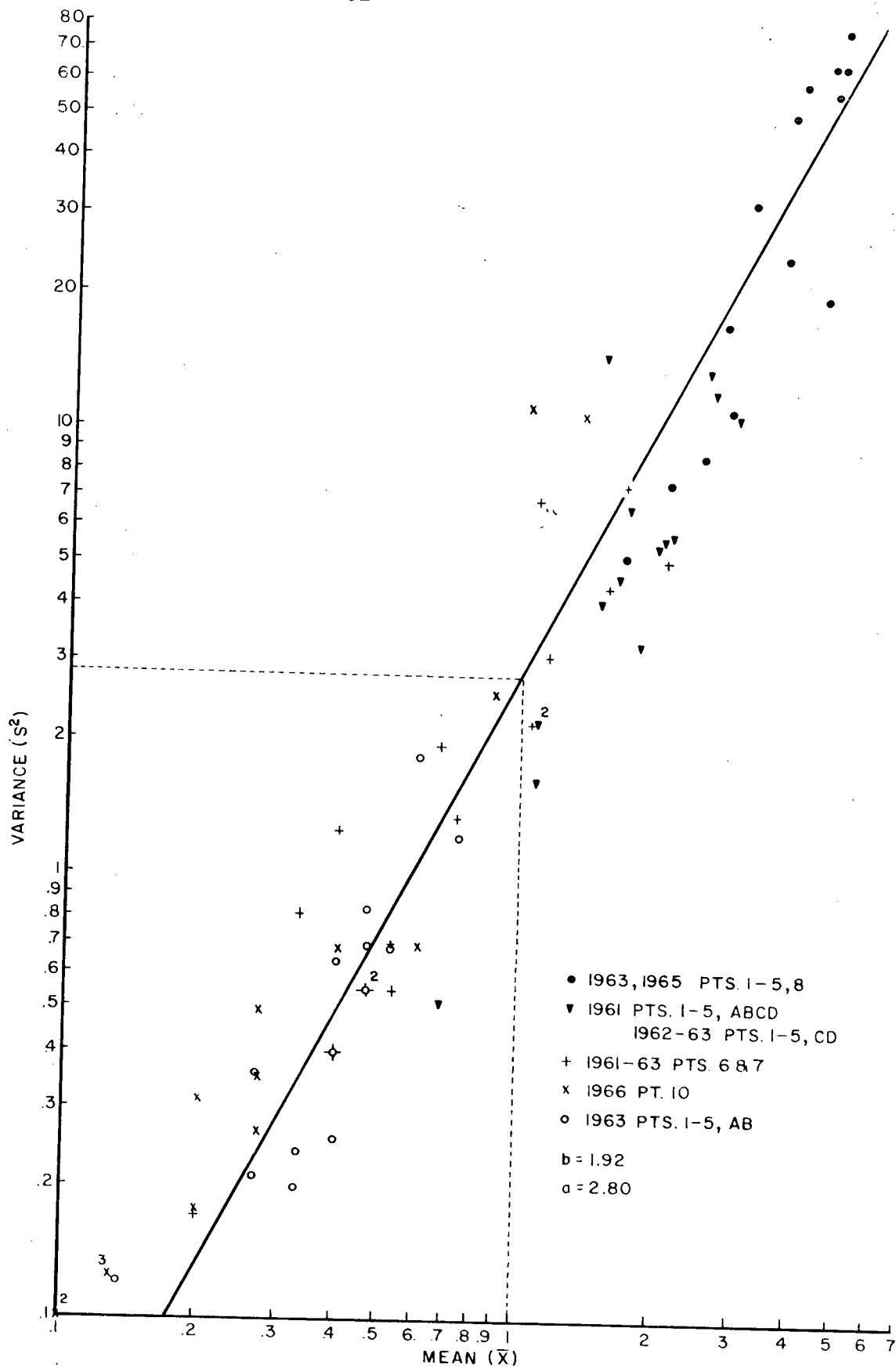


TABLE XVIII. SUMMARY OF THE TREE AND WEEVIL MEASUREMENTS IN PINE STANDS IN THE ROBB AND RICINUS BURN AREAS.

Plot series	No. plots sampled	Total trees sampled	Ave. tree density per plot	Calculated density per acre	Ave. ht. (ft.)	Ave. diam. s.h. (ins.)	% trees attached	Ave.no. weevils per tree	Estimated population per acre
VII	11	327	33.8	4687	9.2	1.5	13.7	0.121	567
VIII	8	107	13.4	1854	8.2	1.7	12.1	0.047	87
IX	10	144	14.4	1996	10.4	2.2	13.6	0.104	208
X	10	389	38.9	5391	6.4	-	2.8	0.028	152

TABLE XIX. SUMMARY OF TREE FREQUENCIES SHOWING WEEVIL DENSITY AND TREE SIZE CHARACTERISTICS.

	Robb Burn Plot series VII, VIII, IX	Ricinus Burn Plot series X	Plot V	Plot VI
No. of trees with:				
1 weevil	39	7	5	9
2 weevils	11	2		
3 weevils	1	0		
Ave. height of trees (ft.) with:				
1 weevil	13.1 (2.5)*	9.0	5.5	6.1
2 weevils	12.3 (2.2)	11.0		
3 weevils	11.5 (3.2)	-		

* Denotes average tree diameter (d.s.h.) in inches.

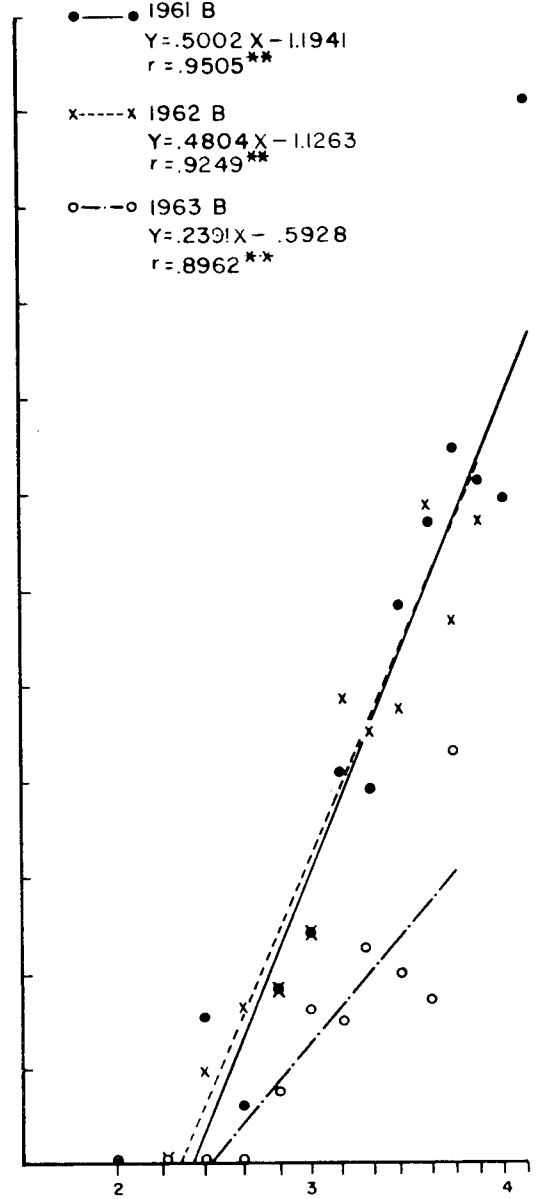
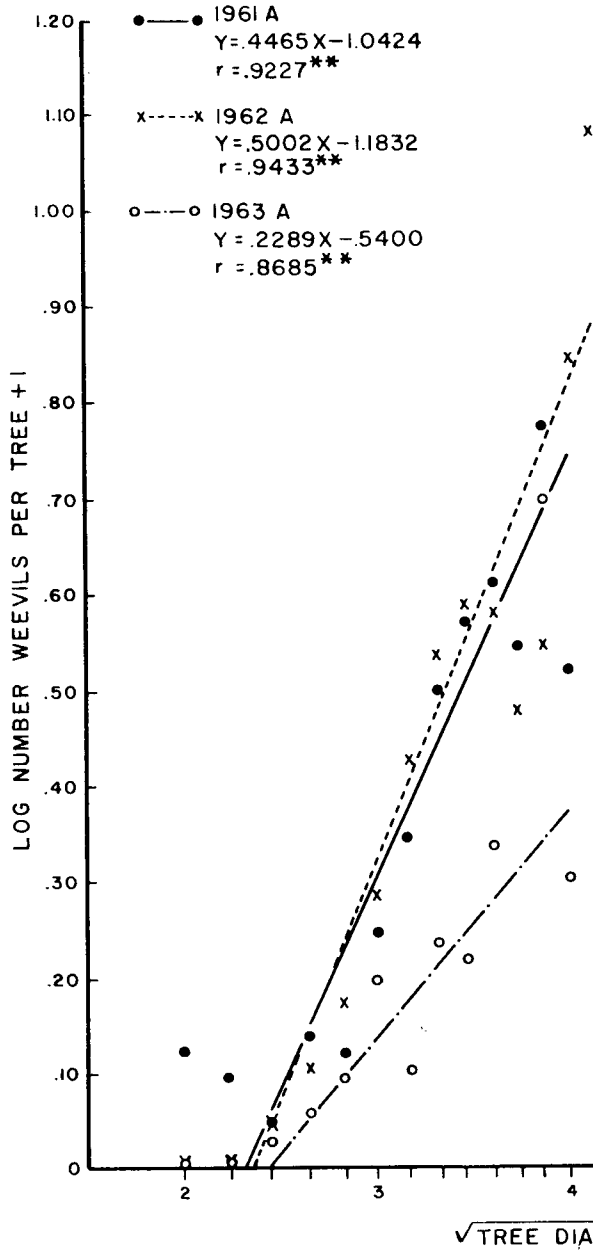
clearcut areas are not comparable because of the age differences between the stands. However, the data show that the largest stems in each stand were preferred.

4. Relationship of Weevil Numbers With Stand Conditions

4.1 Relationship with Tree Size: Lodgepole pine is characteristically a pioneer species and is propagated, both by artificial and natural means, in essentially even-aged stands. All areas of plots 1 to 10 and I to X followed this pattern even though tree sizes varied greatly within stands. Weevil numbers were linearly related to tree size in all stands analysed (Figs. 13, 14, 15, 16, 17 and 18). The log transformation of weevil numbers per tree, plotted over the square root transformation of tree diameters appears to provide the best overall fit of straight line relationships for data in Figs. 13 to 17 inclusive. Large trees consistently supported more weevils than small trees. This pattern was essentially the same for strips A, B, C and D of plots 1 to 5, as well as for different years of sampling. Clearcutting had the effect of decreasing the slope of the line (Fig. 13, 14). A sharp increase in weevil numbers was evident in the C strips of the 1965 sample as compared to previous years (Fig. 15). Similar graph patterns were evident for other mature stands where different levels of populations were recognized (Fig. 17). Although actual insect numbers were not used in the analysis of young stands a similar relationship as described above for mature stands was also evident in the 20-25-year old stand of the Robb Burn (Fig. 18).

4.2 Relationship with Tree Density: The estimated numbers of weevils per block in plots 1 to 6 (1961 data) were analysed in relation to tree density

Figs. 13 and 14. Relationship between weevil numbers per tree and tree diameter size for three different years in strips A and B of plots 1 to 5. Lines were fitted by least squares method of the weighted regression. **Significance of r values is at 0.01 probability.



Figs. 15 and 16. Relationship between numbers of weevils per tree and tree diameter size for four different years in strips C and D of plots 1 to 5. Lines were fitted by least squares method of the weighted regression. **Significance of r values is at 0.01 probability.

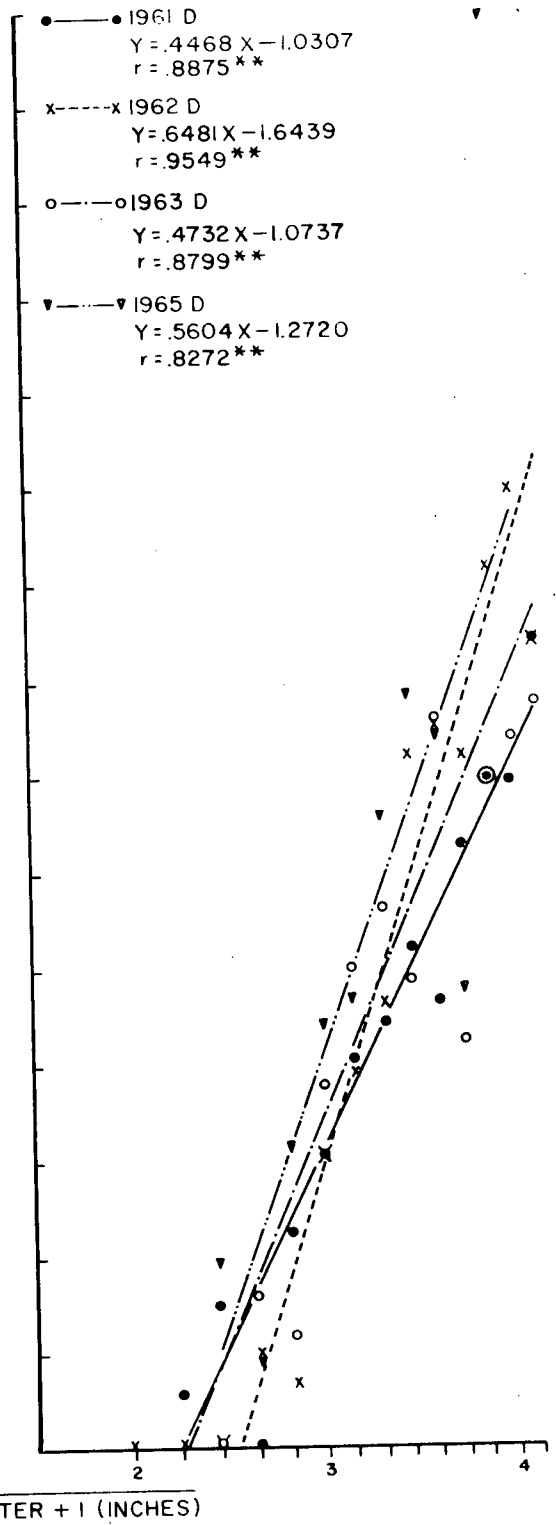
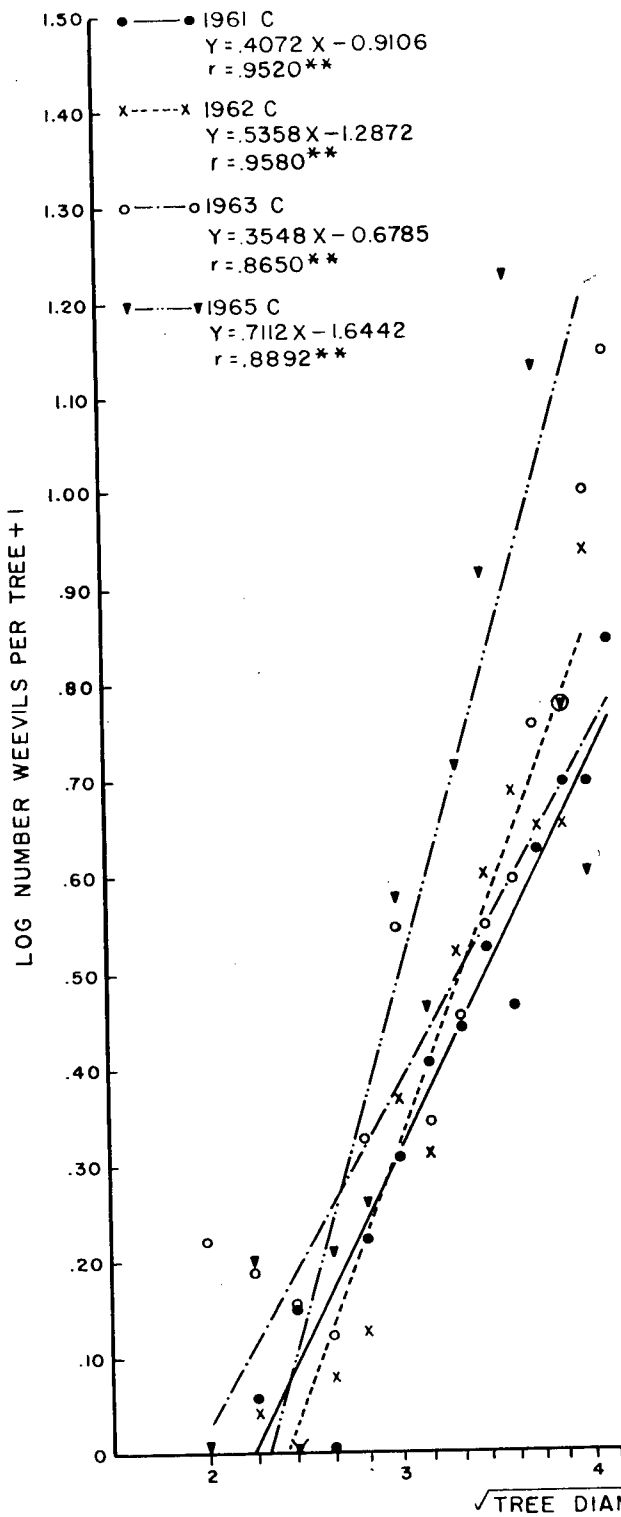
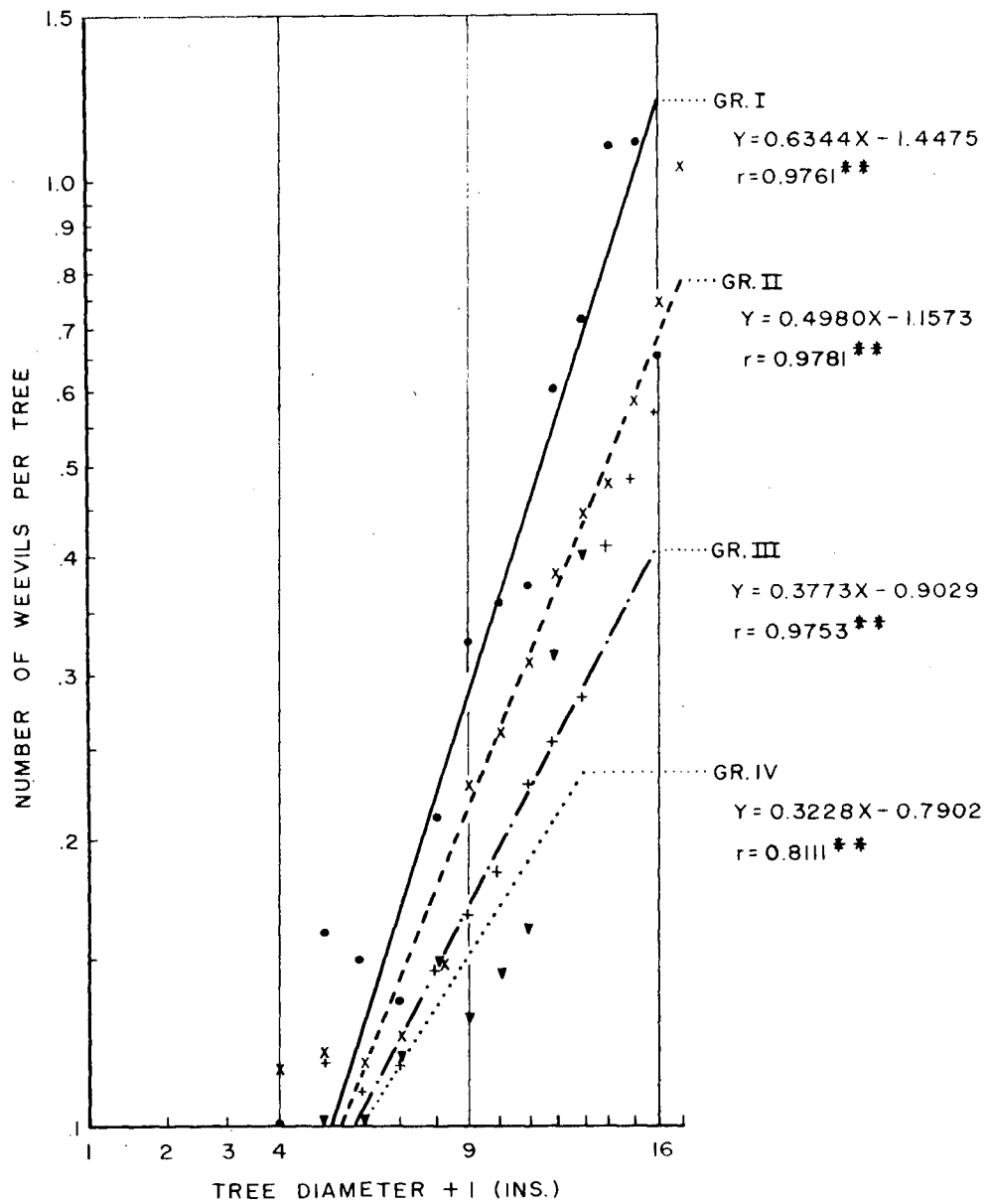


Fig. 17. Relationship between numbers of weevils per tree and tree diameter size for four different levels of abundance. Group I includes plot 8 and plots 1 - 5, CD - 1965; Group II includes plots 1 - 5, ABCD - 1961, CD - 1962 and CD - 1963; Group III includes plots 6 and 7, 1961 - 1963; Group IV includes plot 10. Lines were fitted by least squares method of a weighted regression. **Significance of r values is at 0.01 probability.



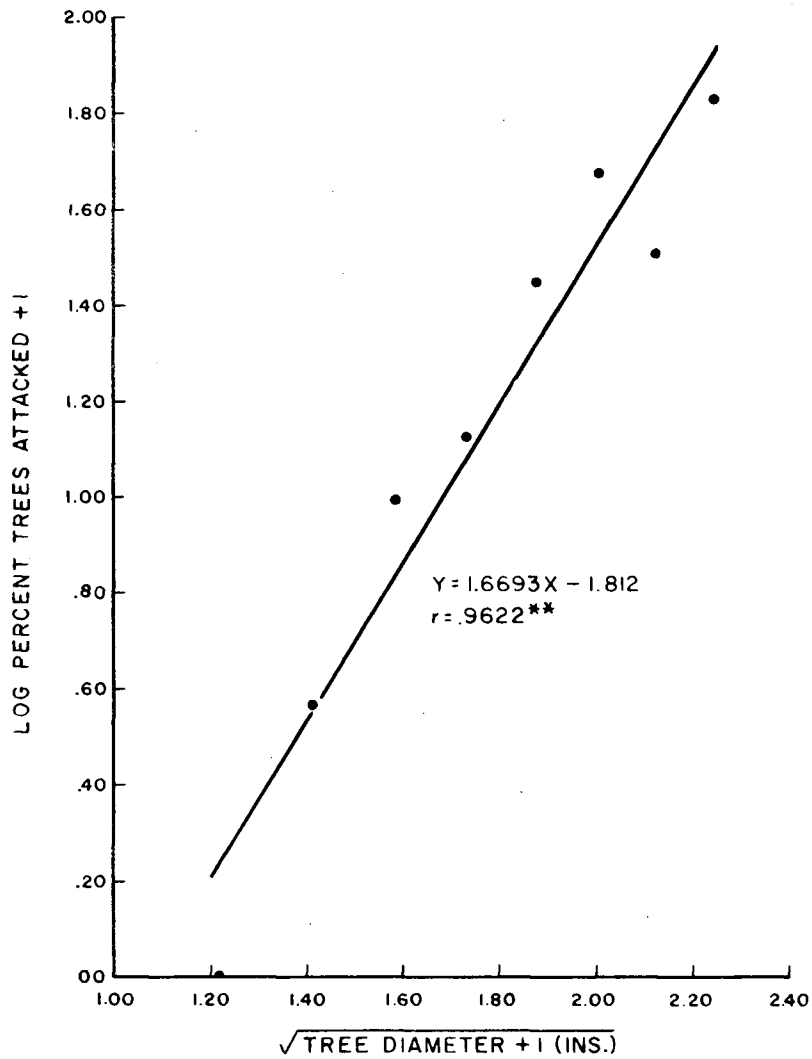


Fig. 18. Relationship between percent trees attacked (old and current attacks) and tree diameter in the 20-25-year old stand of plots VII, VIII and IX. Line was fitted by least squares method. **Significance of r value is at 0.01 probability.

per block (Fig. 19). These data suggested that maximum population levels were attained at a density of between 80 and 95 stems per block, or in the range 426 - 506 stems per acre. In general, low tree density plot areas had low numbers of weevils per acre, and similarly for high density areas.

A tree density relationship could not be clearly established in the regeneration plots VII to X. Figures 20 and 21 provide an indication that the percentage trees attacked may be inversely related to tree density. However, the data are masked by the fact that percentage attacks in these young stands are likely highest at the stand periphery.

4.3 Relationship with Duff Depth: The measurements of duff depth in plots 1 to 10 indicated some variability between sites (Table XX) but that differences between population levels on different sites were not necessarily related to duff thickness. The quality of duff material was also highly variable and may relate to weevil numbers. For example, a forest floor consisting largely of moss species did not appear to be as favorable for the weevil habitat (i.e., plots 6, 7 and 10) as a forest floor comprising a mixture of moss and herb species (i.e., plots 1 to 5).

Within each forest type the depth of duff material around each tree base bears a strong relationship to the pattern of weevil distribution. Figures 22 and 23 describe weevil numbers per tree in relation to duff depth for 4, 8, 10 and 12 inch diameter trees. Three patterns are apparent in Figure 22:

- (1) weevil numbers tend to increase with increasing duff depth, except in the four inch diameter class;
- (2) weevil density increased with increasing tree size and
- (3) the relative steepness of the curves indicate that duff

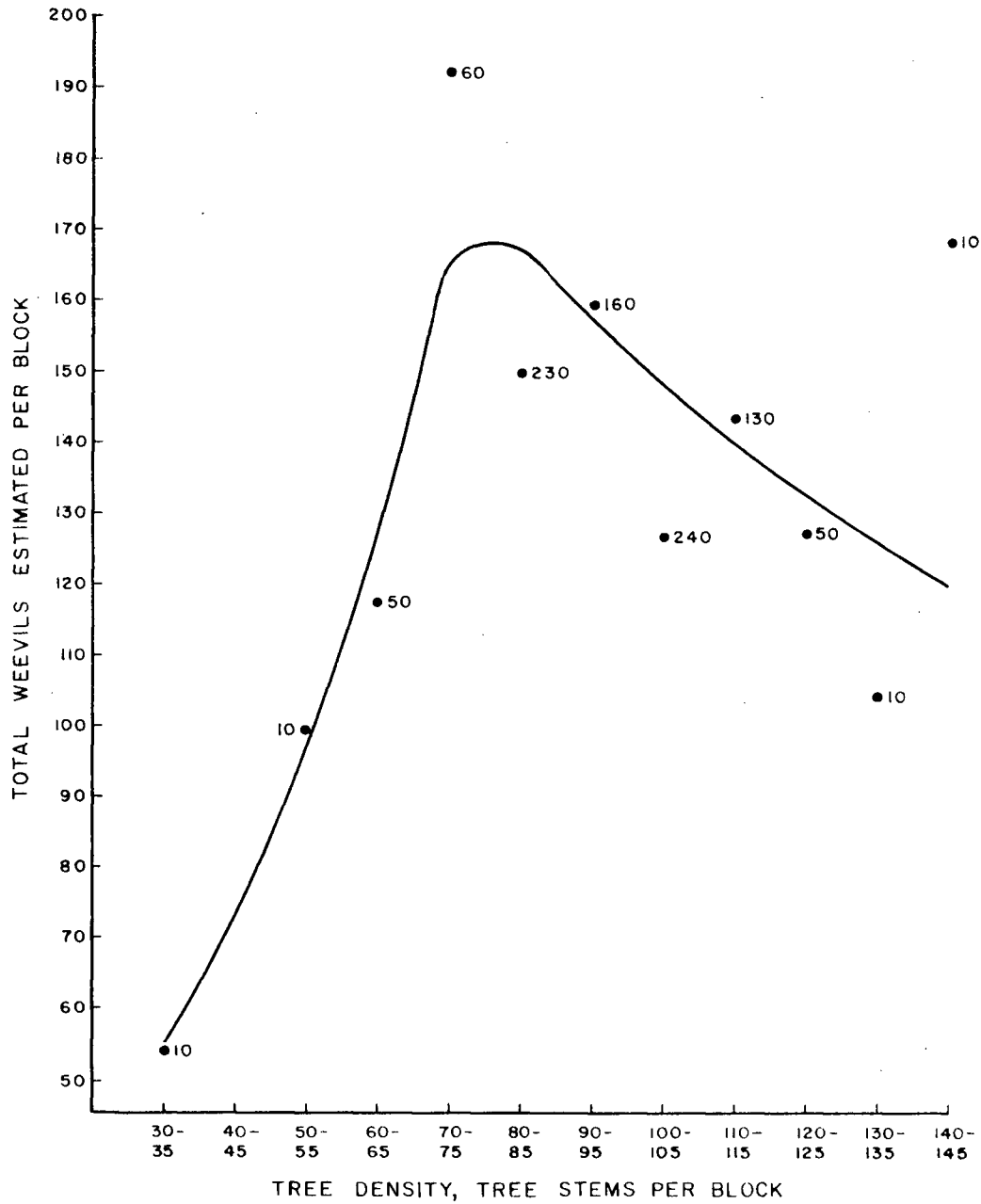
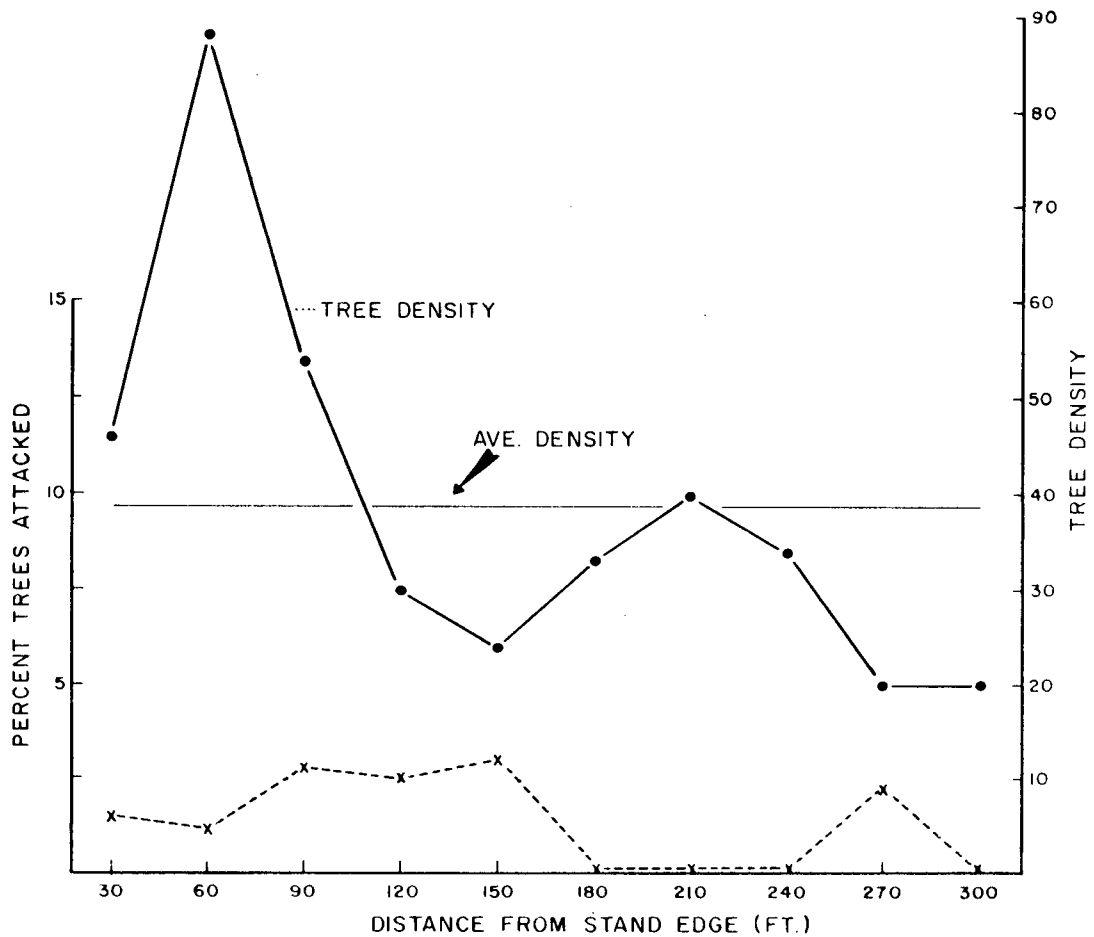
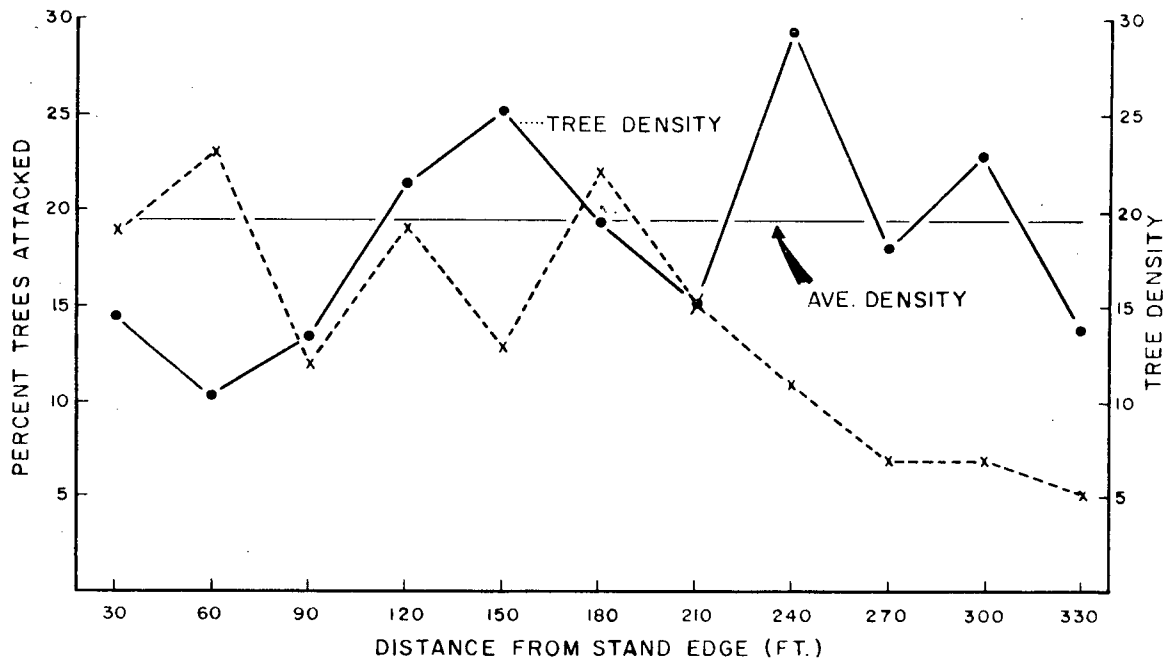


Fig. 19. Relationship between weevil numbers per block and tree density per block in the 65-70-year old pine stand of plots 1 to 6. Numbers beside the dots indicate total trees.

Fig. 20. Tree density and weevil attack pattern in the regeneration plot series VII, VIII and IX combined, and plotted in relation to distance from the stand periphery.

Fig. 21. Tree density and weevil attack pattern in plot X, plotted in relation to distance from the stand periphery.



