DEVELOPMENT OF A TECHNIQUE FOR SAMPLING MOUNTAIN PINE BEETLE POPULATIONS IN LODGEPOLE PINE

by

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ABSTRACT

A technique was developed for sampling the mountain pine beetle, Dendroctonus ponderosae Hopkins, several times during its life cycle for the purposes of estimating within-generation mortality and population trend. The sampling technique is based on a critical study of the density gradients of brood in larval and pupal stages, both vertically and horizontally around the circumference of infested trees. The shape, orientation and size of the optimum sampling unit were investigated by studies of the spatial arrangement of brood, the relationship between edge effect bias and sampling unit shape and size, and by a study of the relationship between total sampling time and sampling unit size. The optimum unit is rectangular, has a width to length ratio of approximately 1:2, and is orientated with long sides perpendicular to the vertical axis of the infested tree. Optimum unit size was approximately eighteen square inches when sampling was at two height levels on the infested stem. A two-stage sampling technique was most appropriate for the sampling problem. The infested surface area of individual trees constituted the primary unit. Variability of brood density estimates between primary units was most efficiently reduced by regression sampling on primary unit size. The variance of brood counts within primary units, on the other hand, was sufficiently reduced by the construction of five within-primary unit strata. Stratum boundaries were determined on the basis of the circular distribution of brood counts (around the stem circum-

ference) and the relationship between brood density and bark thickness. The sampling variances of both attacks and brood counts were related to their respective means by the equation $s^2 = a\bar{x}^b$, where s^2 = variance/secondary unit, $\bar{x}$ = mean brood or attack counts/secondary unit and a and b are constants. Therefore, the counts had to be transformed in order to obtain an efficient estimate of the population variance. Taylor's power transformation, sufficiently removed the variance-mean relationship. Population totals (which have to be estimated in order to estimate population trend) were obtained by developing a surface area function to predict infested surface area for individual trees. This surface area function made possible the estimation of partial surface area to any specified height level. The latter property of the function was utilized to estimate within-primary unit stratum sizes.

An approximate method of population trend prediction was developed for general insect surveys. This method is based on an estimate of brood density from the d.b.h. region of infested trees and on an estimate of the total infested bole area from a partial surface area table. Population trend is estimated by forming the ratio of the product of total infested surface area and brood density from the d.b.h. level in two successive years.

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INTRODUCTION

The availability of suitable sampling techniques is basic to population studies. Intensive studies of insect populations involve the development of life tables, the determination of the mode of action and effectiveness of mortality factors and the prediction of population trend. These studies must be based on measurements of absolute populations; that is populations must be expressed in terms of a unit that cannot change, such as a unit of forest land. Thus, the objective of developing a sampling technique for intensive population studies should be to obtain, by a method economical of time and effort, an estimate of the absolute population for a predetermined degree of precision.

The mountain pine beetle (Dendroctonus ponderosae Hopk.) is an important forest insect species in which population studies have been hindered by lack of adequate sampling techniques. The major problem is that no techniques are available for measuring absolute populations because there is lack of information on how to estimate the surface area of infested bark. The presently available techniques for sampling bark beetles in the genus Dendroctonus are based upon the measurement of densities at fixed height levels within the infested stem of randomly selected sample trees. These techniques give good estimates of relative populations, but in general, lack the stability required for intensive population work.

Bedard and Terrell (1938) developed a method of predicting moun-

tain pine beetle infestation trend in western white pine (Pinus monticola Dougl.) stands. Prediction is based on a sampling system whereby twenty-five infested trees are selected at random from a group infestation and sampling is confined to the bases of the sample trees. Four 3 by 12 inch bark area units are sampled on each sample tree. The sampling units are orientated with long sides parallel to the egg galleries and located on the four major aspects of the sample trees. Broods and attacks are tallied on the sampling units and the former variable is corrected for "basal examination", anticipated mortality and sex ratio. The ratio of the "corrected" number of broods and attacks per square foot multiplied by the bark area ratio of the average susceptible tree and the average currently infested tree is used as an index of infestation trend. The infestation trend index of Bedard and Terrell is simple to use and will give reliable results for survey purposes. However, the method is limited by "built-in" corrections for mortality and include such unpredictable factors as average attack and brood density and average infested bark area per tree which is to occur the following season. Further, as sampling is confined to the bases of the sample trees and as actual infested bark area is not estimated, the sampling technique cannot be adopted for measuring absolute populations.

Knight (1959) sampled at the four to seven foot region of twenty-five randomly selected infested trees to construct life tables and to measure trends of Black Hills beetle (D. ponderosae Hopk.) infestations in pine stands. The selection of sampling height was based on the observation that survival at the end of the beetle's developmental period

is lower above 5 feet than at the five foot level. When comparing the efficiencies of three bark area units for a predetermined degree of precision, Knight found that the 3 by 6-inch and 6 by 6-inch units were more efficient than the 6 by 12-inch unit. Although the 3 by 6-inch unit was more efficient than the 6 by 6-inch unit, Knight used the latter unit because of the large number of zero counts in the former unit. Two sampling units were taken from each infested tree, one from the north and the other from the south side, to account for the circumferential population gradient. Knight's sampling technique facilitates life table construction and population trend measurement on the basis of an easily accessible sampling universe. However, when using this sampling technique for life table studies one has to assume that population changes in the infested bole above the point of sampling are proportional to population changes at the four to seven foot region. Furthermore, the sampling technique cannot be adopted for measuring absolute populations because sampling is confined to a single height level and because total infested bark area is not estimated. Later Knight (1960a, 1960b) used his sampling technique to measure Engelmann spruce beetle (D. engelmanni Hopk.) infestation trend.

To facilitate population studies of the Douglas-fir beetle (D. pseudotsugae Hopk.) in standing Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) trees, Furniss (1962) defined the sampling universe as the total bark area of the middle four-fifths of all infested stems within an area of infestation. Furniss' definition of the sampling universe was based on the observation that Douglas-fir beetle broods are the densest, most successful and least variable between the fifteen and sixty-five foot levels of the infested stem. Fur-

niss compared two bark area units, a 6 by 12-inch unit orientated with long sides parallel to the tree axis and a 0.1 square foot circular unit, and found that the former unit gave a smaller estimate of the number of galleries intercepted but the number of entrance holes and length of galleries were comparable. On the basis of his observations Furniss suggested that sampling be located within the fifteen to sixty-five foot levels on the infested stems but did not elaborate on sampling intensity or on the manner of sample tree and sampling unit selection. This sampling technique can be used to estimate within and between generation changes of Douglas-fir beetle populations but it is not suitable for the evaluation of the importance and mode of action of the various mortality factors.

Shepherd (1962) developed a multiple regression technique to predict within and between generation population trend of the mountain pine beetle in lodgepole pine (P. contorta Dougl. var. latifolia Engelm.) stands. Prediction is based on a sampling technique which involves grouping of the infested trees into two strata by diameter four and half feet from the ground (d.b.h.) and estimation of attack and emerging brood totals for individual trees separately by multiple regression equations. All infested trees are sampled in a group infestation and trees less than or equal to ten inches and those greater than ten inches in d.b.h. constitute the first and second stratum, respectively. Both independent variates, emerging brood and attack totals, are estimated by separate regression equations within the two strata. In trees of the first stratum, sampling is confined to two height levels whereas in trees of the second stratum it extends to three height

levels. The sampling unit is constituted by a one foot wide band of bark strip circumscribing the tree at the point of sampling. The independent variables for estimating emerging brood and attack totals are defined as emerging brood and attack counts, respectively, within a one foot wide band of bark area at a given sampling point. In both strata the number of independent variables in the predicting equations are equal to the number of fixed sampling points on an individual tree. Thus, the predicting equations for the first stratum have two independent variables and those for the second stratum have three independent variates. Between-generation population trend is predicted by forming the ratio of the estimated number of attacks for two successive generations and within-generation population trend by summing the estimated brood and attack totals over all trees, forming the ratio of the two sums and multiplying this ratio by an estimate of the proportion of the emerging female beetles in the population. Shepherd's sampling technique is fast, easy to use and will probably give sufficiently accurate estimates of the total numbers of attacks and emerging brood for population trend prediction. However, the stability of the regression coefficients is considerably affected by the variability of attack and brood density gradients in individual trees. As there is considerable between-tree variation in these density gradients (Shepherd, 1960), the multiple regression sampling technique is not suitable for intensive population work.

Carlson (1963) and later Carlson and Cole (1965) defined the sampling universe for studying the population dynamics of the mountain pine beetle in lodgepole pine as a sub-population contained within a two-foot

wide zone at the d.b.h. level of infested trees. This zone is divided into four quadrants (north, west, south, east) to ensure random allocation of the sampling units with respect to aspect within the zone. One-tenth or 0.25 square foot units are used for sampling. If a 0.1 square foot unit is used each of the four quadrants is divided into six four-inch wide levels, producing twenty-four sampling loci. If a 0.25 square foot unit is used, the quadrants are divided into four six-inch wide levels, producing sixteen sampling loci. The sample trees and sample loci are selected at random and the latter sampled without replacement. The advantage of this sampling method is that an estimate of the within-tree variance can be computed and within-tree variance can be treated as error attributable to replication. However, as sampling is confined to a fixed height level, the sampling method is not suitable for the measurement of absolute populations. Further, for life table studies the sampling plan carries the built-in assumption that the mode of action and effect of the various mortality factors are identical or proportional to those observed at d.b.h. level.

The main object of this study was to develop a sampling technique, based on an analysis of distributional patterns, to measure absolute populations of the mountain pine beetle. Secondary objects were to develop an index of population trend and to attempt to develop a mathematical model to describe the vertical density gradients of attacks over the host.

MATERIALS AND METHODS

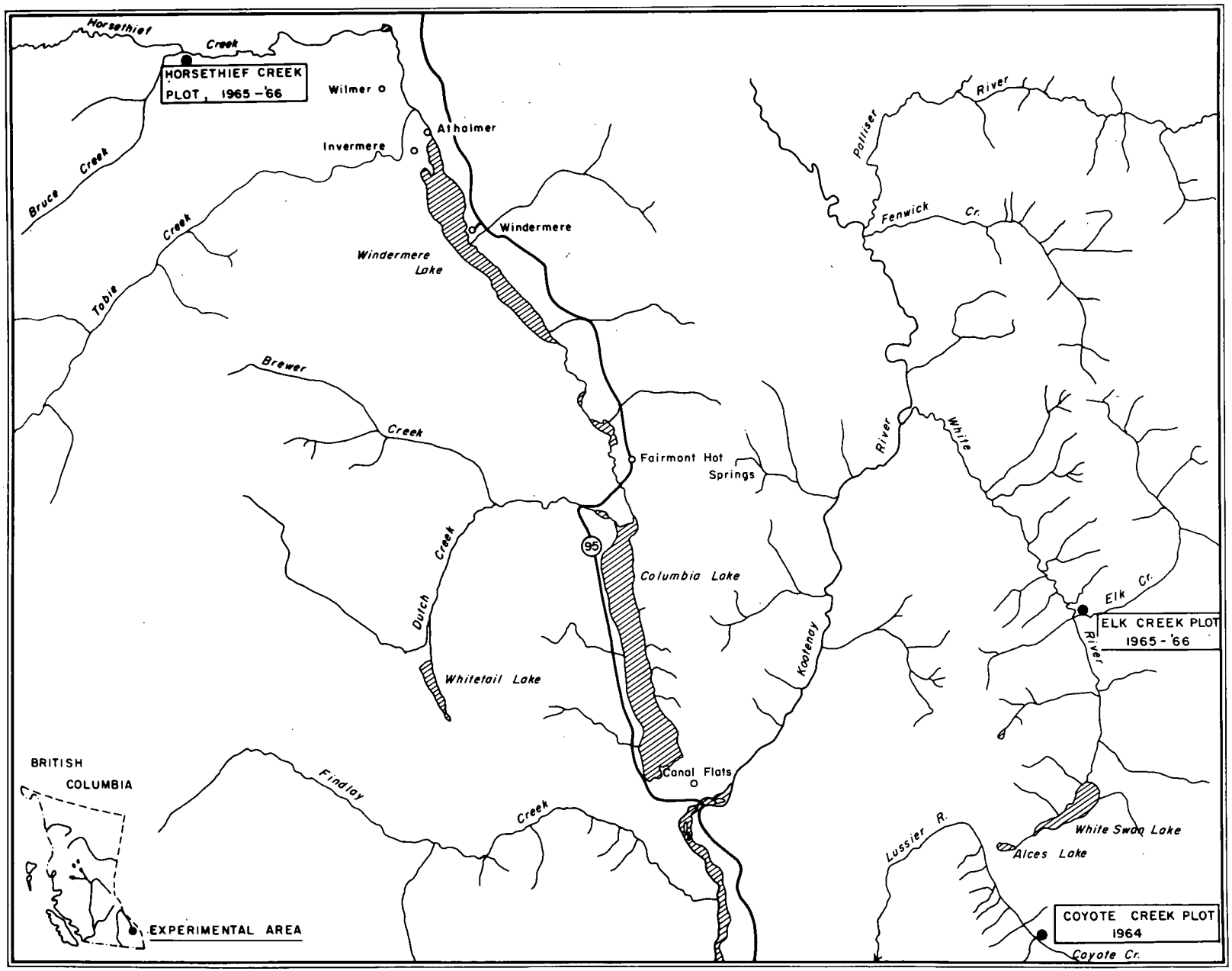
1. Description of the study areas.

The study involved both laboratory and field investigations on three semi-permanent plots, located near Canal Flats and Invermere, British Columbia, from 1964 to 1967 (Fig.1). The Horsethief Creek experimental area was located 7 miles west of Invermere, in the Horsethief Creek valley, at an elevation of 3,500 feet. The forests in the experimental area were a mixture of lodgepole pine and Douglas fir. The lodgepole pine averaged 66 years of age, 66 feet in total height, and 10.3 inches in d.b.h. The Coyote Creek plot was located in the Lussier River valley, at an elevation of 4,200 feet, 16 miles southeast of Canal Flats. The stand was composed of approximately 85% lodgepole pine, 10% Douglas fir and 5% western larch (Larix occidentalis Nutt.) by number of stems. The pine averaged 109 years of age, 78 feet in total height and 10.3 inches in d.b.h. The Elk Creek plot was located 20 miles northeast of Canal Flats (at the foot of Mt. Dorman) at an elevation of 3,800 feet. The stand composition was the same as that for the Coyote Creek plot. The pine averaged 103 years of age, 94 feet in total height and 13.5 inches in d.b.h.