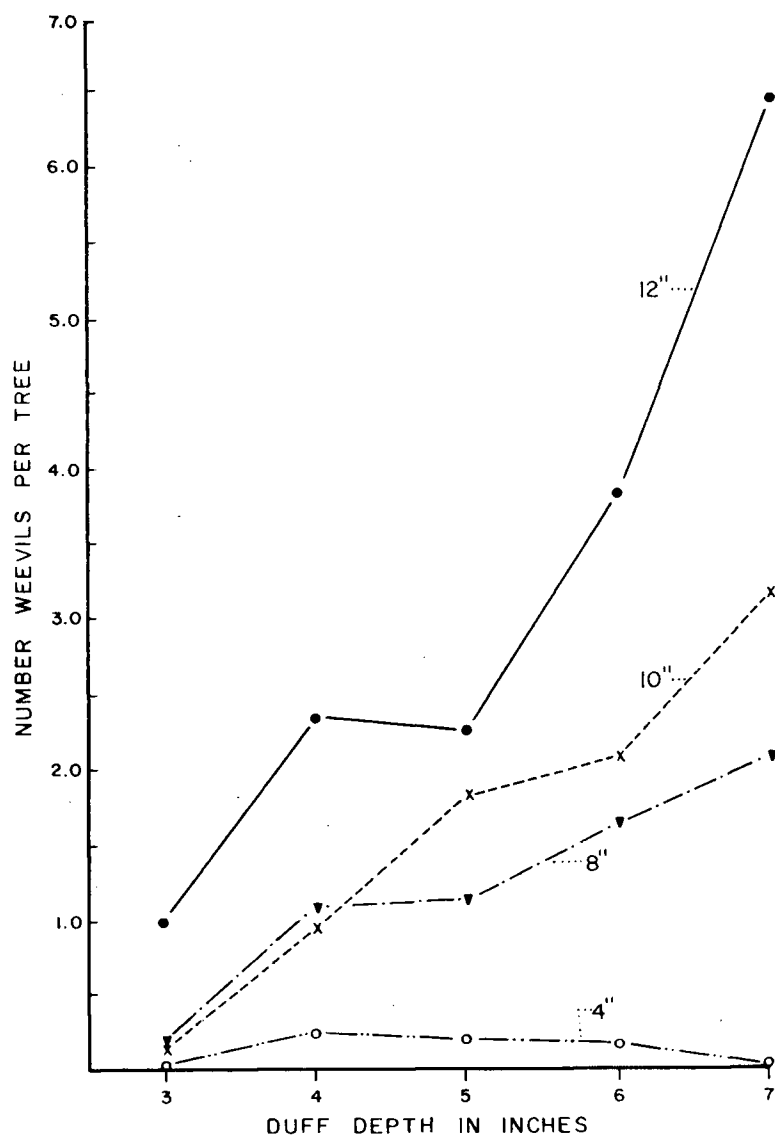


Fig. 22. Relationship between weevil numbers per tree and duff depth of four tree diameter classes in plots 1 to 5.

TABLE XX. AVERAGE DUFF DEPTH IN INCHES MEASURED AT THE BASE OF SAMPLED TREES IN PLOTS 1 TO 10.

	----- Plot number -----									
	1	2	3	4	5	6	7	8	9	10
Average duff depth	4.4	4.9	5.3	5.5	5.7	5.6	4.4	3.6	5.9	7.2

depth becomes increasingly important to weevil populations as tree size increases. Figure 23 includes data from plots 6 and 7 but only the second pattern of weevil abundance is apparent.

The data were further analysed to determine how the pattern of duff depth distribution relates to the four tree diameter classes, and how this might affect weevil abundance. Figure 24 suggests that with increasing tree diameter, there is a proportionately larger percentage of trees with thicker duff material around their bases; trees of the four inch diameter class have the lowest percentage with thick duff while trees of the 12 inch class have the highest.

The duff depth factor was analysed to determine its role in defining the limits of the feeding and developmental zone of immature weevil stages on the host. Figures 25 and 26 show the pattern of weevil numbers in relation to their distribution upon the host tree and to duff depth. The proportion of weevils found on the roots follows a similar pattern as weevils on the collar; i.e., as tree size increases, weevil attacks become more numerous on the main lateral roots. The collar region, however, supports the largest

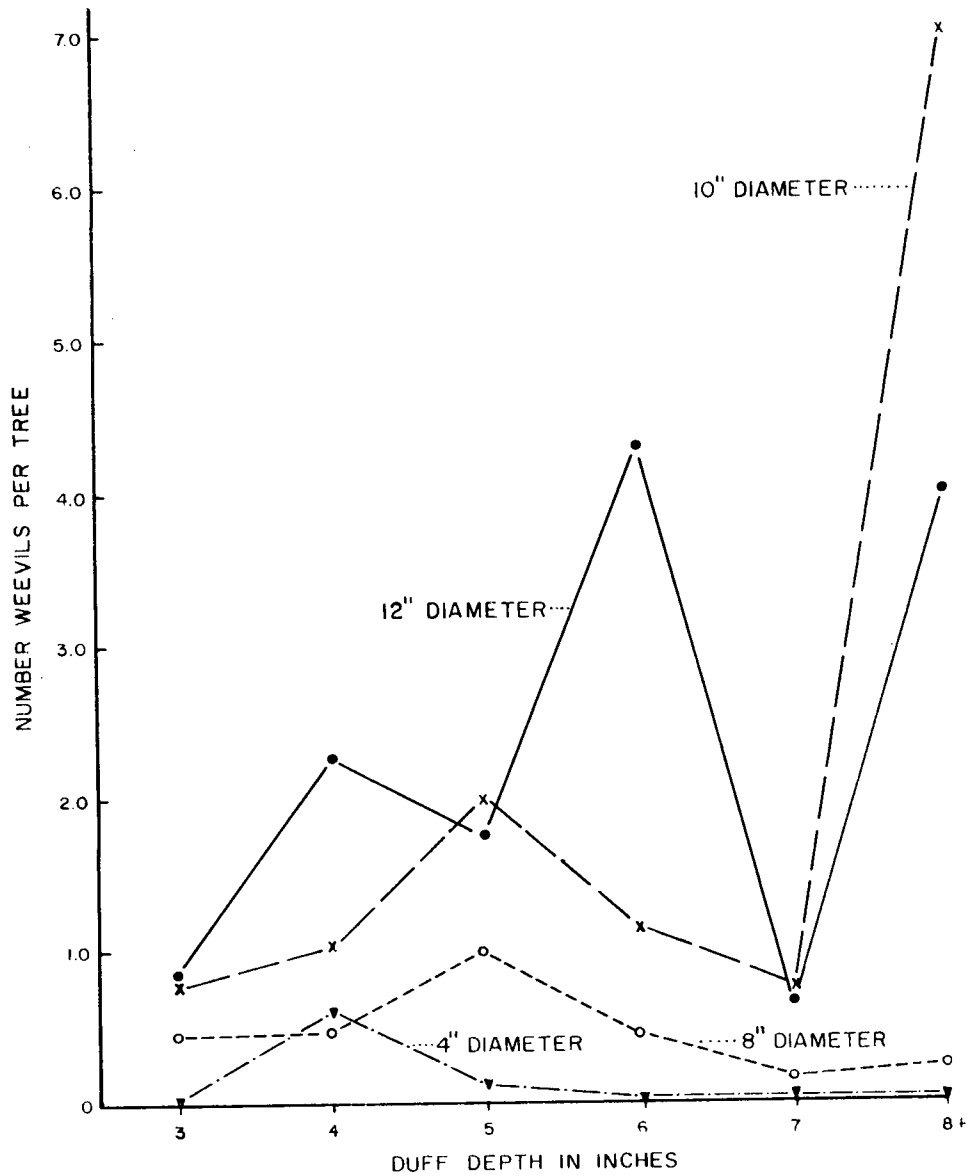


Fig. 23. Relationship between weevil numbers per tree and duff depth of four tree diameter classes in plots 6 and 7.

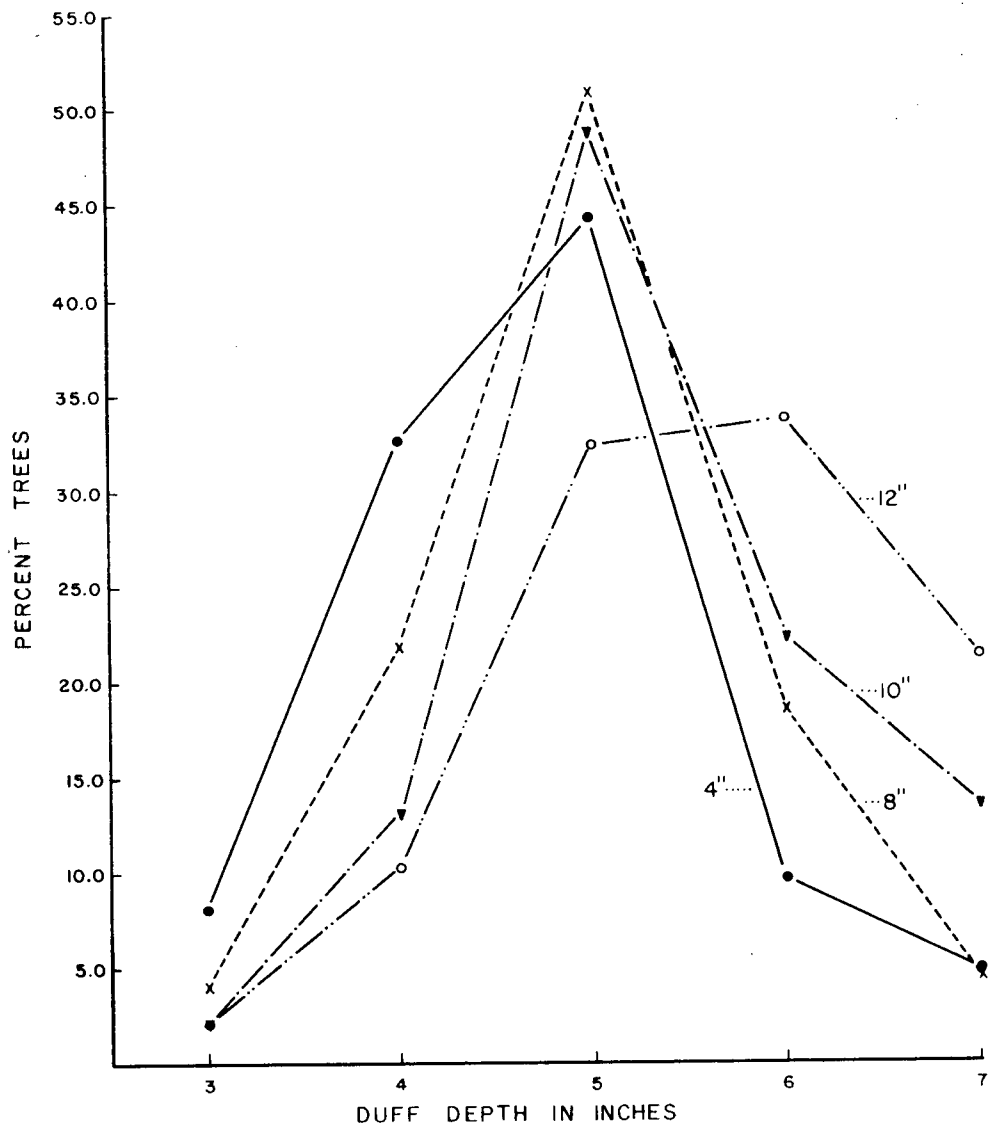


Fig. 24. Frequency distributions of duff depth of four different tree diameter classes in plots 1 to 5.

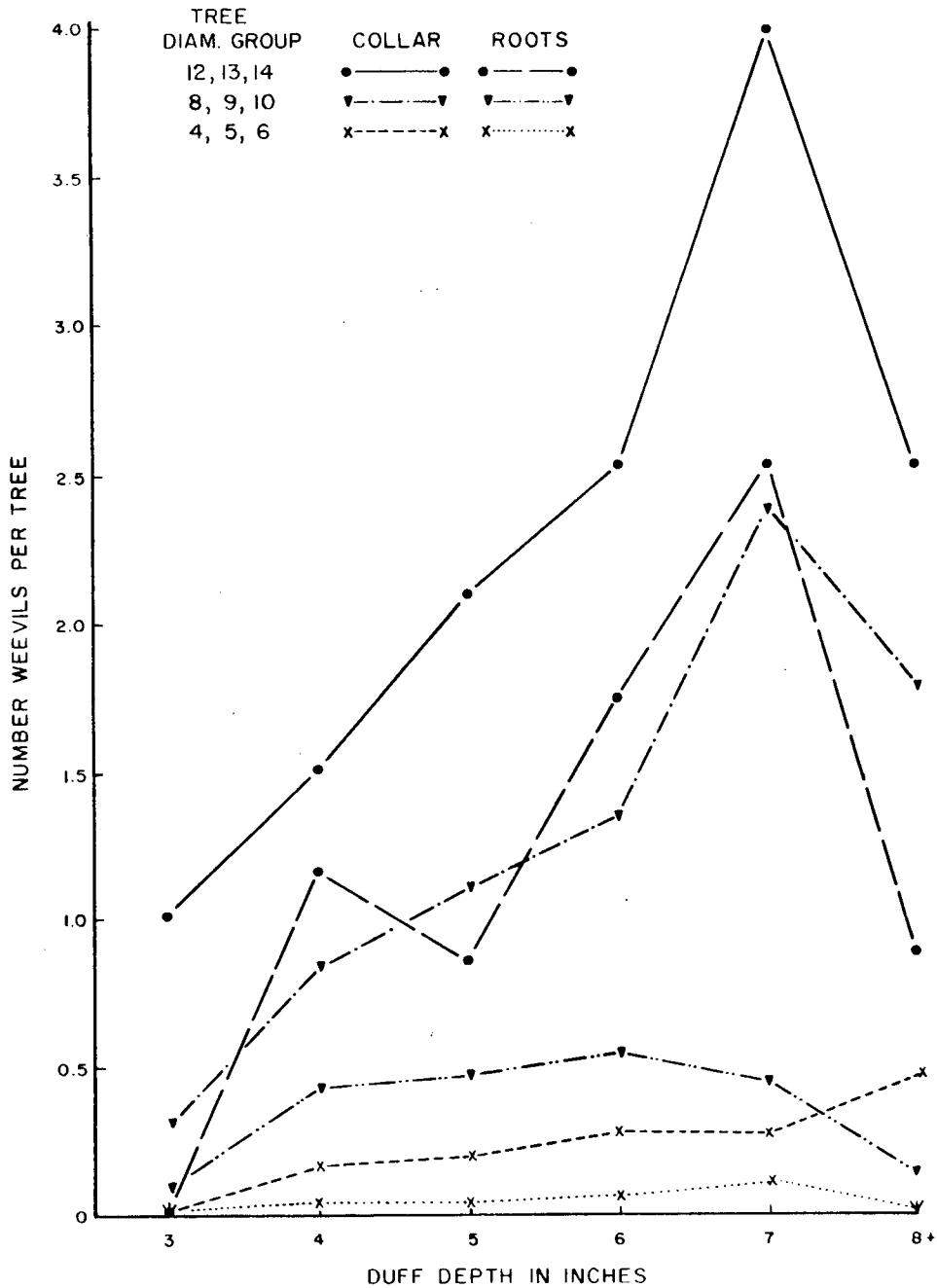


Fig. 25. Relationship of numbers of weevils per tree and duff depth with comparisons for three different tree diameter classes in plots 1 to 5.

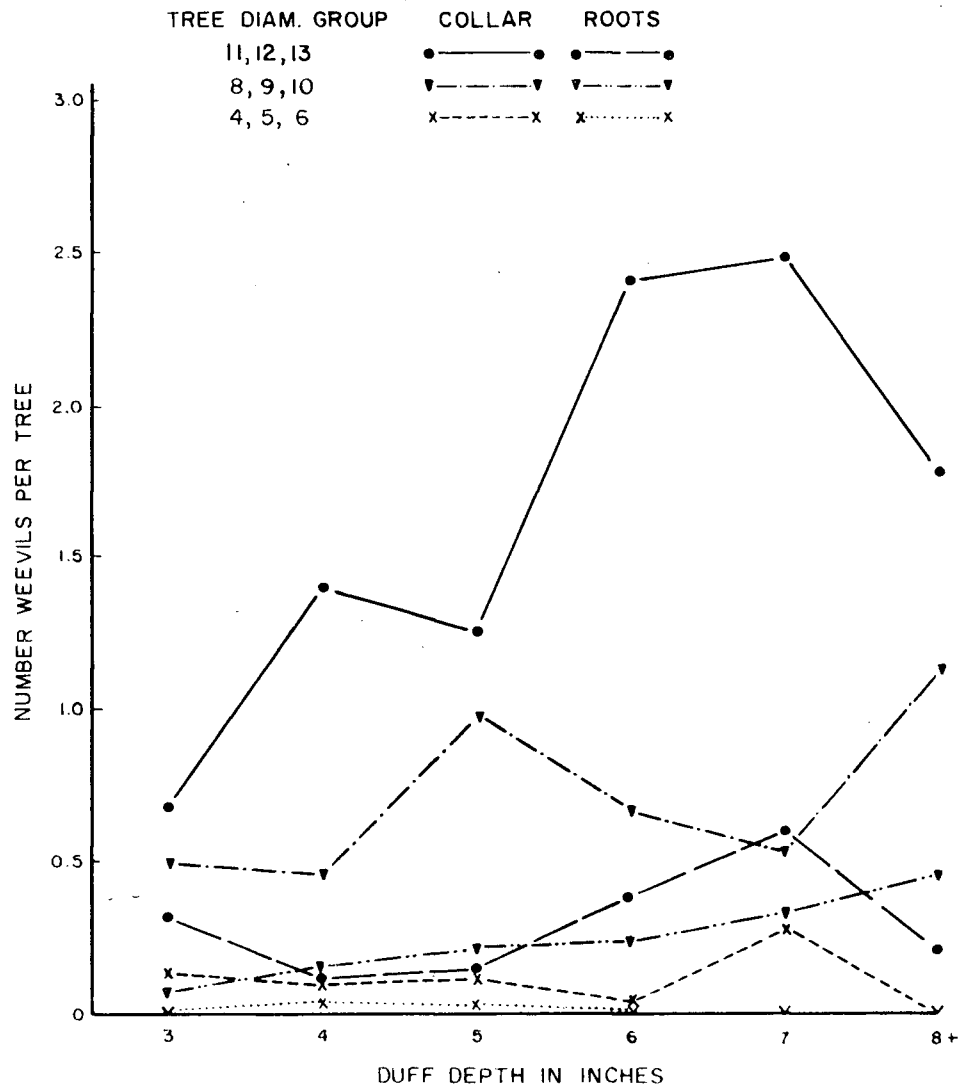


Fig. 26. Relationship of numbers of weevils per tree and duff depth with comparisons for three different tree diameter classes in plots 6 and 7.

proportion of the population (Table XXI). Figure 27 provides evidence that the ratio of weevils on roots to collar increases directly as tree size. This suggests that within the same stand type at least, there is greater utilization of lateral root surfaces for larval feeding on large trees as compared to small trees.

The data in Table XXI suggest that the proportion of weevils found on root and collar areas may vary from year to year. Lower percentages of weevils on the collar generally occurred in 1963 for plots 1 to 5, 6 and 7 as compared to other years. A substantial reduction also occurred in the cutover strips of plots 1 to 5 in 1963 but this probably resulted from different influences operating in the non-cut portions.

4.4. Relationship with Clear Cutting: The sampling in the clearcut halves of plots 1 to 5 showed that some larvae survived in the cut stumps one and two years after tree removal. A small reduction in weevil numbers appeared likely in the first year after cutting while a sharp reduction occurred between 1962 and 1963 (Fig. 10). Between 1961 and 1963 an estimated 67 percent of weevils were unaccounted for and it may be assumed that this value represents the approximate mortality from the 1961 population level in the A and B strips. The population in these strips in 1963 consisted mostly of mature larvae and pupae. The percentage pupation was 59.1 (Table XV). The maximum number of weevils found on any one tree in the A and B strips in 1961, 1962 and 1963 was 19, 14 and 5 respectively, while in the C and D strips the maximum numbers were 24, 20 and 17 for the same years.

Several changes in the weevil habitat were noted in the cleared areas as a result of tree removal. Rapid drying of the bark and sapwood of

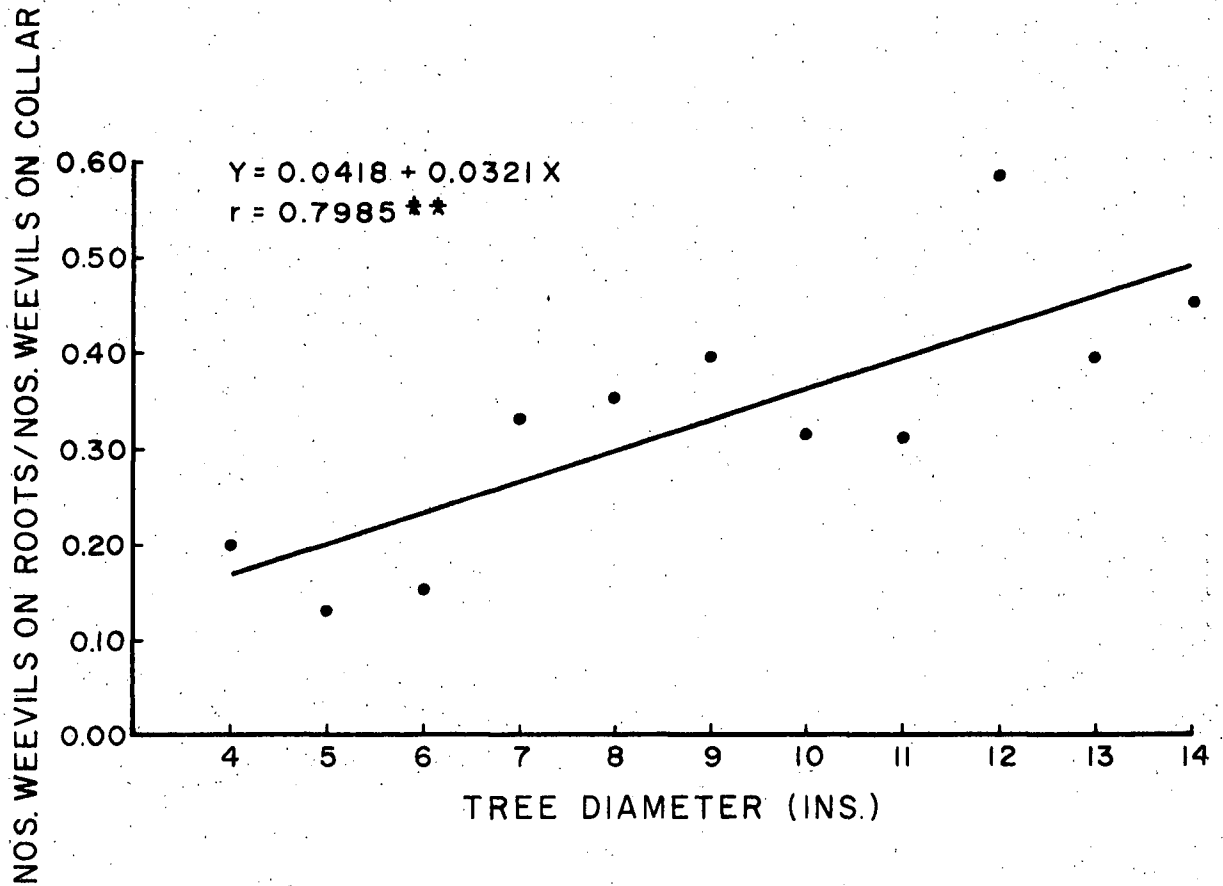


Fig. 27. Graph showing the proportional change of weevil numbers on roots and collar with increasing tree size. The data were taken from plots 1 to 5. Line was fitted by the least squares method.
**Significance of the "r" value is at the 0.01 probability level.

TABLE XXI. SUMMARY OF THE PERCENTAGE OF WEEVIL POPULATIONS FOUND ON THE ROOT AND COLLAR REGIONS OF SAMPLED TREES IN PLOTS 1 TO 10.

Year	Plots	Percentage weevils on roots	Percentage weevils on collar
1961	1-5, AB	19.7	80.3
	1-5, CD	11.1	88.9
1962	1-5, AB	4.9	95.1
	1-5, CD	11.2	88.8
1963	1-5, AB	14.1	85.9
	1-5, CD	28.3	71.7
1965	1-5, CD	38.6	61.4
1961	6	11.0	89.0
1962	6	10.9	89.1
1963	6	37.0	63.0
1962	7	5.0	95.0
1963	7	22.7	77.3
1963	8	68.0	32.0
1966	9	32.0	68.0
1966	10	38.6	61.4

stumps followed immediately after cutting. Duff compaction occurred especially around tree bases during cutting, and additionally when the cut trees were skidded with horses. All branches and tree tops lopped from the pulpwood stems were left in a scattered pattern. They provided some protection as shade to the cut stumps at least during the first year. A variety of phloem feeding insects, such as secondary bark beetles and wood borers invaded the stumps during the first summer after cutting, as well as some wood-decaying organisms. However, the inner phloem retained its whitish appearance for several months after tree harvest. In the regions of larval wounds no fresh resin flow was evident, and many of the galleries were enclosed in hardened masses of resin and bark mixture. The lack of a fresh resin supply appeared to influence the position of pupal case construction since many pupae were found in an upright position on the stump.

The developmental time of larvae and pupae appeared to be altered in the A and B strips. In 1962 and 1963 the sampling data suggested that pupae appeared earlier in the A and B strips as compared to the C and D strips. For example, in the clearcut area the first dates of pupa collections were June 12 and June 11 for 1962 and 1963 respectively. In the non-cut area for the same years the first dates of collection were July 19 and July 9.

4.5. Relationship with Stand Maturity: Differences in measures of weevil population intensity and in absolute numbers were evident in young and old stands of pine. In the 15-year old stand of plot series X the maximum number of weevils found on any one tree was two while three was the maximum number found on trees in the 20-25-year old stand (plot series VII, VIII and IX). Higher numbers were characteristic of all the older stands sampled in plots

1 to 5, 6, 7 and 10 where 31, 15, 17 and 13 weevils respectively were maximum numbers found on any one tree.

Estimates of absolute numbers in plot series X, VII, VIII and IX were 152, 567, 87 and 208 weevils per acre in that order. In contrast, estimates varied from 285 to 1764 weevils per acre in plots 1 to 10. On this scale of measurement considerable overlap in numbers existed between young and old stands. Higher estimates of weevil numbers than those given above for the young stands are possible on good growing sites.

5. Patterns of Weevil Attack

5.1. Initial Weevil Invasion into Regeneration Pine: The results of the pine regeneration survey in the mil-acre plot series I, II, III and IV are summarized in Table XXII. No H. warreni larvae or adults, nor evidence of their feeding was observed in the four plots series during 1963 and 1965. It may be assumed that no immigration of weevils had taken place up to 1965 when the trees were 1 to 7 years old. At this age the mean height of seedlings varied from 6.0 to 8.5 inches.

An examination of trees in plots V and VI in 1966 revealed that 5 and 9 trees respectively were freshly attacked with larvae. This accounted for five percent of the total trees in plot VI. The frequency distribution of tree heights in plot VI is shown in Figure 28. All attacked trees occurred in the dominant and co-dominant classes. Trees in this plot ranged in age from 3 to 9 years. An estimate of the age for susceptibility to attack in this regeneration would be 6 to 8 years, or when the trees are 4 to 5 feet high and have a diameter of about one inch (d.s.h.). No measurement of absolute

TABLE XXII. PINE REGENERATION SURVEY ON CLEARCUT SITES IN THE ROBB STUDY AREA.

Plot series	Total pine seedlings		Ave. no. seedlings/mil-acre		Age range		Ave. ht. (ins.) in 1965	Proportion mil-acres stocked	
	1963	1965	1963	1965	1963	1965		1963	1965
I	41	49	2.73	3.27	-	2-5	7.0	11/15	10/15
II	49	56	3.27	3.73	1-4	2-7	8.5	9/15	10/15
III	122	106	8.13	7.07	1-3	2-5	6.0	13/15	13/15
IV	278	293	18.53	19.53	1-3	1-5	7.0	14/15	14/15

weevil numbers was made in plot VI since the larvae were left undisturbed.

The frequency distribution of tree size and weevil infested trees for plot series X and VII to IX are described in Figures 29 and 30 respectively. The pattern of tree selection appears identical with that described for plot VI. A tally of the infested trees from the Robb Burn showed that almost 70 percent were in the dominant category, while in the suppressed tree class the attacks were rare.

5.2. Rate of Weevil Spread in Young Pine Stands: The rate of advance of weevils into young stands is described in Figures 20, and 21 for the two burn areas of plot series VII to IX and X. The percentage of trees attacked in each 20-foot diameter plot in the Robb Burn suggested that few or no attacks occurred beyond approximately 400 feet from the stand periphery. The time of initial invasion into this stand, as determined by scar dating, was about 1955. Allowing two years for larval development, 12 years is a

Fig. 28. Frequency distribution of tree heights of pine regeneration, 3-9-years old, in plot VI showing the pattern of weevil attacked trees.



Fig. 29. Frequency distribution of tree heights of young pine, 15-years old in plot series X (Ricinus Burn), showing the pattern of weevil attacked trees.

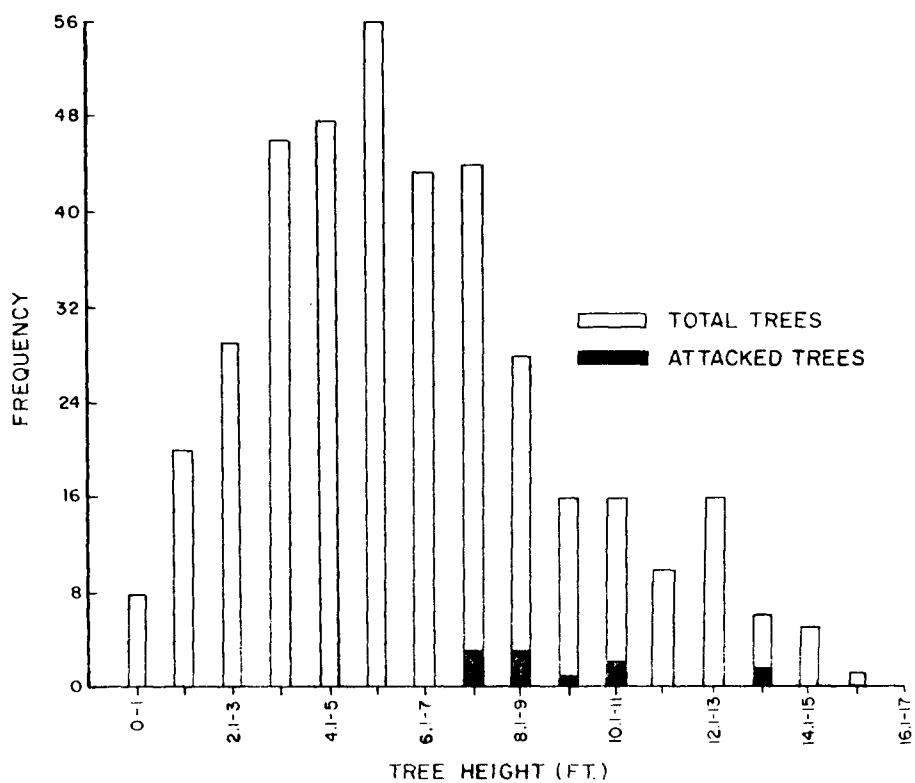
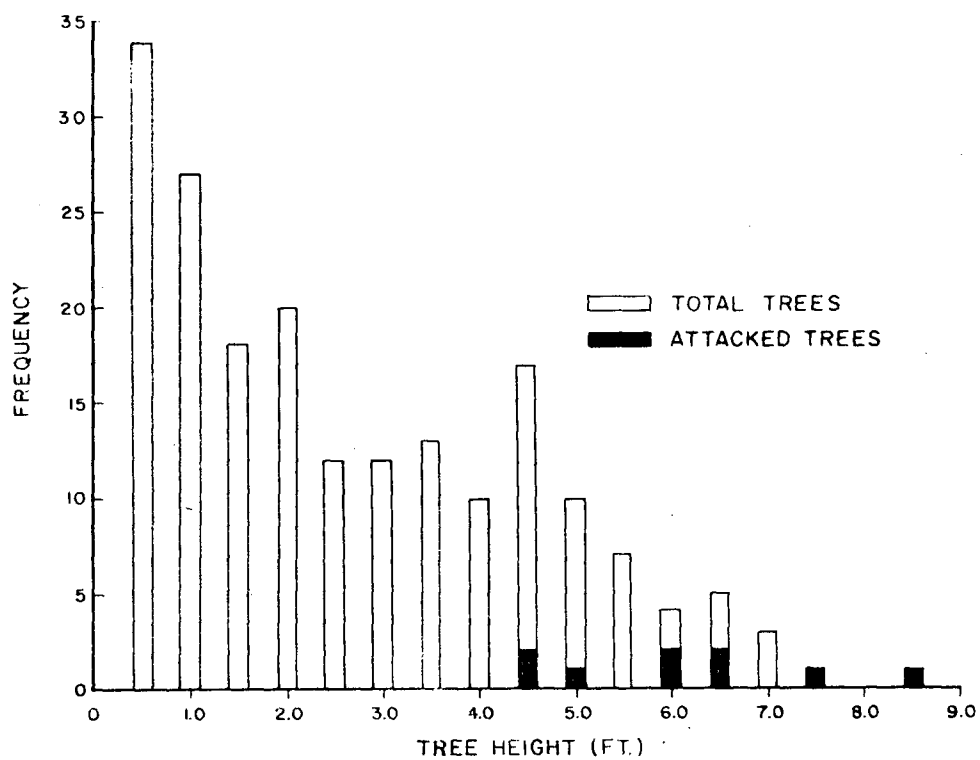
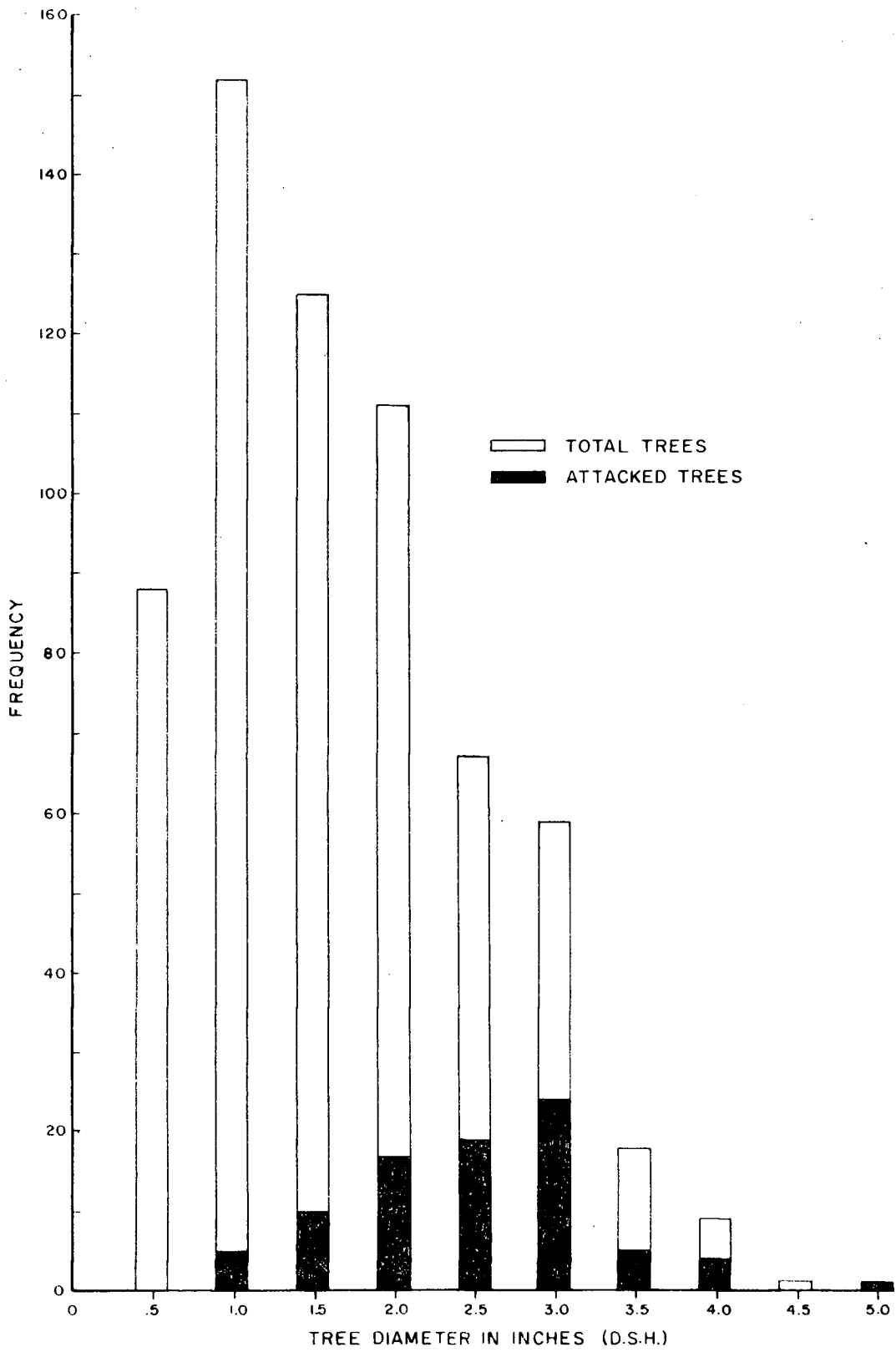


Fig. 30. Frequency distribution of tree diameters of pine, 20-25-years old (Robb Burn) in plots VII, VIII and IX, and showing the weevil-attacked tree pattern.



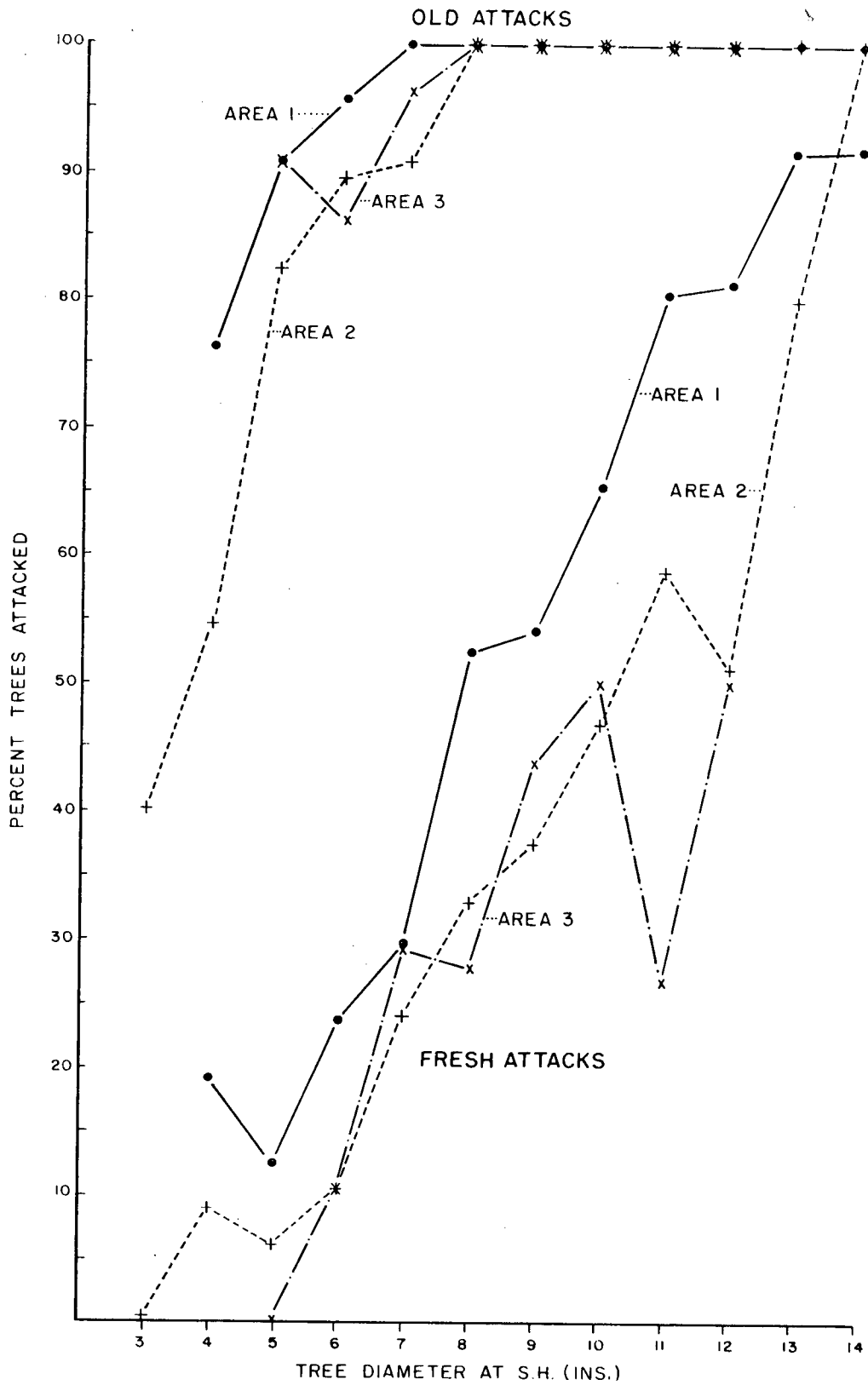
reasonable estimate of the stand age at initial invasion. Since that period the weevils have advanced into the stand at a rate of about 35 feet per year. A similar calculation for plot series X suggested a rate of spread of 45 feet per year. These estimates of 35-45 feet per year must be regarded as only approximate since weevils were found far beyond 400 feet of plot series VII, and therefore, other factors which influence weevil survival and behavior must be taken into account.

An estimate was made of the rate of advance into the pine regeneration of plot VI. This plot was established at least 210 feet from the nearest residual seed block with mature trees. Since the young pine originated after the 1957-58 clearcut it may be assumed that the adult weevil had traversed the 210 feet by at least the eighth year after cutting. However, plot series I to IV suggested that no weevils had entered the stands up to the fifth year after cutting. This would allow 2-3 years to traverse the 210 feet, or at a rate of 70+ feet per year.

5.3. Weevil Attack Pattern in Pine Stands: The pattern of old and current weevil attacks was analysed in relation to tree diameter for three different plot areas (Fig. 31). Population levels were highest in area 1 and lowest in area 3. All trees with a stump diameter of 8 inches or more had 100 percent old attacks, and many of the trees in the smallest size classes showed no evidence of previous attack. No field evidence was found to suggest that small trees provided more unfavorable conditions for larval survival than large trees.

The percentage of trees showing current feeding damage was directly correlated with tree diameter. Areas with high population levels had a

Fig. 31. Comparison of old attack and fresh attack patterns in relation to tree diameter in different pine stands. Area 1 includes plots 1 to 5, ABCD-1961; CD-1962; CD-1963. Area 2 includes plots 6 and 7, 1961-63. Area 3 includes plot 10, 1966.



greater percentage of trees with old and fresh attacks as compared to areas of low population levels. This indicates that population levels are partly a function of tree size and of the percentage of trees with fresh attacks.

The relationship of population levels and percentage of trees with current attacks is shown in Figure 32. For stands 60+ years old (i.e., plots 1 to 10) weevil numbers per tree are linearly correlated with percentage of trees having fresh attacks. Stands less than 60 years old (i.e., plot series VII to X) may be similarly correlated but may have steeper slopes. Four different population levels have been arbitrarily segregated (Fig. 32; Table XXIII) to show the pattern of fresh attacks. The relationship suggests a simple method of population assessment in pine stands.

The nature and pattern of weevil attack since the time of its initial invasion in a 65-70-year old stand is described from scar dating in Figure 33 and Table XXIV. Curves for three tree size classes (small, medium and large) show the pattern of attack for a period of about 50 years. An average of the three graphs provides a general picture for the stand. The data indicate that weevil abundance was maintained at three levels with respect to the three size groups.

All three tree groups appear to have been initially attacked within an interval of about five years; the large group first and the small group last. The corresponding diameters at first attack were largest for the large group and least for the small group.

Figure 33 suggests a characteristic pattern of weevil attack during stand development. For the first 15 years after initial invasion the rate of attack rises slowly. This stage is followed by a period of rapid increase

to a maximum level when the stand attains an age of approximately 45 years; thereafter it declines.

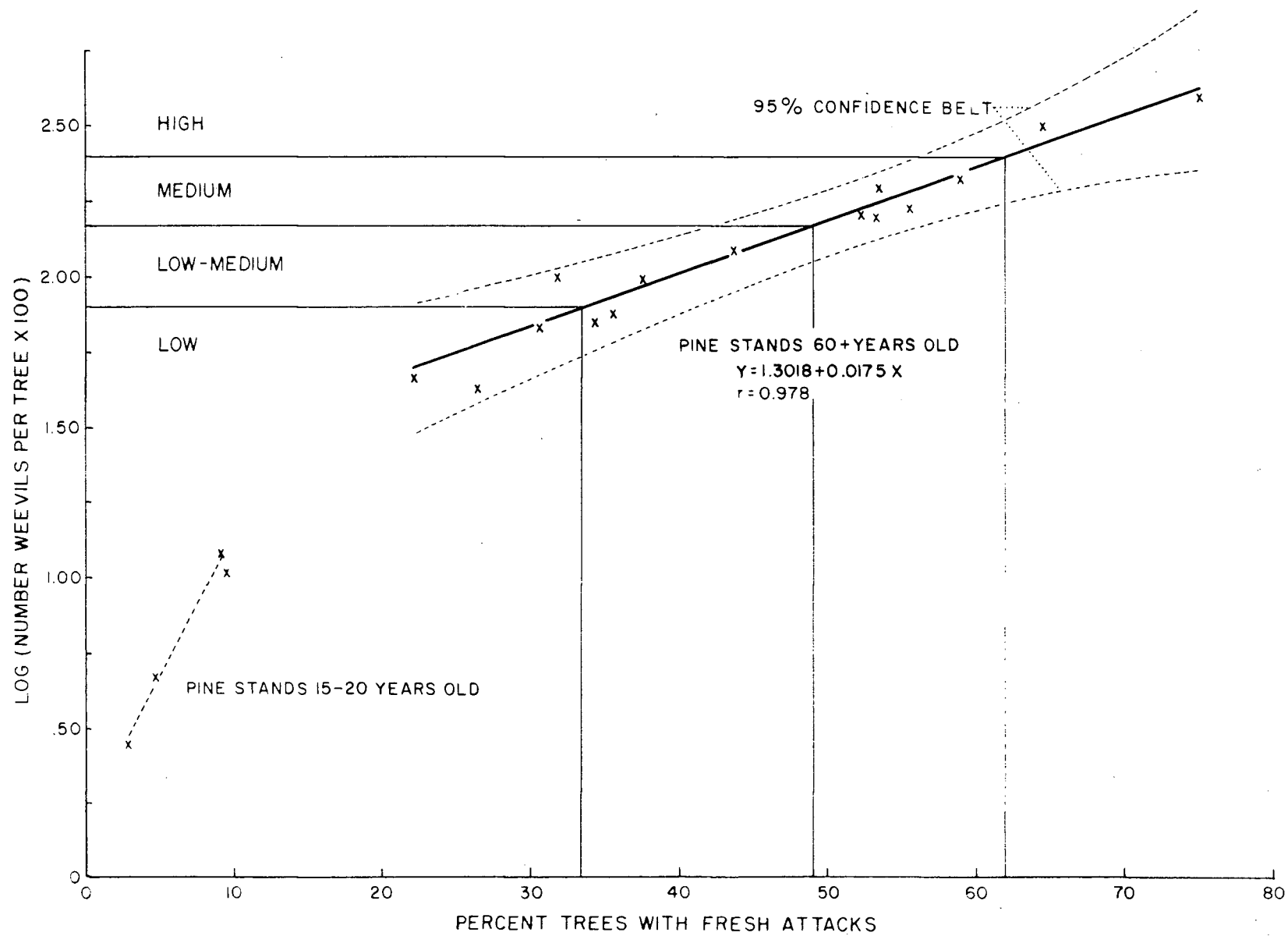
TABLE XXIII. POPULATION INDICES FOR PINE STANDS 60+ YEARS OLD.

Population level	Percentage of trees with current attacks	No. weevils per tree
Low	0 - 33.5	0 - 0.80
Low-medium	33.5 - 49.0	0.80 - 1.50
Medium	49.0 - 62.0	1.50 - 2.50
High	62.0 +	2.50 +

TABLE XXIV. SUMMARY OF H. WARRENI ATTACK HISTORY IN A 65-70-YEAR OLD PINE STAND

Tree groups	Total trees examined	Av. diam. at s.h. in ins.	Av. age	Av. age first attack	Av. diam. first attack (ins.)	No. scars per stump
Small	10	5.5	66.0	32.3	2.75	6.3
Medium	11	8.2	66.7	29.3	3.07	10.7
Large	10	12.3	67.2	27.5	4.26	18.8

Fig. 32. Relationship between weevil numbers per tree and percent trees with fresh attacks. Data for the older stands, 60+ years, were obtained from plots 1 to 10. The four population classes are arbitrary and are defined in Table XXIII. Line was fitted by the least squares method. Data for the younger stand was obtained from plots VII, VIII, IX and X; the line was sight fitted. The factor x100 was used to eliminate negative values.



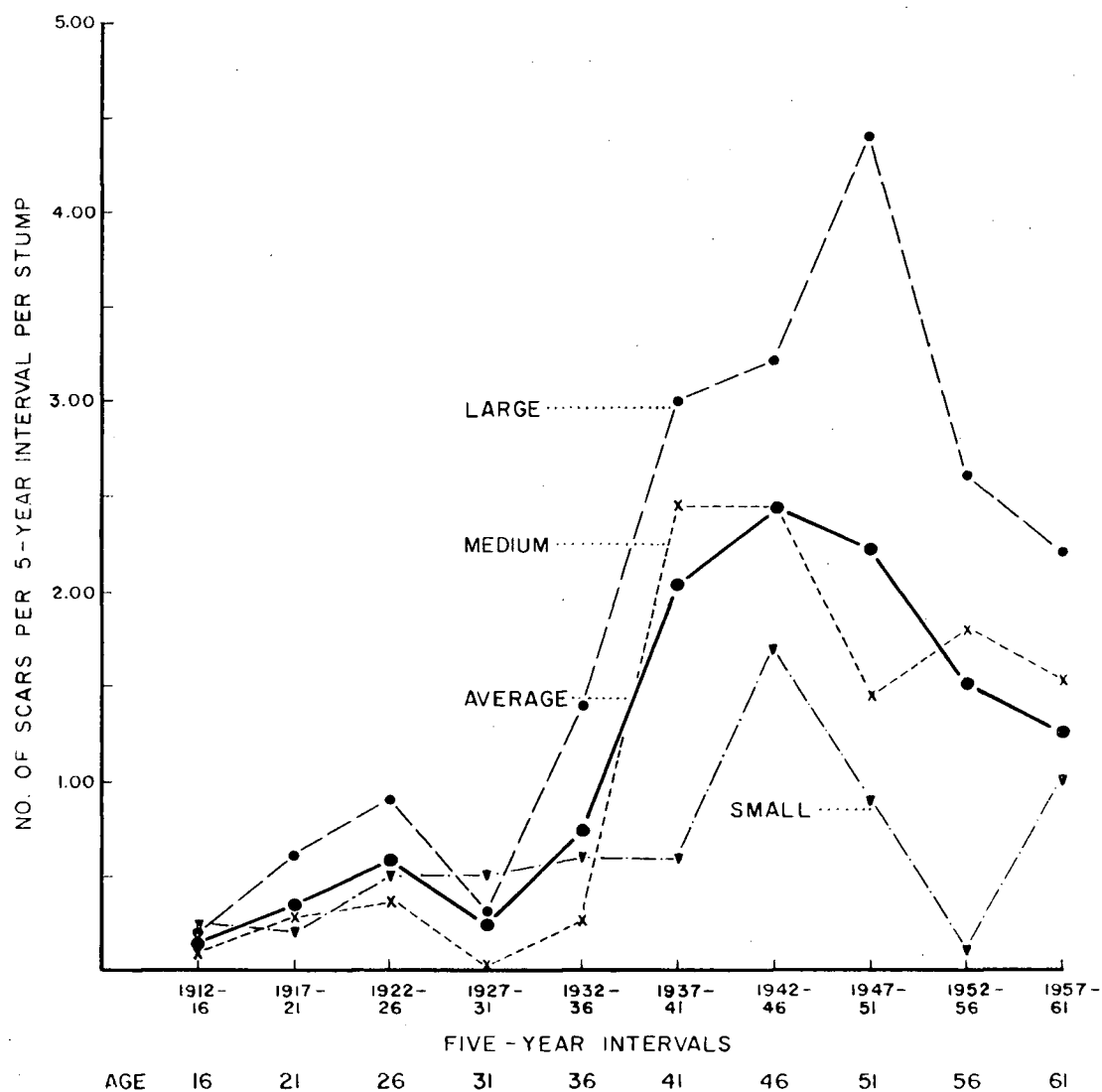


Fig. 33. History of weevil attack frequency on small, medium and large trees, 65-70-years old, and located between plots 1 to 5. Each line represents an average of 10, 11 and 10 trees for the small, medium and large groups respectively.

An analysis of the radial growth patterns of the three tree classes indicate that the trees were maintained in their respective stand positions throughout most of their growth (Fig. 34). The period of maximum attack was taken from Figure 33. Although a slight reduction in growth rate is evident in the small and medium groups during the period of maximum attack, it is unsafe to claim a causal relationship.

The accumulative pattern of weevil attack in naturally stocked pine stands is summarized in Figure 35. A combination of young and old stands is represented to indicate the possible changes expected during normal stand development. The age categories assigned are only approximate since the graph does not include all age classes and site variability within even-aged stands. In the model tree density is seen as a horizontal component which decreases in time as a result of natural thinning processes. Weevil attacks represent a vertical component which increase with decreasing stand density and with stand age.

6. Studies of the Life Stages of *H. warreni*

6.1. Larval Stage:

6.1.1. Larval Instar Determination: The frequency distributions of larval head capsule width measurements indicated that only the first three instars can be clearly defined (Fig. 36). Instar determinations beyond the third are obscured by an overlap of sizes. The prepupal size distribution suggests that six instars are possible.

6.1.2. Feeding Pattern and Development of Larvae: First instar larvae were observed from May to September in old pine stands. Rearings of the first

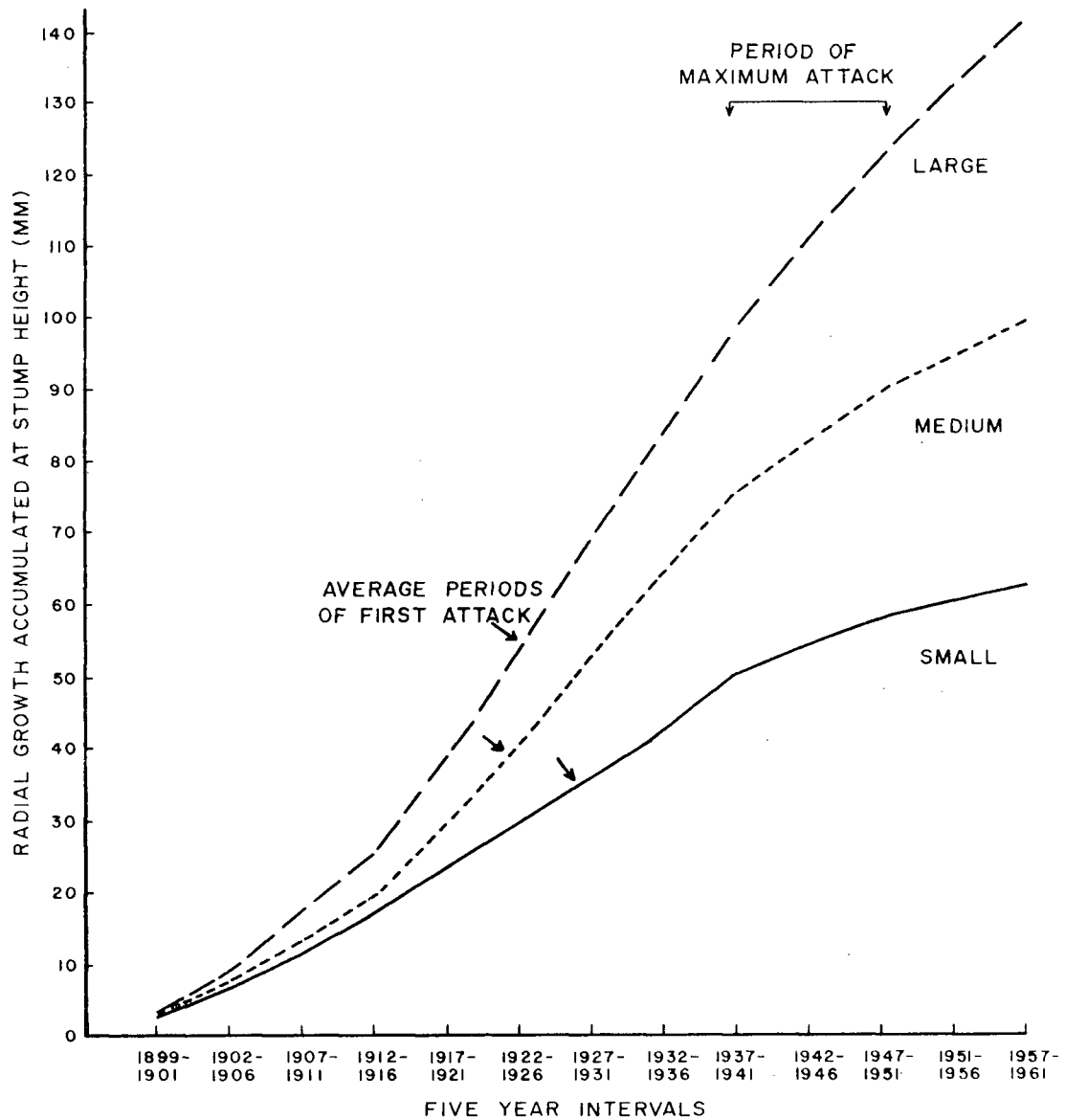


Fig. 34. Radial growth characteristics of small, medium and large weevil-attacked trees, 65-70-years old and located between plots 1 to 5. The period of maximum attack was taken from Fig. 32.

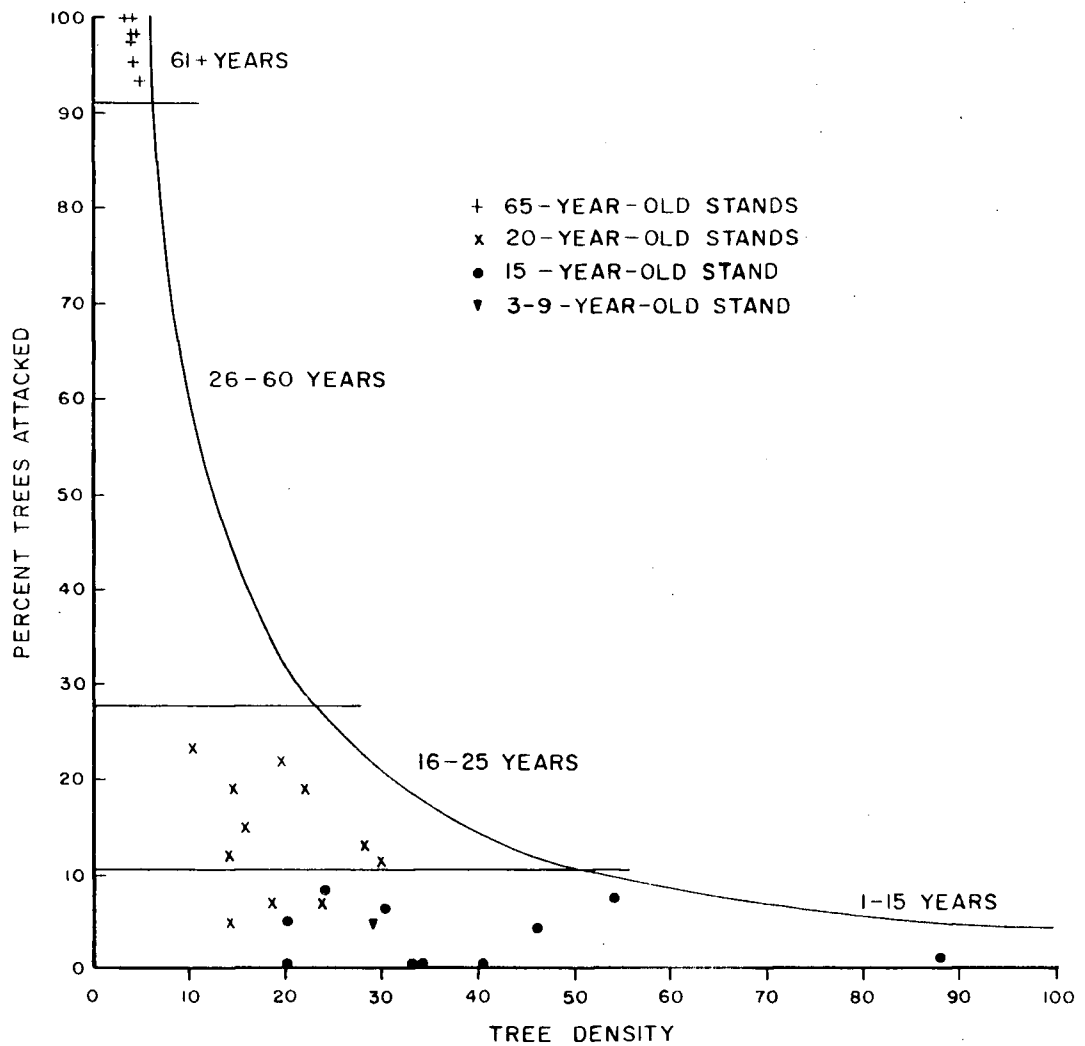
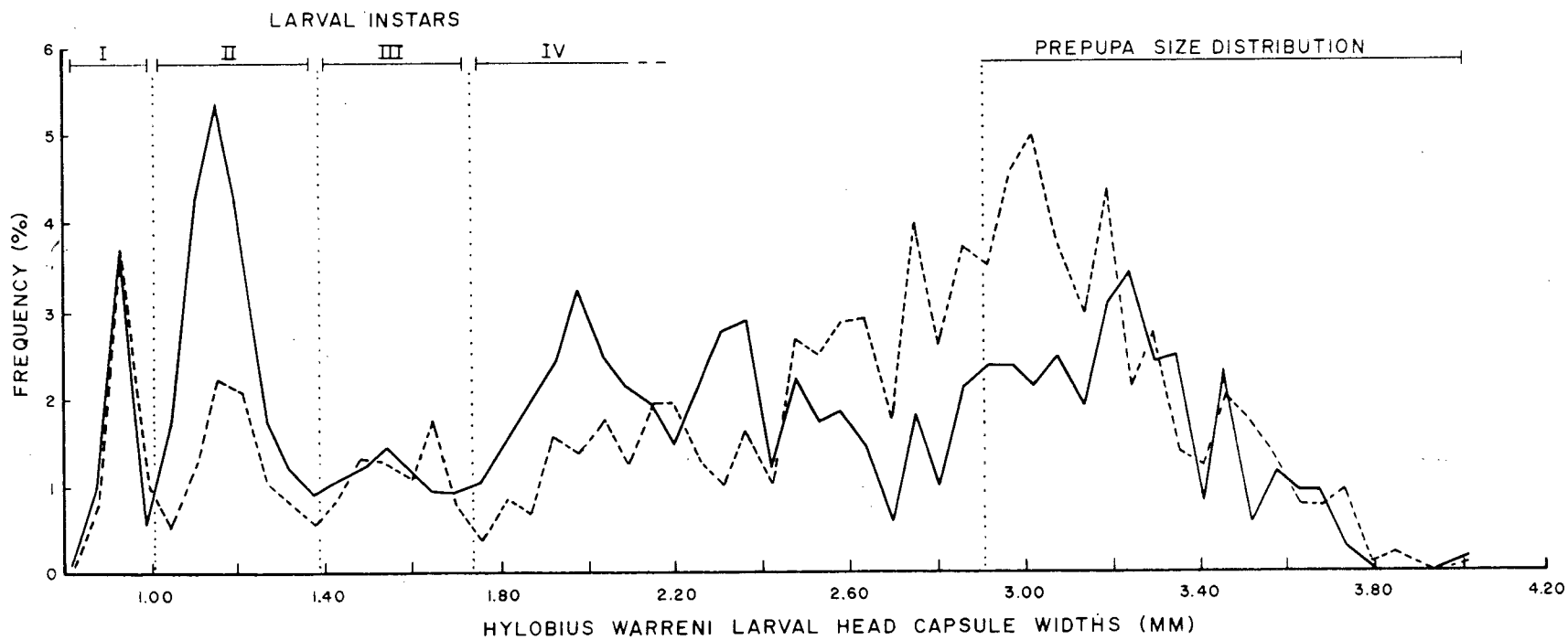


Fig. 35. Pictorial model showing the progressive weevil attack pattern in naturally stocked pine stands ranging in age from a few years old to mature. Age divisions were arbitrarily assigned. All areas sampled were converted to a common unit area equivalent to a 10-foot radius circle.

Fig. 36. Frequency distribution of Hylobius warreni larval head capsule width determinations. Larvae were collected from plots 1-5, ABCD, 1961 (----) and from plots 1-5, CD, 1962 (—); the numbers of larvae measured were 1255 and 778 respectively.



instar without food indicated that they were still active after five days and no mortality occurred at this time. This experiment demonstrated that a five-day period would be sufficient to allow their successful establishment in the bark substrate. Field observations showed that, following hatch, the young larvae may burrow a short distance into the phloem tissue and commence to mine small feeding galleries. The depth of feeding is generally very shallow at first and gallery orientation appears to take no fixed direction. Often the gallery remains very localized until the second or third instar, thereafter it may follow a more directional path. Throughout the feeding period fine particles of chewed-off bark are mixed with fresh resin to form a matrix which the larva molds into a protective covering. The resin material later crystallizes and hardens to provide an effective barrier against most forms of predators and parasites, as well as waterproof protection. The resin-bark mixture of galleries is generally pinkish-brown in color when fresh and turns whitish when dry and hard.

In an experimental situation first instar larvae became oriented beneath bark scales through a series of wriggling motions. Once under the scale they began to chew into the bark tissue. By the second day they were not visible and small amounts of bark frass marked their entry holes. After seven days the larvae had developed to the second instar and had extended small galleries within the bark. Their depth of feeding was greater than had been observed in the field. A necessary requirement for larvae during initial bark penetration appeared to be some form of support to initiate chewing activity. All instars responded negatively in the presence of light. Since they possess two anterior ocelli the larvae may sense the upper limits of its universe visually.

The relationship between larval size and depth of gallery penetration in living phloem of young pine is shown in Figure 37. The data suggest that feeding damage is confined to phloem tissue until the end of the third instar. Larger instars may penetrate into the cambial and occasionally into sapwood tissues. Comparative studies in older pine were not undertaken but general observations suggested a similar behavior.

Larval feeding was confined mostly to the zone of the root collar lying between the surface mineral soil layer and the upper surface of the duff. This zone may be defined as the larval universe. Within this zone the orientation of the gallery extends in almost any direction on the collar and root bases. In many cases, especially in late instars, the gallery network appeared three-dimensional as a result of resinous accumulations. An estimate of the damage potential of mature larvae showed that the galleries scored through to xylem tissue averaged 24 cm. in length by 0.7 cm. in width. These galleries were rarely unidirectional and most damage resulted in patches of dead cambial tissue (Fig. 38).

Some differences in the feeding gallery of late instar larvae were observed between young and old trees. In 10-25-year old stands the galleries were often more circumferentially oriented around the collar than in older and larger trees (Fig. 39), and extension of the gallery onto the roots was less common. Also, penetration into the sapwood was generally more pronounced on the younger trees. Nearly all observed tree mortality attributed to larval girdling occurred in trees less than 30 years old.

The total length of time for development of each instar was not established. However, second instar larvae were obtained at least seven days after hatch as noted earlier. It can be assumed that young larvae should

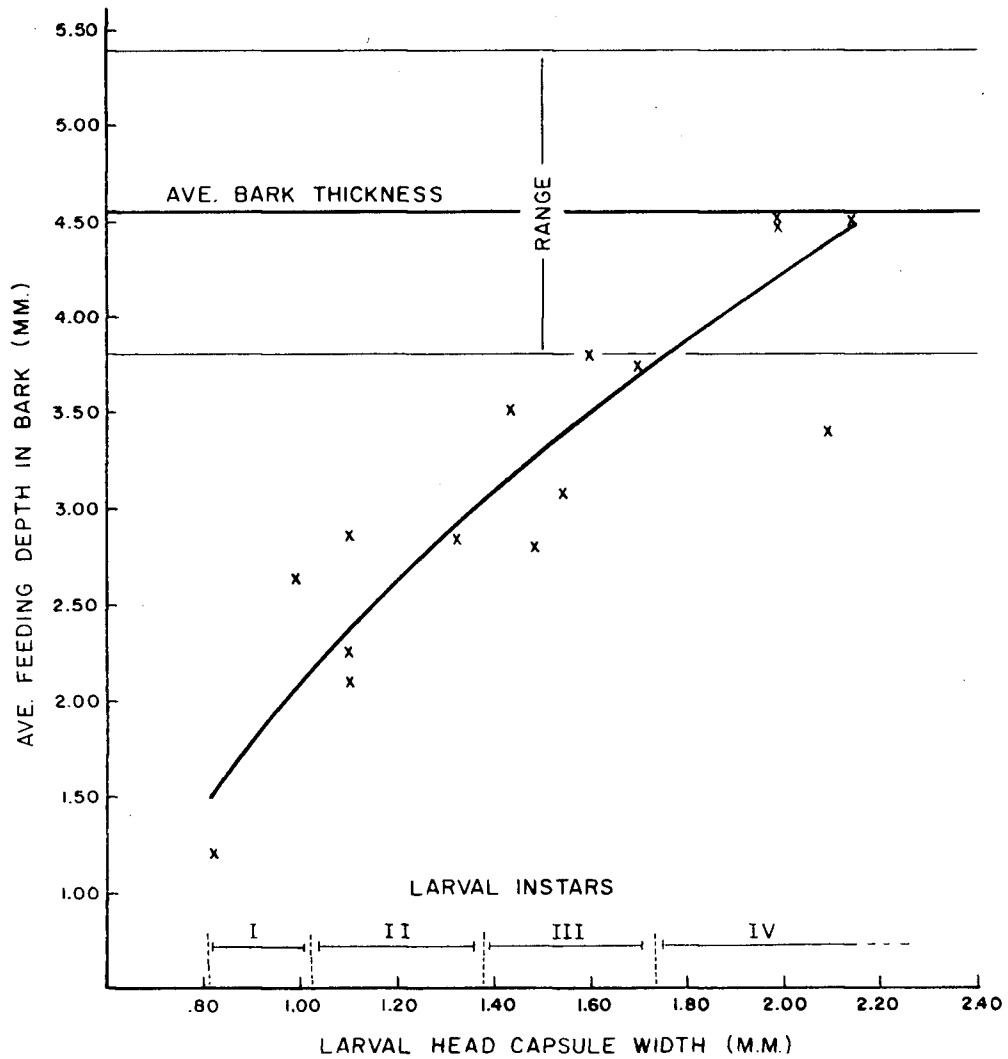


Fig. 37. Relationship between larval size and average feeding depth in the bark tissue of 20-25-year old pine trees.

Fig. 38. H. warreni larval feeding wounds on a 65-year old pine stump with bark removed to show dead cambial areas.

Fig. 39. Fifteen-year old pine stump showing the circumferential pattern of larval feeding in the root collar zone.



reach the second to fourth instars during the first summer of development. Larval development continues throughout the second summer when most of the feeding damage is done. In the following spring growth is terminated with the construction of a special chamber which serves for the prepupa, pupa and teneral stages. Its construction is evident by the middle of May but the prepupal stage does not begin until the early part of June.

During pupal cell formation the larval gallery is usually extended a few cm. away from the tree base. The chamber is formed at the end of the gallery within 2-10 cm. from the duff surface. Rotting logs lying at the base of trees were a common medium for the termination of the gallery. At the completion of its construction the chamber measures 8-10 mm. inside diameter and about 25 mm. long. It has a wall thickness of 4-6 mm. The inside wall is smoothed and the chamber is sealed off behind and in front of the larva. Most chambers lie in a near horizontal plane with the head capsule facing away from the tree.

Large temperature differences were observed in the larval universe between cut and non-cut stumps (Fig. 40). In the natural habitat (non-cut area) daily temperatures may fluctuate between 49 and 63°F. during the summer, while temperatures in the cut stumps may vary between 52 and 82 °F. Little or no difference occurred between north and south aspects of non-cut stumps for each depth level, but 2-5 degree differences were apparent between aspects of each level in the cut area. The temperature differences between cut and non-cut areas likely accounted for the earlier appearance of pupae in the cut area by influencing the rate of larval development (see dates of first pupal collections in section 4.4).