Of the ninety-six sample trees used to develop surface area equations and tables for lodgepole pine, thirty trees were located on the experimental plots and the remaining sixty-six trees were taken from various localities of the Invermere and Canal Flats Forest Ranger

Figure 1.

Map of the experimental area.


Horsethief Creek
HORSETHIEF CREEK PLOT, 1965 – '66
Wilmer
Invermere
Athalmer
Windermere
Windermere Lake
Bruce Creek
Tobie Creek
Brewer Creek
Dutch Creek
Whitetail Lake
Fairmont Hot Springs
95
Columbia Lake
Canal Flats
Findlay Creek
Kootenay River
White River
Elk Cr.
ELK CREEK PLOT 1965 - '66
Elk River
Fenwick Cr.
Palliser River
Lussier R.
White Swan Lake
Alces Lake
COYOTE CREEK PLOT 1964
Coyote Cr.
BRITISH COLUMBIA
EXPERIMENTAL AREA

Districts. Stem analysis data on these sixty-six sample trees were provided by the British Columbia Forest Service, Victoria, B. C. The sample trees ranged from 29 to 125 feet in total height, from 44 to 212 years of age and from 4.3 to 19.8 inches in d.b.h. and were taken from the following forest types: Douglas fir - lodgepole pine (FPl), lodgepole pine - spruce (PlS), and lodgepole pine - Douglas fir (PlF).

2. The experimental insect.

2.1. Taxonomic description. As a result of Wood's (1963) revision of the bark beetle genus Dendroctonus Erichson, the mountain pine beetle (Dendroctonus monticolae Hopk.) and the Jeffrey pine beetle (D. jeffreyi Hopk.) have been synonymized with the Black Hills beetle (D. ponderosae Hopk). Wood's revision was based on analysis of anatomical structures (seminal rod of male genital capsule, surface features of the frons and elytral declivity) and biological characters (character of egg gallery, arrangement of egg niches etc.). Prior to this revision the three species were separated on the basis of size, host preference and geographic location.

Recent work, however, showed that D. jeffreyi is a valid species (Lanier and Wood 1967). In the region where the experimental plots were located previous works referred to this insect as the mountain pine beetle, D. monticolae Hopk.

Dendroctonus ponderosae, monticolae and jeffreyi were described by Hopkins in 1902, 1905 and 1909 respectively. The morphology of the adult was described by Richmond in 1935 and later Reid (1958) and Cerezke (1964) studied some aspects of its internal morphology. Information on the life history and habits were contributed by Hopkins (1909), DeLeon et al. (1934), Struble (1934), Richmond (1936), Even-

den et al. (1943), Struble et al. (1955), Reid (1958a, 1958b, 1961, 1963), and Shepherd (1960).

2.2. Attack pattern and gallery plan. Both the intensity and spatial pattern of attacks over the host are related to the roughness of the outer bark as the attacking female beetle needs a suitable bark scale or niche to lean against in order to initiate the attack (Shepherd, 1960). In individual trees the density of suitable attack sites per unit bark area is directly proportional to bark roughness and both of these variables, in turn, are inversely related to height level. Consequently, in mass attacked trees, attack density is usually highest close to the base and decreases from thereon with increasing height level. In addition to the well defined vertical gradients, attack density differences are often present circumferentially in the lower and middle sections of infested trees. The circumferential attack density gradients are the result of the attacking beetles' reaction to heat and light intensity. High heat and light intensity stimulates the beetles to fly and, therefore, the cooler and shadier northern and northeastern aspects of the clear bole will usually harbor higher attack densities than the warmer and lighter southern and southwestern aspects (Shepherd, 1960).

The female beetles construct J-shaped egg galleries which run parallel to the longitudinal axes of the infested trees and average approximately one foot in length in lodgepole pine. The eggs are deposited in niches on alternate sides during gallery construction. Upon hatching the larvae mine feeding galleries at right angles to the axis of the egg gallery. Larvae from adjacent galleries intermingle but seem to be

somewhat reluctant to cross each other's galleries. The result of this "intermixing" is a characteristic "clumped" spatial arrangement. These "clumps" are long and narrow and their longitudinal axes are approximately parallel to those of the egg galleries. The size and shape of the "clumps" are influenced by egg and egg gallery density, egg gallery length, the developmental stage of the larvae and by the intensity of action of various mortality factors.

Both the density gradients and "clumped" spatial arrangement have considerable effect on the variability of brood density estimates and hence on the sampling problem.

3. The problem of sampling.

3.1. Characteristics of the sampling problem. The problem of estimating within and between-generation population levels of the mountain pine beetle can be divided into two parts; the estimation of total infested bark surface area in the sample universe and the estimation of mean brood and attack density per unit bark area. In individual trees, infested bark area is a function of total and infested tree height and d.b.h. Therefore, total infested bark area can be estimated by regression techniques based on tree volume equations, taper curves, form factors or on form quotients. (Note: tree volume formulae, taper curves, form factors and form quotients are expressions used in forest mensuration to estimate tree volume. The last three expressions are also used to describe tree form). On the other hand, the problem of estimating mean brood and attack density is essentially that of sampling for multiple items. Of the two variables, the coefficient of variation of attack counts is usually smaller than that of brood counts. This is because the frequency distribution of the former variable ap-

pears to be random (Carlson and Cole, 1965) or regular (Shepherd, 1960) and that of the latter variable corresponds to the negative bonomial (Knight, 1959; Shepherd, 1962; Carlson, 1963 and Carlson and Cole, 1965). Therefore, when tallying both brood and attack counts on the sampling units and when the mean of the former variable is estimated with a predetermined degree of precision, the precision of mean attack density will automatically be at least as great as the predetermined level for brood density. Consequently, it will be sufficient to develop an efficient technique to estimate brood density alone.

The precision of mean brood density estimates could be considerably increased by controlling the inter and intra-tree variability of brood counts. The nature of this variability is such that inter-tree variability of brood counts is greater than that within trees (Shepherd, 1962; Carlson, 1963; and Carlson and Cole, 1965). The inter-tree variability of brood counts is the result of between-tree differences in the following variables: density of suitable attack sites, infested bark area, bark thickness, tree resistance, nutritional quality of inner bark, proximity to population source and the surface area/volume (s/v) ratio of the tree stem. All these factors but infested bark area, bark thickness, proximity to population source and s/v ratio have direct influence on brood counts by affecting survival. Bark thickness affects brood counts indirectly by acting as insulator and by influencing the effectiveness of woodpecker predation. The area of infested bark affects brood counts by limiting the size of the beetle's sub-cortical habitat and the s/v ratio by controlling the rate of drying of this habitat. Proximity to the po-

pulation source may affect brood counts by influencing mean attack density within individual host trees. The intra-tree differences in brood counts (intra-tree brood density gradients) are the result of the attack behaviour and egg gallery constructing habit of the adult female beetle, the feeding gallery extention habits of the larvae and within-tree differences in the circumference/cross-section area (c/a) ratios due to tree taper.

In individual trees infested bark area is a function of all those other variables which were previously listed as affecting the inter-tree variability of brood counts. Therefore, the infested bark area of individual trees is logically the best single variable for stratification or regression sampling of trees to reduce the inter-tree variability of brood counts. On the other hand, the within-tree component of the variance of mean brood density estimates is expected to be strongly correlated with bark roughness and aspect. Consequently, this variance component can be effectively reduced by within-tree stratification on bark thickness and aspect.

3.2. Description of the sample design. The definition (or selection) of the various components of the sample design was based on the objective of reducing the variance (increasing the precision) of population size estimates.

3.2.1. The sample universe. In forest insect sampling it is helpful to think of the universe, the total of all individuals of the same kind in a predefined area having a certain property, as an aggregate of habitat units upon which the observations are made. As all the mountain pine beetle stages occur under the bark of the main stem

in lodgepole pine, each infested stem section logically constitutes a unit of habitat. Thus, for the mountain pine beetle, when the object is to estimate within and between-generations population levels, the universe can be defined as the total of all infested stem-sections within a group infestation or other geographically or arbitrarily defined area of forest land.

In this study the definition of the sampling unit and the selection of the sampling method were based on the above given definition of the sample universe.

3.2.2. The sampling unit. The basic unit of sampling was defined as that being constituted by the habitat unit, the individual infested stem-section, for the following reasons: Firstly, infested stem-sections are easy to define, list and identify in the field. Secondly, it is convenient to describe the sample universe in terms of these units. Thirdly, it has been shown (section 3.1) that the inter-tree variability of brood density is considerably greater than intra-tree variability. The above given definition of the sampling unit permits stratification of the sample trees on the basis of external tree characteristics or regression sampling on infested bark area of the units, to reduce the inter-tree variability of brood density.

Total enumeration of a sample of infested stem-sections is excessively time consuming and a wasteful procedure because of the essentially destructive nature of sampling and, therefore, sampling was done in two stages. Infested stem-sections and smaller bark area quadrats constituted the first and second-stage sampling units, respectively. Sampling of the infested stem-sections (second-stage samp-

ling) was carried out with 8 by 12 inch bark area units. These units were orientated with long sides perpendicular to the long axes of egg galleries. The selection of orientation, dimensions and size of the second-stage unit was dictated by convenience in sampling unit delineation and bark removal and by the expectation that certain systematic distortion (bias) of brood counts will be inversely proportional to the circumference/area (c/a) ratio of the sampling unit. (Note: Although the systematic determination of "optimum" second-stage unit size, shape and orientation was an objective of this study, the results were not available until after the sampling has been completed.)

3.2.3. The sampling method. Selection of the sample was based on a modified two-stage sampling method.

The primary units, i.e. individual infested stem-sections, were selected at random, with equal probability and without replacement. This method of primary unit selection was considered more appropriate than random sampling with replacement and probability proportional to primary unit size (the alternative primary unit selection considered) for the following reasons: Firstly, the selection of primary units with probability proportional to unit size is considerably more difficult than equal probability selection. Secondly, when sampling is done with replacement of the units, some units will likely be over-sampled. Although over-sampling can be avoided by using the same sub-sample wherever a particular primary unit appears in the sample, this method gives a rather larger variance than the usual method of selecting a new sub-sample at each successive drawing of a primary unit (Samford, 1962).

Sub-sampling of the primary units consisted of taking two sets of systematic samples, one set from the due North and the other from the due South aspect, with an 8 by 12 inch second-stage unit. The "aspect stratification" of the second-stage units was designed to increase the efficiency of the sample design by reducing that component of the intra-primary unit variation which is caused by horizontal brood density gradients (section 2.2.). The systematic second-stage sampling consisted of tallying brood and attack counts on the secondary units at two foot intervals, from the two foot height level to the uppermost point of infestation, within both "aspect strata" of the primary units. Systematic second-stage sampling was considered more appropriate than random selection of the sub-sample for the following reasons: a) The development of partial surface area equations for the host, lodgepole pine, was one of the objectives of this study and, therefore, primary unit size could not be estimated at the commencement of sampling. The knowledge of primary unit size is essential for the listing of the secondary units if random selection of the latter units is desired. b) Even if primary unit sizes are known, the identification and, thus, random selection of the second-stage units is extremely difficult because of tree-taper. c) The within-primary unit component of the sampling variance is usually considerably smaller than the between-primary unit component. Consequently, a nearly unbiased estimate of the sampling variance can be calculated when second-stage sampling is systematic (Samford, 1962). As brood and attack density form definite vertical gradients, the systematic sample will always be more representative of the distribution of these variables in the population than

some random samples. Furthermore, density gradients tend to be more accurately represented in a systematic sample than in a random sample. Thus, the former can be expected to give more precise estimates of within-primary unit mean brood and attack density than a randomly selected second-stage sample. On the other hand, a systematic second-stage sample tends to give an underestimate of the within-primary unit component of sampling variance (Samford, 1962) and, therefore, this variance will be slightly underestimated.

Following sampling, a regression technique and stratification were used and compared for efficiency in reducing the between-primary unit component of the sampling variance. The regression technique was based on the linearity of the primary unit brood totals vs. primary unit size relationship. On the other hand, stratification of the primary units was done on the basis of an "abundance index"; the product of primary unit size and an estimate of brood density at the breast height region of the sample trees. The breast height brood density was used in the "abundance index" because this region supports the heaviest broods and is generally considered the most stable single height level for sampling (Knight, 1959; Carlson, 1963; Carlson and Cole, 1965). Three primary unit strata were formed by arbitrarily dividing the "abundance index" range of the units into three parts.

Following sampling the two within-primary unit "aspect strata" were further sub-divided transversely into three vertical strata each. This was in an attempt to reduce the intra-primary unit component of the sampling variance of mean brood density. The vertical stratum boundaries were established by studies of the brood density vs. bark

closely related to the mean cannot be analysed without the risk of errors (Beall, 1942). Therefore, the data have to be transformed: that is the observations on the original scale are replaced by a function whose distribution is such that it normalizes the data or stabilizes the variance. Hayman and Lowe (1961) pointed out that "as non-normality must be extreme to invalidate the analysis of variance it is better to concentrate on stabilizing the variance of the samples." A correct transformation for variance stabilization will also ensure the additivity of the variance and, therefore, for practical purposes the distinction between transformation for normality and that for stabilizing the variance need not be emphasized (Southwood, 1966).

When the variance changes with the mean, variance estimates based on the original values of the observations will provide a consistent but inefficient estimate of the population variance (Finney, 1941; Cochran, 1953). This inefficiency arises from the fact that the population variance, V, will be inflated due to non-normality of the parent distribution. The formula for V is as follows:

$$V = \frac{2\sigma^4}{n-1}\left(1 + \frac{n-1}{2n} G_2\right), \text{ (Cochran, 1953)}$$

Where, V = variance of the sampling variance; n = sample size; σ^4 = = fourth moment and G_2 = Fisher's measure of kurtosis. The term inside the brackets is the factor by which V is inflated due to non-normality. For a normal distribution the term $(n - 1)G_2/2n$ is equal to zero and may take positive or negative values in other distributions. The revelance of these observations to practical sampling is that comparisons of the precision of various sampling methods and the estimation of sample size for a specified degree of precision should

involve the use of consistent and efficient estimates of the sampling variance. When data are transformed to a new scale, which makes the variance independent of the mean and "normalizes" the distribution of the transformed observations, the dispersion of the transformed values will be consistently and efficiently estimated by the sampling variance. Therefore, in non-normal parent distributions the precision of the various methods of sampling and the estimation of sample size should be based on the variance of the transformed values.