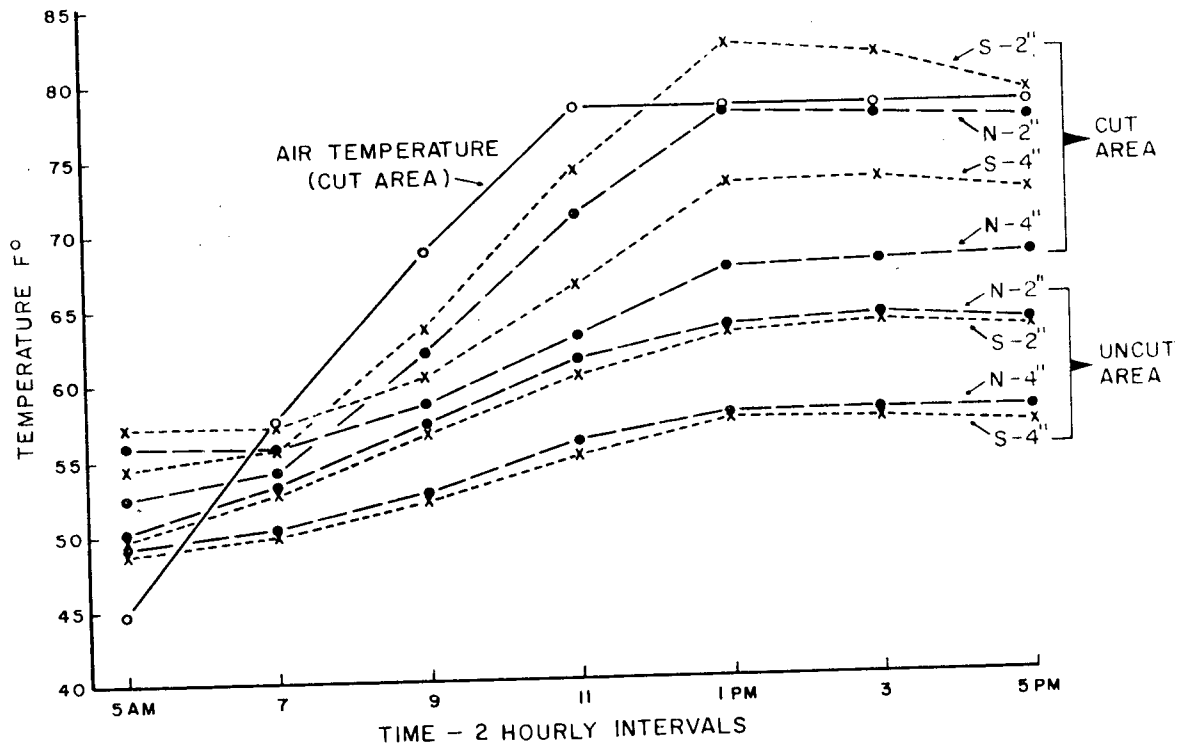


Fig. 40. Comparison of weevil habitat temperatures at cut stumps and at non-cut stumps. N-2" = two inch depth on north aspect; S-2" = two inch depth on south aspect; etc.

6.1.3. Bark Microhabitat Studies: Studies of the larval microhabitat on pine trees which took into account bark thickness and resin pockets, showed that certain patterns were apparent in the larval feeding universe of the root-collar zone. Bark thickness was minimal on lateral roots and reached a maximum two inches above the root base (Fig. 41). This level of the stem coincided approximately with mid-duff layer. No change in bark thickness was detected above 16 inches.

Resin pocket diameter was least in lateral root bark and increased almost two-and-a-half times at a level of four inches on the main stem (Fig. 42) while resin pocket area was least on lateral roots and increased almost five-fold at a height of four inches up the stem (Fig. 43). The number of resin pockets per mm^2 was also minimal on the lateral roots and reached a maximum about eight inches up the stem (Fig. 44).

The values comparing area and numbers of resin pockets to bark cross-sectional area were small but most of the larger pockets occurred near mid-alignment circumferentially in the living phloem (Fig. 45). Their effectiveness as a protective barrier against damaging agents is thereby enhanced. The pockets provide an immediate source of resin in liquid form and many were a mm. or more in diameter.

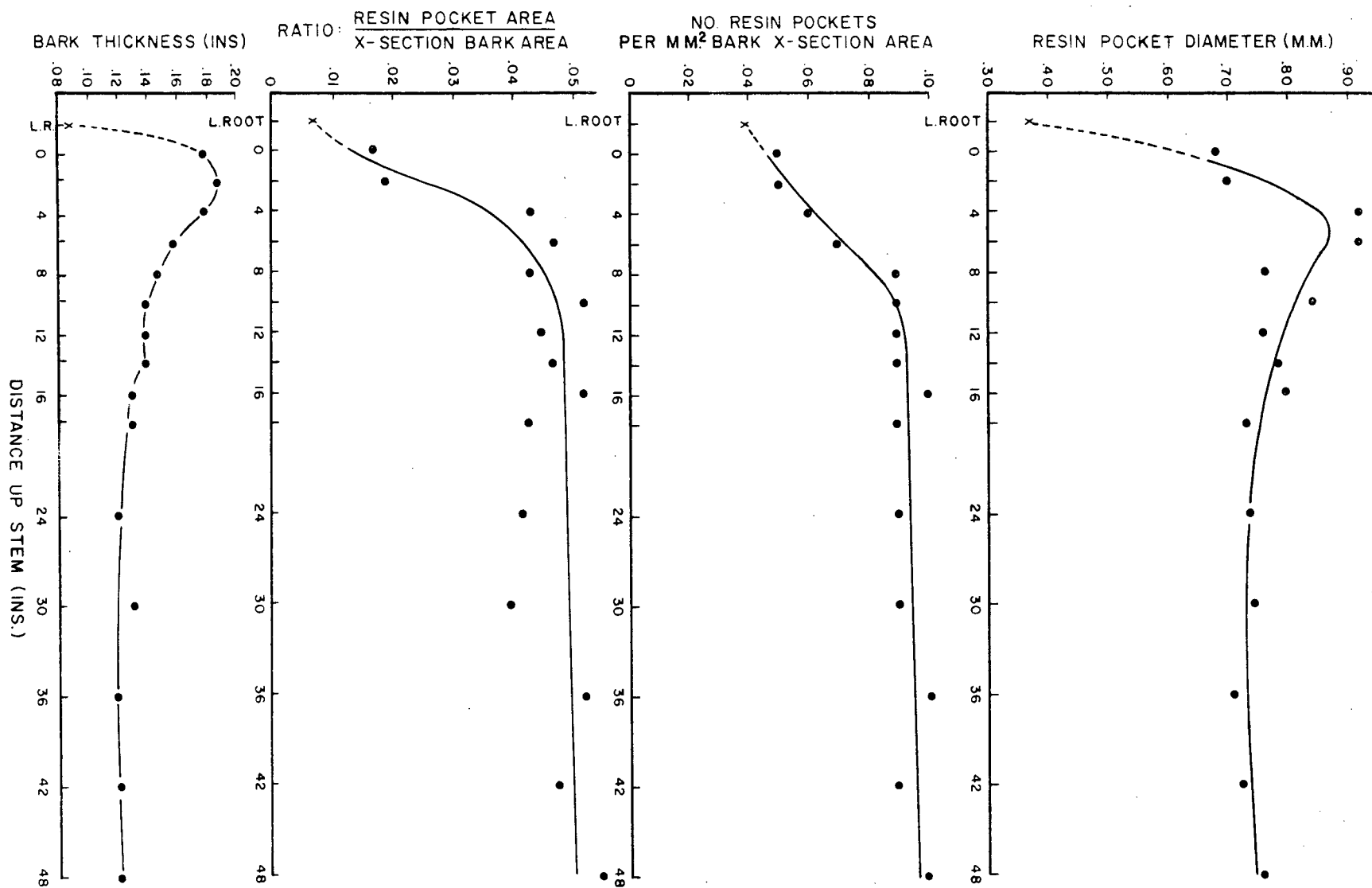
6.1.4. Mortality Factors of Larvae, Pupae and Teneral: In all weevil study areas sampled during 1961 to 1966 observations of larval mortality under natural conditions was relatively rare (Table XXV). Of those recorded a common cause appeared to be from excess moisture in the gallery. Most of the dead larvae were in the first to third instars. Moisture from stem runoff can accumulate in galleries and other cavities within the resinous matrix around attacked tree bases.

Fig. 41. Relationship between resin pocket diameter and position on the lateral roots (l-root) and main stem.

Fig. 42. Relationship between numbers of bark resin pockets per bark cross-sectional area and position on the lateral roots (l-root) and up the main stem.

Fig. 43. Ratio of bark resin pocket area to bark area on a transverse plane of lateral roots (l-root) and main stem.

Fig. 44. Relationship of bark thickness and position on the lateral roots (l-r) and main stem.



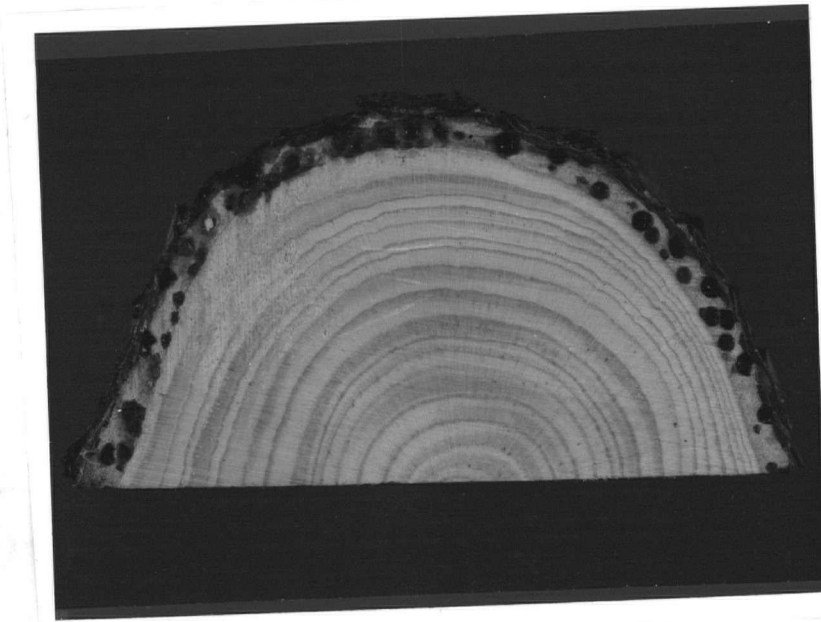


Fig. 45. Cross-sectional view of a disc cut four inches above the root collar on the main stem of a 21-year old pine showing bark resin pockets.

TABLE XXV. SUMMARY OF THE MORTALITY INCIDENCE TO IMMATURE STAGES OF H.
WARRENI IN PLOTS 1 TO 10.

Year	Plot	-----Stage of mortality-----				No. of para- sites	% mortal- ity of weevils in pupal cells	% mortal- ity of total population
		Larva	Prepupa	Pupa	Teneral			
1961	1-5, AB	-	-	-	-	0	0	0
1961	1-5, CD	-	1	-	-	0	1.4	0.26
1962	1-5, AB	2	1	-	6	0	5.3	1.37
1962	1-5, CD	-	-	4	5	1	7.0	1.26
1963	1-5, AB	1	8	2	3	5	15.0	10.00
1963	1-5, CD	-	2	8	4	4	18.9	2.19
1965	1-5, CD	1	2	17+1*	8	3	44.3	4.81
1961	6	1	-	-	-	0	0	0.66
1962	6	-	-	-	-	1	4.2	0.62
1963	6	-	1	-	2	0	50.0	2.70
1962	7	-	2	4	6	0	30.8	9.02
1963	7	-	-	-	3	0	17.6	2.65
1963	8	1	-	4	5	0	34.6	3.16
1966	9	1	3+1*	-	1	0	22.7	3.14
1966	10	-	-	-	2	0	20.0	3.39

* Denotes specimens covered with white fungus.

Total mortality of newly hatched larvae could not be assessed because of the low incidence of eggs found in the field. Of a total of 16 eggs found on mature trees the oviposition sites varied from within the outer bark to about 5 cm. from the bark surface. Some mortality is likely during the period between egg hatch and establishment of the larva in the phloem tissue, although no evidence of parasitism, predation or disease was observed in first or in later instars. Mortality was not observed to result from overwintering.

Several mortality factors of the prepupal and pupal stages were recorded (Table XXV) and identified. Pupae appeared to be particularly susceptible to moisture accumulated in their chamber. In some instances, free water appeared to weaken the case structure, and moistened chambers readily took on a blackish appearance with the development of fungal mycelia. A dry environment had a similar detrimental effect on reared pupae. Body fluid was lost and the weevils shrivelled and died. Collections of pupae and young adults still in the chamber were made in May and early June of each sampling year but in no instance were these pupae found alive. This suggested that pupae are unable to withstand overwintering conditions, whereas tenerals can.

Several specimens of a Hymenopterous parasite were collected and reared from weevil pupal chambers. These were identified as Dolichomitus tuberculatus tuberculatus (Fourc.) (Fig. 46) and belong to the family Ichneumonidae. They were identified by Mr. G. S. Walley at the Entomology Research Institute in Ottawa. The distribution of the parasite may coincide with that of H. warreni since collections in Alberta were made at Embarras (near Lake Athabasca), Robb, near Edson and 10 miles west of Ricinus.

Fig. 46. Female adult of Dolichomitus tuberculatus tuberculatus (Fourc.) and the weevil pupal chamber containing the case from which the parasite emerged. Scale in mm.

Fig. 47. Two live H. warreni pupae in cases and one dead prepupa (left) in a pupal case with the larval parasite, Dolichomitus tuberculatus tuberculatus (Fourc.). XI.



The life cycle of this parasite was reconstructed from field observations as follows. The adult emerges from about mid-June to mid-July and deposits an egg in a pupal chamber containing a weevil in the prepupal stage. The newly hatched parasite larva feeds externally on its host (Fig. 47) and develops in about two weeks to a mature larva. At this time it has consumed the body contents of its host. Parasites found in late July and August were usually enclosed in a greyish-brown case within the old weevil chamber. Here they remain as larvae until the following spring. Development to the pupal stage commences soon after the frost leaves the ground in May. Both male and female adults were collected in the field although the latter were most common. The incidence of the parasite may account for up to five percent mortality of weevils in the pupal cell (Table XXV), however, excess moisture appeared to be the main mortality factor. The values shown in Table XXV are probably conservative since some plots were sampled too early in the year to detect mortality of prepupae, pupae and teneralis.

Two specimens of a second insect organism (Fig. 48) causing weevil mortality of the prepupa and pupa stages were identified as Dipteran larvae belonging to the family Laphriinae (Asilidae). These were identified by Dr. J. R. Vockeroth at the Entomology Research Institute in Ottawa.

A few dead prepupae, pupae and young adults in pupal cells were found covered with a white fungal mass believed to be the entomogenous fungal parasite, Beauveria bassiana (Bals.-Criv.) Vuill. This same organism was positively identified on a number of dead adult H. warreni, but in either case the degree of virulence was not established.



Fig. 48. Dipteran larva of the family Laphriinae (Asilidae) collected from the pupal chamber of H. warreni (X 2.5).

6.2. Pupal Stage: Under natural field conditions pupae first appeared between the third week of June and the early part of July, while the peak of abundance occurred near mid-July. The prepupal and pupal stages combined may last up to eight weeks in the pupal chamber. Teneral adults were generally observed after mid-August and some vacated the chamber before the end of this month. They do this by chewing through the distal end of the chamber. Most tenerals emerge in the fall while some may overwinter in the chamber and emerge in May and early June.

6.3. Adult and Egg Stages:

6.3.1. Numbers of Adults and Sex Ratios: The numbers of adults collected by the different methods are summarized in Table XXVI, along with the corresponding sex ratios. Adults collected under (1)-a and -c consisted of dead specimens found at tree bases. Many of these may not represent mortality of the same year since they were in different stages of deterioration. Only the abdomens were available for identification of some of these.

Wide variations in the sex ratios were apparent from the adults collected by the different methods. There was less variation between collections made by the same or similar sampling method. Reared adults from 214 field collected pupae suggested that females were somewhat more abundant than males (method 6). Using the tree base-duff search method on trees within stands, more females than males were obtained (methods 1-b and 1-d), while the converse was true for adults collected on trees bordering cut strips (method 2). Similarly, more males than females were obtained on border trees as compared with within trees by the trap method (methods 3, 4 and 5). The collections from plots A and B showed similar sex ratios

TABLE XXVI. NUMBERS OF ADULTS AND THE SEX RATIOS OF H. WARRENI COLLECTED BY DIFFERENT METHODS IN DIFFERENT YEARS IN THE 65-70-YEAR OLD STAND.

Method of sampling and location	Year	Number of adults			Sex ratio ♀/♂
		females	males	total	
(1) Tree base-duff search within stand:					
(a) dead adults	1961	13	20	33	0.65
(b) living adults	1961	32	28	60	1.14
(c) dead adults	1962	16	11	27	1.45
(d) living adults	1962	44	26	70	1.69
(2) Tree base-duff search border of cut strip:					
(a) living adults	1965	30	65	95	0.46
(b) living adults	1966	5	40	45	0.13
(3) Traps on 60 trees:					
(a) 30 traps on border	1965	36	47	83	0.77
(b) 30 traps 50 ft. within	1965	27	26	53	1.05
(4) Traps on 43 trees at border of cut strip:	1966	21	48	69	0.44
(5) Traps in plots A and B:					
(a) Traps on 93 trees, A	1964	32	14	46	2.29
(b) Traps on 251 trees, A-B	1965	130	57	187	2.28
(c) Traps on 251 trees, A-B	1966	64	50	114	1.28
(6) Collected as pupae on cut and non-cut stumps:	1964	115	99	214	1.16

for 1964 and 1965, but a significant change occurred in 1966.

Observations made during collections may suggest an explanation for the discrepancies in the sex ratio patterns. During the tree base-duff search on border trees males were found inactive in the daytime and were most commonly near the surface of the duff layer within a radius of about 15 inches from the tree base. Females were generally on the tree base but lower in the duff. They appeared to spend considerable time on the root base and collar regions, presumably in search of oviposition sites and for egg laying activity. During the hours of darkness both sexes may disperse laterally within the stand in search of new hosts, or they may ascend the tree trunk to feed in the crown. The greater numbers of females collected by hand searching and in traps within the stand may suggest that both feeding and lateral dispersion are more frequent for females than males. This may also explain why more males were found on border trees since many could have originated from the adjacent cutover area and remained for longer periods on border trees. Tree removal on the cutover areas referred to, took place during 1961-62.

Relative abundance of adults captured during the three and four periods of the summer are summarized in Figures 49, 50, 51 and 52 for plots A, B, C and D. The trend for both sexes is similar in the two stand age classes, except that fewer males than females were generally captured during most periods of the summer. Although the general trend from spring to fall is a decrease in catch per day, the patterns vary within the same plots between years. However, the periods of catch were short and low numbers of adults were characteristic of most catches. The highest catches were recorded in June, except in plots A and B, 1966. Although mortality may account for

Fig. 49. Numbers of male and female adult weevils captured throughout the summer of 1965 in plots A and B.

Fig. 50. Numbers of male and female adult weevils captured throughout the summer of 1966 in plots A and B.

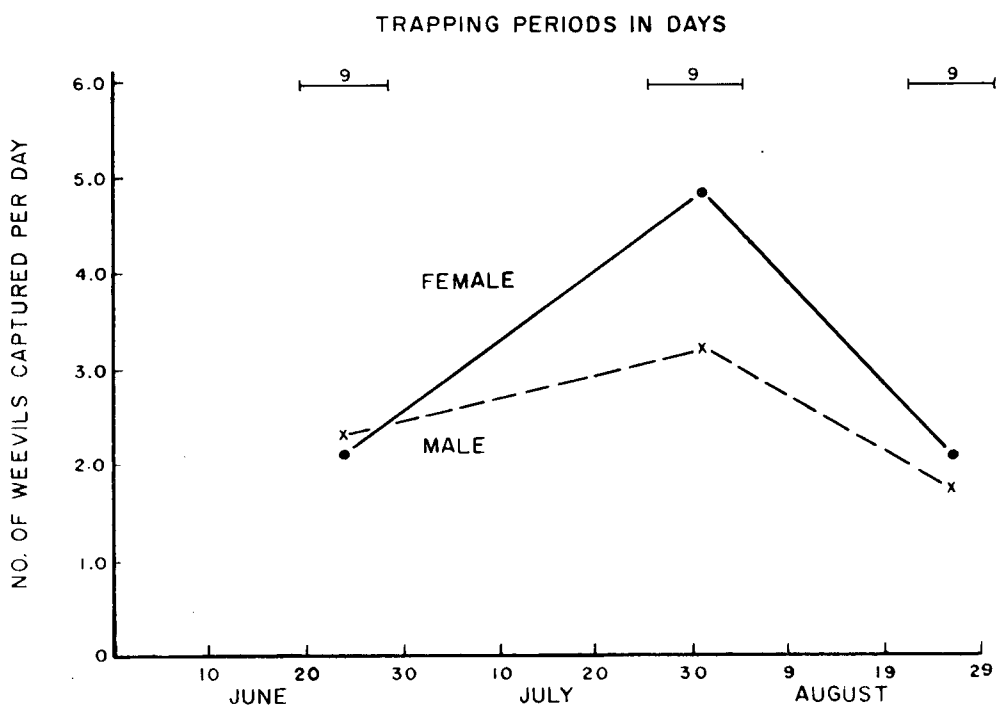
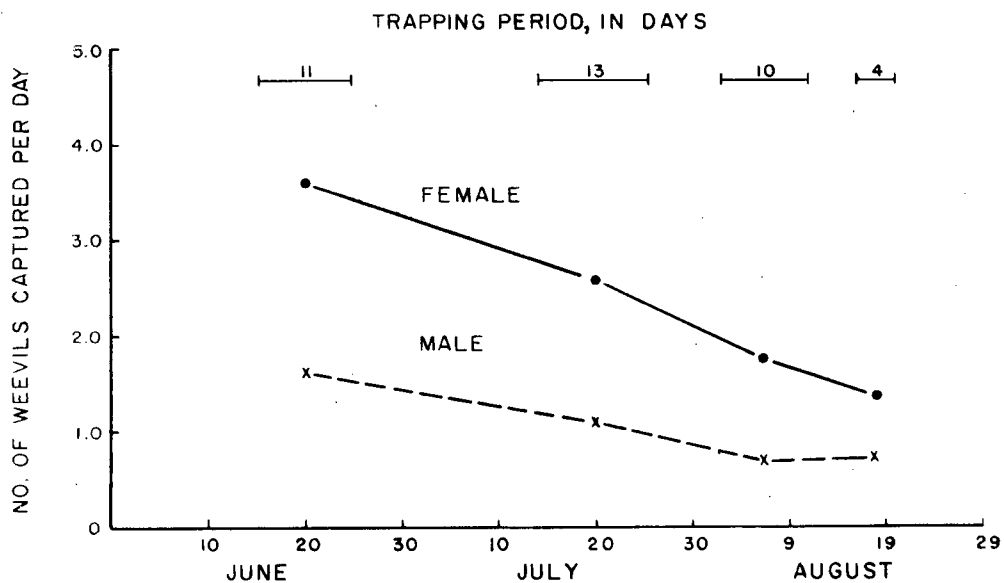
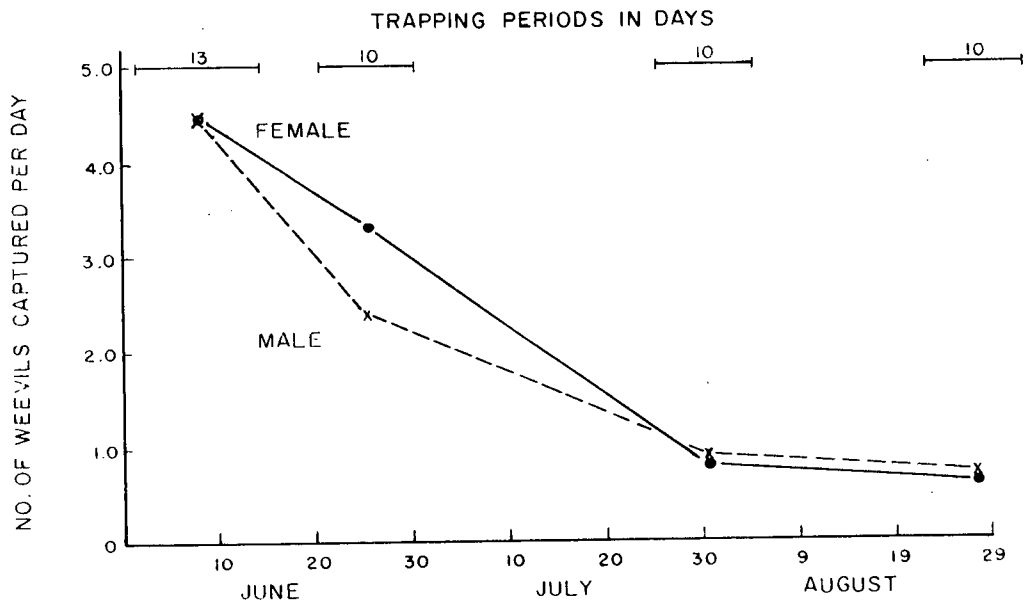
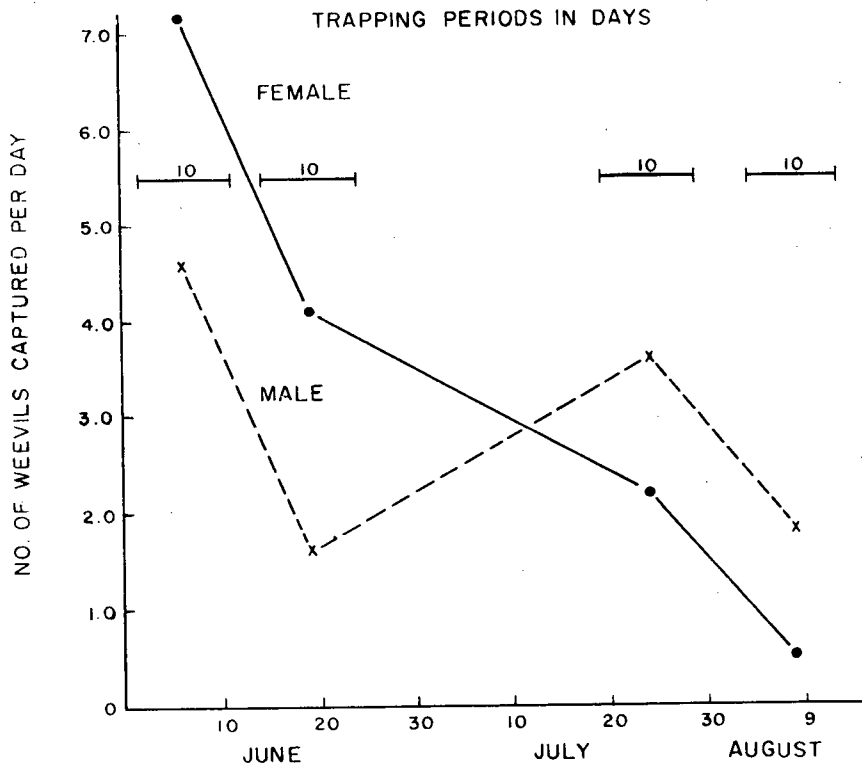


Fig. 51. Numbers of male and female adult weevils captured throughout the summer of 1965 in plots C and D.

Fig. 52. Numbers of male and female adult weevils captured throughout the summer of 1966 in plots C and D.



some of the rate of decrease this aspect was not investigated.

There was some evidence that a change in the behavior pattern of females may have occurred in different years in plots A and B. Calculated numbers of female captures per day per trapping day indicated high numbers in 1964, a slight decrease in 1965 and a sharp decrease in 1966 (Table XXVII). This decrease was of similar magnitude in both plots. The calculations for males suggested little or no change in the population levels between plots and in different years. The data in Table XXVII also show that the frequency of recaptures was similar for both sexes.

Numbers of adult captures in plots C and D during 1965 and 1966 showed a decline for both sexes, and a change in the sex ratios (Table XXVIII). The fact that weevil catches were higher in the spring of 1966 as compared to the fall of 1965 suggested that mortality did not account for all of the decline. It was therefore, likely that a combination of mortality and a change in behavior pattern was responsible for the spring to fall decline.

6.3.2. Relationship of Trapped Adults and Tree Size: The frequency distribution of tree sizes in plots A and B combined is given in Figure 53 and male and female captures in Figure 54. The tree size with greatest numbers of adult captures does not coincide with peak numbers of trees, suggesting a preference for larger trees. Both sexes are distributed similarly except that fewer males were captured than females. A straight line relationship describes the distribution pattern for each sex in relation to tree size (Fig. 55). Further evidence for selection of large trees is illustrated in Figure 56.

6.3.3. Dispersal Patterns of Adults in the Forest: The analysis of adult terrestrial movement patterns in plots A and B suggested that males and

TABLE XXVII. SUMMARY OF THE RELATIVE ABUNDANCE AND RECAPTURE CHARACTERISTICS OF MALE AND FEMALE H. WARRENI IN PLOTS A AND B DURING 1964-66.

	Plot A			Plot B	
	1964	1965	1966	1965	1966
% females captured 1+ times	37.5	37.0	51.5	36.8	43.2
% males captured 1+ times	59.1	33.3	44.0	40.0	44.0
No. female captures per trap per trapping day	0.025	0.022	0.014	0.027	0.016
No. male captures per trap per trapping day	0.012	0.010	0.011	0.011	0.011

TABLE XXVIII. SURVIVAL OF MALE AND FEMALE ADULT H. WARRENI RELEASED IN 1964 IN PLOT ARENAS C AND D.

	Year	Plot C		Plot D		Plots C + D	
		♀	♂	♀	♂	♀	♂
Total adults released	1964	30	20	30	20	60	40
Sex ratio	1964	1.50 : 1		1.50 : 1		1.50 : 1	
Total individuals recaptured	1965	24	20	22	15	46	35
Sex ratio	1965	1.20 : 1		1.47 : 1		1.31 : 1	
Total individuals recaptured	1966	24	18	16	13	40	31
Sex ratio	1966	1.33 : 1		1.23 : 1		1.29 : 1	

Fig. 53. Frequency distribution of tree diameters of all trees in the 1/5-acre plots A and B located in the 65-70-year old pine stand.

Fig. 54. Catch frequency of adult male and female H. warreni on different sized trees in plots A and B. The data were compiled from 1964, 1965 and 1966, captures.

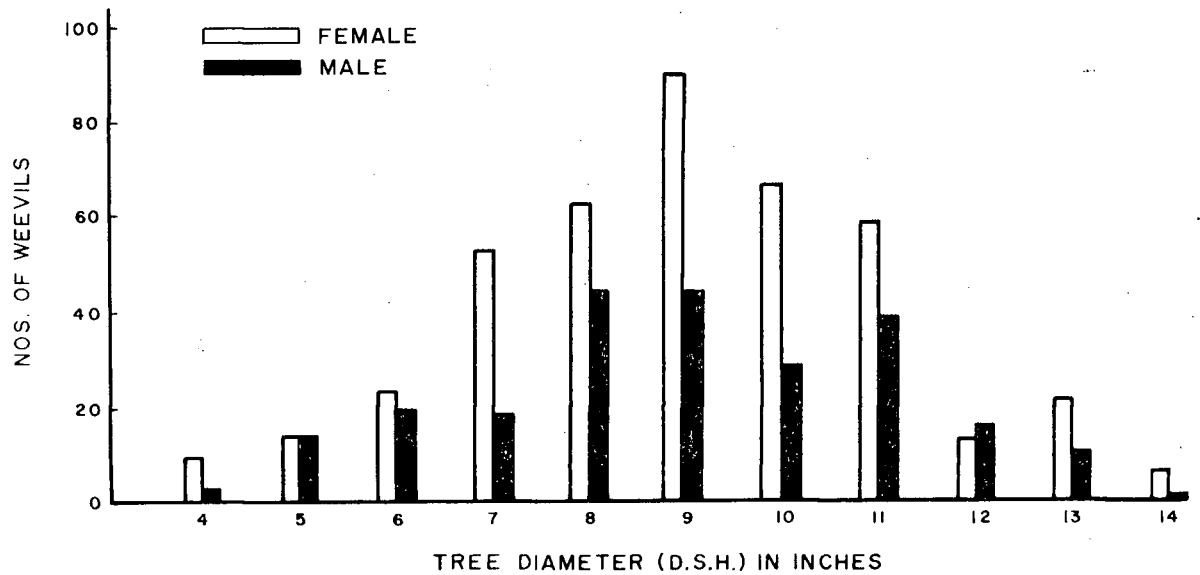
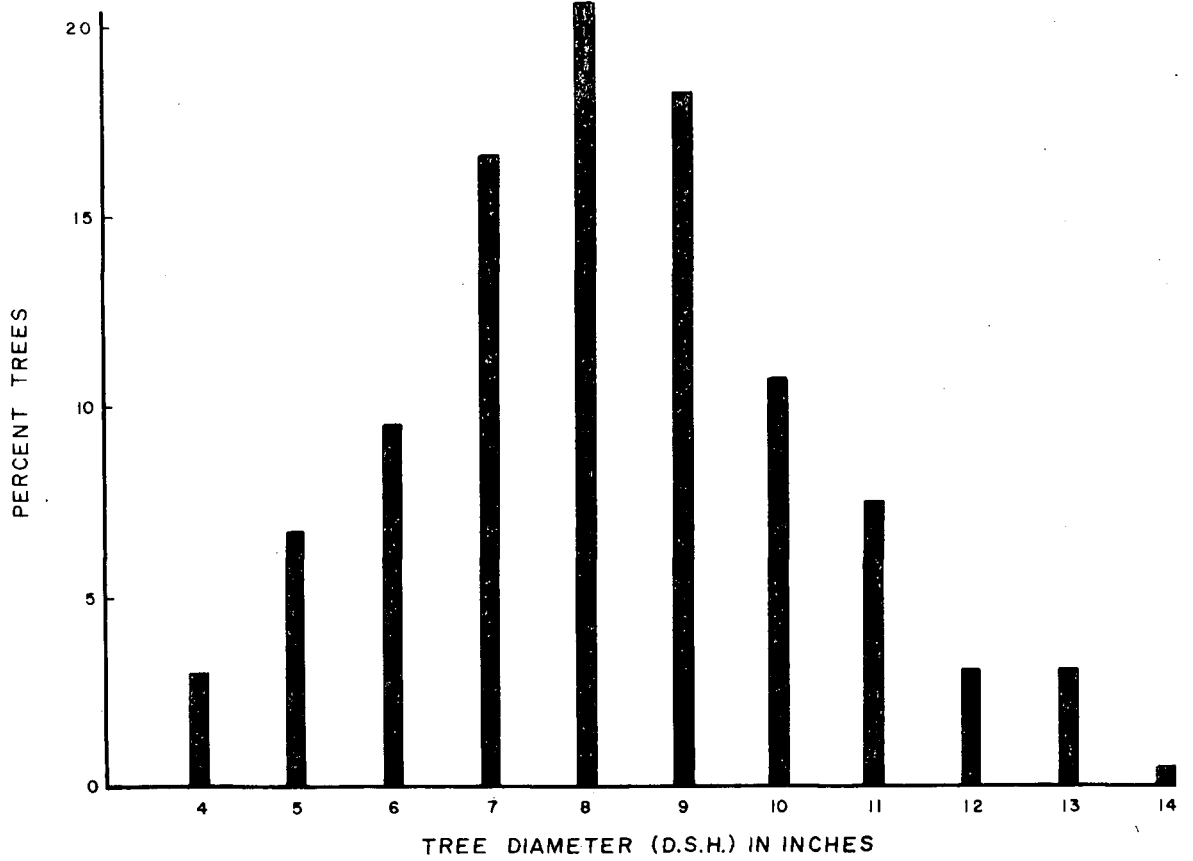
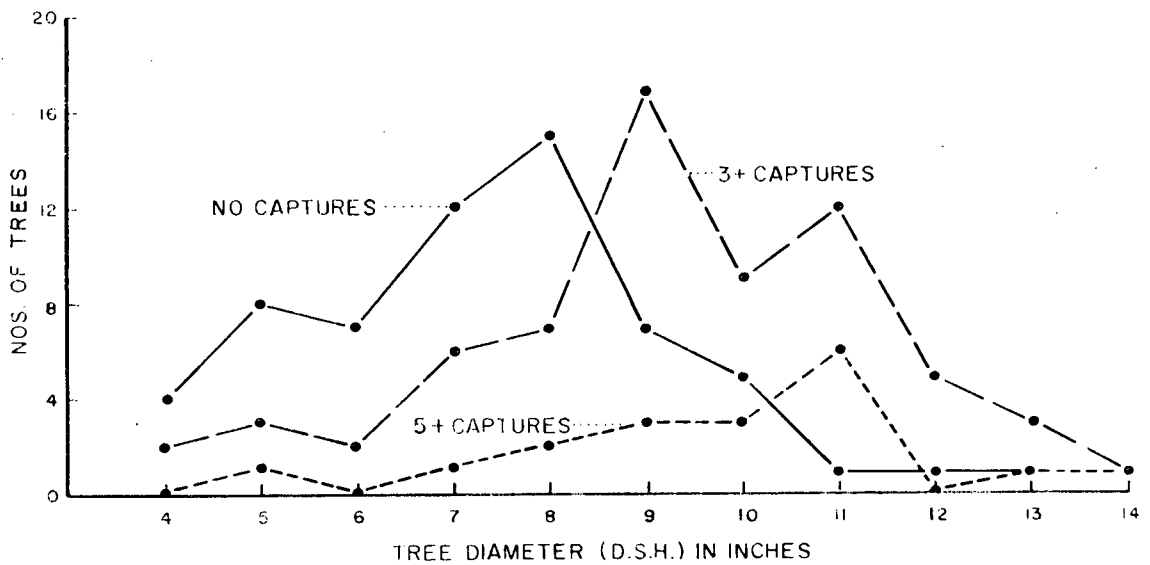
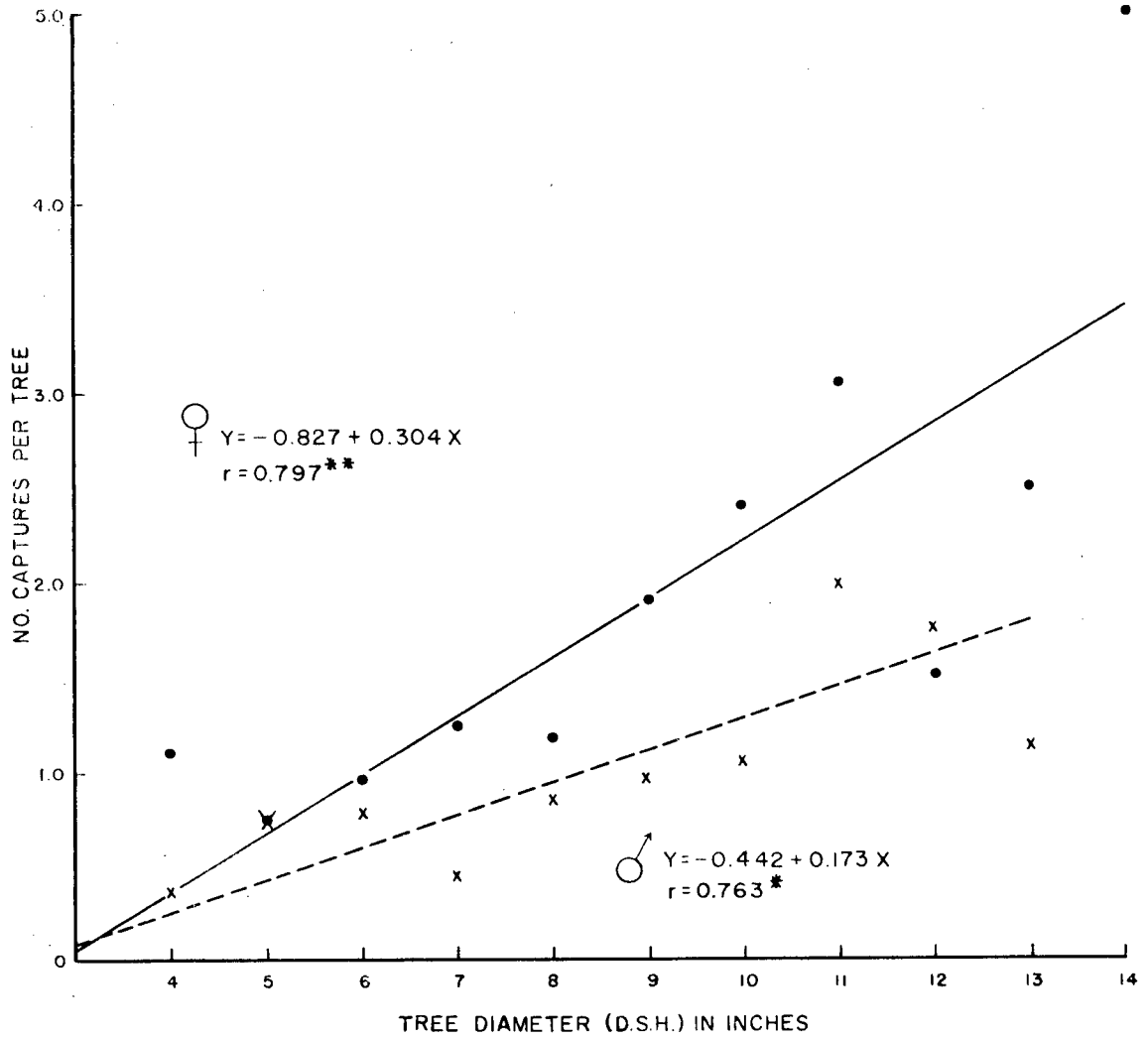


Fig. 55. Relationship between captured adult weevils and tree diameters in plots A and B during 1965 and 1966. Lines were fitted by the least squares method. ** r value significant of .01 probability level. * r value significant at .05 probability level.

Fig. 56. Frequency of tree size with no adult weevil captures, with three or more captures and with five or more captures. The data were compiled from plots A and B during 1965 and 1966.



females dispersed at the same rate in feet per day (Fig. 57). Slight differences in the rate of dispersal may exist between plot areas (Fig. 58) as a result of differences in site. The graphs suggest a pattern of random movement where the greatest distance travelled from a point source, such as a tree, takes place during any one night of travel. However, over long periods of time, after 8-10 days, the rate remains constant. The average rate of linear travel for any single night for males and females compares favorably with the average distance between trees which was estimated as 8.2 feet, but does not compare with the average distance of nearest neighbor tree (4.0 ft.). The maximum linear distance recorded between trees traversed by the same weevil during one night was 37 feet. It is therefore possible for individuals to visit more than one tree per night. Male and female individuals were also recaptured in the same trap two nights in succession on several occasions. The amount of activity, however, appeared to be limited partly by night temperatures. Little or no movement was observed when temperatures were below 40° F.

When adults left a tree in search of another tree there was evidence that they moved randomly from the tree of origin, at least initially (Figs. 59 and 60). The chi-square test for a directional preference showed that deviations of the calculated ratios from the theoretical ratios were not significant at the 0.05 probability level (Table XXIX) for males and females separately.

6.3.4. Weevil Reproduction:

Experiment 1: Tree diameter frequencies for plots C and D are shown in Figure 61. The graph indicates that the two plots were very similar in stand composition and structure.

Fig. 57. Rate of dispersion of male and female adult weevils. The data from plots A and B during 1964, 1965 and 1966 were combined.

Fig. 58. Rate of dispersion of male and female adult weevils separately in plots A and B. Data were compiled from 1964, 1965 and 1966 captures.

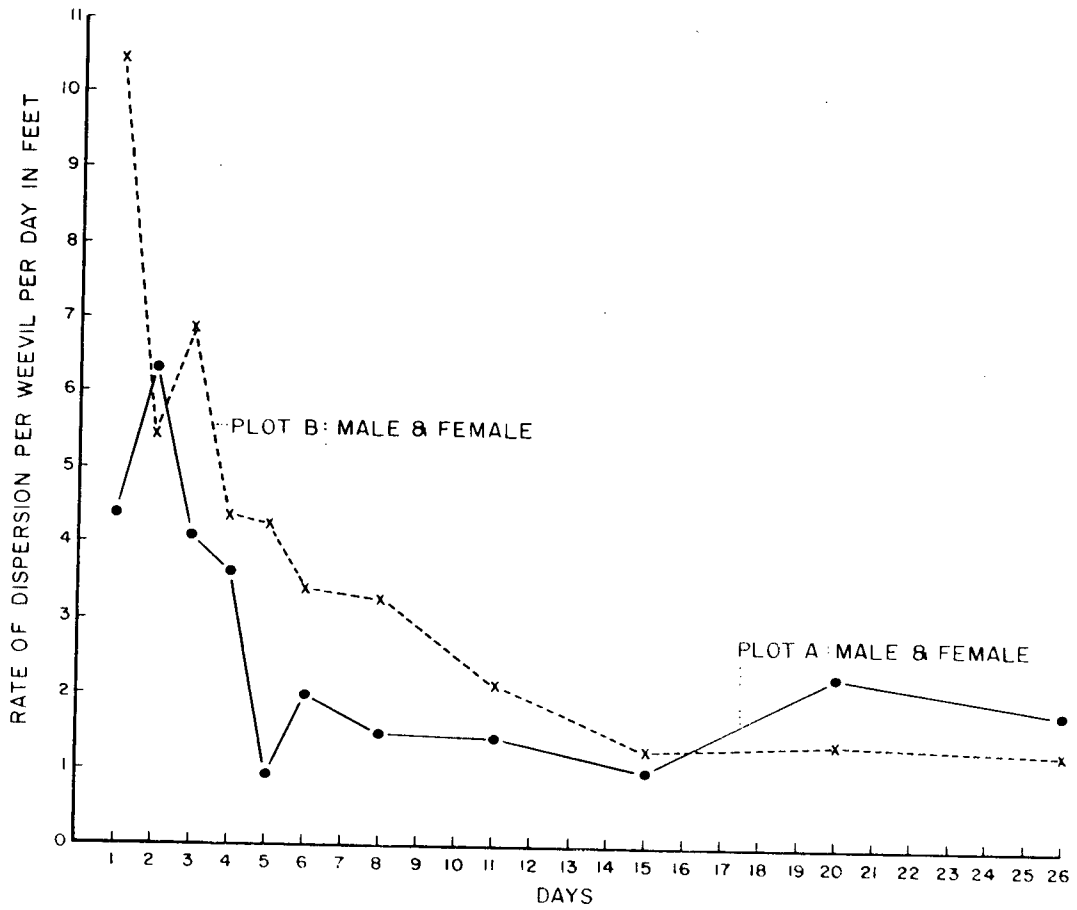
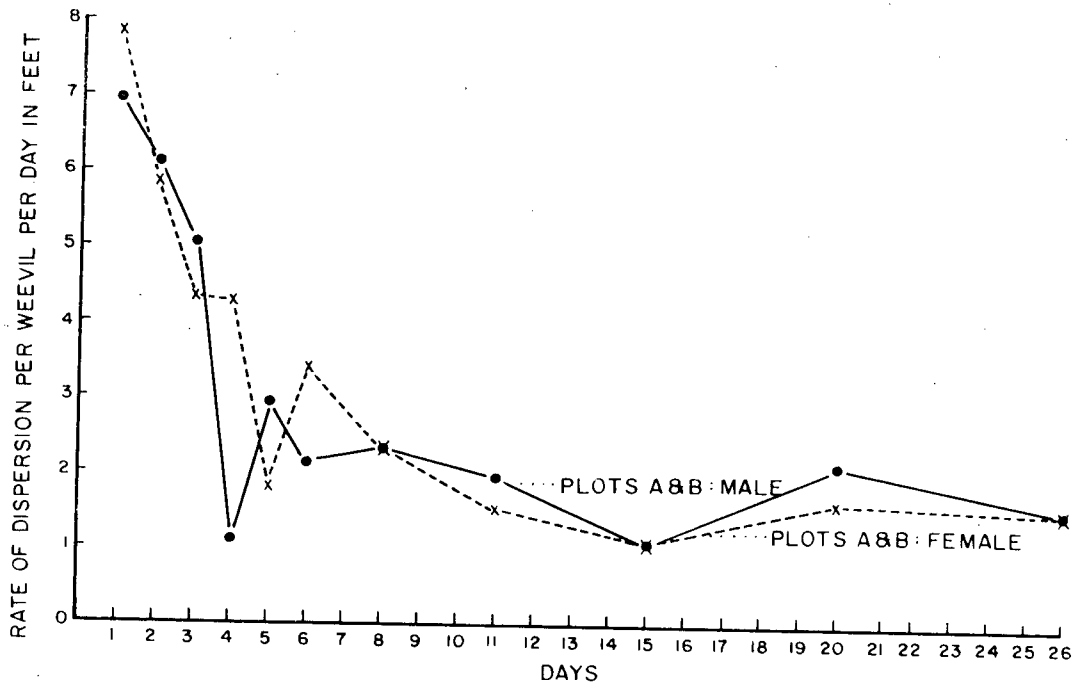
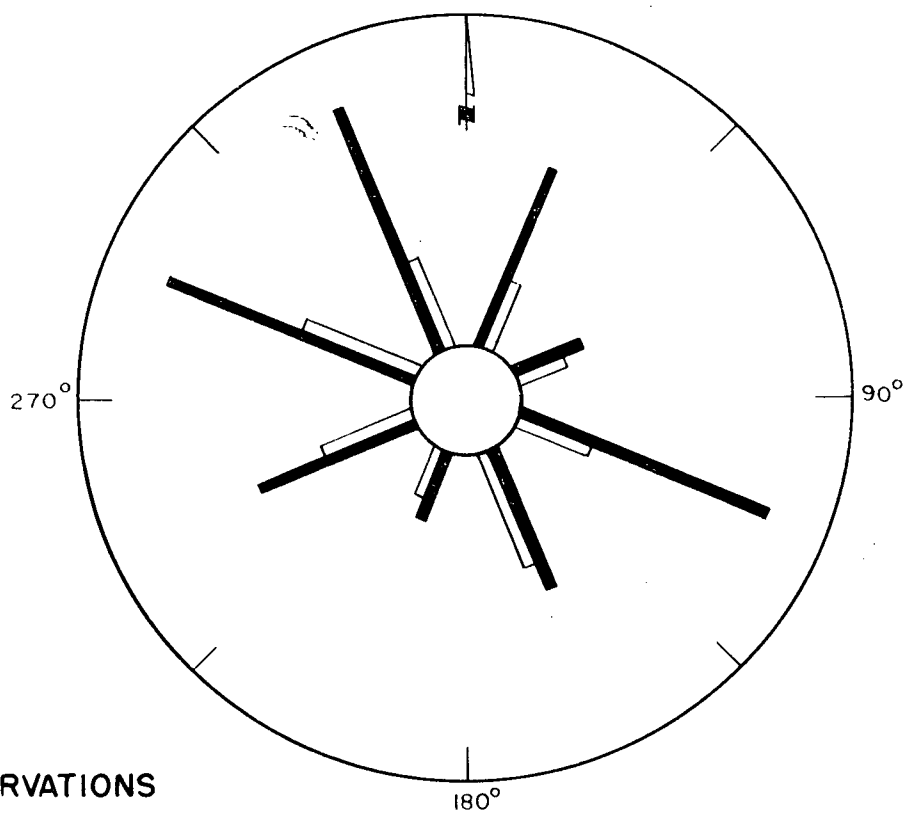


Fig. 59. Directional movement of adult male and female weevils in plot A.
Data were compiled from 1964, 1965 and 1966 captures.

Fig. 60. Directional movement of adult male and female weevils in plot B.
Data were compiled from 1965 and 1966 captures.



■ FEMALES
□ MALES

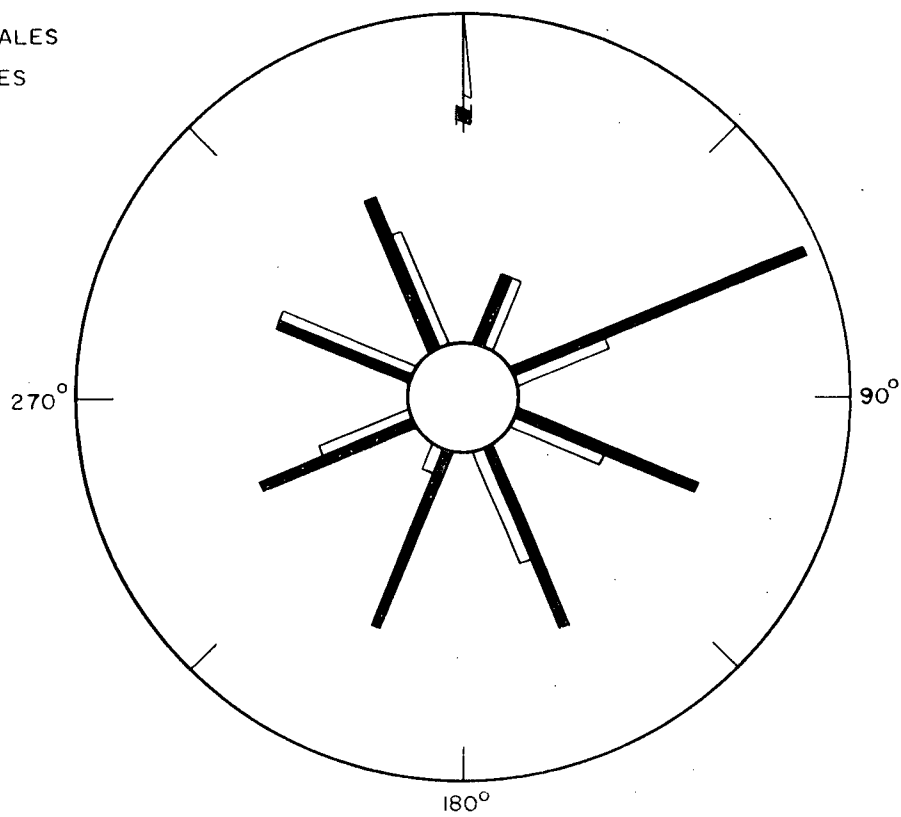


TABLE XXIX. CHI-SQUARE TEST OF DIRECTIONAL MOVEMENT OF MALE AND FEMALE ADULT H. WARRENTI IN PLOTS A AND B ACCORDING TO A 1:1:1:1:1:1:1:1 RATIO.

Plot no.	Sex	Total observations	D.f.	χ^2	P	Significance
Plot A	female	60	7	2.857	0.90 to 0.80	n.s.
Plot A	male	28	7	10.667	0.20 to 0.10	n.s.
Plot B	female	60	7	4.000	0.80 to 0.70	n.s.
Plot B	male	32	7	7.200	0.50 to 0.30	n.s.

D.f. = degrees of freedom; χ^2 = chi-square; P = probability; n.s. = not significant

Observations of oviposition and egg hatch on all tree bases in plots C and D are summarized in Table XXX. Few eggs and larvae were found during the 1965 search in both plots compared with the 1966 search. Since all males and females were virgin when released in 1964, and that experimental conditions were as close as possible to the natural weevil habitat, the data provide strong evidence that egg laying does not occur until the second summer of adulthood. About twice as many eggs were found in plot C in 1966 as compared to D of the same year, while percentage hatch was about the same for the two plots. Although fewer adults were trapped in plot D in 1966 (Table XXVIII) as compared to plot C there appears to be a sizeable difference in numbers of eggs per female. It is suggested that by increasing the duff thickness, conditions for egg laying were enhanced. The bark surface area available for oviposition sites was increased with the

Fig. 61. Frequency distributions of tree diameters in plots C and D.

Fig. 62. Relationship between numbers of weevil progeny per tree and tree diameter in plots C and D during 1966. Sphagnum mosses were placed around the tree bases in plot C. Lines were fitted by the least squares method of a weighted regression and each vertical bar indicates \pm one standard error of the mean. ** indicates significance at the .01 probability level; * indicates significance at the .05 level.

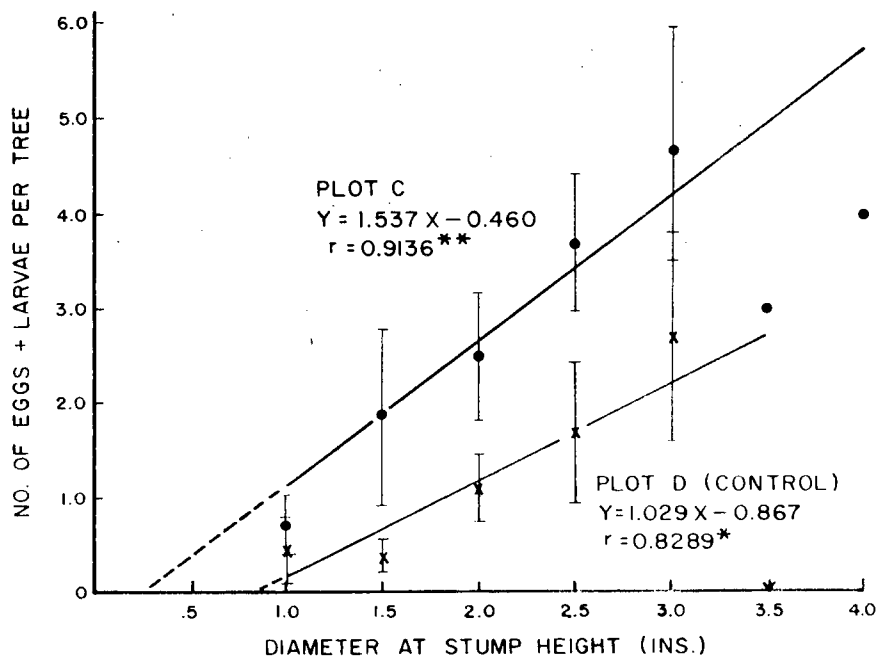
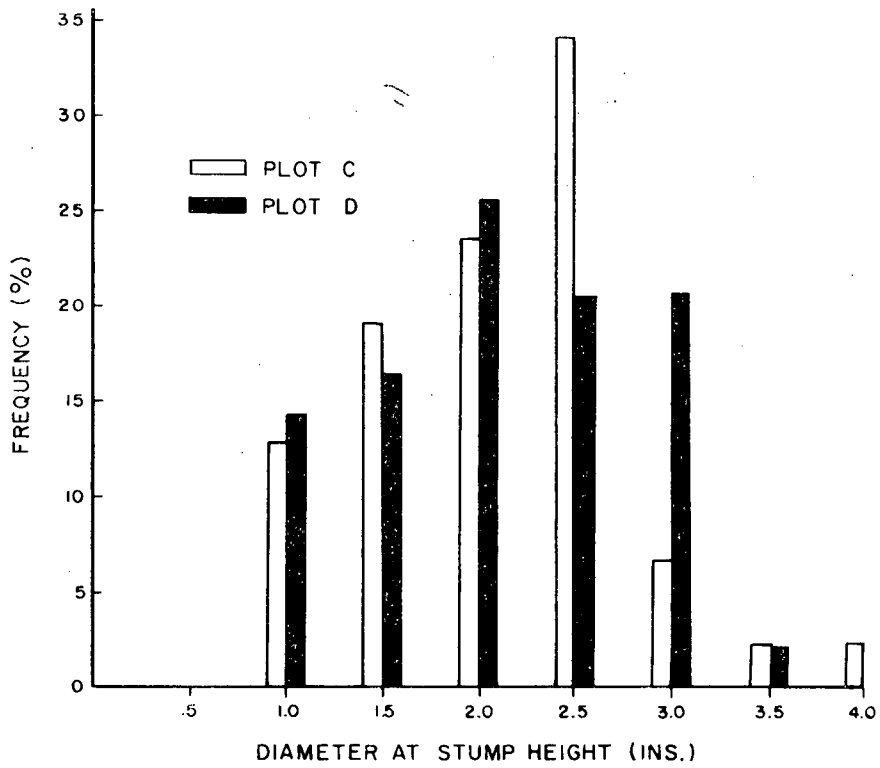


TABLE XXX. SUMMARY OF TREE STAND, OVIPOSITION AND EGG HATCH CHARACTERISTICS IN PLOTS C AND D DURING 1965 AND 1966.

Plot	Year	Total trees	Ave. diam. (s.h.-ins.)	Total eggs + larvae	Ave. no. eggs + larvae/tree	No. larvae	No. eggs per female *	% hatch	% eggs in niches
C	1965	47	2.1	4	0.09	0	0.17	-	-
C	1966	47	-	129	2.74	9	5.37	7.0	72.5
D	1965	49	2.1	1	0.02	0	0.05	-	-
D	1966	49	-	64	1.31	5	4.00	7.8	55.9

* Values in this column were computed from data given in Table XXVIII where 24, 24, 22 and 16 individual females were recorded in plots C and D respectively.

addition of mosses. In addition, the microhabitat around the root collar was made more moist. A higher percentage of eggs was deposited in niches constructed by the female in the bark tissue in plot C as compared to plot D, and many of these were located on the collar within the zone covered by sphagnum. This indicated that females did utilize the increased bark surface area in plot C and that females were comparatively more active at egg laying than in plot D.

The number of eggs and larvae found in plots C and D were linearly correlated with stump diameter (Fig. 62). Plot C showed a higher rate of oviposition per tree diameter class than did plot D.

Experiment 2: Out of a total of 37 eggs laid by females caged in plastic cups, nearly all were deposited in small niches chewed in the bark

and covered over with excreta. Eggs were rarely laid side-by-side. No egg hatch was observed throughout the fall of 1964, nor in the spring of 1965. At the time of the last examination in the spring of 1965, most eggs appeared partially collapsed or destroyed.

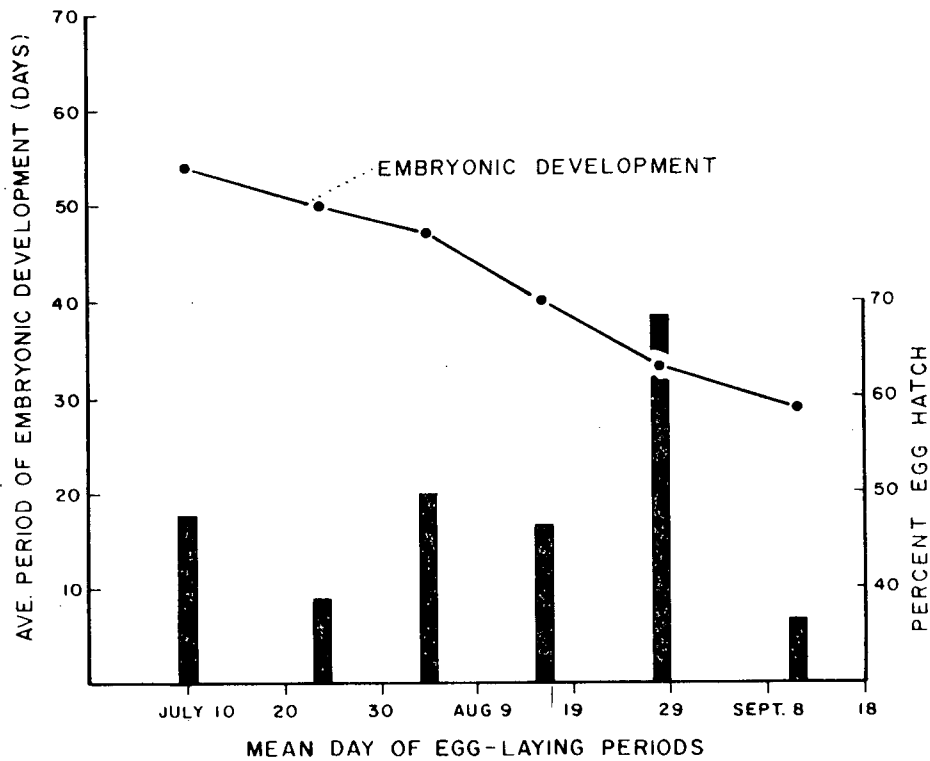
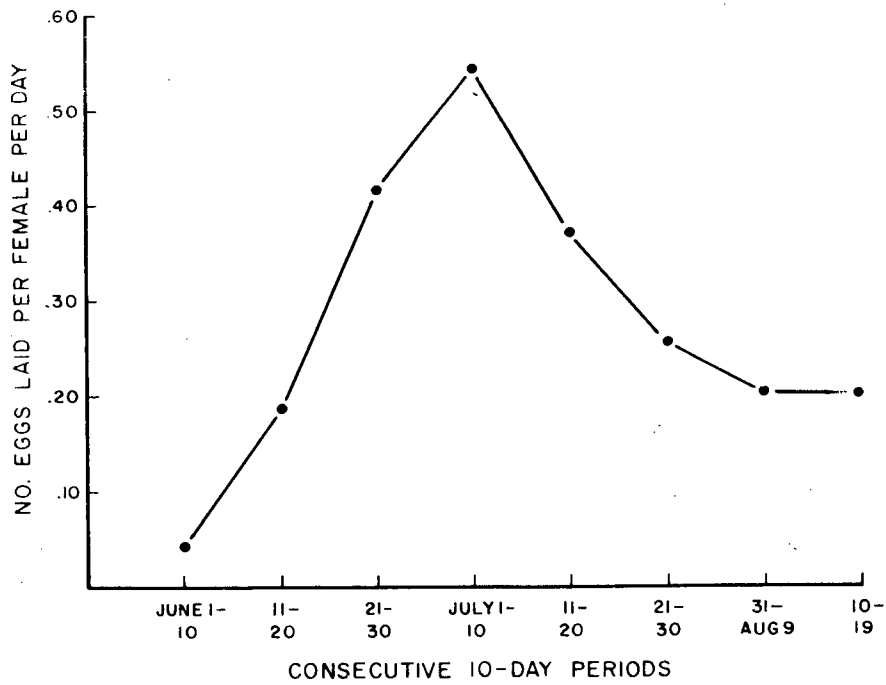
Experiment 3: Female weevils reared in paper cups inverted over bark sections laid most of their eggs on the screen surface and a few were deposited in niches chewed in the bark. The maximum number of eggs recorded per female during a period of 84 days varied from 2 to 36 with a mean of 12.2 eggs based upon 24 female layers. On a per day basis the average number of eggs was 0.236 per female per day. Using this value and a possible maximum egg laying period of about 103 days, the total egg productivity during a season could be 24.3 eggs ($= 103 \times 0.236$) per female. This may be an over estimate for females in the natural habitat since the laboratory rearing conditions were maintained at slightly higher temperatures and females had a readily available food supply.

The periodicity of oviposition, as determined from total egg output per 10-day interval consecutively throughout the summer, indicated that a maximum peak of egg production occurred during the early part of July (Fig. 63). The rate of oviposition dropped rapidly after this date but some eggs were still found up to August 23. During this experiment a total of 294 eggs were collected from the 24 females but none of these hatched after storage in petri dishes. It is possible that the level of moisture was inadequate.

Experiment 4: The percentage hatch of eggs laid by females reared in vials varied from 36.8 to 68.4 and average 45.6 (Fig. 64). Under the

Fig. 63. Summer egg laying pattern of H. warreni reared in paper cups inverted over pine bark during 1964.

Fig. 64. Percentage egg hatch and the period of embryonic development of H. warreni eggs stored in moist vials under natural temperature conditions.



experimental conditions the average period of embryonic development was calculated as 42 days but varied from 29 to 54 days. The longest period of development was recorded from eggs laid during the early part of the experiment, while the shortest period was recorded for eggs laid during the final 10-day period..

Experiment 5: The data collected from adults reared in plastic cages showed that almost all eggs were located in the root-collar zone corresponding to the larval universe. However, the exact placement of the egg during oviposition varied considerably. In cages 1 to 20 (1966) about 75 percent were deposited in niches, while in cages 21 to 30 (1966) only 51 percent were in niches (Table XXXI). These niches were small pockets chewed

TABLE XXXI. SUMMARY OF H. WARRENI EGG LAYING EXPERIMENT IN PLASTIC CAGES ON PINE STUMPS.

Year	Cage nos.	Starting date	Duration (days)	Total eggs deposited	% eggs in niches	Total larvae	% hatch	No. eggs per female per day
1965*	1-10	July 5	59	164	85	62	37.8	0.278
1965*	11-16	July 27	38	42		0	0	0.184
1966	1-10	June 21	50	121	73	8	6.6	0.242
1966	11-20	June 13	50	138	75	70	50.7	0.276
1966	21-30	July 15	50	45	51	0	0	0.082

* Data from previous experiment; see Cerezke (1967).

out by the female, usually within the outer bark. The eggs were deposited in

these niches, one per niche, and were covered with bark particles or excreta. Some eggs were also loosely placed under bark scales or in the moss immediately adjacent to the bark. The eggs were almost invariably placed singly in each oviposition spot. These observations agreed generally with eggs observed under natural conditions in the field. For example, in plots C and D many eggs occurred loosely in the soil adjacent to the root-collar. On one mature tree in plot 10, five eggs were found within an area of about two square inches on the root collar bark, and none of these were side-by-side. Still other instances were observed where 6-8 first-second instar larvae were removed from similar sized areas of bark surface. This suggested that the larvae were from eggs deposited about the same time, and likely by the same female.

The rate of egg laying varied considerably between cages 1-10, 11-20 and 21-30 of the 1966 data (Table XXXI). The low value obtained from cages 21-30 may reflect an influence of lower temperature conditions. In general, the rates reported for cages 1-10 and 11-20 (1966) are similar to the rate observed in Experiment 3 above. It was not established, however, whether females were capable of laying the same number of eggs each year until death.

Experiment 6: The results of 36 dissected females collected during 1964 and 1965 are summarized in Table XXXII. The data suggest that little or no change in the size of fat body or expansion of spermathecal gland and germaria were detected between the non-mated, non-laying condition and the mated, egg laying condition. Ovary size, total number of oocytes and the number of mature-sized oocytes showed maxima in the late June collections. This pattern agrees with the peak period of egg production

TABLE XXXII. SUMMARY OF THE OBSERVATIONS OF THE FAT BODY AND REPRODUCTIVE STRUCTURES OF FEMALE H. WARRENI COLLECTED DURING 1964 AND 1965.

Date of collection	No. females	Fat body condition *	Ovary condition *	Total oocytes	No. mature eggs	Length of germarium (mm)	Length of spermathecal gland (mm)	Proportion mated	Spermatophore present	
									Fresh	Old
June 1-5, 1964	5	S	M	31	2	1.925	2.475	3/5	-	-
June 23-25, 1965	5	M	L	40	5	2.035	2.530	4/4	3/4	0/4
June 30, 1964	5	S	L	38	6	1.980	2.420	4/4	3/4	1/4
July 22-23, 1965	5	S	M	28	4	2.145	2.585	5/5	3/5	2/5
July 30, 1964	5	S	M	25	2	1.925	2.420	5/5	1/3	2/3
Aug. 11, 1965	6	M	M	26	0	1.980	2.420	6/6	0/6	5/6
Aug. 31, 1964	1	S	S	-	0	1.925	2.530	-	0/1	0/1
Aug. 31-Sept. 7, 1965	4	M	M	26	0	1.925	-	4/4	0/4	1/4

* The fat bodies and ovaries were given general ratings of size; S = small, M = medium and L = large. The criterion of ovary size was based upon counts of oocytes per four ovarioles present in each female as follows: S = 12-24; M = 25-36 and L = 36+ oocytes. The fat body and oocyte ratings represent an average for each collection group of females.

described in Figure 63.

Mated and non-mated females were clearly discernable by the presence or absence of sperm in the spermathecal gland. In addition, freshly mated females possessed a single spherical shaped spermatophore which expanded the vaginal pouch and was whitish in appearance. These were observed most commonly during June. At least two females in the first collection had not mated. As the summer progressed the number of freshly deposited spermatophores decreased but they were still recognizable, being smaller in size, yellowish in color and irregular in shape. The most active period of mating appeared to be throughout June and part of July. Spermatozoa were found in the spermathecal glands of all females except two from the earliest collection; these two were likely newly developed females.