In samples drawn from non-normal parent distributions, the arithmetic mean will also be an inefficient estimator of the population mean (Finney, 1941). When appropriate transformation is applied to the data, the central tendency will be consistently and efficiently estimated by the mean on the transformed scale. Although the transformed mean will be sufficient for the purposes of most statistical tests, Morris (1955) pointed out that the transformed mean would give rise to complications in computations of population levels, as well as in interpretation of the results. The "back transformed" means (i.e., geometric mean for log. transformation) would be attended by the same difficulties because they usually underestimate the arithmetic mean. Therefore, for the purposes of estimating population size, population and mortality trends, and for life table studies, it is advisable to present the means in terms of the original variates (i.e. numbers of insects).

The frequency distribution of brood and attack counts displayed strong positive skewness and, therefore, studies of the efficiencies of within-and between-primary unit stratifications and the calculation

of sample size were based on variance estimates obtained from transformed data. Estimates of the population mean and total, however, were given in terms of the original variates (i.e. numbers of insects). When estimating the variance of the population total, the sampling variance of brood counts was "back transformed" to the original scale.

Two transformations were considered: the logarithmic and Taylor's power law, and the more efficient of the two was accepted as the proper form of transformation. Efficiency was judged by the success with which the two transformations removed the variance vs. mean relationship of brood and attack counts.

3.2.5. Precision and sample size. The sampling variance of mean brood density per secondary unit was affected by systematic distortions of brood counts due to faults in the following experimental procedures: a) delineation of the second-stage units and b) tallying of broods.

Delineation of the sampling units was done manually with a template, chisel and hammer. Consequently, it was difficult to attain consistency and accuracy in sampling unit area delineation. On smooth bark surface it was considerably easier to obtain an accurate delineation than on rough bark surface. Therefore, the "area delineation bias" of the second-stage units was a function of bark roughness. On the other hand, tallying of the brood was carried out simultaneously with bark removal and, consequently, some insects were missed or mutilated beyond recognition during the debarking process.

In view of the above defined systematic distortions of brood counts it would have been unjustified to strive for a very high degree of precision in the estimation of the sampling mean and, therefore, the size

of the standard error was set at 10% of the mean. Consequently, this standard of precision was used for estimating sample size. In estimating sample size, the second-stage sampling fraction was set at 2% of the size of the primary units for the following reasons: Sampling is a destructive process and, excessive disturbance of the bark surface may induce artificial brood mortality close to the sampling unit boundaries by accelerating the natural drying process of the inner bark and outer sapwood. In studies of within-generation population and mortality trends it is desirable that four or five consecutive samples be drawn from the original sample trees during the life cycle of the beetle. Five sets of samples would eliminate 10% of the total infested bark area, if the sampling fraction was set at 2% for each sample. Observations on woodpeckered infested trees indicate that a sampling intensity much greater than about 10% of the infested bark area would seriously affect brood survival.

The calculation of sample size and the comparisons of the precision of various modified two-stage sampling methods were carried out on data collected from ten sample trees, on the Elk Creek plot, in 1965. This sample was characterized by large within-and between primary unit variation in brood counts and by large variation in primary unit size.

3.3. Determination of the orientation, shape and size of the "optimum" secondary unit. As all stages of the mountain pine beetle form clumped spatial patterns and density gradients (both, parallel and perpendicular to the main axis of the stem), these studies were based on the following interrelations of precision, sampling unit shape,

size, orientation and population pattern:

If the distribution of individuals in a population is completely random, the size, shape and orientation of the sampling unit is immaterial except from the point of view of convenience and edge effect. (Note: Edge effect is a systematic distortion of brood counts resulting from the consistent inclusion or exclusion of those individuals which are located on the sampling unit boundaries.) However, when individuals form "clumped" spatial patterns or density gradients, the size, shape and orientation of the long, narrow units with respect to the density gradients, may profoundly affect the precision of the density estimate and the cost of the sample survey. The nature of this relationship is such that the precision of the estimate is at minimum when the size, shape and orientation of the sampling unit are approximately equal to those of a "clump" of individuals.

Thus, for the purposes of sampling the mountain pine beetle (or all bark beetles in the genus Dendroctonus, in general), the optimum sampling unit can be defined on the basis of the above described interrelations of precision, cost, sampling unit dimensions and orientation, and population pattern. The optimum unit is that which gives the desired precision of the density estimates at the smallest cost, or the greatest precision for fixed cost, subject to the restriction that the circumference/area (c/a) ratio shall not exceed a certain pre-established limit. The restriction was superimposed on this definition of the optimum unit because the c/a ratio increases logarithmically with decreasing sampling unit size and the edge effect bias of mean brood density is expected to be proportional to c/a. Edge effect bias of mean brood density is one of the important problems of

sampling sub-cortical insects because a common feature of all three presently used sampling unit delineation techniques, namely; chisel and hammer, "arch punch" circular "hole saw", is that they destroy or mutilate all individuals located on the boundaries. Consequently, these individuals may be missed entirely or, on the other hand, the separated halves counted as two independent individuals. In mountain pine beetle sampling, the edge effect problem is intensified by the current trend toward reducing the size of the sampling unit. The primary reasons for this trend are that: a) sampling is mainly in the lower bole of infested trees where brood density, in all stages, is the highest and the use of small units will not result in excessive numbers of zero counts and b) there is a tendency to use hole saws and arch punches for sampling unit delineation and the excessive curvature of small diameter trees necessitates the employment of units of small radii. However, it was pointed out previously that "edge effect" bias of brood density is expected to be directly proportional to the ratio c/a and, therefore, minimum sampling unit size has to be established on the basis of a study of the nature of this relationship.

In this study, the determination of the orientation and shape of the optimum unit was attempted through analyses of the relations between precision of mean brood density estimates, sampling unit dimensions and spatial pattern. On the other hand, optimum sampling unit size determination was based on a time study of sampling units of optimum shape and on studies of the c/a ratio vs. edge effect bias relationship.

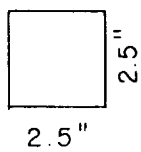
4. Experimental Procedure.

4.1. Techniques of observation. Both field and laboratory studies were based on quantitative observations taken on the density gradients of brood and attack counts, the spatial pattern of larvae and on the external characteristics of sample trees.

The accuracy and precision of various sampling unit shape and sizes for measuring late stage brood density were studied by sampling forty-five infested trees with a set of six units superimposed in a nested fashion (Fig. 2). The nested arrangement was designed to reduce that component of the intra-sampling unit variability of brood counts which results from differences in the sampling universe when the units are selected in a non-overlaping fashion. The sample trees were selected at random from within the Coyote Creek experimental plot. Sampling was confined to the four-foot height level and to the northern and southern aspects. The selection of the four-foot height level was based on convenience in sampling and on the fact that brood density is usually the highest and most stable in the four to seven-foot region of the infested stem (Knight, 1959). The northern and southern aspects, at the four-foot height level, were known to support different brood densities (Knight, 1959; Carlson, 1963; Carlson and Cole, 1965) and, therefore, sampling at both of these aspects permitted the testing of the performance of the sampling units at two different density levels. The nested lay-out included circular, square and rectangular sampling units. The longitudinal axis of one of the two rectangular sampling units was orientated parallel, and the other perpendicular, to the main axes of egg galleries. In addition to the six sampling units, a seventh, half circumference by 14.4 inch unit has been taken from each sampling location. This unit

Figure 2.

Nested lay-out to study the effect of sampling units shape and size on the precision and accuracy of mean brood density estimates.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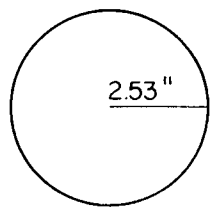
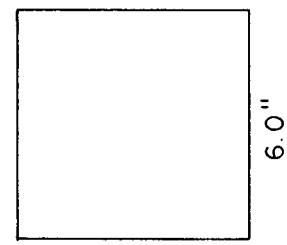

2.53"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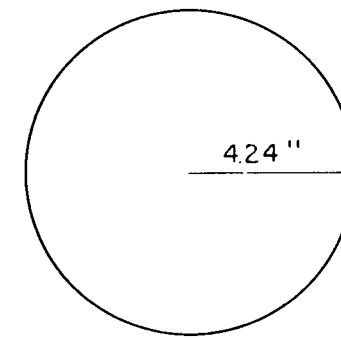
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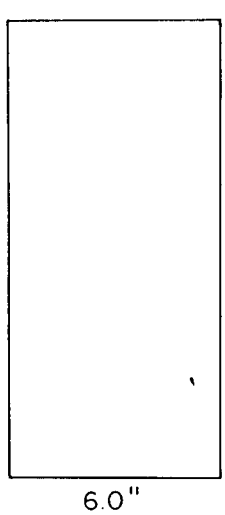
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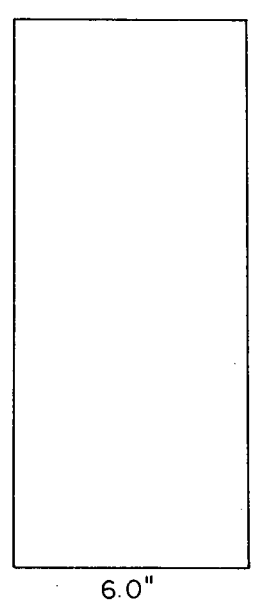
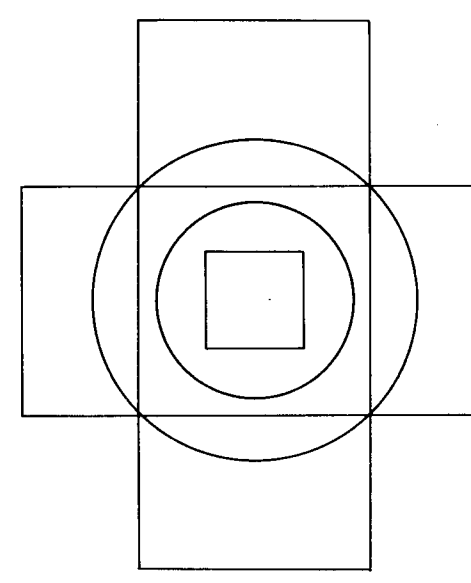
6.0"


14.4"
6.0"



served as a "standard" for comparisons in subsequent analyses. The sampling unit sizes included in the nested lay-out (6.25, 20.10, 36.00, 56.45, 72.00 and 86.40 square inches) have been selected on the basis of convenience in sampling and record keeping. Sample unit boundaries were delineated by two flexible aluminium templates, one for the circular units and the other for the square and rectangular units, (Fig. 3). The cutting of the boundaries was done by chisel and hammer and a wide-blade hunting knife was used to remove the bark from within the sampling unit boundaries. Owing to the nested arrangement of the sampling units, bark removal and subsequent tallying were carried out according to a predetermined plan (Fig. 4). The numbers of late stage mountain pine beetle brood and attacks, insect predators and parasites, egg galleries and total inches of egg galleries were recorded for each sampling unit. Gallery length was measured to the nearest one-tenth inch with a flexible steel ruler. A cheesecloth bib, fastened to the sampler's waist at one end and to the tree, immediately below the point of sampling at the other, was used to prevent accidental loss of brood during sampling. On June 14, 1964, when sampling began, mountain pine beetle broods were in third and fourth larval stages. Brood development progressed to the fourth instar-pupal stage at the time of the completion of sampling on July 6, 1964. All data have been converted to a square foot basis prior to analysis.

Six two-foot long, naturally infested logs were used to study the magnitude of the edge effect bias of mean density estimates and the relationship between sampling unit size and sampling variance. The logs were cut from the three to five foot levels of six trees located within

Figure 3.

Templates to delineate sampling unit boundaries within the nested arrangement.

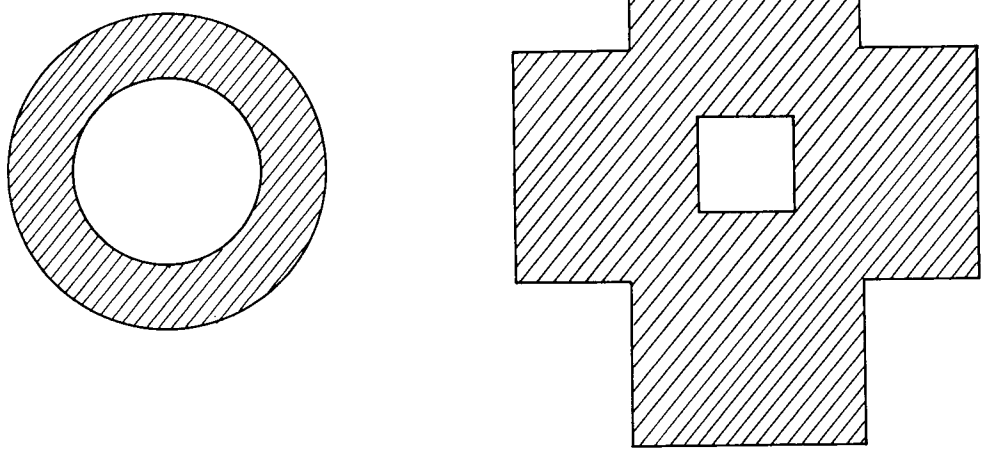
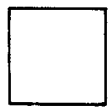
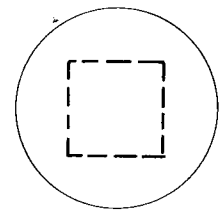


Figure 4.

The sequence of sampling unit enumeration within the nested arrangement.



Step 1



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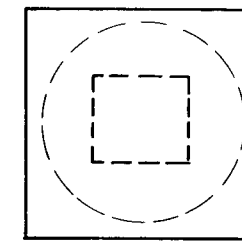

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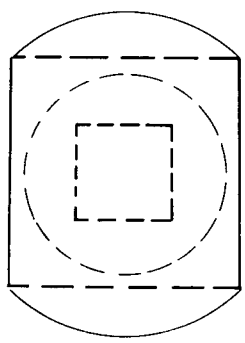

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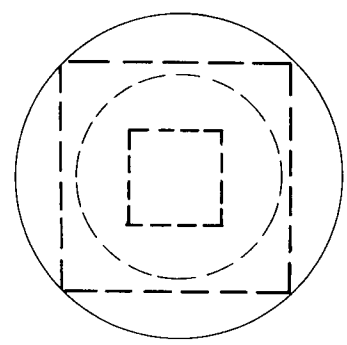

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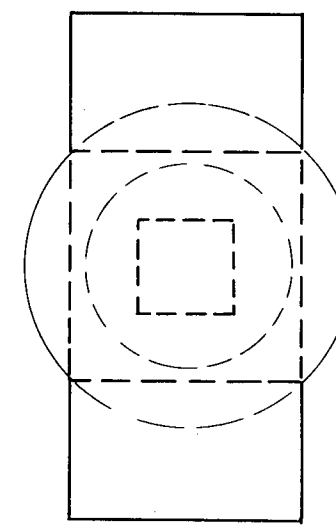

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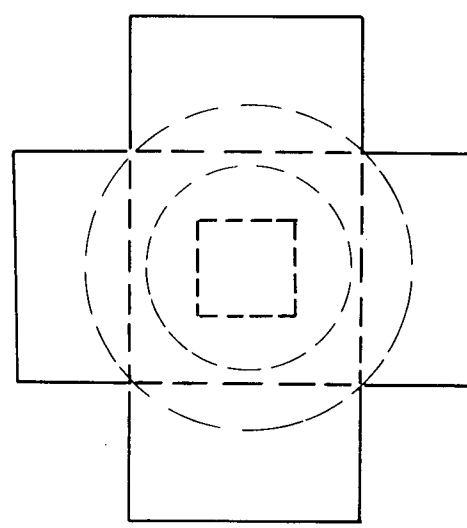


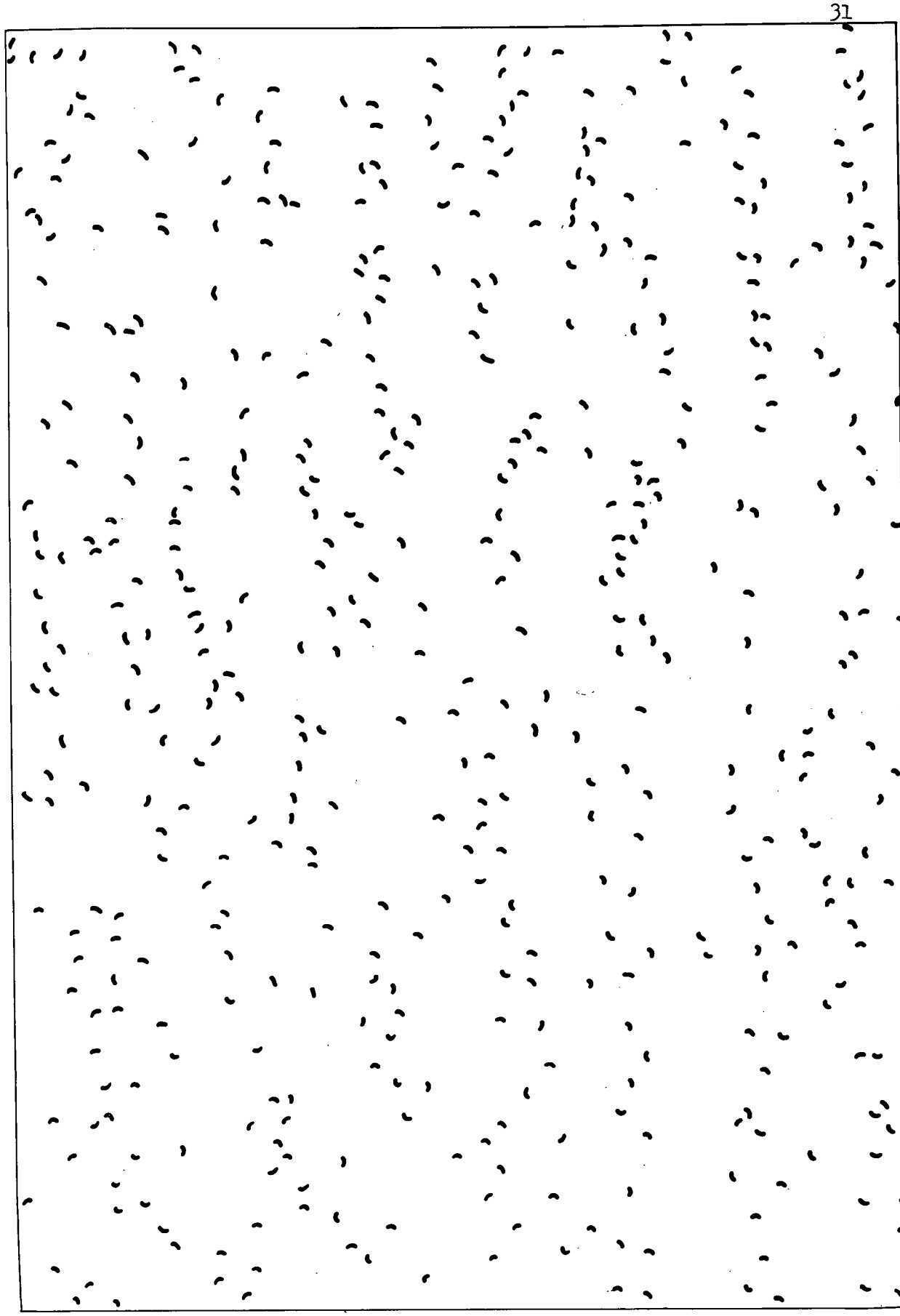
Step 7

the Elk Creek experimental plot, on September 10, 1964. The bolts were taken to the laboratory, there they were end sealed with paraffin, and the brood was allowed to develop to the third and fourth larval stages. When the majority of the larvae reached the desired developmental stages, the bark was carefully removed from each bolt and the positions of the larvae marked with map tacks. The top and bottom six-inch bolt sections were discarded at this stage because the brood suffered excessive mortality in these regions due to edge drying of the bolts. Following the marking of the larval positions the surface area of each bolt was divided into five, one fifth circumference by twelve inch, strips parallel to the longitudinal axes of egg galleries. Twelve of these strips were selected at random, two strips per bolt, and the map tack positions traced, separately from within each strip boundary, to transparent overlays. The overlays, in turn, were assembled in random fashion, four strips per row and three strips per column. The larval positions were then retraced from the assembly of overlays to a single, transparent master sheet. Positions of the larvae (measuring 2.4 by 5.5 millimeters) were stamped on this master sheet with a "larval stamp" made from an ink eraser. The orientations of the "larvae" were randomized prior to "stamping". The completed spatial map is shown on Figure 5.

One hundred randomly selected sample centers were placed on this spatial pattern map, inside a three inch buffer zone around the edges. A set of two, four, eight, twelve and sixteen square inch circular, square and rectangular sampling units was taken from each sample center. The sampling unit templates were made of transparent drafting

Figure 5.

Spatial pattern "map" to study the effect of sampling unit shape, and size on the edge effect bias of brood counts.



paper and sampling was done by placing the spatial pattern map over a light table, transposing the templates, one at a time, over the sample centers and recording the number of larvae entirely within the sampling unit boundaries and those falling on or touching the boundaries, separately. The rectangular sampling units had a width/length (w/l) ratio of one half and were orientated with longitudinal axes both parallel and perpendicular to the main axes of egg galleries.

The effect of sampling unit shape and orientation on precision was explored in more detail, on two additional population maps. These maps were prepared from the butt section, between the two and five foot levels, of two naturally infested trees. The "maps," when trimmed to 32 by 32 inch final dimensions, contained densities of 1.21 and 0.27 larvae per square inch. A total census was taken of the larval population of each map with a series of rectangular and square units and the variance of the larval counts was used in subsequent tests of efficiency.

Nine, three-foot long bolts, three bolts per tree, were cut from infested trees on the Horsethief Creek experimental plot for studies to determine the average size of larval clumps. Bolts were cut from the one to four foot section of the bole, from half way between the ground and the base of the crown, and from that position of crown which supported the longest live branches. The bolts were debarked in the laboratory and the positions of the larvae and galleries marked with a red felt pen. When marking was completed, the resulting pattern was traced to polyethylene sheets wrapped around each of the nine bolts. The nine spatial pattern maps obtained thereby, were

trimmed to thirty-two inch square sizes (Fig. 6). These spatial pattern maps had a mean brood density range of 0.043 - 1.217 larvae/square inch. Complete census was taken of each spatial pattern map with a series of 1, 4, 16, 64 and 256 square inch square units. Average larval clump size was determined by analyses based on Morisita's (1959) index of dispersion. This study was carried out within the period from June 19, 1965 to May 28, 1966.

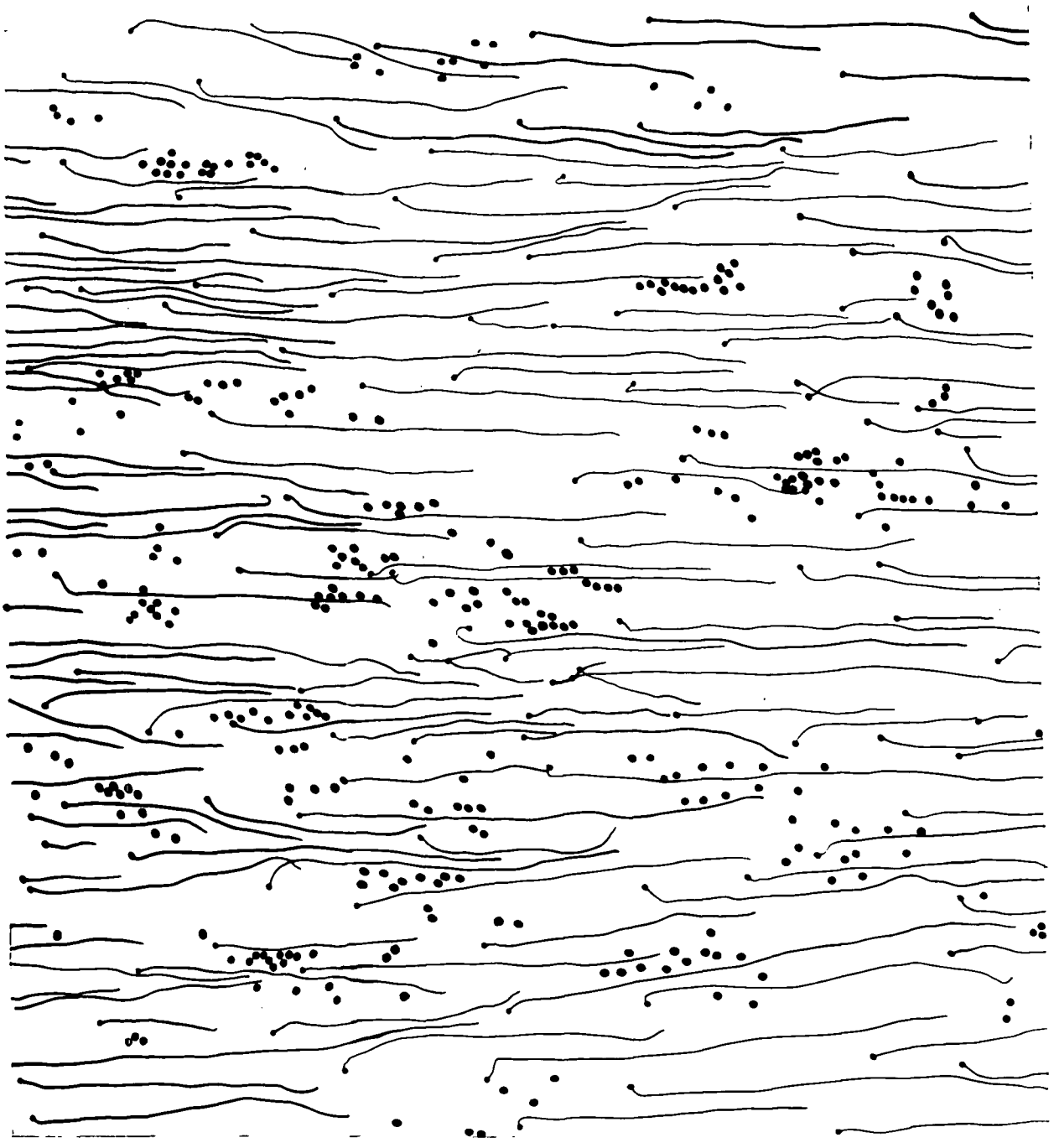
Spatial pattern maps prepared from the bottom logs of two infested trees were used to study average clump dimensions. The maps were totally sampled with a series of rectangular units, the long axes of which were orientated parallel to the long axes of clumps (and egg galleries). The sampling units were grouped in three series of the following dimensions: series 1-- 1 x 1, 1 x 2, 1 x 4, 1 x 8, 1 x 16 and 1 x 32 inches; series 2-- 2 x 2, 2 x 4, 2 x 8, 2 x 16 and 2 x 32 inches; series 3-- 4 x 4, 4 x 8, 4 x 16 and 4 x 32 inches. Average clump dimensions were determined by analyses based on Morisita's index of dispersion.

The analysis of distributional patterns of late stage brood was based on the same data which were used for studying the accuracy and precision of various sampling unit shapes and sizes in estimating mean brood density.

In order to establish optimum sampling unit size, in terms of minimum sampling time needed to establish mean densities of late stage mountain pine beetle broods with a predetermined degree of precision, a time study was made of five rectangular sampling units. The units had a $\underline{w/l}$ ratio of one half and were orientated perpendicular to the main axes of egg galleries. The following sampling unit sizes were

Figure 6.

A spatial pattern "map" to study the effect of sampling unit shape and size on the precision of mean brood counts and to study clump dimensions in relation to brood density.



studied: eight, eighteen, thirty-two, seventy-two and ninety-eight square inches. Flexible aluminium templates were used to delineate, and chisel and hammer to cut, sampling unit boundaries. A wide-blade hunting knife was used for bark removal. The time study was carried out at the five and fifteen foot levels and on the northern and southern aspects of thirty infested trees located on the Elk Creek experimental plot. The times spent in sampling unit allocation and delineation, bark removal and brood counting, gallery length measurement, attack counting and in data recording were measured by two stop watches. One of the stop watches was started immediately prior to sampling unit allocation and allowed to run continuously until sampling and data recording were completed, while the second stop watch was started every time a distinct sampling operation commenced, and was stopped on completion of that operation. This method of time keeping enabled the sampler to keep a separate time record of each distinct sampling operation. Furthermore, this method made possible the calculation of the total time spent on non-sampling operations such as; data recording, tool handling (including handling and climbing an extension ladder when sampling at the fifteen foot level), branch cutting and clearing the bark surface of loose scales prior to sampling unit delineation. This "time waste" was calculated by subtracting from the total sampling time, recorded by one stop watch, the total working time spent in actual sampling, recorded by the second stop watch. In the morning, and after lunch break, on each sampling day, a ten to fifteen minutes "dry run" sampling excercise was carried out to familiarize the observer with the tools and the sequence of operations and to al-

low him to settle down to a steady speed in sampling. The sampling was carried out by the author from July 2 to July 11, 1965. Data from the northern and southern aspects were pooled for subsequent analyses.