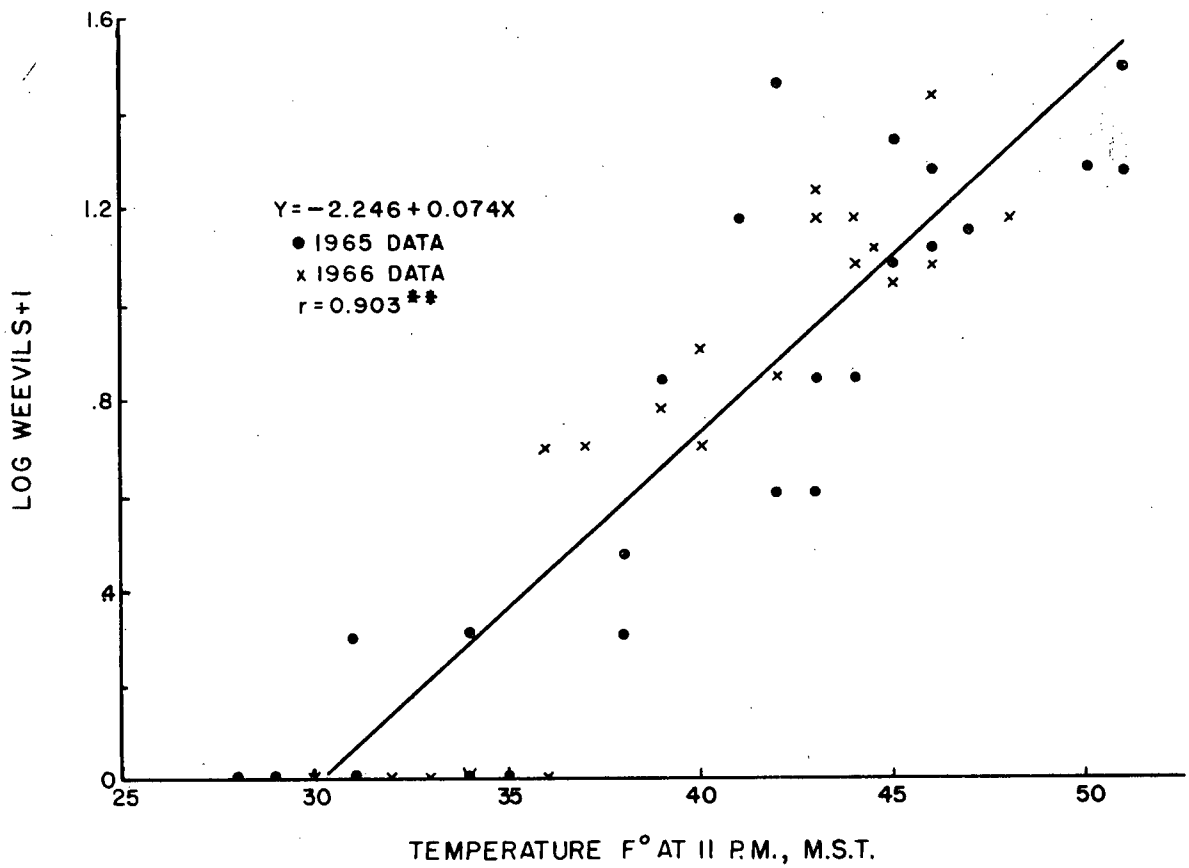
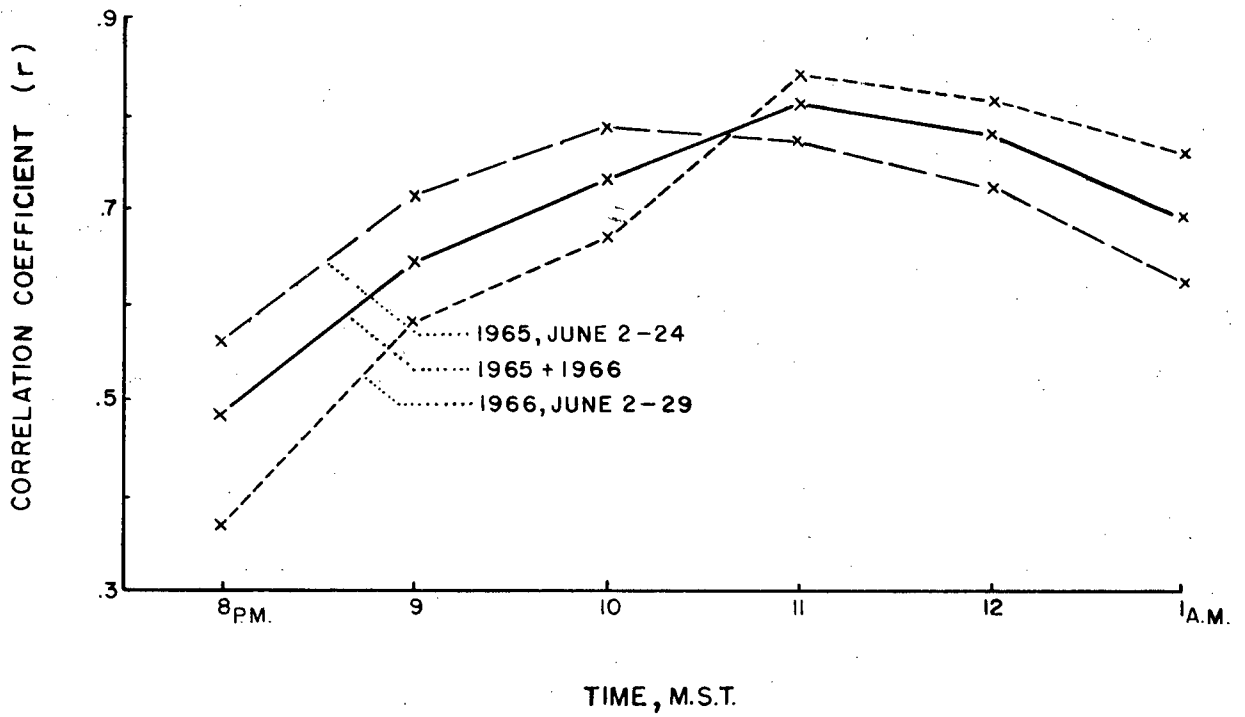
6.3.5 Light and Temperature Response and Orientation of Adults:

Experiment 1: The daily numbers of captured adults in plots C and D were correlated with temperatures at each hour-interval of the previous night. The data indicated that temperatures recorded at 11:00 p.m. provided the highest correlation coefficient (r) value (Fig. 65). This suggested that most emergence from the duff occurred shortly prior to this hour. Figure 66 describes the relationship between weevil numbers captured and temperatures recorded at 11:00 p.m. of the nights prior to collections. The graph shows that few weevils were caught when the temperature fell below 36-40 °F by 11:00 p.m.

Experiment 2: When adult weevils were placed under moss in the center of a small arena their maximum peak of emergence through the moss occurred between 10:00 and 10:30 p.m. (Fig. 68). This corresponded to about

Fig. 65. Correlation of adult weevils captured in plots C and D with night temperatures.

Fig. 66. Relationship between adult weevil catch in plots C and D and temperatures recorded at 11:00 p.m., Mountain Standard Time. Line fitted by least squares method. r value significant at 1 percent level.



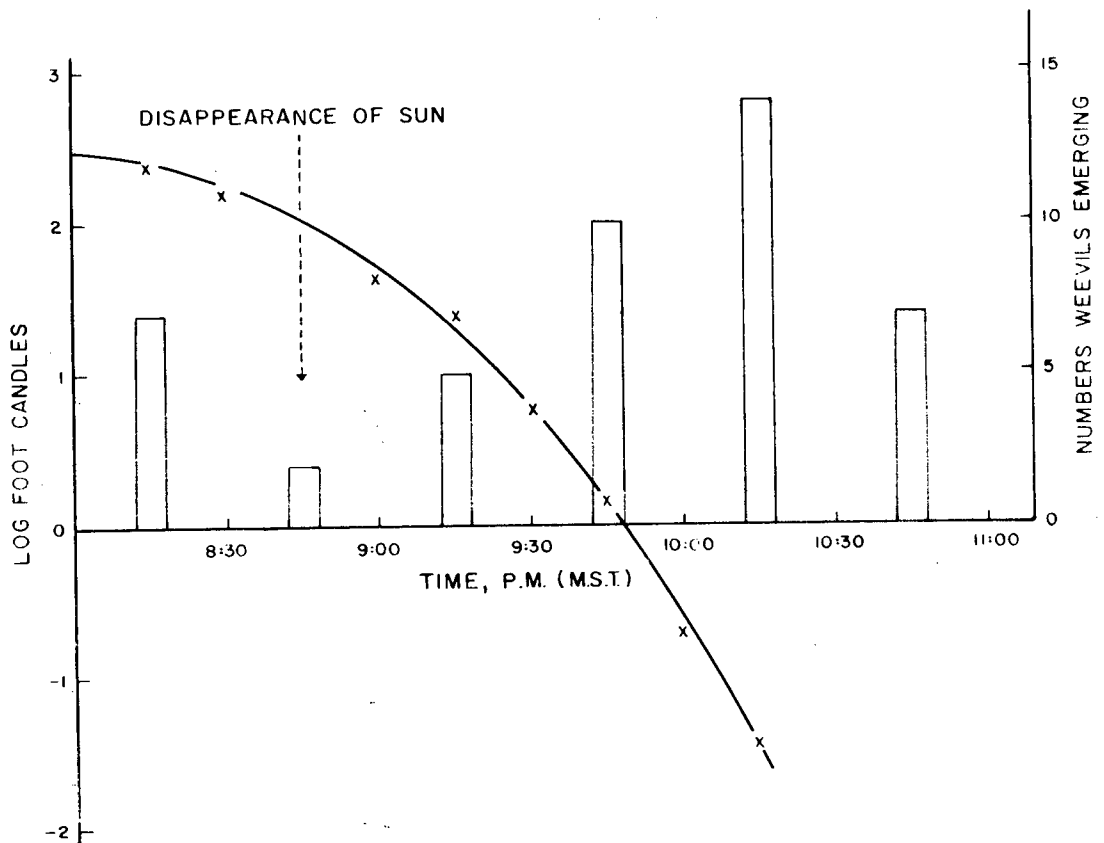
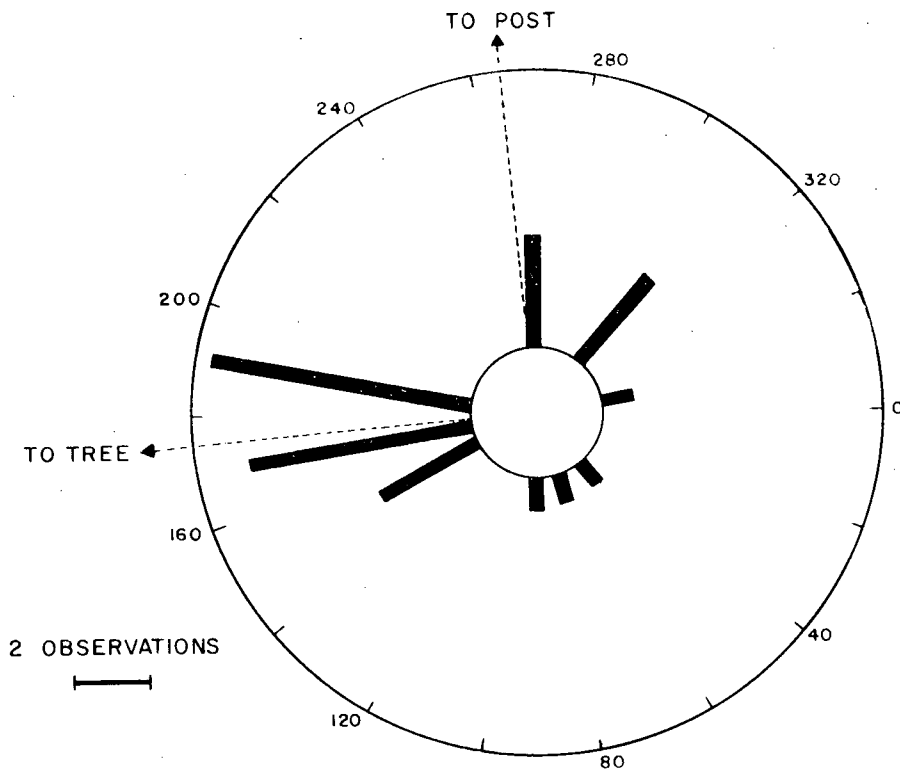
two hours after sunset. Light intensity recordings taken concurrently indicated a possible relationship with weevil emergence. Throughout the experiment all temperatures recorded were above 40 °F. Several adults emerged prior to sunset and some of these began movement as soon as they were placed in the arena. At least some of this initial behavior may be abnormal in that it appeared to be in response to disturbance through handling.

Many weevils climbed vertically through the moss while others crawled laterally. Once at the exterior of the moss they invariably stopped all movement for a few minutes to over half an hour. Some weevils, especially those that emerged from the top, assumed a characteristic pose as if seeking out some aspect of the habitat. They extended their antennae, stood motionless for a few minutes and then began a turning movement. Following this the weevil either relaxed its antennae and remained motionless for a short period, or commenced crawling horizontally. Once lateral crawling had begun most weevils continued in a straight line with little deviation from this directional path until an obstruction was met. The directional response of adults in the arena is analysed in Figure 67. There is evidence that the weevils chose the direction of the pine tree more consistently than any other direction.

Experiment 3: Some general patterns of behavior were summarized from the adults retained in a small arena enclosing two pine trees. Nearly all observable activity of the adults occurred between the hours from 7:00 p.m. to 5:00 a.m. during the three day experimental period. Greater attractiveness to the larger tree than to the smaller tree was common to both sexes. Females appeared to be more active than males in terrestrial movement; i.e., 58 percent compared to 46 percent for males. Males were more abundant

Fig. 67. Directional response of adult H. warreni confined within a 90-cm. diameter arena.

Fig. 68. Numbers of adult H. warreni emerging from moss in relation to time during the evening. Decreasing light intensity before and after sunset is also described.



on the large tree than females; i.e., 50 percent compared to 30 percent of females.

The time of initial evening activity varied widely but the peak period occurred between 10:00 p.m. and 1:00 a.m. Several weevils were observed at the 21.5-foot level above ground on both trees.

The speed of crawling upon the host was slow. For example, one male ascended a distance of five feet on the tree stem in 12 minutes. During this period 5-6 stops were made, each 3-5 seconds in duration.

Feeding was observed on branches of the smaller tree a few inches from the main stem. Adults in the mating position were observed up the tree, on the ground surface and in the duff.

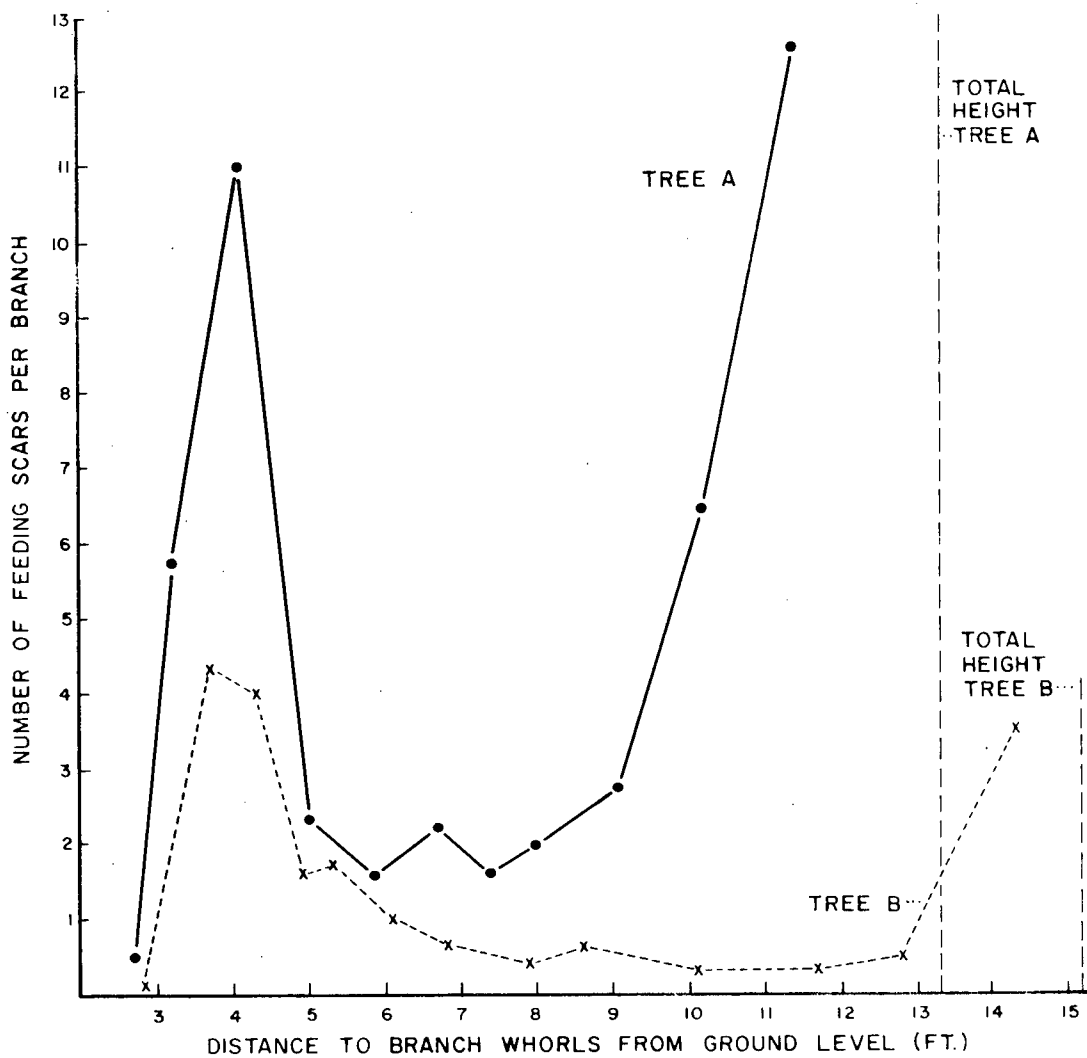
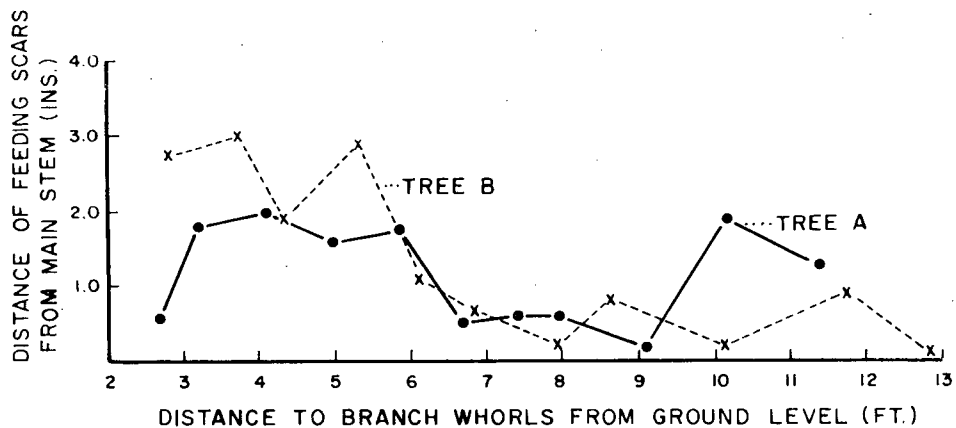
6.3.6. Adult Feeding Patterns:

Experiment 1: The feeding patterns of adults on two co-dominant trees, 20-25-years old, are analysed in Figures 69 and 70. The arena around tree A was established earlier than for tree B, thus accounting for the lower values on B. Both trees show a similar pattern with two peaks of almost equal height. This suggested that adults fed mostly on the lower and on the upper branches. Many of the latter feeding sites occurred in the terminal buds where females were more commonly observed than males.

The distance out on the branch from the main stem was also variable but some pattern is evident (Fig. 69). In general the feeding scars were farthest out on the lower branch whorls. Natural needle drop extended farthest out on the lower branches and this may have influenced the distance for feeding since the needles impeded their movement on the bark surface. Few scars were found among needle covered areas. During movement or when at

Fig. 69. Pattern of adult weevil feeding scars on branches in relation to height above ground.

Fig. 70. Frequency distribution of adult weevil branch feeding scars in relation to height above ground.



rest on a branch the adults clung tenaciously, indicating a preference for a solid substratum. Nearly all feeding scars were located on the upper surface of branches.

Experiment 2: Although adult feeding is insignificant in its effect on trees some terminal shoots may become distorted as a result of feeding (Fig. 71). In addition to branch and terminal bud feeding, adult scars have also been observed on the root base and collar regions.

When adults were retained in two-foot-square arenas only two pine seedlings showed evidence of feeding. This damage was considered negligible. This indicated that little or no damage would occur to pine seedlings in newly cutover areas from adults emerging from cut stumps, or from adults immigrating from adjacent areas.

6.3.7. Mortality Factors of Adults: Little is known of the mortality factors of H. warreni adults, and the trapping studies in plots C and D indicated a life span of at least three years. The possibility of Beauveria bassiana has been mentioned (see section 6.1.4.) and is illustrated in Figure 72. The examination of stomach contents of shrews (Sorex cinereus cinereus) provided no evidence of adult weevil predation. Sclerital fragments of carabid beetles were a common constituent of the gut contents and these were easily identified.

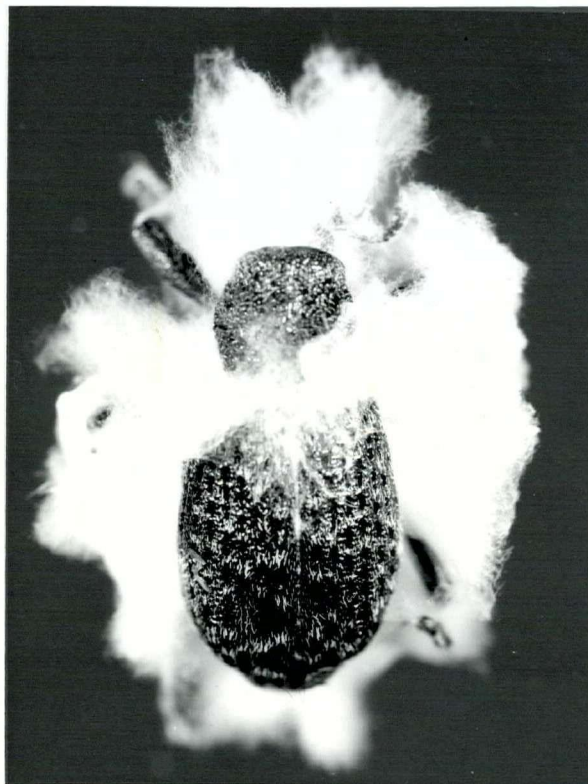
One female weevil collected for dissection had 10 internal parasites (Fig. 73) within its abdominal cavity and external to the digestive tract. The parasites were subsequently identified as nematodes belonging to the family Tylenchoidea by Dr. Gertrud R. Kloss, Sao Paulo, Brazil, and verified by Dr. W. Rühm, Hannover, Germany (personal communications). According to

Fig. 72. Dead adult H. warreni showing the white mycelial mass of the fungal parasite, Beauveria bassiana. (X 5).

Fig. 73. Nematode parasite (family Tylenchoidea) found within the abdomen of a female adult weevil. (X 40).



Fig. 71. Adult weevil feeding damage on terminal shoots of 6-8-year old lodgepole pine.



Dr. Kloss the nematode parasite stage in the weevil is hermaphroditic while the succeeding stage would be gonochoristic and would be spent in the soil. The effect of the parasite upon the health of the weevil is unknown but it is almost certain to affect fecundity since each nematode measured about three mm. in length. Most of them occupied the region of ovary expansion in the dorsal abdomen.

Externally attached mites were common on the adult weevil and appeared most abundant after June. Out of 74 mites collected 72 were on females and only two were on males. A sample of 12 specimens was identified by Dr. E. E. Lindquist, (personal communication) Ottawa, Canada, as Saproglyphidae, Carpoglyphinae : Hericia sp. (near H. fermentationis Vitz.). Dr. Lindquist indicated that the externally attached mites were an immature form and that the adult form may live upon the sap oozing from the trees. The effect of the mite upon the weevil may be negligible and its presence may be primarily for dispersion.

7. Studies of the Effects of Weevil Damage to Trees

7.1. Anatomical Effects: Several inherent mechanisms of lodgepole pine appeared to be evident in helping to overcome the damaging effects of the weevil. One effect is illustrated in a cross-sectional view of a cut stump from the 65-70-year old stand (Fig. 74). Periods of attack on this stem were dated since the age of 28 years, and heaviest damage occurred at the age of 43-45 years. At this time 50 percent or more of the root collar was girdled to xylem tissue. Partial recovery from the loss of the perimetrical distance of cambial and phloem tissue since age 43-45 was brought about by a



Fig. 74. Cross-sectional view of a 66-year old pine stump cut at the root collar level. Numbers beside the larval feeding scars indicate approximate years of attack. Note bud-like growth pattern of wood increment adjacent to scar areas.

budding type of growth adjacent to the wound areas. Rate of growth of both ring width and lateral extension of cambium in the "bud" areas was greatly increased over the normal growth pattern. This had the effect of partly sealing off damaged areas, and at the same time, helped to increase laterally the area of conductive tissue.

A second mechanism of defense occurred in response to wounding, resulting in the formation of traumatic resin ducts (Figs. 75 and 76). Large numbers of vertical ducts were produced in the outermost xylem ring when larval feeding extended through the cambial tissue; their production may occur annually until larval feeding is terminated. Traumatic ducts were found to extend above and below the wound area and were a source of the resin which exuded at wound openings. As a result open wound areas appeared relatively resistant to entry of fungal decay organisms.

In addition to surface resinosis, some infiltration of the tracheids with resin occurred contripetally from the wound (Figs. 77 and 78). This was observed especially in young stems when damage extended through the cambial layer. Such areas were often pie-shaped in the transverse plane and extended toward the pith. Resin-soaked xylem areas were observed to extend above and below the wound area.

A third mechanism of defense was observed on wound damaged trees in the Strachan area west of Rocky Mountain House, on a 15-year old pine (Fig. 79) and on several mature pine (Fig. 80). These trees developed adventitious roots directly above the wound areas. They may function to partially compensate for the loss of weevil-killed roots and damaged collar regions.

Many trees sampled in plots 1 to 5 which had severe damage around

Fig. 75. Wood discs cut at two-inch intervals up the main stems of 20-year old pine trees in the Robb Burn. Upper three (left to right) were removed from a weevil damaged tree; the lower three from a non-attacked tree. Note the large number of vertical traumatic resin ducts produced in the two outer growth rings of the attacked tree. Resin ducts were made more clearly visible with a starch-reacting stain of iodine (0.4 gms. I_2 + 1.8 gms. KI per 100 ml. water). Ruler scale is in inches.

Fig. 76. Transverse section of a disc cut at root collar level from a weevil attacked tree showing a portion of the outer four wood increments. Note the vertical traumatic resin ducts (accentuated by the starch-staining iodine solution) in the outer two increments. The formation of two tangential bands of traumatic ducts are evident in the first and second rings. (X 12).

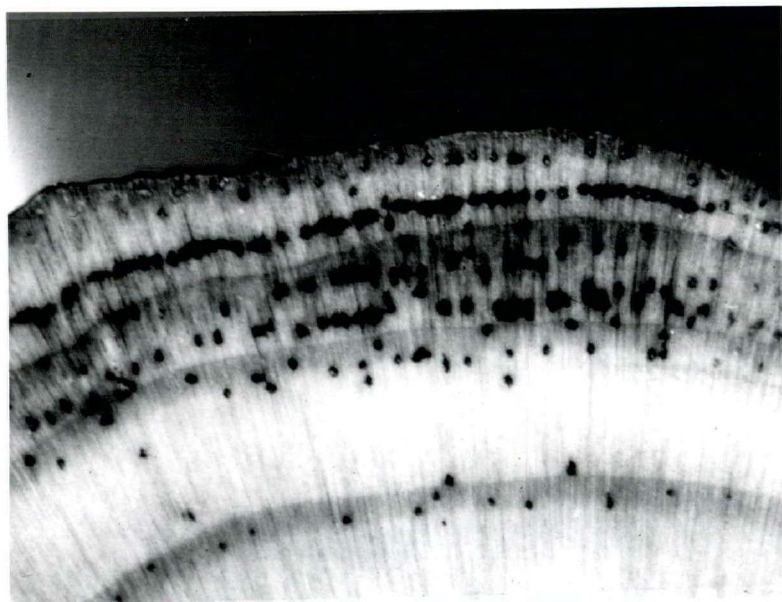


Fig. 77. Radial view of the lower stem of a weevil attacked 20-year old pine tree. Note wound area on the root collar and resin-soaked sapwood.

Fig. 78. Transverse view of discs removed from the taproots of a weevil damaged tree (left) and a non-attacked tree (right). Note the light colored resin-soaked sapwood areas on the attacked tree. Scale in inches (upper) and mm. (lower).



Fig. 79. Lower portion of a stem from a 15-year old pine tree showing small adventitious root development immediately above a weevil larval wound.

Fig. 80. Lower portion of a stem from a 95-100-year old pine tree showing a small adventitious root immediately above a weevil larval wound area on the root collar. The large lateral root visible on the left was killed from larval feeding.



the root collar showed a slight swelling above the wound or a reduction in growth within the wound region. For example, one 12-inch diameter tree had a root collar circumference of 41 inches around the damaged level while immediately above the wounds, the circumference was 42 inches.

7.2. Growth Loss Effects: The assessments of weevil larval feeding damage to pine was made with respect to partially girdled stems at the root collar zone. All pine trees were in the dominant and co-dominant categories. Table XXXVIII shows the pooled measurements of attacked and non-attacked groups of trees. The data indicate a fairly homogeneous selection of trees. The percentages of root collars girdled were 45.7 for the Robb Burn trees and 49.0 for the Grande Prairie trees. Average years of initial damage were 1961 and 1963 for the two areas respectively.

Data presented in Table XXXIV suggests that attacked trees on the average (except 1965 branches) produced more lateral branches on the top whorl than did non-attacked trees. However, the differences are small, especially on the Grande Prairie sample. It was noted that in this sample, internodal branches were more common than in the Robb Burn sample and this may have influenced the growth pattern.

There were no appreciable differences in lengths of needles on the 1963 and 1964 lateral branches of the top and second top whorls between attacked and non-attacked trees from the Robb Burn (Table XXXV). Terminal and lateral branch length measurements indicated a reduction in the attacked tree groups as compared with the controls. In general, shoot elongations showed an annual decrease on both terminals and laterals for the two and three year periods of the Robb Burn and Grande Prairie areas respectively.

TABLE XXXIII. MEASUREMENTS OF WEEVIL ATTACKED AND NON-ATTACKED TREES IN THE ROBB BURN AND GRANDE PRAIRIE STUDY AREAS.

Area	Tree group	Ave. age (years)	Ave. height (ft.)	Ave. diam. at s.h. (ins.)	% root collar girdled	Ave. year first attack
Robb Burn	Attacked (trees 1A-10A)	20.4 (20-21)	15.8 (12.6-18.7)	2.33 (2.07-2.54)	45.7 (27-62)	1961 (1957-1964)
	Non-attacked (trees 1N-10N)	20.6 (17-23)	16.4 (13.2-19.4)	2.25 (1.85-2.39)	- -	- -
Grande Prairie	Attacked (trees 1A-11A)	21.7 (19-24)	20.7 (17.2-25.8)	2.39 (2.40-3.40)	49.0 (28-64)	1963 (1961-1965)
	Non-attacked (trees 1N-10N)	22.0 (19-24)	20.8 (17.3-24.8)	2.85 (2.50-3.20)	- -	- -

Values in brackets indicate range of measurements.

TABLE XXXIV. NUMBERS OF LATERAL BRANCHES ON THE TOP WHORL OF ATTACKED AND NON-ATTACKED TREES IN THE ROBB BURN AND GRANDE PRAIRIE AREAS.

Area	Tree group	Ave. number of lateral branches on the top whorl			
		1963	1964	1965	1966
Robb Burn	Attacked	4.5	4.7	-	-
	Non-attacked	3.9	4.2	-	-
Grande Prairie	Attacked	-	4.6	3.8	4.4
	Non-attacked	-	4.4	4.3	4.2

TABLE XXXV. NEEDLE LENGTH, TERMINAL LEADER AND TOP LATERAL BRANCH LENGTHS OF ATTACKED AND NON-ATTACKED TREES IN THE ROBB BURN AND GRANDE PRAIRIE AREAS.

Area and tree group	Ave. needle length (mm)		Ave. terminal length (ins.)				Ave. lateral branch length (ins.)			
	1963	1964	1963	1964	1965	1966	1963	1964	1965	1966
Robb Burn										
Attacked	65.1	69.8	15.5 (8.9)	18.2 (12.9)	-	-	7.2 (12.2)	8.5 (14.1)	-	-
Non-attacked	67.0	70.0	17.2	20.9	-	-	8.2	9.9	-	-
Grande Prairie										
Attacked	-	-	-	15.1 (10.1)	13.3 (3.6)	14.1 (17.5)	-	7.4 (1.3)	6.5 (3.0)	7.5 (2.6)
Non-attacked	-	-	-	16.8	13.8	17.1	-	7.5	6.7	7.7

Values in brackets indicate percentage reduction based upon non-attacked tree lengths.

Attacked trees in the Robb Burn showed a decrease in terminal lengths of 8.9 - 12.9 percent, while lateral elongations were decreased by 12.2 - 14.1 percent. Reduced elongations of terminals of attacked trees from the Grande Prairie area ranged from 3.6 to 17.5 percent, while laterals were reduced from 1.3 to 3.0 percent. Over the two and three year periods of measurements recorded from the Robb Burn and Grande Prairie areas respectively the mean losses of tree heights were estimated as follows:

Robb Burn: 2.2 ins. per year or a total of 11.5 percent

Grande Prairie: 1.7 ins. per year or a total of 10.9 percent

The patterns of growth increment for the oblique sequence are shown in Figures 81, (a) to (e) and 82, (a) to (g) for the Robb Burn and Grande Prairie areas. Both graph series indicate a pattern of decreasing widths from the earliest increment to the last of attacked tree groups as compared with controls. The quantitative changes of mean annual widths of each increment are given in Table XXXVI.

TABLE XXXVI. AVERAGE RING THICKNESS PER YEAR AND PER TREE GROUP OF ATTACKED AND NON-ATTACKED TREES AS DETERMINED FROM OBLIQUE SEQUENCE MEASUREMENTS.

Area and tree group	Ave. yearly oblique sequence ring measurements (mm)								
	1958	1959	1960	1961	1962	1963	1964	1965	1966
Robb Burn									
Attacked	2.15	2.02	-	-	2.65	2.28	2.49	-	-
Non-attacked	2.22	2.19	-	-	2.81	2.47	2.99	-	-
NA - A *	+0.07	+0.17			+0.16	+0.19	+0.50		
Grande Prairie									
Attacked	-	-	2.37	2.42	2.37	2.39	2.29	2.27	1.90
Non-attacked	-	-	2.12	2.18	2.22	2.27	2.24	2.34	2.12
NA - A *			-0.25	-0.24	-0.15	-0.12	-0.05	+0.07	+0.22

* NA - A = non-attacked minus attacked values.

It was noted that trees from the Robb Burn did not show the full characteristics of the oblique sequence pattern as described by Duff and Nolan (1953), while the Grande Prairie sample trees did (Figs. 81 and 82).

Fig. 81. (a) to (e). Oblique growth sequence patterns of attacked and non-attacked trees from the Robb Burn. Graphs (a) and (b) represent pre-attack years; graphs (c), (d) and (e) represent post-attack years. The mean year of attack occurred in 1961.