The distribution of late stage mountain pine beetle brood around the circumference of the host was studied on three-foot long bolts, cut from infested trees located on the Elk and Horsethief Creek experimental plots. The bolts were cut from the one to four-foot section of the trunk, from half-way between ground level and the base of the crown and from the lower crown, at a position where the longest live branches have been located. Twenty-four bolts were obtained in this manner, three bolts per tree and twelve bolts per plot. The bolts were taken to the laboratory and their circumference divided into twenty degree sections, on both ends, from a starting position of due South. The bark was then carefully removed from each of the one eighteenth circumference by three foot strips and the numbers of mountain pine beetle brood and attacks were recorded. The mountain pine beetle brood was in the pupal and teneral adult stages at the time of sampling which took place from July 14 to July 21, 1965.

Ninety-six trees, taken from various localities of the Invermere and Canal Flats Forest Ranger Districts of British Columbia, were used for developing surface area equations and tables for lodgepole pine. Data on sixty-six trees were supplied by the British Columbia Forest Service, Victoria, B. C. The data obtained from the Forest Service consisted of diameter measurements, to the nearest tenth inch, taken at the one and four and half foot height levels and at ten more equal intervals between the four and half foot level and the top of

the tree. The author took diameter measurements, to the nearest tenth inch, at the one, two, and four and-a-half foot levels and at every two foot interval from thereon. The diameters were converted to circumference by the following formula: $C = D \times \pi$, where D = diameter, outside bark (d.o.b.) and $\pi = 3.14...$ The surface area of each trunk section was calculated as $S = ((C_1 + C_2)/2)H$, where S = surface area (sq. ft.), and C_1 and C_2 = the lower and upper circumference of the section in feet, and H = the length of the section in feet. The cumulative total of the surface areas of the sections to any one height level provided the partial surface areas of the sections to any one height level provided the partial surface area data, and the cumulative total of the surface areas of all sections gave the total surface area data for the sample trees. In addition to the sectional diameter data, total height, age and d.b.h. were recorded for the sample trees and served as independent variables in subsequent regression analyses of surface area.

The vertical gradients of attack and brood density over the host, the relationship between bark thickness and attack density and the relationship of brood density at the d.b.h. level and overall brood density were studied on sixty-five naturally infested trees during the summers of 1965 and 1966. These studies provided the basis for the development of an index of population trend, for testing models to estimate mean brood and attack densities within individual hosts and for inter- (and intra-) tree stratification of brood densities when comparing the precision of various sampling techniques. Forty-three trees were felled and sampled on the Horsethief Creek experimental

area, twenty-eight in 1965 and fifteen in 1966. On the Elk Creek plot a total of twenty-two trees were sampled, ten in 1965 and twelve in 1966. The twenty-eight trees sampled in 1965, on the Horsethief Creek experimental plot, were felled on September 19, 1964 to prevent woodpecker predation of the mountain pine beetle brood. The rest of the sample trees were felled immediately prior to sampling. Sampling commenced when brood development reached the fourth larval and pupal stages.

Sampling was done by removing an eight by twelve inch bark area, at two foot intervals, from the northern and southern aspects of the sample trees. The lowest sampling point was taken at the two foot level, and sampling continued up the stem to the uppermost point of infestation. This point was ascertained by removing the bark to a level four feet higher than the level of the last recorded attack. The longitudinal axes of the sampling units were orientated perpendicular to the main axes of the egg galleries. The following data were recorded for each sample tree; age, total height, infestation height, crown width, crown length, the width of the last five and last ten growth rings at one foot stump height and the sum of the distances to the three nearest neighbours greater than four inches in d.b.h. The following data were collected on the sampling units: combined thickness of the outer and inner bark, number of attacks and brood, total gallery length and total inches of resin soaked galleries, and number of insect parasites and predators. Some of the variables recorded were not used in the present study but were retained for future investigation of the population dynamics of the mountain pine beetle.

Bark thickness was measured to the nearest thirty-second inch,

with a caliper, and the measurements were converted to millimeter scale prior to analysis. Each time the bark was being removed from a sampling unit, a section (about four square inches in area) was retained, from close to the center of symmetry, and measured at its thickest part (perpendicular to the run of bark ridges where these were present). Gallery length was measured, to the nearest quarter inch, with flexible steel rulers. Tree height, infestation height, crown length and width, and the distances to the three nearest neighbours were measured, to the nearest half foot, with a hundred foot long steel chain. Tree age was ascertained by counting the number of growth rings from the pith to the periphery of one foot high stumps and by correcting these counts for stump height using a correction of 3 years. Age correction was based on B. C. Forest Service site curves and correction tables for boring height (Forestry Handbook for British Columbia, 1959). The widths of the last five and ten growth rings on the stump were measured to the nearest thirty-second inch, in four places, at ninety degree intervals, and the average of the four measurements was recorded on the data sheets.

4.2. Statistical techniques and handling of data. Detailed descriptions of only special statistical concepts and techniques are given in this section. Standard statistical tests are described without giving the assumptions underlying their use.

4.2.1. Calculation of sample size for various sampling unit shapes and sizes drawn at random from "population maps". As the means, obtained by units of various shapes for a fixed size were slightly different because of random variation, direct comparison of the sampling variances was not a reliable method for evaluating the efficiency of different

sampling unit shapes. Therefore, sampling unit shapes were also compared by calculating the number of sampling units (of a certain shape and fixed size) needed to establish the mean with a predetermined degree of precision. Sampling was done by replacement and sample size, n, was calculated, assuming simple random sampling method, as follows:

$$n = (t_p/k)^2 \times (s/\bar{x})^2 \quad (1)$$

When, n = sample size, t = Student's "t" parameter, p = probability level, k = constant, s = standard deviation $\bar{x}$ = mean. Sample size calculated for a half confidence belt of $.1\bar{x}$ and p = .01.

4.2.2. Calculation of relative efficiency. Efficiency (E) of a sampling unit is defined as the reciprocal of the product of the cost per unit (C) and the squared coefficient of variation (CV) (Freese, 1962). That is

$$E = 1/(C)(CV)^2 \quad (2)$$

The relative efficiency (RE_i) of the i-th unit (E_i) relative to the "standard" unit (E_1) is defined as in the following equation:

$$RE_i = E_i/E_1 = (C_1)(CV_1)^2/(C_i)(CV_i)^2 \quad (3)$$

As mean density and cost per unit were held constant (the latter only approximately) by holding sampling unit size constant in these experiments RE was simplified to the following expression:

$$RE_i = S_1^2/S_i^2 \quad (4)$$

Where, S_1^2 = variance of the "standard" unit and S_i^2 = variance of the i-th unit. This formula was used to compare the efficiencies of samp-

ling units of various shapes and orientations.

4.2.3. The Id index of dispersion (Morisita, 1959). This index is applicable for analyses of distributional patterns. Id will take a value of unity if the individuals are distributed at random over the area. When the distribution of individuals is uniform, Id will take a value smaller than unity, and when the distribution of individuals is contagious, the Id value will be greater than unity. Id is defined as follows:

$$Id = \frac{S(fn^2 - fn)}{(Sfn)^2 - Sfn}(Sf) \qquad (5)$$

Where, n = frequency class midpoint (number of individuals), f = frequency and S = sum over all sampling units.

The significance of the departure from randomness of Id values greater than unity may be tested by the following formula with Sf - 1 and ∞ degrees of freedom.

$$F = \frac{Id(Sfn - 1) + Sf - Sfn}{Sf - 1} \qquad (6)$$

Where, ∞ = infinity and F = Fisher's F statistic.

Significance of Id values smaller than one was tested by the departure of the variance/mean ratio from unity with the following formula:

$$S_{\bar{x}} = (2/(n - 1))^{.5}, \qquad (7)$$

Where, $S_{\bar{x}}$ = standard error of the mean and n = sample size.

Id is affected by sampling unit size when the distribution of individuals is uniform Id increases from zero to unity with increasing sampling unit size. When, however, the distribution of individuals is contagious Id will either stay constant or increase to a sampling

unit size not much smaller than the "clump" sizes, and beyond this point the index value will approach unity. When the intra-clump distribution of individuals is at random, Id will stay approximately constant, with increasing sampling unit size, up to a point where the unit and the clump will be equal in area. Id will increase to the same point, with increasing sampling unit size, when the intra-clump distribution is uniform. Morisita showed that Id can also be used to find the approximate size of the clumps by plotting Id(a)/Id(ma) (where Id(a) is the Id value of sampling unit size a and Id(ma) is the Id value of sampling unit size ma.) for each sampling unit size taken as ma. The peaks in the Id(a)/Id(ma) curves will correspond, approximately, with mean clump size.

4.2.4. Determination of optimum sampling unit size: Optimum sampling unit size was established by plotting the total sampling time (T) over sampling unit size. Optimum sampling unit size corresponded with minimum total sampling time on the T vs. sampling unit size free-hand graphs. T was calculated as follows:

$$T(\text{hours}) = (\text{sample size}) \times (\text{sampling time (hours)/unit}) \quad (8)$$

Sample size, n, was calculated, for a probability level of $p = 0.99$, for each unit at two height levels assuming simple random sampling. Sample size, n, was calculated as in equation (1). In this method of optimum sampling unit determination, it was assumed that sampling is multivariate and that number of attacks and gallery length, besides number of brood, will be tallied on the sampling units. Sample size, however, was calculated only for brood data because, of the three variables, brood counts have the greatest variability.

4.2.5. Analysis of circular distributions: The density gradients of attacks and late stage larvae around the stem circumference was studied by the concept of circular distribution.

Circular distributions are a special kind of two dimensional distributions, where the total probability is spread out on the circumference of a circle (Batscelet, 1965). As ordinary distributions on a straight line are usually described by their moments, the circular distributions are described by trigonometric moments. The first trigonometric moment, the mean, is a vector quantity. The length of the mean vector can take up positive values between zero and one and has a mean angle. The mean vector length (r_1) and its angle (λ_1) are defined as follows:

$$r_1 = \sqrt{\left(\frac{1}{n}\sum_{i=1}^{n} \sin\alpha_i\right)^2 + \left(\frac{1}{n}\sum_{i=1}^{n} \cos\alpha_i\right)^2} \qquad (9)$$

$$\cos\lambda_i = \frac{1}{n}\sum_{i=1}^{n} \sin\alpha_i / r_1 \qquad (10)$$

Where, α_i is the i-th class interval.

The measure of dispersion, called mean angular deviation (s), of the circular distribution is defined as follows:

$$s = \sqrt{2(1 - r)(\text{in radians})} \qquad (11)$$

If the value of s is not greater than 50°, approximately 67% of the observations will fall within the limits "mean ± s". If, however, s is greater than 50°, the percentage values contained in that interval decreases gradually from 67% to 45%. The measure of skewness (g) is defined as in the following equation:

$$g = r_2 \sin(2\lambda_1 - \lambda_2) \qquad (12)$$

Where, r_2 and λ_2 are defined as r_1 and λ_1 by substituting $2\alpha_i$ for α_i in the appropriate equations.

The significance of the concentration of the observations toward the mean direction can be tested by the following statistic:

$$z = nr^2 \tag{13}$$

Critical values of z are tabulated for the 1% and 5% levels of significance (Batscelet, 1955). This test is valid only for unimodal distributions. The half confidence interval (ϵ) for the mean angle, for 1% significance level and n greater than 15, can be calculated as follows:

$$\cos\epsilon = \sqrt{n^2 r^2 - x^2 \tfrac{n}{2}}/nr \tag{14}$$

Where, x^2 denotes the upper critical value of x^2 with one degree of freedom and significance level p.

4.2.6. Taylor's power law. Taylor's power law (Taylor, 1961, 1965) expresses the relationship between variance (s^2) and mean ($\bar{y}$) and holds for distributions from regular through random to highly aggregated. The law is expressed by the relationship:

$$s^2 = a\bar{y}^b \tag{15}$$

Where, a and b are constants (a is a sampling factor and b appears to be a true index of aggregation characteristic of the species), s^2 and $\bar{y}$ are defined earlier.

The parameters of equation (15) can be found by transforming the (s^2,$\bar{y}$) pairs of observations to logarithmic scale and by fitting the following least squares equation to the transformed data:

$$\log_{10}(s^2) = \log_{10}(a) + b \log_{10}(\bar{y}) \tag{16}$$

4.2.7. Taylor's "Z" transformation. The "Z" transformation is based on the assumption that the relationship between variance and mean follows Taylor's power law. If this assumption holds, the appropriate variance stabilizing function, f(y), is of the form:

$$f(y) = Q \int \bar{y}^{-b/2} \, d\bar{y} \tag{17}$$

Therefore, the transformed observations will take the following form:

$$Z = y^{(1 - b/2)} \tag{18}$$

Where, Z = transformed value of an observation; y = observation on original scale; b = Taylor's power constant; Q = integral constant; $\int$ = integral sign.

4.2.8. Estimation of the gain in precision of the inter-primary unit component of the population total due to stratification and regression sampling and that of the intra-primary unit variance component due to stratification. Since the primary units were selected without replacement and with equal probability, the following variance of population total estimator was used for calculating precision (Samford, 1962):

$$s^2(Y) = \frac{N^2 \bar{M}^2 s_b^2}{n}(1 - f_1) + \frac{N}{n} S_n \frac{M_j^2 s_j^2 (1 - f_2)}{m_j} \tag{19}$$

Where, $s^2(Y)$ = variance estimate of the population total; N = number of first-stage units in the population; $\bar{M}$ = population mean of the number of secondary units per first-stage unit; n = sample size of first-stage units; f_1 = first-stage sampling fraction; f_2 = second-stage sampling fraction; M_j = number of second-stage units in the j-th primary unit; s_j^2 = within-primary unit variance for the j-th primary unit; m_j = second-stage sample size in the j-th primary unit; S_n = sum

over "n" primary units and s_b^2 = between-primary units variance and is defined as:

$$s_b^2 = \frac{1}{n-1} S_n \frac{M_j^2 (\bar{y}_{mj} - \bar{\bar{y}})^2}{\bar{M}^2} \qquad (20)$$

$\bar{y}_{mj}$ = mean of the "m" secondary-units in the j-th primary and $\bar{\bar{y}}$ = overall sample mean per second-stage unit. The second term on the right hand of equation (19), following the equation sign (s_{ws}^2), was modified to allow second-stage stratification of the units. The modified form is as follows:

$$s_{wst}^2 = S_n(S_k M_{ij}^2 s_{ij}^2 (1 - f_{2ij})/m_{ij}) \qquad (21)$$

Where, M_{ij} = number of second-stage units in the i-th stratum of the j-th primary unit, m_{ij} = sample size of the secondary-units in the i-th stratum of the j-th primary unit, s_{ij}^2 and f_{2ij}, respectively, = the variance and sampling fraction in the i-th stratum of the j-th primary unit, S_k = sum over "k" number of strata and s_{wst}^2 = within-tree sampling variance for stratified samples.

The efficiency of the within-primary unit stratification was calculated by expressing s_{wst}^2 as a % of s_{ws}^2. That is:

$$E(\%) = 100 (s_{ws}^2/s_{wst}^2) \qquad (22)$$

In calculating the within-tree variance component of the population total, the factor $(1 - f_{2ij})$ was ignored. Further, it was assumed that a total census was taken of the primary units and, therefore, the factor N/n was equated to unity.

The expression for calculating the inter-primary unit component of the sampling variance from a simple random sample of the primaries

(s^2_{br}) was rewritten to permit the estimation of this variance component from a stratified random and a regression sample of the primary units. For the stratified random sample, the inter-primary unit component of the sampling variance (s^2_{bst}) was calculated from the following expression:

$$s^2_{bst} = \bar{M}^{-2} S_k \frac{N_i^2 s^2_{bi}(1 - f_{1i})}{n_i} \qquad (23)$$

Where, s^2_{bi} = between-tree variance in the i-th stratum, n_i = sample size in the i-th stratum, N_i = total number of primary units in the i-th stratum and the other notations are as defined previously.

For regression sampling of the primary units on primary unit size, the between-primary unit variance component of the population total (s^2_{bre}), was calculated as:

$$s^2_{bre} = \frac{N^2 \bar{M}^{-2} s^2_{x.y}}{n} (1 + \frac{1}{n})(1 - f_1) \qquad (24)$$

Where, $s^2_{x.y}$ = variance of the estimate and the other notations are as defined previously.

4.2.9. Estimation of sample size from the sample design. The appropriate variance of mean formula, when the primary units are unequal in size, is

$$s^2_{\bar{y}w} = \frac{s^2_c}{n} - \frac{s^2_b}{N} \text{ (Samford, 1962)} \qquad (25)$$

Where,

$$s^2_c = s^2_b + (1/N\bar{M}^2) S_n \frac{M_j^2 s_j^2(1 - f_{2j})}{m_j} \qquad (26)$$

and the other symbols are the same as defined previously.

From formula (24) sample size may be calculated if the first stage

sampling fraction is known in advance or if all m_j are equal.

For the purpose of estimating sample size, the individual s_j^2 values were replaced by the pooled variance, S_p^2, in equation (25). Thus, the second half of this formula, after the equation sign, changes to

$$S_p^2 \left(\frac{1}{f_2 \bar{M}} - \frac{1}{\bar{M}} \right) \tag{27}$$

$$S_p^2 = S_n \frac{S_k(m_{ij} - 1)\, s_{ij}^2}{S_k(m_{ij}-1)}, \tag{28}$$

Where, the symbols are the same as before.

The sampling variance was estimated from data transformed by Taylor's Z transformation and, therefore, the following condition was specified in mathematical terms: The standard error on transformed scale must correspond to 10% of the mean on the original scale. That is:

$$s_{\bar{\bar{y}}} = \frac{((\bar{x}p)^c - ((1 - 0.1)\bar{x}p)^c + (((1 + 0.1)\bar{x}p)^c - (\bar{x}p)^c)}{2} \tag{29}$$

Where, $s_{\bar{\bar{y}}}$ = required standard error on transformed scale, $\bar{x}$ = population mean estimate on original scale, c = (1 - b/2) = Taylor's Z transformation constant and p = $(100\bar{x}_w/\bar{x}$ = "back transformed" mean ($\bar{x}_w$) as a % of $\bar{x}$.

4.2.10. Calculation of the standard error of mean brood density per secondary unit on original scale. The standard error of the "back transformed" mean (the equivalent of the geometric mean for log. transformation) was calculated by the following formula.

$$s_{\bar{x}w} = \frac{(\sqrt[c]{(\bar{\bar{y}}_w + s_{\bar{\bar{y}}})} - \sqrt[c]{\bar{\bar{y}}_w}) + (\sqrt[c]{\bar{\bar{y}}_w} - \sqrt[c]{\bar{\bar{y}}_w - s_{\bar{\bar{y}}}})}{2} \tag{30}$$

Where, $s_{\bar{x}w}$ = standard error of "back transformed" mean, c = (1 - b/2), b = Taylor's power constant, $\bar{\bar{y}}_w$ = mean on transformed scale. Formulae (30) is the mathematical equivalent, for Taylor's Z transformation, of the method described by Morris (1955) for calculating the standard error of a geometric mean. Further, this formula defines the inverse of the operations defined by equation (29). The standard error of the mean on the original scale ($s_{\bar{x}}$) was calculated from $s_{\bar{x}w}$ by multiplying the latter by the ratio $\bar{x}_w/\bar{x}$. That is

$$s_{\bar{x}} = (\bar{x}_w/\bar{x})s_{\bar{x}w} \tag{31}$$

Where, $\bar{x}_w/\bar{x}$ = the ratio of the "back transformed" mean and the mean on the original scale and the other symbols are as defined previously. In formula (30), $s_{\bar{\bar{y}}}$ was estimated by the equation:

$$s_{\bar{\bar{y}}} = \frac{s^2_{x.y}}{n}(1 + \frac{1}{n})(1 - f_1) + \frac{f_i}{n^2\bar{M}^2} S_N(S_k M^2_{ij} s^2_{ij}(1 - f_{2ij})/ m_{ij}) \tag{32}$$

Where, $s^2_{x.y}$ = varience of estimate and the other symbols are the same as before.

This formula is a modification of Samford's (1962) equation (8.22) for regression and stratified sampling of the primary and secondary units, respectively. The estimate of $s_{\bar{\bar{y}}}$ given by formula (32)is slightly biased because the variables M_{ij} and $\bar{M}$ are treated as constants. (Note: M_{ij} and $\bar{M}$ were estimated by regression techniques.)

4.2.11. Estimation of population total and population mean per second-stage unit. The population mean per second-stage unit was estimated by the following formula:

$$\bar{x} = S_n(S_k M_{ij}\bar{y}_{ij})/S_n(S_k M_{ij}) \tag{33}$$

Where, $\bar{y}_{ij}$ = the mean of the i-th stratum within the j-th primary unit and the other symbols are the same as defined earlier.

The population total was estimated by multiplying $\bar{x}$ with the product of the number of primary units in the population (N) and average primary size ($\bar{M}$). That is

$$Y = (N\bar{M})\bar{x} \tag{34}$$

Where, Y = estimate of the population total.

4.2.12. Estimation of the variance of the population total. Estimation involved finding the variance of the product in equation (34), where $\bar{M}$ and $\bar{x}$ are variables and N is a constant. The variance of $N\bar{x}$ was calculated as:

$$S^2(N\bar{x}) = N^2 s^2_{\bar{x}} \tag{35}$$

Where, $S^2(N\bar{x})$ = variance of the product $N\bar{x}$.

$\bar{M}$ was calculated as the product of the "mean" proportion of infested surface area/tree ($\bar{p}$) and average surface area/tree ($\bar{a}$). Therefore, $S^2(\bar{M})$ is estimated as in equation (36).

$$S^2(\bar{M}) = \bar{M}^2(s^2_{\bar{p}}/\bar{p}^2 + s^2_{\bar{a}}/\bar{a}^2) \tag{36}$$

Where, $s^2_{\bar{p}}$ and $s^2_{\bar{a}}$ are the variance estimates of $\bar{p}$ and $\bar{a}$, respectively. The variance of $\bar{p}$ was estimated as:

$$s^2_{\bar{p}} = s^2_{y.x}\left(\frac{1}{n_1} + \frac{1}{n}\right)\left(\frac{\bar{x}_p(1 - \bar{x}_p)}{\bar{x}_p(1 - \bar{x}_p)}\right), \text{ (Appendix B)} \tag{37}$$

Where, $s^2_{\bar{p}}$ = variance of $\bar{p}$, $s^2_{y.x}$ = variance about the regression of p on x_p, x_p = infested height/total height, n = sample size for regression equation, n_1 = number of primary units in the sample, $\bar{x}_p = S_n W_i x_{pi} / S_n W_i$, $W_i = (\text{Ht. x d.b.h.})_i$ and $\bar{x}_p = 0.5$.

The variance of $s_{\bar{a}}^2$ was estimated by the following equation:

$$s_{\bar{a}}^2 = s_{y.x}^2 \left(\frac{1}{n_1} + \frac{1}{n} + \frac{x^2}{S_N x^2}\right), \text{ (Steel and Torrie, 1960)} \quad (38)$$

Where, $s_{y.x}^2$ = variance about the regression of total surface are on (D.b.h. x Ht.), n = sample size for regression, n_1 = size of the sample, x^2 = squared difference between the regression mean and the sample mean and $S_N x^2$ = sum squares of the (D.b.h. x Ht.) values for the regression equation.

The variance of $\underline{Y}$ (equation (32)) was estimated by applying the variance of the product formula to the independent components $\underline{S^2(N\bar{x})}$ and $\underline{S^2(\bar{M})}$.

4.3. Model building concepts and techniques.

4.3.1. Experimental determination of the edge effect bias of mean brood density (L_c%). In order to experimentally determine $\underline{L_c}$%, one hundred sets of circular, rectangular and square sampling units were drawn, at random, from a "spatial pattern map" (Fig.5). The number of larvae falling entirely within the unit (I) and those falling on the circumference (C) were recorded, separately, for each sampling unit shape-size combination considered.

The best estimate of the larval counts on the k-th trial of a sampling unit (k = 1, 2....100) was obtained by the following expression:

$$\frac{C_k}{2} + I_k \quad (39)$$

Thus, in terms of the above defined expression the "true" mean density estimate ($\bar{x}$) can be defined as in equation (40).

$$\bar{x} = \frac{\sum_{k=1}^{100} C_k}{200} + \frac{\sum_{k=1}^{100} I_k}{100} \quad (40)$$

Where, S = sum.

Then, the biased density estimate resulting from the inclusion of all individuals from the sampling unit boundaries ($\bar{x}'$) will be as in equation (41), and the biased density estimate resulting from the exclusion of all individuals from the circumference ($\bar{x}''$) will be as in equation (42).

$$\bar{x}' = \frac{\sum_{k=1}^{100} (C_k + I_k)}{100} \tag{41}$$

$$\bar{x}'' = \frac{\sum_{k=1}^{100} I_k}{100} \tag{42}$$

Further, the over and under estimation of mean density resulting from edge effect will be given by equations (43) and (44), respectively.

$$\bar{x}' - \bar{x} = + \frac{\sum_{k=1}^{100} C_k}{200} \tag{43}$$

$$\bar{x}'' - \bar{x} = - \frac{\sum_{k=1}^{100} C_k}{200} \tag{44}$$

Therefore, L_c (in %) relative to $\bar{x}$, the "true" mean density estimate, is given by equation (45).

$$L_c\% = 100 \left| \frac{\frac{\sum_{k=1}^{100} C_k}{200}}{\bar{x}} \right| = \left| \frac{\sum_{k=1}^{100} C_k}{2\bar{x}} \right| \tag{45}$$

Where, $|\ |$ designates absolute value.

An $L_c\%$ was calculated for each planned sampling unit size-shape combination as in equation (45). The calculated $L_c\%$ values then, were plotted over sampling unit size (A_s), separately for each selected samp-

ling unit shape. In order to calculate the equation of $L_c\%$ on A_s, both of these variables were transformed to common logarithms and a least squares linear regression line was fitted to the transformed values.

4.3.2. Assumptions for the mathematical model expressing the relationship between L%, sampling unit shape and size, and the size of an average larva. This model was based on the following simplifying assumptions: a) The sampling unit circumference bisects the vertical projection of a larva at random, relative to the insect's orientation. b) The proportion of sampling unit circumference occupied by insects is approximately equal to that occupied by insects of the sampling unit area. c) The edge effect bias of mean brood density is directly proportional to the c/a ratio of the sampling unit.

4.3.3. Mathematical model to express attack intensity as a function of bark thickness. The development of the mathematical model was based on the following assumptions:

a, At any given level of the attacking population mean attack density, at any height level, will be directly proportional to the mean number of suitable attack sites per unit bark area.

b, The number of suitable attack sites per unit bark area is indirectly related to bark thickness through bark roughness.

c, The density of suitable attack sites will asymptotically approach an upper limit with increasing bark thickness.

As no reliable methods are available to identify suitable attack sites on the bark surface, the combined thickness of the inner and outer bark was used as the most important independent variable in the mathe-

matical model. Further, it was postulated that the mode of influence of bark thickness on attack density was subject to modification by tree resistance and height above ground level. Accordingly, in mathematical terms, we could write

$$Y = f(X_1, X_2, X_3) \tag{46}$$

Where, Y = attack density, X_1 = bark thickness, X_2 = proportion of unsuccessful egg galleries (an expression of localized tree resistance) and X_3 = height above ground (ft.). Further, in accordance with the predefined assumptions the rate of change of $\underline{Y}$ with respect to $\underline{X_1}$ will be as in equation (47).

$$\frac{dY}{dX_1} = b(Ymax - Y) \tag{47}$$

Where, dY/dX_1 = first derivative of $\underline{Y}$ with respect to $\underline{X_1}$, b = constant, Ymax = the maximum value of $\underline{Y}$ and $\underline{X_1}$ are defined as in equation (46). Equation (47) integrates to equation (48).

$$Y = Ymax(1 - e^{-bX_1}) \tag{48}$$

This basic equation may be conveniently written as in equation (49),

$$Y = Ymax(1 - 10^{-b'X_1}) \tag{49}$$

by replacing the natural logarithms with logarithms to base 10. Equation (49), can be transformed into linear form as in equation (50).

$$LOG_{10}(Ymax/(Ymax - Y)) = b'X_1 \tag{50}$$

Thus, if equation (48) describes the relationship between $\underline{Y}$ and $\underline{X_1}$ adequately, then the plot of $LOG_{10}(Ymax/(Ymax - Y))$ on $\underline{X_1}$ yeilds a straight line with slope = b' and zero intercept.