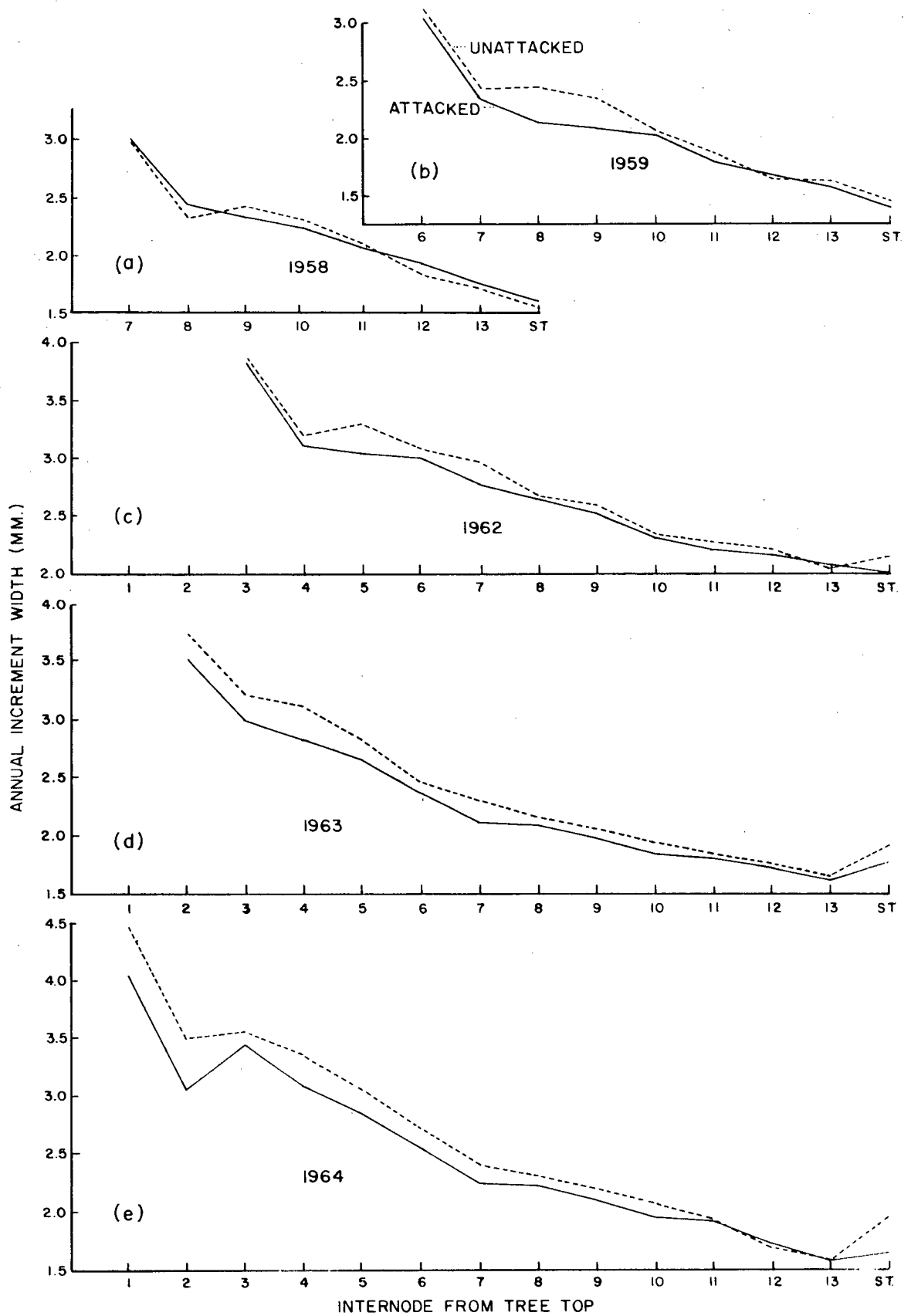
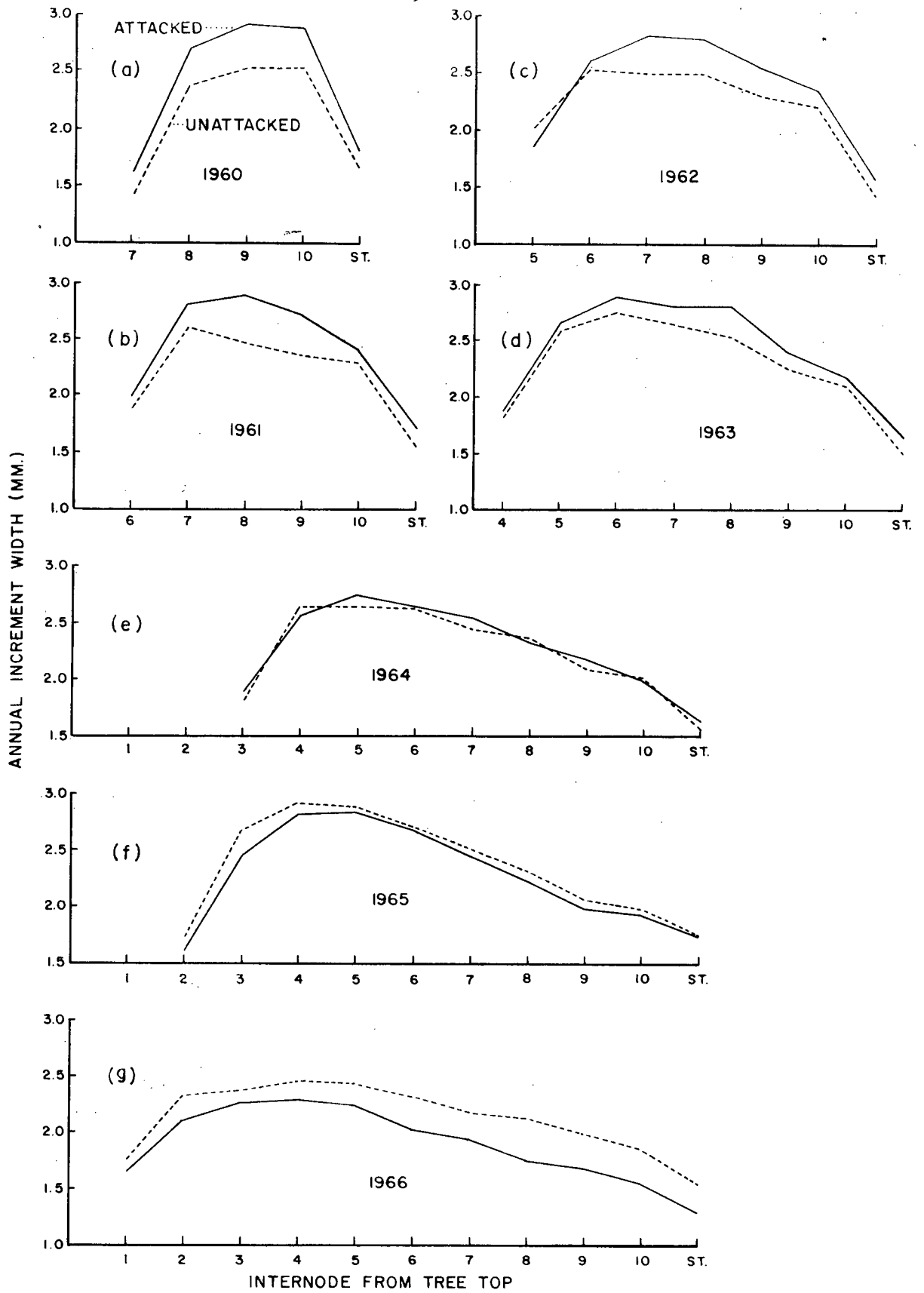


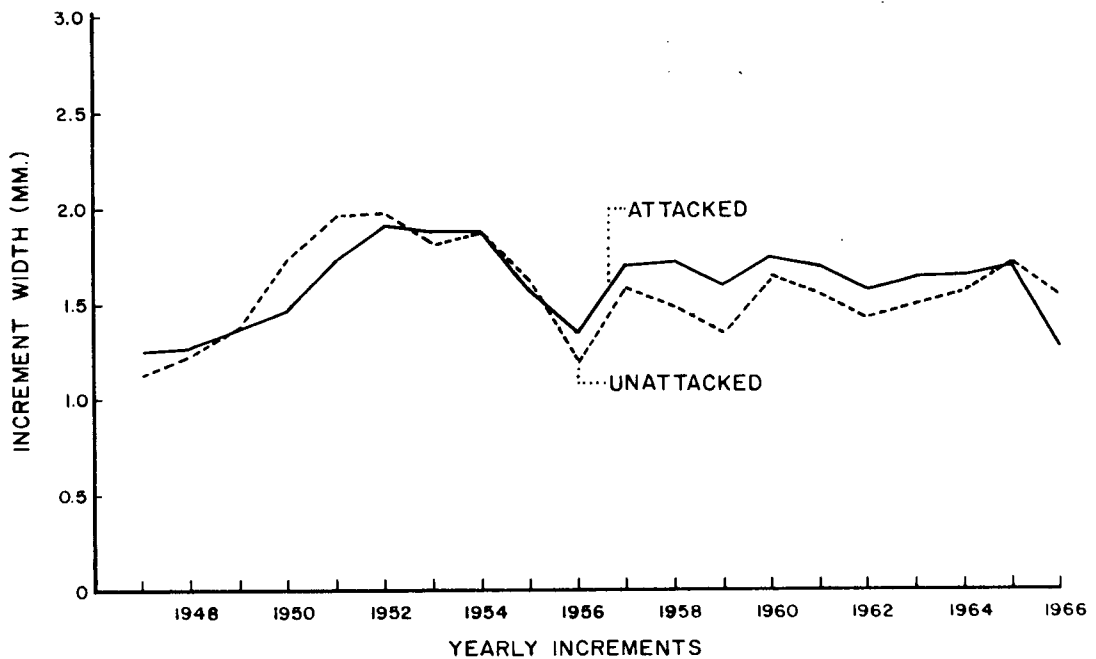
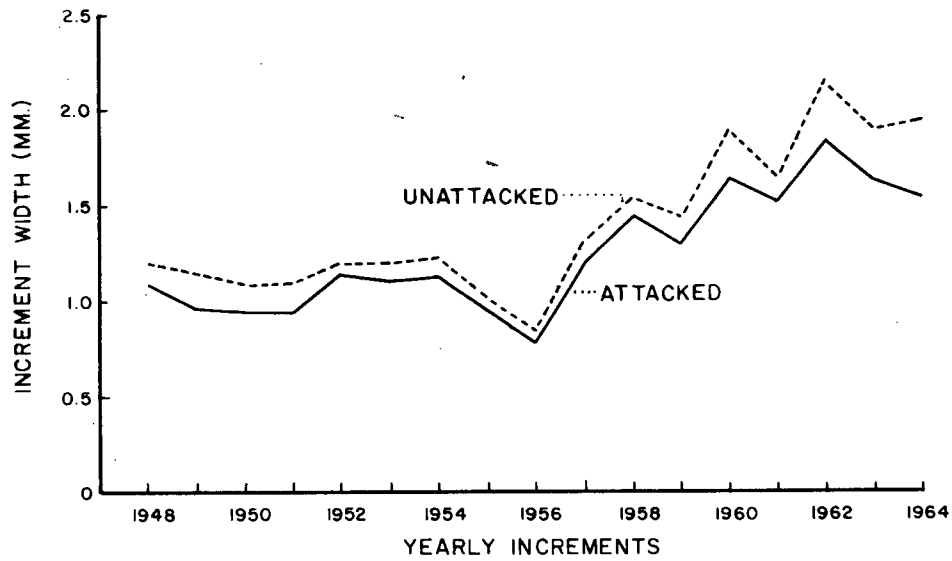
Fig. 82. (a) to (g). Oblique growth sequence patterns of attacked and non-attacked trees from the Grande Prairie area. The mean year of attack occurred in 1963.



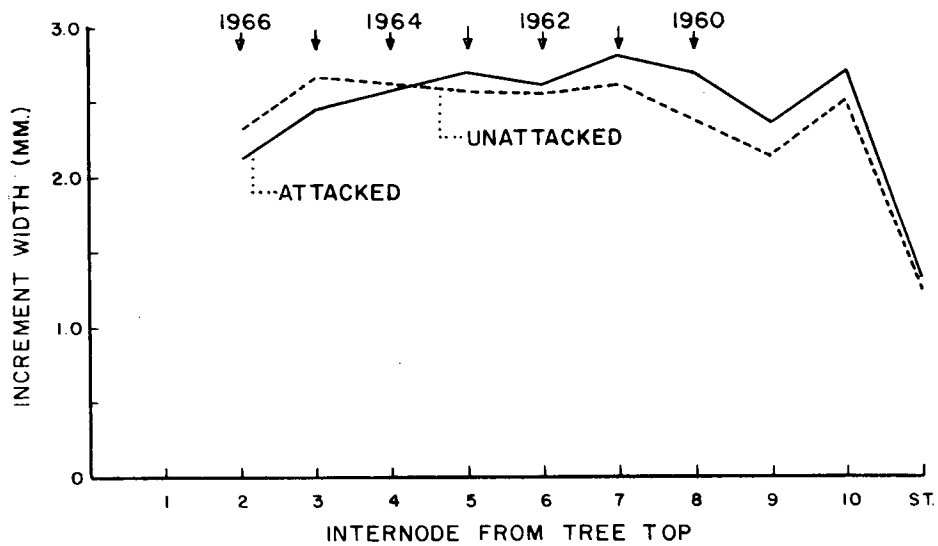
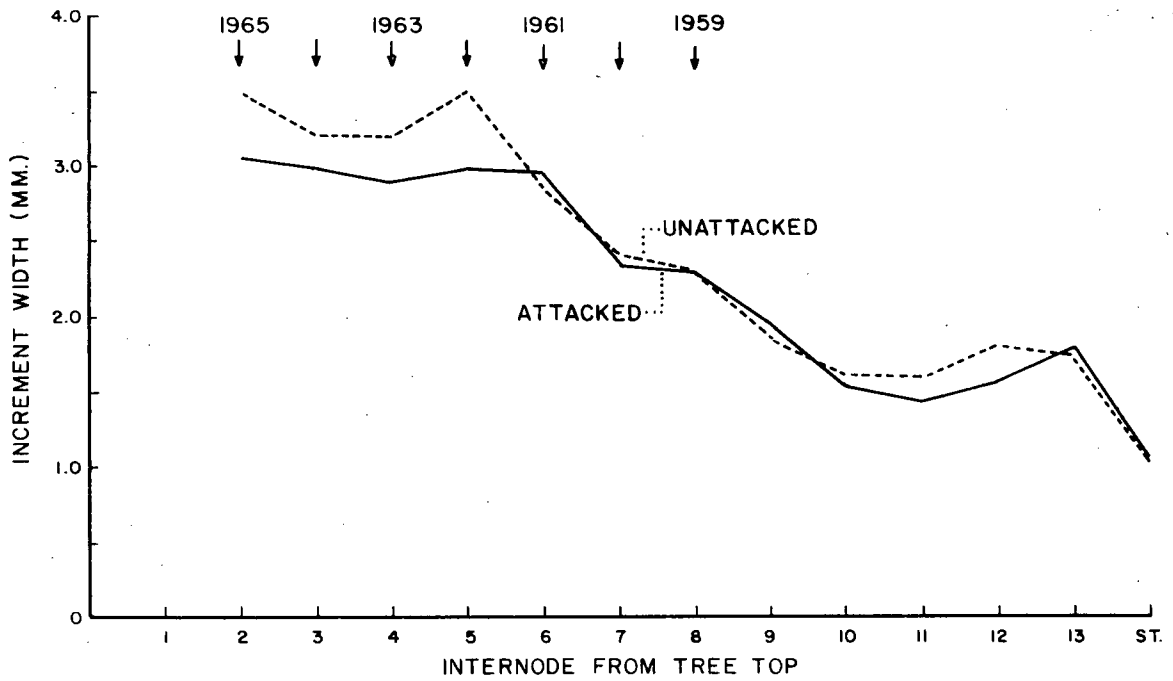
The horizontal growth sequences shown in Figures 83 and 84 do not indicate a clear description of the attack periods. Only a slight indication of a gradual widening of the two lines is evident in Figure 83, particularly since 1961 for the Robb Burn trees. Figure 84 shows a similar slight divergence of lines after 1963.

Figures 85 and 86 depict the vertical sequence patterns and provide the best indication of the three growth sequences in expressing the effects of weevil damage on pine. In the Robb Burn sample a sharp deviation from the control group is indicated after the 1961 increment. In contrast, the greatest deviation from the control group of the Grande Prairie sample occurs between 1961 and 1963. These patterns agree reasonably well with the average years of initial attack shown in Table XXXIII. The data suggest that growth loss effects on trees having approximately 50 percent of the root collar circumference girdled may appear in the first or second year after damage.

Figs. 83 and 84. Radial growth sequence patterns at the 10-inch stump height level of attacked and non-attacked trees. Fig. 83 (top) describes the pattern of trees from the Robb Burn; Fig. 84 (bottom) describes the pattern for the Grande Prairie trees.



Figs. 85 and 86. Vertical growth sequence patterns of attacked and non-attacked trees. The second increment from the pith at each internode was used for all measurements. Fig. 85 (top) describes the pattern in trees from the Robb Burn where the average year of attack was 1961. Fig. 86 describes the pattern in trees from the Grande Prairie area where the average year of attack occurred in 1963.



DISCUSSION

The geographical distribution pattern of H. warreni in Alberta agrees generally with earlier studies (Ann. Rpt. Forest Insect and Disease Survey 1956; Stark 1959b). Although the distribution of lodgepole pine extends to well over 6000 feet in elevation in the Alberta foothills (Rowe 1959) it was not determined why the weevil was generally absent above 4500 feet. Descriptions of these higher elevations provide some clues. The Upper Foothills Section (B.19c of Rowe 1959) forms a sharp transitional zone between the Lower Foothills Section and the Subalpine Region (Horton 1956). This section typically has high forested hills up to 6000 feet with deep valleys between 4000 and 6000 feet. Major vegetation differences as compared to the Lower Foothills include a greater proportion of white and black spruce and a lower incidence of poplar species. Thus the rapid transitional change toward a dominant spruce species complex of the Subalpine Region likely contributes to an unfavorable environment for weevil survival. There is evidence from the present studies that white spruce is attacked secondarily to pine in the Alberta foothills, and that black spruce is attacked only occasionally. Temperature data (Smithers 1962) suggest that mean summer soil temperatures decrease with increasing altitude and with increasing stand density (Millers 1965). This would have the effect of increasing developmental time of immature stages. Studies in Nordic countries have demonstrated that the length of the developmental time and the life cycle of H. abietis is largely dependent upon temperature (Nordic Forest Entomologists' Research Group 1962). It is also possible that the total summer period of

favorable night temperatures for adult activity (i.e., temperatures above 36 - 40 °F) relates inversely to altitude. Other limiting factors may be related to the ground vegetational and physiographic differences described for the higher elevations (Horton 1956; Smithers 1962).

Within the Lower Foothills Section natural stocking of lodgepole pine varies widely but stand density is generally lower and crown differentiation is better than in the Subalpine (Smithers 1962). The reasons for these differences are unknown but it was suggested that they are due to soil, species composition, especially the abundance of poplar, and possibly to genetic differences. Heavy overstocking occurs on mesic and dry sites (Horton 1956), but these sites on the whole, have not been as favorable to the weevil as moist sites.

The fact that no H. pinicola adults were found on lodgepole pine strengthens the view that this species inhabits moist sites characterized by spruce and larch species. It is therefore unlikely that immature stages of this insect occurred in the population samples of H. warreni.

The detailed analysis of the weevil habitat in the 65-70-year old and in the 20-25-year old stands provided a basis from which to judge habitat relationships with weevil abundance elsewhere. However, even within these two stands weevil habitat conditions were highly varied and complex. Apart from the dominant pine host tree growing in an even-aged condition, certain other characteristics common to both areas may be singled out as favorable weevil site factors. In general, the highest weevil incidence occurred where the ground floral complex was rich and where soil conditions were moist. These sites usually had a strong component of moss species mixed with a variety of herb species. This supports the studies of Warren (1956b) in

white spruce habitats. Pine areas with a forest floor carpet of predominantly moss species did not appear as favorable a site as did a more varied floral carpet. This may have been due to excess moisture.

Unevenness of a forest floor may constitute an important characteristic of a weevil habitat, especially if decaying logs are abundant. Warren (1956b) pointed out the importance of these logs lying adjacent to successful larval feeding sites, and the studies in plots 1 to 5 particularly bore this out. The data suggested that the logs provided extra moisture to the larval universe and also added protection to pupae against excess moisture and parasites. Warren suggested that the adult weevil sought out the moister sites for placement of eggs.

It was postulated that the weevil habitat changes in time with, and is partly dependent upon the age of the stand when destroyed by fire. Fallen burnt snags 80-years old, for example, would likely create a more favorable habitat in the new stand than would fallen burnt snags 40-years old. The larger snags provide deeper and larger depressions when they fall and decay more slowly. Thus the former situation may be longer lasting in its effects upon the habitat. It is reasonable to suppose that, in intensely managed pine forests of the future, the favorability of weevil habitats may be reduced since there would be little or no uprooting as in many of the present day stands preceded by fire.

Several sources of error were inherent in the sampling system. The tree as a basic sampling unit varied in size, in root-collar surface area, in root branching patterns and in depth of root submergence below the forest floor. These aspects give rise to an ever changing microenvironment

in the root-collar zone of each tree. In all probability they accounted for much of the variability in weevil numbers within plots, as well as between plots. Another source of error was related to the ease with which different life stages were located. Large larvae and pupae were generally easy to locate, while early instars required extra fine scrutiny of the root-collar surface. In addition, some trees showed evidence of heavier previous attacks than others. This was especially true of larger trees where thick accumulations of hardened resin-soaked soil often ringed the collar zone for 3-4 inches. These masses required considerable effort to chip them loose, thus giving rise to different tactics in sampling procedure. The greatest sources of error appeared to have involved the early instars as suggested by the frequency distribution of head capsule widths.

Since sample trees were selected randomly it was not likely that systematic errors arose as a result of improper representation of tree sizes, even though weevil numbers were biased toward larger trees. It appeared that the sample trees followed the same size gradient as in the natural habitat.

There seems little doubt that weevil populations were maintained at characteristically low numbers. It is doubtful that the relatively small root-collar universe could account for this alone since a large portion of the potential feeding sites were not utilized in any one year. There was also no evidence in plots 1 to 7 of a violent shift in weevil numbers between years. Only strip C of plots 1 to 5 in the 1965 sample showed a marked change in weevil abundance, and it was suggested that this occurred in response to an artificial situation created by clearcutting.

Weevil abundance recorded in 85-90-year old pine stands in 1957

within the vicinity of plot 10 was comparable to those in plots 1 to 5 during 1961 to 1965. In undisturbed stands the average number of larvae per tree varied from 1.25 to 2.86 ($\bar{x} = 1.83$) (Stark 1959a) while the estimates per acre were mostly within the range 600 to 1200 weevils. In a variety of other mature stands sampled along the Alberta foothills by Stark (1959a) similar population levels were recorded; numbers of larvae per tree varied from 1.00 to 2.44. In plantations of Scotch, jack and red pines in the eastern United States populations of Hylobius radicis have generally been higher. In Scotch pine they varied from 6 to 8 weevils per tree (Maxwell and MacLeod 1937; Schaffner and McIntyre 1944). Other values reported have been in terms of numbers of larvae per inch circumference (Millers 1965). These values varied from 0.23 to 0.96 larvae.

It is worth noting that plot 10, sampled in 1966, was located within the Block number 5 area sampled by Stark in 1957. His data (1959a) showed that the population level was 1.91 larvae per tree or 1226 larvae per acre. The 1966 data suggested that weevil abundance was less than one-quarter that observed in 1957. While it is impossible to ascribe a reason for this decline, certain significant changes were noted in the stand in 1966. Tree density per acre had been reduced from 642 to 610 stems per acre since 1952 (Crossley 1955), while the mean diameter increase (d.b.h.) during this 14-year period was estimated at only 0.3 inches. The stand appeared in a general state of decadence as the crowns were very thin and dead snags were evident in most diameter classes. In addition, many sampled trees had one or more major lateral roots killed by the girdling activity of weevil larvae.

The attack density patterns and tree size relationships were evident in two dimensions; according to stand age and according to habitat suitability. Within each stand type weevil numbers increased with tree size, regardless of stand age. In young stands the largest trees supported the most weevils as did the largest trees in the older stands, but fewer weevils per tree were characteristic of the younger stands. Stands of the same age (i.e., plots 1-5, 6 and 7) differed from one another by suitability of habitat; the less suitable ones carried fewer weevils per tree.

The absolute estimates of weevil numbers per acre indicated that, although weevil numbers increased with tree size, similar levels of abundance were found in young and old stands. This suggests that weevil abundance remains relatively constant in time. Stand density changes in time as a result of natural thinning processes, and as each surviving tree grows, its capacity to support more weevils increases. It is therefore logical to assume that the rate of increase in weevil numbers per tree is in proportion to tree mortality and in proportion to the rate of increase of habitat space due to tree growth.

The reason for a peak development of weevil abundance at 426-506 stems per acre in the 65-70-year old stand is difficult to explain since it is likely inherent in several variables which evolve with successional changes during stand development. It might be postulated that "optimum conditions" of 426-506 trees per acre represent a balance between minimal tree spacing and maximum stem diameter; the former characteristic may relate to adult weevil-host and mate finding efficiency while the latter factor may relate to total habitat space available for egg laying and larval feeding

sites. Millers (1965) noted also that there were stand density effects which influenced the abundance of H. radicis. He suggested that cooler soil temperatures associated with dense stands as compared to open grown stands may be the reason for a near absence of this weevil in dense stands. If lower soil temperatures in dense stands reduce the rate of larval and pupal development, greater mortality could be expected in the pupal stage. Evidence for this was given in Figure 40 and from the fact that no pupae were ever found to overwinter successfully.

Stand density relationships in young pine were not sufficiently clear to compare with that of mature pine. However, it is possible that the relative importance of tree density in maintaining populations in young stands may not be of the same magnitude as in older stands.

The duff depth factor appears to play a key role in defining the limits of the feeding and developmental zone of immature weevil stages upon the host tree. It is no less important to the adult since most of its inactive period as well as some active periods are spent in the duff. In general, it is the duff layer which adds protection to all stages of the life cycle. The duff layer may vary in both quantity and in quality, depending upon the floral complex, soil conditions, stand density and stand maturity. Thus the relationship of weevil numbers and duff depth is interrelated with these other factors.

This distribution of duff depths around the bases of different sized trees within the same stand suggests an explanation for the changing slope of line observed in Figure 22. The greater proportion of 12-inch diameter trees with thick duff provides a proportionately larger root-collar surface area, and hence, a proportionately larger larval universe in

comparison with smaller diameter trees. This explanation may apply equally well to the pattern of weevil distribution on both collar and root regions.

There was evidence that the proportion of weevils on roots and collar regions varied from year to year and between stands. The differences observed in plots 1 to 10 may be partially explained by the fact that some years were more moist than others. It might be postulated that during dry years, or during dry intervals of the summer, oviposition may occur farther down the roots, or lower on the collar. Similarly, larvae may respond in a comparable manner to avoid or seek out more moist conditions. Thus the time of sampling during a season or in different years may account for some of the observed variability. In contrast to these studies Stark (1959a) observed 85 percent of larvae on roots and only 13 percent on the root collar. His data, however, included trees of all sizes. Warren (personal communication) noted that the roots of white spruce were more severely damaged than the roots of jack pine, where as the root collar of jack pine was preferred more by the weevil than the root collar of white spruce.

Data analysed from plots 1 to 5 suggested that the proportion of weevils on the roots tended to increase with tree size. This may result from two things. Firstly, it may relate to the duff depth distribution as mentioned earlier. Secondly, it may be due to the larger root sizes upon which there is greater expansion of egg laying activity.

In the clearcut strips of plots 1 to 5 it was unlikely that any successful oviposition occurred on the cut stumps during 1962 and 1963, so that most of the weevils collected in 1963 were from eggs laid during the summer of 1961. This indicates that at least two years are necessary for

to adult
egg development. Other workers have postulated a similar developmental period (Reid 1952; Warren 1956b and Stark 1959b).

The question may be asked what happens to adult weevils after tree removal. There was evidence that some adults migrated from the cut area to adjacent non-cut trees. Evidence for this migration was provided in the population sample in strip C of plots 1 to 5 between 1963 and 1965, and from collections of adults on border trees. A similar pattern of events likely occurred in plot 8 after the clearcut operation of 1957-58. The population level recorded in this plot was higher than reported elsewhere. Further evidence of adult migration was given by Stark (1959b) who suggested that the effect of a cutting method which reduced the number of stems per acre resulted in concentrating the population in the residual trees. In plots 1 to 5, 1965 it appeared unlikely that the increase in the C strips was due to migration of adults from within the stand. Populations in the D strips showed a fairly uniform trend of increase from 1961 to 1965, and any movement into C was probably normal.

The changes in weevil abundance within stands of different degrees of maturity appear to be effected through two main variables of stand development; stand density and tree growth. The rate at which natural thinning takes place appears to be extremely variable (Smithers 1962) and no reports were found which suggested a consistent pattern. The analysis of old weevil scars by dating on 65-70-year old trees suggested that populations increased most rapidly between the ages of 30 and 45 years, while radial growth was most rapid between 15 and 45 years. The latter period may represent a time of peak thinning for this particular stand.

During the period of rapid population growth the change in numbers of weevils reflects more of an increase in intensity (weevils per tree) than an increase in absolute numbers. The increasing tree size and reduction in stems per acre have the effect of making populations more highly aggregated.

A maximum peak of weevil abundance in the 65-70-year old stand was suggested at the age of about 45 years. However, the method of dating weevil scars did not take into account certain changes in attack pattern during the growth of the stand and with increasing stem diameter. Evidence was presented which indicated an expansion of the larval universe to include portions of the roots as tree size increases. The error involved in estimating numbers of scars may therefore be highest for measurements of the past 15-20 years, due to an increasing number of feeding sites on roots. Some scars on the lower portion of the collar may also have been missed. The sharp decline indicated in Figure 33 since the stand age of 46 years is more apt to be a levelling-off or a more gradual decline.

It is noteworthy that basal area of fully stocked pine stands attains a maximum at 60 years of age (Smithers 1957). This supports the view that population intensity levels may not increase significantly beyond this age.

From an examination of the attack patterns in all sampled areas it is possible to reconstruct a schematic sequence of events which describes the development of H. warreni populations during the normal growth of lodgepole pine stands. This pattern may be considered typical of good growing sites in the Lower Foothills Section of Alberta. Adult weevils immigrate initially into pine stands 8-10-years old. Their attack pattern

remains essentially the same throughout stand growth; the order of preference for oviposition is on dominant, co-dominant, intermediate and suppressed trees in that order. Population build-up appears to be slow for the first few generations. Presumably this is partly dependent upon the density of immigrating adults, and partly due to survival in the new habitat. The rate of advance into the stand is at least 35-45 feet per year on average sites. During the early years of attack; i.e., up to the age of 20-25 years, there may be up to five percent mortality of the larger trees caused directly by larval girdling. Only scattered mortality may occur thereafter. The attack density on most of the young trees may not exceed 1-2 larvae per tree. As the tree grows, so also does the rate of oviposition and the larval universe increases in area. Dominant trees approaching maturity may have an attack density of 20 or more larvae each. Between the period of stand ages 10 years and maturity, stand density may be reduced from over 5000 stems per acre to 500 stems per acre. Thus, while weevil population intensity increases with stand age, absolute numbers of weevils may remain relatively constant at some level between 500 and 1500 weevils per acre. It is expected that, within this range, annual fluctuations would normally occur.

Following the initial slow phase of population build-up there is a rapid increase from about the age of 30 years to 45 years, thereafter there is a levelling-off. As stand maturity is reached near 80 years a slow decline can be expected in population intensity and in absolute numbers.

The sampling system used appears to have been adequate for showing general trends in abundance, for describing population structure and in defining weevil habitat relationships. However, some refinements are possible.

if the system is to be used for detailed population studies.

Southwood (1966) has indicated that a stratified random sample is recommended for most ecological work in that it provides best representation of the total area to be sampled. Essentially, this condition was partially fulfilled in the design used within the 65-70-year old stands of plots 1 to 7. In each plot the block was a minimum sized area in which a fixed number of trees were randomly chosen.

In even-aged pine stands, which is the most common situation in the Alberta foothills, the individual tree is probably the simplest to handle as a basic sampling unit. Each tree can be regarded as a complete biological unit in itself. Additionally, weevil numbers expressed on a per tree basis can be related directly to absolute numbers, or to degree of tree damage.

Contagion in the weevil habitat appeared to be due to two things when the tree was taken as the sampling unit. It was due to the adult weevil recognizing large trees for greater oviposition as compared to small trees. It was also due to the gradient of tree sizes in natural pine stands. These two characteristics are interrelated, the former being a determinant of oviposition sites, while the latter provides the source of attraction. It is suggested that in pine plantations where little gradient of tree size exists a more random weevil distribution might be expected since the trees should be attacked with almost equal probability and intensity.

The degree of contagion caused some statistical problems in the analysis of weevil populations from individual trees. In plots 1 to 10 the high proportion of trees with zero weevil counts (up to 75 percent for low population levels) added the problem of selecting a suitable transformation.

While Taylor's power law suggested that a logarithmic scale would be adequate ($b = 1.92$) this did not provide normality to the data. However, when weevil numbers were pooled from groups of five trees, then transformed to a logarithmic scale, the requirements of normality and stabilization of variance were fulfilled. From this it appears that a stratified random sampling system in which clusters of five trees are randomly selected might offer the best approach to detailed sampling. Because of the lower weevil densities per tree in the regeneration plots the cluster size may have to be increased considerably. The number of such cluster units required to give a chosen degree of precision was not established.

One alternative to the use of the tree as the sampling unit might be to equate weevil numbers per tree to a common unit area of the tree surface, measured from the total larval feeding universe. While this would not decrease the number of zero counts, it might relate more directly to the available space for oviposition.

The studies of the relationship between tree size and weevil numbers within stands indicated that all trees do not have equal probability of attack. However, the actual measurement of the root-collar surface area available to the weevil would pose several problems. Surface area estimates may vary with tree size, with rooting patterns, with duff depth and probably with tree density. Special techniques would have to be devised for estimating surface area.

The method of sample tree selection for plots 1 to 7 allowed a residual of 40-50 percent of unsampled trees at the end of the four annual samples. Further disruption of the larval and adult habitat may interfere

with the normal pattern of weevil distribution, and may have the effect of concentrating the population upon the residual non-sampled trees. If weevil populations are to be followed over a greater period of time a stratified sampling system using a plot size which would allow more than 40-50 percent of unsampled trees would be desirable.

Since weevil numbers were found to be directly related to percentage of trees with fresh attacks, direct application of this relationship could be made use of in designing a sampling system for general surveys of weevil abundance and damage appraisals. The system would use the tree as the basic sampling unit, and each tree would require a minimum amount of effort to determine the presence or absence of fresh weevil attacks. When the first live weevil is located the sampler would then proceed to the next tree. Each freshly attacked tree would be scored positively. The total percentage of trees with fresh attacks would provide an estimate of population density, or be an indication of potential and actual damage. By this system stands with high population levels would require less time to assess than would stands with low populations since, on the whole, trees in the former category would require less searching than trees in the latter.

The present studies were in agreement with Stark's finding (1959a) that all stages of larval development could be found throughout the summer, and that egg laying also occurred during most of the summer period. Since the life cycle is not synchronized, therefore, it is questionable whether the life table approach would provide reliable information regarding a mortality with age relationship. Larvae born in June, for example, may be confronted with different mortality factors than larvae born in August.

Thus, while they may be of the same age they are separated by different biological events. The mortality of eggs may be similarly difficult to assess.

The frequency distribution of larval head capsule widths did not show distinct peaks beyond the third instar, indicating the unreliability of such data in determining total numbers of instars. Seven instars were recorded from artificial rearings of larvae by Warren (1960a), while Stark (1959b) defined six on the basis of head capsule measurements. Similar problems have been encountered in the determination of instars of other Hylobius species. Measurements of H. radicis field collected larvae provided only an indication of the number of instars, while five, six and seven were reported for artificially reared material (Finnegan 1962a). Five and six instars were recorded for H. pales, but the smallest larvae in the fifth instar group generally transformed to a sixth instar before pupating (Finnegan 1959).

In Europe, H. abietis develops through at least five instars and certain differences exist between pine and spruce reared material (Nordic Forest Entomologists' Research Group 1962). Five instars were noted for H. piceus (Scherf 1964). It is possible that the number of instars of H. warreni may vary from five to seven.

The extent of mortality and the factors involved of first instar larvae could not be determined since the larvae were always located within small galleries of the outer phloem. The site of oviposition varied from within the adjacent soil to frass-covered niches in the bark. Some mortality due to predation can be expected between the period of hatch and establishment in the bark, especially when the oviposition site is external to the bark.