The appropriateness of equation (49) to describe the attack density

vs. bark thickness relationship was tested by experimental data. The experimental data consisted of gradient samples of both attack density and bark thickness. These variables were recorded at two foot intervals, on the northern and southern aspects of infested trees. Sampling commenced at the two foot level and continued to the upper most point of infestation. Sampling was done by a 96 sq. in. rectangular sampling unit which was orientated with long sides perpendicular to the egg galleries. Forty-three trees have been sampled in this manner on the Horsethief Creek plot, twenty-eight trees in 1965 and fifteen trees in 1966. On the Elk Creek plot similar data have been collected from ten trees in 1965.

Attack density was summarized by 1/32 inch (0.79 mm.) bark thickness classes, and a mean attack density was calculated for each class. There was an unequal number of observations in the various bark thickness classes because the logarithm of bark thickness, rather than the arithmetic values, was inversely proportional to height above ground level. Consequently, in the higher bark thickness classes there were fewer samples than in the smaller bark thickness classes. Whenever a particular bark thickness class contained less than three observations, this class has been combined with the immediately greater class for subsequent analysis.

Ymax in equation (50) was solved by an iterative technique. The Ymax value that maximized the correlation coefficient was considered to be the correct value. Then, weighted linear regression lines were fitted to the transformed values of the experimental data. The mean attack density values were weighted by the number of observations in

the various bark thickness classes.

To test the modifying influence of tree resistance (X_2) and height above ground level (X_3) on equation (50), it was expressed in the following form:

$$b = \frac{LOG_{10}(Ymax/(Ymax - Y)) + a}{X_1} \qquad (51)$$

Where, a = intercept, b = slope and Y, Ymax, and X_1 are the same as for equation (50). For testing, the data was resorted on X_2 and, then, on X_3 and b was plotted against these independent variables.

4.3.4. Surface area equations for lodgepole pine. Stem surface area of individual trees is a function of stem volume and, therefore, the former variable may also be estimated by methods similar to those used for estimating stem volume. Total stem volume of individual trees is well described by mathematical expressions of the stem volume-diameter-height relationship. This relationship is expressed in various forms, on both arithmetic and logarithmic scale. Arithmetic solutions tend to be more precise (Spurr, 1952) and less biased than logarithmic methods (Cunia, 1964) and, therefore, the former methods are preferred. The most commonly used arithmetic volume functions express the stem volume-diameter-height relationship in terms of the stem profile (or taper curves); a reference cylinder volume or in terms of field measures of d.b.h. and total height. The quantification of taper curves requires the use of polynomials or ratios of polynomials (Grosenbough, 1966) and, therefore, this method will likely lead to complicated volume (and surface area) integrals. The reference cylinder volume method involves the calculation of a form factor and will, in general, afford accurate estimates of total tree volume.

Heger (1965) and later Stanek (1966) achieved excellent results in estimating the form and volume of lodgepole pine trees with Hohenadl's method of stem form and stem volume estimation. Unfortunately, the calculation of form factors require a diameter measurement on the upper stem, in addition to the measurement of d.b.h. The measurement of upper stem diameters is time consuming and troublesome, therefore, the advantages offered by the "reference cylinder" volume estimation methods tend to be eclipsed by the additional effort required for sampling, relative to the sampling effort needed to establish volume functions based on field measures of only d.b.h. and total height.

In this study, total surface area of individual trees was estimated by regression techniques based on total cubic foot volume functions. Two general stem volume equations were used as models for the development of surface area functions.

The stem volume equations were as follows:

$$V_t = a + b(D^2H) \tag{52}$$

and

$$V_t = D^2/(a + b/H) \tag{53}$$

Where, V_t = total stem volume/tree, D = d.b.h., H = total height and a and b are constants.

The former equation is the widely used "combined variable" total cubic foot function and the latter equation is the new "transformed variable" function proposed by Honer (1965). Spurr (1952) achieved excellent results in fitting the combined variable formula and concluded that the function ($V = a + D^2H$) "cannot be significantly improved by the addition of other variables." These conclusions were verified by Smith et al

(1961), Golding and Hall (1961) and Kirby (1968). Smith and Breadon (1964) and Kirby (1968), showed that the combined variable equations can be converted to volume/basal area ratios for point sampling. The combined variable formula tends to over estimate tree volumes in the small d.b.h. classes (Spurr, 1952; Golding and Hall, 1961) but gives excellent volume estimates for the medium to large d.b.h. range. For lodgepole pine in Alberta the critical d.b.h. class is approximately 3 inches (Kirby, 1968). Honer (1965) demonstrated that the "transformed variable" function (equation (52)) gives good estimates of stem volume for all d.b.h. classes and, at the same time, stabilizes the variance about the regression line.

The general surface area equations were derived from formula (52) and (53) by substituting $\underline{D}$ for $\underline{D}^2$. Thus

$$S_t = a' + b'(DH) \tag{54}$$

and

$$S_t = D/(a' + b'/H) \tag{55}$$

Where, S_t = surface area, a' and b' are constants and D and H are as before.

The bole area function suggested recently by Whittaker and Woodwell (1967) has the same general form as equation (54) but these workers used the basal half circumference of the bole (instead of d.b.h.) as a second variable to total height, in their "conic surface" equation.

Prior to analysis, equation (55) was re-arranged as in equation (56) to permit linear least squares regression fit.

$$D/S_t = a' + b'(1/H) \tag{56}$$

The estimation of partial surface area was based on Honer's (1964) method of merchantable cubic volume determination. Honer and later Smith and Munro (1965) demonstrated that the section volume (V_s)/total

volume (V_t) ratio can be estimated with a high degree of accuracy by regression equations which express V_s/V_t as a function of the section height (ΔH)/total height (H) ratio.

The partial surface area (S_p) of individual trees was estimated as in equation (57).

$$S_p = S_t f(\Delta H/H) \tag{57}$$

Where, f = functional notation and S_p, S_t, ΔH and H are as defined previously. The ($\Delta S_t/S_t$) ratio was estimated from the following multimple curvilinear regression:

$$\Delta S_t/S_t = a + b(\Delta H/H) + c(\Delta H/H)^2 + d(\Delta H/H)^3 \tag{58}$$

Where, a, b, c, and d are constants, ΔS_t = section surface area and the other symbols are the same as before.

Equation (58) was fitted to section surface area data by electronic computer and the best two independent variables were formed by the "all variable combinations" method. After eliminating the least significant independent variable from equation (58), $\Delta S_t/S_t$ was substituted for $f(\Delta H/H)$ in equation (57) and a "partial surface area table" was calculated for lodgepole pine in the fashion of "merchantable" cubic volume tables.

EXPERIMENTAL RESULTS

1. Studies of the relationship between the shape, size and orientation of the sampling unit, the spatial pattern of late stage larvae and the accuracy and precision of mean brood density estimates.

1.1. The relationship between the size and shape of the sampling unit and its circumference. The relationship is shown on Figure 7. It is presented in such a manner as to show the change in the circumference/area (c/a) ratio with changing sampling unit shape. The rectangular units shown, had a w/l ratio of one quarter. The equations for the curves are based on the circumference formulae of square, circular and rectangular plane geometrical forms and were derived as follows:

If a represents sampling unit area in square inches, c circumference in inches and $\pi = 3.14...$, then the circumference, in terms of sampling unit area, is given by equations I, II, and III for square, circular, and rectangular units (w/l = 0.25), respectively.

$$c = 4\sqrt{a} \qquad \text{(I)}$$

$$c = 2\sqrt{\pi a} \qquad \text{(II)}$$

$$c = 5\sqrt{a} \qquad \text{(III)}$$

Dividing both sides of these equations by a, the following relationships are obtained.

$$c/a = \frac{4}{\sqrt{a}} \qquad \text{(IV)}$$

$$c/a = \frac{2\sqrt{\pi}}{\sqrt{a}} \qquad \text{(V)}$$

$$c/a = \frac{5}{\sqrt{a}} \qquad \text{(VI)}$$

These last three equations were then solved for various values of a and expressed in graphical form (Fig. 7).

It is apparent from Figure 7 that both sampling unit size and shape considerably affect the c/a ratio. Of all shapes, circular units have the smallest and rectangular units the greatest c/a ratio for any fixed size. The c/a ratio of the rectangular units increases with decreasing w/l ratio. Further, the c/a ratio drops sharply with increasing sampling unit size, from zero to about twelve square inches, for all sampling unit shapes. For sampling units greater than about twelve square inches, the rate of change in the c/a ratio with respect to sampling unit size becomes more gradual. Equations (IV) to (VI) indicate that the nature of the c/a ratio vs. a relationship is such that, on logarithmic scale, the rate of change of the former variable with respect to unit size is constant for all sampling unit shapes (on log-log scale equations (IV) to (VI) have identical slopes).

1.2. Theoretical and experimental determination of the relationship between sampling unit shape and size and the edge effect bias of mean brood density. The mathematical formulae, to describe the edge effect bias vs. sampling unit size relationships for various sampling unit shapes, were derived on the basis of a set of simplifying assumptions (section 4.3.2.,Materials and Methods) in the following manner:

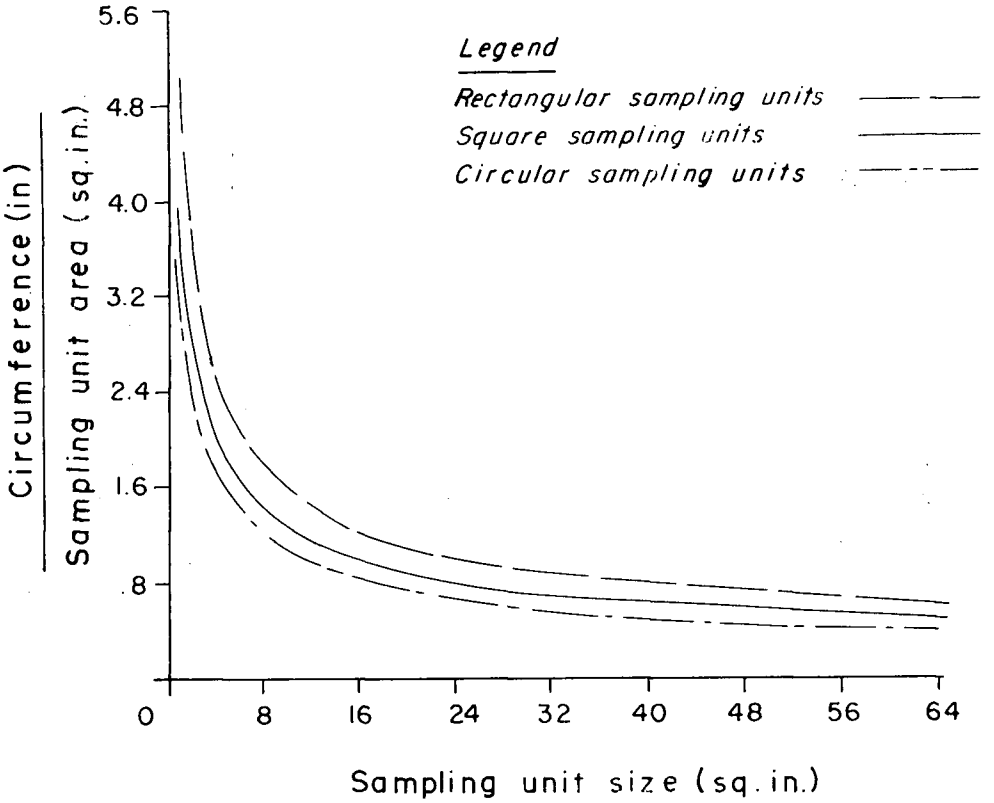
Let D = "true" population density per unit area, a = average width and b = average length of an insect, A_i = (a)(b) (cross-sectional area or vertical projection of an average individual) and A_s = sampling unit size (in the same unit of measure as A_i). Then the proportion of a unit

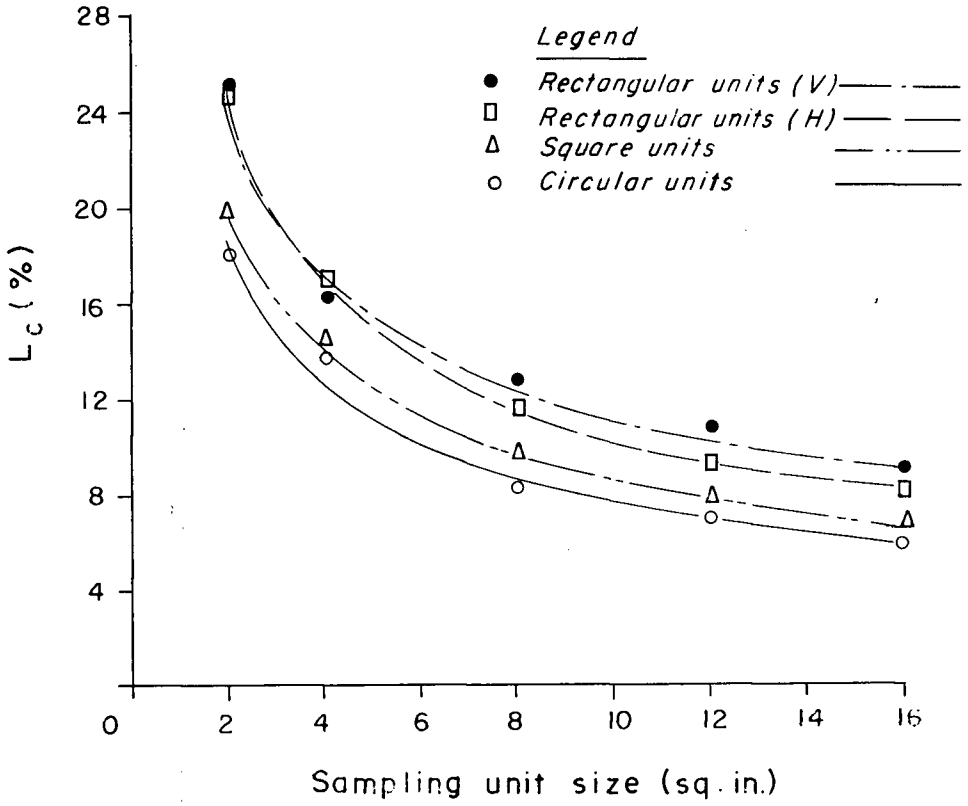
Figure 7.