Once feeding began the larvae were usually confronted with fresh resin flow which they used continuously as a protective covering. There appeared to be little evidence that excessive resin flow could be a mortality factor, except indirectly by trapping moisture. Studies of the feeding behavior indicated that young larvae adjusted their feeding depth in the phloem as they increased in size. This may be an adaptive feature for survival.

Throughout its development the larva destroys a large quantity of inner phloem and cambial tissues (9+ inches of gallery), and much of this is used directly as food. Where patches of dead phloem and cambium appear as a result of feeding, it can be assumed that this represents an actual destruction of feeding area to succeeding larvae. The feeding pattern of later larvae may be altered depending upon the extent of previous damage. It has also been noted that large accumulations of resin-soaked soil, up to 3-4 inches thick, occur adjacent to the wound areas of some trees. This material becomes sufficiently hard to be impenetrable by the adult weevil, as well as to early instar larvae. Thus the oviposition pattern and larval feeding patterns can be affected by direct loss of cambial and phloem areas, and to some degree by the hardened masses of resin-soaked soil. In addition, the behavior of the adult can be affected through an increase in time spent in searching out oviposition sites as damage intensity increases.

Although the sloughing-off process of bark scales, tree growth and the healing process combined would tend to reduce damaged areas in time, the implication is that weevil numbers become partly a function of attack density and of the frequency of re-attack. If the tree is heavily attacked during one particular period this would immediately influence the pattern of re-attack

for several subsequent years. This provides one explanation why many trees of all sizes in mature stands had no weevils, while adjacent trees had many. In most sample plot areas the percentage of trees with current attacks did not exceed 55. Similar findings were obtained by Stark (1959a).

The measurements of bark thickness and resin cavity statistics showed that the nature of the larval universe between the lateral roots and main stem is transitional in these microhabitat characteristics. There appear to be distinct advantages for egg deposition and initial feeding to occur on root bases since there is minimal contact with resin cavities as compared to the tree stem base. Within the collar zone bark thickness is maximal; this provides a maximum food supply for larvae and may require about the least amount of mechanical effort to obtain it.

In all sample plots the highest incidence of mortality occurred in the prepupal, pupal and teneral stages. However, these higher values may reflect the ease with which these stationary stages were located. Mortality of eggs and adults could not be assessed quantitatively inasmuch as only some of the factors were identified. Pupae were found very susceptible to moisture in the chamber. Other workers have observed similar findings for H. radicis (Finnegan 1962a; Millers 1965). Millers also demonstrated that submersion of H. radicis eggs in water for more than a day caused mortality, and that contact with free water could prevent development. The eggs of H. warreni appeared to be slightly more resistant to moisture. Rearing studies suggested that egg hatch was most successful in a saturated atmosphere.

In the prepupal and pupal stages the two main parasites, B. bassiana

and D. tuberculatus tuberculatus may tend to increase in response to increasing weevil populations but observations were too few to confirm this. Highest numbers of the Hymenoptera parasite were recorded in 1963 in plots 1 to 5. With the exceptions of plots 1 to 5, AB, 1963 and 7, 1962, the incidence of mortality of entire populations was less than five percent. The higher percentage in the cut stumps of 1963 (plots 1-5, AB) is reasonable because of the drastic changes effected through clearcutting. In plot 7, 1962, however, mortality in the pupal cells was especially high in relation to the overall population level. This may have been related to the predominantly moss forest floor cover and to the relatively high stand density.

Several authors, including Benham and Miranda (1953) and MacLeod (1954) have maintained that B. bassiana attacks a large variety of insect hosts, and the possibility of its use as a controlling agent has been described (Angus 1960). In Europe an integrated method of control for H. abietis has been described using a weak insecticide (DTHP) with a suspension of B. bassiana spores (Samšínáková and Novák 1967).

Little is apparently known of the habits of the larval stage of Laphriinae Diptera. According to Imms (1957) they inhabit soil, wood and leaf mould and are either predacious or scavenging. Elton et. al. (1964) provided evidence that certain species inhabiting cut pine stumps in Holland were predacious on larvae of Hylobius abietis.

The relatively large numbers of dead adults found at tree bases (Table XXVI) may suggest that they died from old age or from internal parasites. However, only one of the 36 dissected females was observed with

internal nematodes. Dr. Rühm (personal communication) stated that four different species of nematodes are associated with Hylobius abietis.

No effects of the attacked mites (Hericia sp.) upon the longevity or fecundity of weevils were observed. However, there is evidence that mites cause sterility in the Corixid, Cenocorixa bifida Hung. (J. Simpson, personal communication), and the possibility of a similar effect in the weevil should not be overlooked.

Although no evidence of adult weevil predation by shrews was detected from stomach content examinations, Warren (personal communication) noted that S. cinereus cinereus in captivity readily accepted adult H. warreni as food. It is possible, therefore, that they do in fact prey upon the weevil in the natural habitat. However, the sampling procedure for collecting shrews may have failed to detect predation for two reasons. Firstly, adult weevil locomotion on the duff surface and up tree stems was greatest between the hours of 10:00 p.m. and 1:00 a.m., and it is during this time that greatest predation should be anticipated. Since shrews were collected in the morning between 9:00 - 10:00 a.m., the time lapse would be sufficient for complete digestion. Secondly, since adult weevil populations appeared to be very low, the prey-capture behavior and diet of shrews were likely conditioned to the more abundant insect species such as carabid beetles. This was evident from the stomach content examinations.

The numbers of adult weevils collected by the different methods show few distinct patterns for interpretation. Newly developed males and females occurred in about equal numbers and a 1 : 1 ratio was also described by Stark (1959a). It was apparent that the two sexes differed in behavior

as evidenced by the greater numbers of males collected from border trees as compared to trees within stands. Several reasons may be postulated to explain the differences. Females may tend to be more active than males in lateral dispersion as well as in feeding. Evidence for this is suggested by the greater numbers of females captured in plots A and B. The fact that males were found nearer to the duff surface than females may account for the higher numbers by the tree base-duff search method, but does not account for the higher numbers caught in traps on border trees. A second reason may be that females are more sensitive to moisture requirements in the root-collar environment, and hence were more active in locating these areas. This is also a reasonable assumption since the bases of border strip trees appeared considerably dryer than tree bases within the stand. Warren (1956b) suggested that adults may seek out oviposition sites in the environment best adapted to their requirements. A third possibility may be that mortality of females was higher on the border trees than of males, although there appears to be no direct evidence for this. Another possibility may be that males disperse more laterally than females. However, the evidence from trapping and behavior studies tend to favor the first two postulates.

As indicated by the trap method of collection in plots A and B (Table XXVI) females were more than twice as abundant as males during the 1964 and 1965 periods, but in 1966 they were almost equally abundant. Data in Table XXVII suggests two alternative explanations. The rate of capture indicated that the male population in the plots remained constant during the three year trapping period, and that the change in sex ratio in 1966 was proportional to the lower capture rate of females in 1966. It was

suggested that a differential mortality rate accounted for the apparent decline in the female catch rate, or that this reduction was brought about by a change in behavior pattern. The first explanation appears most plausible since the age structure of adults should remain relatively constant in time. In contrast, a drastic change in behavior pattern, as a result of maturity, or immaturity does not appear likely. Further studies are required to clarify the differences in distribution and abundance of the sexes within stands.

When the percentages of captures, 1+ times (Table XXVII), are pooled for different years and plots, but separately for the sexes, the values indicate that males and females were recaptured at about the same rate (females 41.2% and males 44.1%). This suggests that females were in fact more abundant than males in plots A and B, and that their tree climbing behavior was similar. The data describing the numbers of adult captures in relation to tree size support this idea. The tree size relationship also indicates that it is the selection pattern of trees by females which accounts largely for the subsequent distribution pattern of larval, pupal and teneral numbers.

The interpretation of the graphs describing rate of dispersion implies that after one night of travelling an adult can be expected about 8 feet, on the average, from its tree of origin. After two nights it can be expected about 12 feet, after 10 nights about 20 feet and after 20 nights about 40 feet. While this suggests a very local pattern of terrestrial movement it is difficult to ascribe biological meaning to the pattern. When leaving a tree of origin the directional response was random, at least

initially, and movement tended to be unidirectional. In locating host trees, however, there was evidence that they do so partly by vision. In this respect the correlation of weevil movement, during one night's travel, with average distance between trees is reasonable.

The studies of weevil reproduction have demonstrated a relatively low fecundity for H. warreni. Studies by other authors generally agree with this. Warren (1955) noted that the maximum number of eggs laid by a single H. warreni female during a summer period was 33, while Stark (1959a) observed nine eggs. Warren (1956a) also observed that the highest oviposition period occurred during May, June and July. He obtained percentage hatches which varied from 7.6 to 70.0 for different years.

Several authors have studied the oviposition habits of other Hylobius species. Finnegan (1962a) reported up to 40 eggs per female per season for H. radicis, but noted that there was wide variation among them. He obtained an average of 17.5 and 14.2 eggs per female during the first and second years of rearing respectively. His findings for H. pales (Finnegan 1959) were slightly higher than for H. radicis for first and second summer rearings. Shaffner and McIntyre (1944) and Millers (1965) obtained maximums of 64 and 67 eggs respectively per female H. radicis from laboratory rearings. A maximum of 33 eggs for one female was also recorded for H. rhizophagus by Millers (Kearby 1965), while Heqvist (1957) obtained 10 eggs per female from laboratory rearings of H. piceus. Hylobius abietis and H. cribropennis showed higher egg productivities; i.e., 60-80 eggs per female (Scherf 1964) and 70-80 per female per season (Matsuzawa et. al. 1963) respectively for the two species.

The egg laying period of H. radicis appears similar to that of H.

warreni. Finnegan (1962a) and Millers (1965) both observed oviposition of H. radialis from May to September. These authors also observed an egg laying rate of 1-4 eggs per female per day; similar observations were noted for H. cribropennis (Matsuzawa et. al. 1963).

The habit of constructing a special niche in the bark for placement of eggs and subsequently covering them over with excreta, appears to be common to several Hylobius species. The female H. radialis excavates a small chamber in the inner bark in which one egg is usually placed (Millers 1965). The cavity is then covered with tightly packed excrement. A similar habit was described for H. cribropennis (Matsuzawa et. al. 1963). This appears to be a special adaptive feature which confers safety on the egg from excess moisture and from predation during the relatively long developmental period of the embryo. Survival is additionally enhanced through the habit of depositing eggs singly in any particular laying site.

The attempts made to estimate total summer egg productivity for H. warreni showed considerable variability. While 36 eggs may represent a potential maximum per female, the average was only 12.2 eggs per female. This is about half the value obtained (24.3 eggs) by calculating from 103 possible egg laying days. This implies that less than half this number of days may be suitable for oviposition in the field. Data presented in Table XXX tend to support this, where only 4.00-5.37 eggs per female were estimated in a natural habitat situation. These values should be considered minimal, however, since eggs were difficult to locate. Low night temperatures, periods of drought and periods of heavy rain fall may contribute to periods of non-laying activity.

The long pre-oviposition period of about one year suggested from rearing H. warreni in plots C and D is uncommon in the insect world. However, Matsuzawa et. al. (1963) also described a pre-oviposition period of two to three months for H. cribropennis. This period would seem to be a weak link in the life history since H. warreni females appeared to carry on all life functions except egg laying (Tables XXVIII and XXX) during their first year.

The percentage of eggs in niches may provide an indication of suitability of microhabitat conditions in the root-collar zone. Under the most favorable conditions observed in plots C and D (Table XXX), and by experimentation (Table XXXI), the percentages of eggs in niches were all above 70. While no studies were undertaken to compare survival of eggs and first instar larvae in niches versus other egg laying sites, the niche would seem to provide maximum protection. Not only are eggs maintained in a relatively constant and stable environment in the niche but the newly emerged larva is provided with an immediate and protected source of food. It is thus free from the risk of predation during translocation from within the adjacent soil to the bark environment. Unfavorability in the microenvironment for oviposition may be critical when the duff layer is shallow and dry (Table XXX, plot D, 1966). This condition was improved in plot C by adding sphagnum mosses around tree bases. A duff layer which is extremely moist may also have an inhibiting effect on oviposition. This was suggested in cages 21-30 (Table XXXI) where the moisture level may have been excessive. The lower temperature conditions of these cages likely had the effect of reducing the rate of oviposition but should not have effected the position of egg laying sites.

During the rearing experiments described in Table XXXI some error in fecundity may have been due to the timing of each set of cages. It was shown that oviposition attained a maximum in early July. Cages which were established after this date may reflect the reduced laying activity period.

The trapping experiments in plots A, B, C and D suggested that weevils were most active in dispersal in June as indicated by numbers of captures per day. It was not established, however, whether this represents a period of active migration. Feeding requirements would likely be highest during this period of maximum dispersal. In addition, mating activity was most common during the months of June and July (table XXXII). Thus the overall seasonal trend of activity, including egg laying, slackens after July. The most active period coincides with the month of June when temperature and moisture conditions in the Alberta foothills are likely optimal for the weevil. High temperatures and low moisture are characteristic of July and August. Studies of night time temperatures in plots C and D showed that few nights in May are suitable for adult activity since the temperatures fall below 40 °F. by 11:00 p.m. on most nights.

Studies of the feeding habits of H. warreni generally agree with observations by Warren (1956b). However, in contrast to his studies, there was little evidence that the adults fed upon the needles of lodgepole pine.

The maxima of feeding scars shown in Figure 70 may have been due to a sexual difference, with females preferring the upper crown areas and males the lower crown areas. Another possibility is that falling temperatures or wind in the evening may have restricted their movement to the lower canopy.

The impact of weevil damage to its lodgepole pine host has

implications in the survival, growth and development of individual trees and upon the stand as a whole. Sampling studies in infested stands indicated that up to 100 percent of trees may show evidence of larval feeding, but the degree of damage varies widely among trees within the same stand. Warren (1956b) has adequately assessed larval feeding damage on white spruce to show its cumulative characteristics with each successive attack. Stark (1959b), however, indicated that the "Damage Index" rating method used by Warren, based upon degree of girdling of collar and roots, was unsatisfactory in expressing tree injury to lodgepole pine. He suggested that some modification was necessary for the pine. According to Kramer and Kozlowski (1962) death by girdling is probably caused by desiccation resulting from injury to the root system through lack of carbohydrates. Mortality was rarely observed, however, in trees over three inches in diameter, or after the age of 30 years. Trees smaller than this showed less resistance, probably because fewer larvae were required to do an amount of damage equivalent to that on larger trees. In addition, the pattern of larval feeding and gallery orientation was shown to differ between young and old trees. With increasing tree size weevil damage becomes more extensive down the roots and this may tend to reduce the impact of damage to the tree. Most of these feeding sites occur on the upper and lateral aspects of the root, and only occasionally are they present on vertical roots and sinkers. Horton (1958) showed that root sinkers developed from the underside of major lateral roots and from the taproot, usually before the polewood stage (about 40 years). He suggested that the vertical roots function significantly in anchorage and absorption. Thus the change in developmental pattern of root

structure as the tree passes from the sapling stage may confer resistance against the wounding effects of larvae.

The claim that weevil damage is cumulative with each successive attack may not be strictly true. Some allowance is needed for tree growth characteristics and the natural healing process. Damage assessment values do not remain static in time as long as the tree continues active growth. Total damaged areas may decrease if no further wounding occurs. Therefore, damage is cumulative as it relates to the time of measurement, and any subsequent measurements might give higher or lower values.

While the results of growth measurements in the two young pine stands indicated growth losses in the vertical and horizontal dimensions of the tree, the data can be interpolated into the stand as a whole only in a limited way. A small percentage of trees in a stand (i.e., less than 10 percent) may have girdling damage equal to or exceeding 45-50 percent of the root collar circumference. Trees with this amount can occur in the dominant, co-dominant and intermediate categories. However, since dominant and co-dominant trees receive most of the initial attacks total growth loss over the developmental period of the stand may be considerable, especially on the better sites. This assumes, of course, that the degree of tree height reduction is comparable for all ages or sizes of trees having an equivalent amount of partial girdling.

Some sampling results of Warren (1956b) and Stark (1959a) in mature pine near Strachan, Alberta in 1954 and in 1957 respectively, indicated average damage indices of the order 4.5 and 4.2. This may be equivalent to 5-25 percent girdling of roots and collar regions for the stand as a whole. The 1966 examinations of the same stand (plot 10) revealed that many trees

had one or more major lateral roots killed from weevil feeding. While 5-25 percent girdling may be an insufficient quantity to cause a detectable growth reduction to all trees in the stand, a small proportion may be seriously affected. The overall effect would not appear severe enough to cause a notable change in stand structure, such as a shift in crown levels of different sized trees or large stand openings. On the other hand, any tree mortality caused directly or indirectly by weevil feeding would affect tree spacing and competition. On good pine sites which maintain weevil populations over long periods of time the total impact of the weevil likely plays a role in the hastening of stand decadence by contributing to a general overall reduction in growth, by allowing entry of root and stem decay organisms, by reducing the effective root system and by making trees more prone to windthrow. Evidence in support of this comes from several workers, including Nordin (1956), Warren (1956c) and Stark (1959b). The implication of the total impact is that natural successional changes may proceed at a faster rate than normal with the aid of the weevil.

It is apparent that several factors are responsible for the spacial variability in abundance of weevils in forested areas. The weevil tolerates pine forests of nearly all ages growing on a variety of sites from dry to wet. Their greatest abundance coincides with the medium to moist sites, and usually these are characteristic of high quality sites. Within these stands the weevil is distributed according to four main stand variables; stand maturity, tree size, tree density and duff depth. Favorability of the microhabitat of the weevil is inherent largely in these four variables. For example, stand maturity, tree size and duff depth dictate the number of eggs which can be laid and the amount of space available for larval feeding.

Tree density regulates to a degree host and mate finding efficiency and has interactions with all other stand variables. In addition, the rate and degree of forest succession, as well as habitat conditions of moisture and temperature, are influenced by stand density. The quality and quantity of duff relates directly to specific requirements of the weevil, affecting adult dispersal, oviposition, hatchability, development of larvae and survival of all stages. In essence the combination of these four stand variables accounts largely for the different levels of abundance in different stands.

Providing that the four stand variables allow successful survival and growth of a weevil population, a fifth factor comes into play. This factor is inherent in the behavior patterns of the weevil. The female was found to deposit her eggs according to a tree size relationship. This suggested some regulatory mechanism in distributing her eggs according to a root and root collar surface area basis. Where previous larval wounds occur the space available for new oviposition sites, as well as larval feeding areas are reduced accordingly, so that weevil numbers become partly a function of host attack density and the frequency of re-attack. This idea derives support from the fact that damage is cumulative and that up to 100 percent of trees in a stand may show old attacks. The rate of tree growth, rate of wound healing and natural thinning processes in turn influence attack density and the frequency of re-attack. This implies that the overall numerical restraint and stability of the weevil is accomplished largely through its own behavior patterns.

The special adaptations of the weevil which provide the mechanisms through which its variability in abundance, numerical restraint and stability

are made possible are many. These include a low fecundity rate, a long pre-oviposition period, a life cycle of up to five years long or more, a reduced period of activity in the adult stage and slow means of dispersal. Its flightless condition and nocturnal habits significantly reduce the period and rate of activity. The habit of climbing trees may have survival value since it reduces the possibility of predation. Placement of eggs in special niches and the construction of the pupal chamber may enhance survival. The long period of embryonic development and establishment of early instar larvae require the special protection of the bark niche. In the larval stage a major adaptation is the ability to withstand resin flow of the most vigorous trees, and to utilize this material for its own protection.

The relationships of weevil numbers with forest conditions in the Alberta foothills suggest that there exists an ecological feedback which limits the abundance of the weevil in stands. On the whole, the weevil does not appear to increase at a rate, or inflict damage to an extent greater than the normal recovery rate of its host. In theory, extensive host mortality and low density stands would tend to reduce host finding ability, and thereby lower the rate of increase. There appears strong selective advantage to attack most heavily the largest and most vigorous trees in a stand since this allows maximum population levels to be maintained, and at a tolerance level that allows little or no tree mortality. For the same reason the most productive growing sites of lodgepole pine appear to have the potential to support and maintain the greatest levels of abundance.

The overall studies of the weevil suggest several avenues for implementation of cultural control measures against the weevil. Initially,

the decision to carry out control can be based upon an assessment of weevil abundance in mature stands prior to cutting. This would help to establish a site potential rating of future weevil activity. The assessment can be done by the sampling technique described in Figure 33 and Table XXIII.

Stands showing population levels in the "high" category (62.0 percent or more of trees with fresh attacks, or an average of 2.50 or more weevils per tree) may be considered a reasonable criterion for initiating control measures. Various site factors may also be used to recognize high priority sites. These include stands having a predominance of pine, a density of 300-600 stems per acre, good growth characteristics, rich floral complex including a large proportion of mosses and a duff depth of 5-7 inches. In general, concern for the weevil in stands with these characteristics need apply only in the Lower Foothills Section of Alberta.

Following the establishment of a high population index in a mature stand most attention should be directed toward keeping out weevils from regeneration pine established after clearcutting. Because of the persistence of weevils in stands it is not felt economically justified to attempt control once populations become well established, at least in forests utilized for pulpwood or related uses. In infested mature stands clearcutting destroys a large portion of the weevil population (estimated 67 percent), but larvae can still complete their development one and two years after tree removal. The newly developed adults from cut stumps pose a problem to any advanced regeneration pine or uncut trees. Since they are long-lived the adults are also of concern in the timing of initiating the new stand and in the clearcutting of residual strips or blocks. For this reason a complete

clearcut of the stand, including any advanced regeneration pine and white spruce would be most effective in reducing weevil abundance. Scarification treatment applied soon after cutting would likely hasten mortality of larvae and pupae in the cut stumps.

Where pine areas are clearcut in alternate strips or in block patterns, the residual strips and blocks should not be retained longer than 2-4 years. This period would allow sufficient time for natural regeneration or planting on the cut areas and would decrease the chance of re-invasion into the young stand. It would also reduce the chance of population build-up in the border trees. The 2-4 year period takes into account survival of larvae in the cut stumps as well as adult longevity. Since the rate of adult dispersal into young stands may be 35 feet or more per year there is merit in increasing the size of area of clearcutting.

Immigration of weevils into young stands may be retarded initially in overly dense stands. However, since dense stands can lead to stagnation (Smithers 1962) an early pre-commercial thinning might favor a build-up in population intensity. By concentrating the weevils on the residual trees, and by creating a stand situation analogous to a plantation, considerable tree mortality and growth loss could result. The encouragement of an aspen intermixture or an underplanting of black spruce would tend to favor a decrease in the rate of population build-up.

Within stands Warren (1956c) postulated that H. warreni may be controlled by removing the humus from the vicinity of the root collar and basal portions of major roots. He suggested that the humus layer provided protection to the insect's habitat by maintaining a high humidity. The

present studies agree with this but suggest that the main effect of duff removal is in reducing the area available for successful oviposition. Studies by Wilson (1967) demonstrated that removal of lower branches and tree base duff material, and the scraping of surface soil around the tree base reduced H. radicis larval populations to below an economic level, at least for the first year. Wilson suggested that the greater exposure to light or heat, or both, at the tree base created an unfavorable habitat for the adult weevil.

SUMMARY

Ecological studies of the root weevil, Hylobius warreni Wood were conducted in lodgepole pine forests in Alberta. The main objective was to evaluate this insect pest in terms of its potential destructiveness to forests. Answers to two ecological questions were sought: what factors are responsible for the weevil's spatial variability in abundance in forests and what factors are responsible for its apparent numerical restraint and stability. In the first stage of study the geographical range of the insect was mapped with particular emphasis upon the distributional range of its pine host. In the second stage plot areas within a variety of pine stand conditions were sampled to ascertain patterns of weevil abundance, their change with time and their correlation with stand conditions. The physical nature of the weevil habitat was analysed in the main study areas to provide a basis for comparison with other infested stands. This included vegetation,

soil, climate and topographic characteristics.

Weevil abundance was followed in 7, 3-acre plot areas over 2-, 3- and 5-year periods. Thirteen additional plots were sampled for weevil numbers and attack incidence. Levels of abundance were related to stand maturity, tree size, tree density and duff depth. Clearcutting treatment was applied to some of the plots to assess this practice as a method of control, and for its effects upon weevil survival.

Weevil numbers and the attack distribution upon the host were described from a variety of stands, a few years old to mature, to illustrate the chronological patterns of change with normal stand development. Related information was collected from mature attacked trees through an analysis of dated larval scars. Stand susceptibility was analysed in a variety of young stands by scar dating, and by determinations of the age and size of trees when initial attacks occurred. The rate of weevil spread within stands was estimated from plot areas extended into young stands from boundary trees which supported reservoir populations. Their selection of hosts and attack density patterns were related to stand maturity.

A third phase of study dealt with casualty factors operating on all stages of the life cycle of the weevil. In the adult stage relative abundance was assessed over a 3-year period by the use of a specially designed trap and the mark-recapture principle. By the use of this trap in a variety of field plots the longevity of adults, their survival rate, egg laying behavior, daily and seasonal activity patterns, host selection and the direction and rate of dispersal on the forest floor were investigated. The fecundity of adults was studied in several field and laboratory experiments,

and by examinations of the female internal reproductive system. Other experiments were used to explore the influence of environmental conditions on activity. Mortality factors of all stages were investigated, and assessed quantitatively in the larval, pupal and young adult stages. Limited field and laboratory experiments were conducted on the survival, percentage hatch and embryonic development of eggs. Attempts were made to assess the feeding behavior and early survival of young larvae upon its host, and of its adaptations for survival in the root-collar zone. Two aspects of concern were bark thickness and bark resin cavity characteristics. The structure and development of larval populations were analysed by head capsule width measurements. The period of pupal development and the characteristics of the pupal case structure were described.

A fourth phase of study was concerned with the effects of weevil injury to its host tree. Anatomical changes in the host which resulted from direct larval feeding wounds were described. Growth losses resulting from partial girdling of pine root collars were measured in the vertical and horizontal dimensions of the tree, using the three growth sequences described by Duff and Nolan (1953). Some interpolations of these results were made of the forest as a whole to indicate economic effects, and to aid in the understanding of weevil population development and survival.

The biological factors considered most likely to influence weevil abundance and regulation of numbers are discussed in relation to lodgepole pine stand development in the Alberta foothills. Recommendations for control of the weevil through forest management are made for stands supporting high infestations.

CONCLUSIONS

1. In Alberta the geographical distribution of H. warreni extends generally throughout the coniferous forest areas of pine and white spruce, except all stands above 5000 feet in elevation. Lodgepole pine is the primary host in Alberta and within its range greatest abundance of the weevil occurs in the Lower Foothills Section (B19a of Rowe, 1959), between 2500 and 4000 feet in elevation.

2. Within even-aged lodgepole pine stands weevils are most abundant on good growing sites characterized by a rich ground floral complex of mosses, herbs and low shrubs, and where soil conditions are mesic to moist. Stands with a predominant moss carpet are generally associated with low levels of weevil abundance.

3. Decaying logs lying at tree bases are associated with heavy larval feeding damage in the immediate areas of the roots and root collar of host trees. Their presence enhances moisture conditions in the larval universe and provide a safe medium for mature larvae, pupae and teneralis. A relatively high degree of forest floor undulation and indentations, caused by tree uprooting and decaying logs, tend to favor high weevil populations as compared to stands having a smooth forest floor.

4. Within even-aged pine stands weevil numbers vary according to four main stand variables: stand density, tree size, stand maturity and duff depth. Variability in the patterns of weevil abundance is manifest in the interactions between these variables.

5. Weevil numbers measured on an absolute scale attained a maximum

at a stand density range of 426 - 506 stems per acre in a 65-70-year old stand. In stands 15-25-years old the density range for maximum numbers appeared to be far greater.

6. Within each stand type the numbers of weevils vary directly with tree size, being the highest on dominant trees and lowest on suppressed trees. Their numbers may be directly proportional to the surface area of the root-collar region inhabited by larvae. The relationship is applicable in young and old stands.

7. The effect of stand maturity on weevil numbers is manifest in the distribution of tree sizes in that attack density per tree is lower in young stands than in older stands. On individual trees up to 25 years old the numbers of larvae rarely exceed 3 while in 65-70-year old trees the numbers often exceed 15 weevils. Absolute numbers of weevils can occur at similar levels in young and old stands, thus reflecting the influences of tree size and stand density.

8. The pattern of weevil abundance in relation to duff depth is complex, being influenced largely by duff depth at tree bases, duff quality and the effect of tree size. Within even-aged stands weevil numbers tend to increase directly with duff depth for each tree size class, but the slope of line increases with tree size class. This seems due to the finding that a greater proportion of large trees have deeper duff than small trees of the same stand, and to the finding that the larval universe expands down the roots as the tree grows.

9. The distribution of the weevil on its host tree varies in time as the tree grows. The greatest percentage of weevils occur in the root

collar zone and a lower percentage occur on roots. As tree size increases there is a tendency for the percentage of weevils on roots to increase accordingly. Weevil numbers on the root collar and on roots each display a similar pattern of increase with increasing duff depth, but the pattern is modified by tree size in both cases.

10. The proportion of weevils on root and collar areas may change from year to year or during a summer period, in response to changing moisture conditions around the tree base.

11. A clearcut form of tree harvest reduced a weevil population by an estimated 67 percent, but some larvae developed to adults in the cut stumps one and two years after tree removal. The rate of development of surviving larvae and pupae appeared to be increased in the cut stumps, probably due to higher soil temperatures at the base of cut stumps as compared to soil temperatures in residual stands. A build-up of weevils occurs on border pine trees surrounding cut areas following clearcutting; their origin appears to be from adults dispersing from cut stumps, rather than from trees within residual stands.

12. Initial weevil invasion into young stands occurs when the trees are 6-10 years old, or when they are 4-5 feet high and have a stump diameter of about 1 inch. During initial invasion dominant trees are selected first and the rate of dispersal is at least 35 - 45 feet per year.

13. Throughout the life of the stand weevil attacks accumulate, being the highest on dominant trees and least on suppressed trees. The percentage of trees with current attacks in mature stands relates directly to tree diameter, while the log of weevils per tree relates in a linear

positive pattern with the percentage of trees having current attacks. The latter relationship forms the basis of a simple survey sampling technique for assessing weevil abundance and damage intensity.

14. Four general stages of weevil population development may be defined for even-aged lodgepole pine stands. The stages take into account the period from initial invasion until stand maturity. Stage I: extends from stand age 10-30 years; population development characterized by slow rate of increase. Stage II: extends from age 30-45 years; population development characterized by rapid rate of increase. Stage III: extends from age 45 to 70-80 years; population development characterized by a general levelling-off. Stage IV: extends beyond age 70-80 years; population development characterized by a slow decline. The developmental patterns reflected in these stages are more of an expression of population intensity than of absolute numbers.

15. Weevil populations are highly aggregated in mature stands; "k" values of the negative binomial varied from 0.09 to 0.68 while Taylor's power law provided an aggregation index "b" value of 1.92.

16. The tree collar zone of the larval habitat is transitional between lateral root bases and the lower portion of the main stem with respect to bark thickness and bark resin cavity characteristics. Placement of eggs and young larvae in this zone may increase their survival.

17. The life cycle of H. warreni extends about 2 years in the Lower Foothills Section of Alberta for complete development. In the larval stage only the first 3 instars are distinguishable by head capsule width measurement, but 5-7 instars are possible. Undetected high mortality or sampling errors may account for low numbers of early instar larvae in field samples. The

period of pupal development is relatively constant from year to year.

Pupae which do not develop to young adults by fall do not appear to withstand overwintering conditions, whereas teneral adults can. The proportion of the population undergoing pupation varies from year to year and with stand conditions, but most values lie in the range 5-20 percent. Most young adults emerge from the pupal chamber before September.

18. The longevity of adults is at least 3 years and eggs are laid during the second and third summers, the first summer of adulthood being an extended pre-oviposition period. Maximum egg productivity per female per season may be 36 but under natural field conditions the average may not exceed 12.2 eggs per female per season. The oviposition period extends from late May to September with a peak in early July. Most eggs are deposited in special niches excavated by the female in the bark of the root-collar zone, and subsequently covered over with excreta. Other eggs are deposited loosely under bark scales or in the adjacent soil. Under field conditions the average period of embryonic development is about 42 days.

19. First instar larvae can survive 5 or more days in the field without food. During initial bark penetration they require some form of support for leverage when chewing. All instars respond negatively in the presence of light and each larva possesses 2 anterior ocelli. The depth of larval feeding in the bark relates directly to larval size up to the fourth instar. Feeding damage is confined to the phloem until the fourth instar and thereafter it extends through cambial tissues as well. The average total length of gallery scored through cambium by mature larvae may not exceed 24 cm. The feeding gallery tends to be more circumferentially oriented

around the collar zone of small trees as compared to large trees, but as the tree grows the tendency is toward irregularly-shaped patches of dead cambium on the root-collar surface. This change of pattern likely reflects the influences of accumulated damage as well as weevil attack density.

20. An important mortality factor of larvae, prepupae, pupae and tenerals is excess moisture in the gallery and pupal chamber. The incidence of parasites and predators on pre-pupae and pupae does not appear to account for more than 5 percent mortality of these stages. In the adult stage the incidence of mortality and factors affecting fecundity were partly identified. On the whole, the observed mortality of weevil populations, exclusive of eggs and adults, was generally less than 5 percent. In some forest habitat situations eggs and early instar larvae may be the most crucial, while in other habitat situations the pre-pupal and pupal stages may be most vulnerable to mortality. Successful oviposition appeared to be highly variable, being strongly dependent upon microhabitat conditions.

21. Newly emerged males and females occur in about equal numbers. Differences in their behavior account partly for varying sex ratios in collections made in different locations within stands as well as during different summer periods. Males tend to be more abundant at stand peripheries while females tend to be more numerous within the stand.

22. Adults are most active at terrestrial dispersion, mating, feeding and oviposition during June and early July, after which time there is a general decline in these activities. The decreasing trend coincides with generally hot and dry conditions in July and August.

23. Examinations of the internal reproductive structures of female

weevils can provide a reliable index of sexual activity and of the general fecund condition.

24. The daily and hourly activity patterns of adults suggest a dependence upon temperature, light and probably moisture conditions in the forest. Throughout day light hours the adults remain in the forest duff and emerge about 2 hours after sunset. Almost no emergence occurs if temperatures at the forest floor fall to 36-40 °F. by 11:00 p.m. At night adults climb trees to feed, or they disperse laterally in search of new hosts. When leaving a tree of origin their initial direction of dispersal is random, while their rate of dispersal from a fixed point tends to be maximal during any one day, but declines rapidly to a constant after 8-10 days. The rate of linear travel during any one night may relate to the mean distance between trees. Host trees are located at least partly by vision and the pattern of selection appears identical for both sexes.

25. On young trees adult feeding occurs most heavily on lower branch bases and on upper branches of top whorls. On large trees feeding also occurs in the main canopy.

26. The studies provide insight into some weevil-host interactions. Different patterns of oviposition and larval distributions occur between small and large hosts. These differences account for some of the higher incidence of mortality recorded in regeneration pine. Various degrees of partial girdling, accumulated throughout stand development, may account for height and diameter growth losses, but the overall effect of weevil damage does not influence significant changes in stand density or stand structure. The vertical sequence of stem analysis appeared to be the most useful of the

three sequences in expressing the effects of weevil damage on pine. In the temporal sense natural successional changes may be hastened through the effects of the weevil, especially in stands where populations remain high over long periods of time. Anatomical changes in the root-collar zone arise as a result of larval feeding, and they provide some resistance against the direct and indirect effects of wounding. At the site of wounds a continuous resin flow is imperative to the safety of developing larvae. Pre-pupae, pupae and teners also derive protection from a resin-bark fragment matrix.

27. The investigations have provided several techniques to measure and evaluate weevil abundance in a variety of pine stand conditions. These include a simple sampling system for general surveys, a sampling system for intensive population studies and a method of live-trapping adults for field behavior studies and numerical assessment using the mark-recapture principle.

28. The studies have revealed insight into the possible mechanisms by which weevil abundance is regulated in lodgepole pine forests, in both the short and long term sense.

29. The studies provide a biological basis for prescribing several control measures against the weevil through forest management.

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