Theoretical relationship between the size and shape of the sampling unit and its circumference.

Figure 8.

Relationship between the precentage edge effect bias of brood density and sampling unit size for various sampling unit shapes.


Legend
Rectangular sampling units
Square sampling units
Circular sampling units
Circumference (in) / Sampling unit area (sq.in.)
5.6
4.8
4.0
3.2
2.4
1.6
.8
0
8
16
24
32
40
48
56
64
Sampling unit size (sq.in.)


Legend
Rectangular units (V)
Rectangular units (H)
Square units
Circular units
L_c (%)
28
24
20
16
12
8
4
0
2
4
6
8
10
12
14
16
Sampling unit size (sq.in.)

circumference occupied by insects can be expressed as $\underline{DA_i}$, and the number of insects bisected by a unit circumference will be equal to $DA_i / \sqrt{A_i} = D\sqrt{A_i}$, where $\underline{\sqrt{A_i}}$ is the average "diameter" projected by an insect on the circumference. Further, as circumference, in terms of sampling unit area, is expressed by equations I to III, the average number of insects (C) bisected by the sampling unit circumference will be given by equations VII, VIII and IX for square circular and rectangular units, respectively.

$$C = 4D\sqrt{A_i A_s} \qquad \text{(VII)}$$

$$C = 2D\sqrt{\pi A_i A_s} \qquad \text{(VIII)}$$

$$C = 5D\sqrt{A_i A_s} \qquad \text{(IX)}$$

When taking a tally of the number of insects on a sampling unit C/2 of the individuals from the boundaries should be included. Therefore, edge effect bias of the density estimate ($L_c\%$) resulting from the inclusion or exclusion of all individuals located on the unit boundaries will be given by equations X,XI and XII for square, circular and rectangular units, in that order.

$$L_c\% = 100(4D\sqrt{A_i A_s})/2DA_s = 200\sqrt{A_i/A_s} \qquad \text{(X)}$$

$$L_c\% = 100(2D\sqrt{\pi A_i A_s})/2DA_s = 100\sqrt{\pi A_i/A_s} \qquad \text{(XI)}$$

$$L_c\% = 100(5D\sqrt{A_i A_s})/2DA_s = 250\sqrt{A_i/A_s} \qquad \text{(XII)}$$

Where, $\underline{DA_s}$ is an expression of the "true" average number of insects per sampling unit. It is apparent from equations VII to IX that, $\underline{C}$, the average number of insects bisecting the circumference of the sampling unit is directly proportional to density, the square root of the cross-sectional area of individuals and to the square root of sampling unit size. On the other hand, equations X to XII show that

$\underline{L_c}$, the % edge effect bias of the density estimate, is independent of density and is directly proportional to the square root of the cross-sectional area of individuals and inversely proportional to the square root of sampling unit size.

The sample survey data for the experimental determination of the $\underline{L_c}$ vs. sampling unit size and shape relationship (which was obtained by sampling the "population map" on Figure 5, at one hundred randomly selected sampling points, with a set of sampling units superimposed in a nested fashion) is summarized in Table I. Reference to Table I indicates that the mean number of larvae bisected by the sampling unit circumference ($\bar{C}$) increased logarithmicly with increasing sampling unit size, for all sampling unit shapes considered (rows 2, 8, 14 and 20 in Table I). On the other hand, $\underline{L_c}$, the % edge effect bias of mean brood density, decreased logarithmicly on sampling unit size for all unit shapes (rows 5, 11, 17 and 23 in Table I). The graphical form of the $\underline{L_c}$ vs. sampling unit shape and size relationship is shown on Figure 8 and the regression equations, on arithmetic scale (the equations were fitted by the method of least squares after logarithmic transformation of both axes), correlation coefficients and standard error of estimates are shown in columns 3, 4 and 5 of Table II, respectively. The least squares equations have high correlation coefficients and their parameters are in good agreement with those of the corresponding theoretical equations which appear in column 2 of Table II. (Note: The theoretical equations were derived from formulae X to XII by substituting 2.4 x 5.5 square millimeters for A_i (the actual width-length dimensions of the "stamped" larvae of Figure 5.)). The "t"-test

TABLE I. STATISTICS FOR THE EXPERIMENTAL DETERMINATION OF THE $L_c(\%)$ VS. SAMPLING UNIT SHAPE AND SIZE RELATIONSHIP.

	Sampling unit size (sq. in.)					Row no.
	n	2	4	8	12	16	
Circular units							
Mean no. of larvae inside s. unit boundaries ($\bar{I}$)	100	1.510	3.100	6.220	9.080	12.890	1
Mean no. of larvae on s. unit circumference ($\bar{C}$)	100	0.650	0.990	1.100	1.470	1.550	2
$\bar{I} + \bar{C}/2 = \bar{x}$	100	1.835	3.605	6.765	9.825	13.665	3
$s_{\bar{x}}$	100	0.110	0.134	0.220	0.244	0.295	4
$L_c(\%)$	100	17.934	14.008	7.988	7.583	5.671	5
$s_{L_c(\%)}$	100	3.830	3.480	2.710	2.640	2.310	6
Square units							
Mean no. of larvae inside s. unit boundaries ($\bar{I}$)	100	1.430	3.030	5.980	9.080	12.150	7
Mean no. of larvae on s. unit circumference ($\bar{C}$)	100	0.710	1.000	1.290	1.480	1.780	8
$\bar{I} + \bar{C}/2 = \bar{x}$	100	1.785	3.530	6.625	9.820	13.665	9
$s_{\bar{x}}$	100	0.110	0.125	0.228	0.238	0.310	10
$L_c(\%)$	100	20.112	14.164	9.736	7.488	6.825	11
$s_{L_c(\%)}$	100	4.000	3.480	3.100	2.630	2.520	12
Rectangular units (w/l = 0.25, long sides perpendicular to egg galleries)							
Mean no. of larvae inside s. unit boundaries ($\bar{I}$)	100	1.200	2.710	5.740	8.950	12.100	13
Mean no. of larvae on s. unit circumference ($\bar{C}$)	100	0.810	1.100	1.530	1.820	2.210	14
$\bar{I} + \bar{C}/2 = \bar{x}$	100	1.650	3.260	6.505	9.860	13.205	15
$s_{\bar{x}}$	100	0.083	0.147	0.184	0.193	0.236	16
$L_c(\%)$	100	24.848	16.870	11.680	9.220	8.360	17
$s_{L_c(\%)}$	100	4.310	3.750	3.170	2.880	2.760	18
Rectangular units (w/l = 0.25, long sides parallel to egg galleries)							
Mean no. of larvae inside s. unit boundaries ($\bar{I}$)	100	1.260	2.720	5.400	8.940	12.050	19
Mean no. of larvae on s. unit circumference ($\bar{C}$)	100	0.830	1.070	1.580	2.120	2.420	20
$\bar{I} + \bar{C}/2 = \bar{x}$	100	1.675	3.250	6.190	10.000	13.260	21
$s_{\bar{x}}$	100	0.146	0.211	0.259	0.294	0.338	22
$L_c(\%)$	100	25.000	16.436	12.762	10.600	9.125	23
$s_{L_c(\%)}$	100	4.320	3.700	3.340	3.070	2.880	24

n = sample size, $s_{\bar{x}}$ = standard error of $\bar{x}$, s_{L_c} = standard error of $L_c(\%)$ and $L_c\%$ was calculated as in equation (45), Materials and Methods section.

comparison of the slopes (on log - log scale but powers on arithmetic scale) of the least squares equations and their corresponding theoretical models indicated that there were no significant differences (column 6, Table II). Also, there is excellent correspondence between the constants (intercepts on log - log scale) of the least squares equations and those of the corresponding theoretical models. Figure 8 shows that, for all sampling unit sizes, rectangular units with long sides orientated parallel to the egg galleries (V) have the greatest edge effect bias and circular units the smallest. Square and rectangular units orientated with long sides perpendicular to egg galleries (H) have edge effect biases intermediate between those given by circular units and rectangular units of (V) orientation. The edge effect bias of mean brood density decreases rapidly with increasing sampling unit size from zero to about twelve square inches, for all sampling unit shapes. For sampling units greater than about twelve square inches, the change in $\underline{L_c(\%)}$ with respect to sampling unit size becomes more gradual. $\underline{L_c(\%)}$ and $\underline{c/a}$ (equations IV to VI) are both proportional to the reciprocal of the square root of sampling unit size and, therefore, the former variable is a linear function of the latter variable with zero intercept. Thus, edge effect bias is directly proportional to the circumference/area ratio of the sampling units.

1.3. Studies of the effect of sampling unit size and shape on the accuracy of mean brood density estimates. The effect of sampling unit shape and size on the accuracy of mean brood density estimates was studied by analysis of variance of the brood counts at two density levels, i.e. on the northern and southern aspects of the sample trees (for sample design see section 4.1. and Fig. 2., Materials and Methods) and the results are given in Tables III and IV.

TABLE II. THEORETICAL AND EXPERIMENTAL RELATIONS BETWEEN $L_c\%$, THE EDGE EFFECT BIAS OF MEAN DENSITY AND SAMPLING UNIT SIZE.

Sampling unit	Theoretical model	Least squares model			
		Equation	r	$s_{x.y}$	t.05
(1)	(2)	(3)	(4)	(5)	(6)
Circle	$L_c\% = 25.70\ A_s^{-.5}$	$L_c\% = 27.00\ A_s^{-.552}$	0.987	0.0393	0.977^{ns}
Square	$L_c\% = 28.60\ A_s^{-.5}$	$L_c\% = 29.30\ A_s^{-.534}$	0.998	0.0240	1.110^{ns}
Rectangle, long side parallel to egg gallery (V)	$L_c\% = 35.75\ A_s^{-.5}$	$L_c\% = 33.80\ A_s^{-.468}$	0.996	0.0334	1.170^{ns}
Rectangle, long side perpendicular to egg gallery (H)		$L_c\% = 35.60\ A_s^{-.532}$	0.998	0.0199	0.712^{ns}

ns = not significant, r = simple correlation coefficient, $s_{x.y}$ = standard error of estimate, t = Student's parameter.

In the analysis of variance table the sampling units are designated by the following symbols: 6.25 sq. in. square unit = 21, 36,00 sq. in. square unit = s2, 20.10 sq. in. circular unit = c1, 56.45 sq. in. circular unit = c2, 72.00 sq. in. rectangular unit, long side perpendicular to egg galleries = r_h, 86.40 sq. in. rectangular unit, long sides parallel to egg galleries = r_v and half circumference by 14.4 inch "control" unit = cyl.

The analysis of variance shows that there were highly significant tree-to-tree (replication) and aspect differences in brood counts. Of the pre-planned single degree of freedom comparisons of the sampling units, however, only those two comparisons were significant which involved the sampling unit s_1. These comparisons were significant at the 5% probability level. Although, the "control" (cyl) vs. rest comparison of the sampling units was not significant it had a high "F"-value ($F = 3.77$ as compared to $F_{0.05} = 3.84$). Reference to Table IV shows that the significance of the two comparisons involving sl and the high "F"-value of the cyl vs. rest comparison resulted from the high mean brood density estimate given by smallest unit (sl), relative to that of the other units. The aspect-sampling unit size interaction was not significant indicating that the change in brood counts with respect to the two density levels (aspects) was approximately the same for all sampling unit shape-size combinations considered in the sample survey.

1.4. Studies of the effect of sampling unit shape, size and orientation on the percision of mean brood density estimates. The relationship between sampling variance and sampling unit size, for various

TABLE III. ANALYSIS OF VARIANCE OF THE EFFECT OF VARIOUS SAMPLING UNIT SHAPE-SIZE COMBINATIONS ON BROOD COUNTS PER SQUARE FOOT ($LOG_{10}(x + 1)$ TRANSFORMATION).

Source of variation	Df	Net sum squares	Mean squares	F	$F_{.05}$	$F_{.01}$	Remark
1 Trees (Blocks)	44	68.9340	1.5667	14.01	1.38	1.46	**
2 Treatments	(13)	(10.7636)					
Aspects (a)	1	7.3426	7.3426	65.68	3.84	6.63	**
Sampling units (u)	(6)	(2.3174)					
cyl vs. rest	1	.4320	.4320	3.77	"	"	ns
sl vs. s^2	1	.6848	.6848	5.16	"	"	*
cl vs. c^2	1	.4010	.4010	3.58	"	"	ns
r_h vs. r_v	1	.0382	.0382	0.35	"	"	ns
clc2 vs. $r_h r_v$	1	.2573	.2573	2.30	"	"	ns
sls2 vs.$(clc2 + r_h r_v)$	1	.5110	.5110	4.57	"	"	*
(a)(u)	6	1.0172	.1695	1.52	"	"	ns
3 Error	572	63.9491	.1118				
Total	629	143.6467					

** = significant at the p = 0.01 probability level, * = significant at p = 0.05 probability level, ns = not significant.

TABLE IV. AVERAGE BROOD DENSITY PER SQUARE FOOT.

Sampling unit size (sq. in.)	Sampling unit shape	n	Average brood density per sq. ft.
6.25	square (sl)	90	112.05
20.10	circular (cl)	90	101.52
36.00	square (s2)	90	105.00
56.45	circular (c2)	90	104.50
72.00	rectangular (r_h)	90	103.71
86.40	rectangular (cyl)	90	99.94
14.4 x half circumference	rectangular (r_v)	90	103.00

n = sample size.

sampling unit shapes and two orientations, is shown on Figure 9. (Note: The sampling variance vs. sampling unit size relationship was studied on the same set of sampling units and samples which were used for the experimental determination of $\underline{L_c}$ in section 1.2. of the Experimental Results.)

For sampling units smaller than about 6 square inches, there were no differences between the variances of the density estimates given by the square, and circular units and those rectangular units which were oriented with long axes perpendicular to the egg galleries (marked with H on Figure 9). For units larger than 6 square inches, however, rectangular units of H orientation gave consistently smaller variances for the density estimates than either the circular or square units. The rectangular units, which were oriented with long axes parallel to the egg galleries (marked with V on Figure 9), gave consistently higher variances for the density estimates, for the entire size-range investigated.

The sampling variance vs. sampling unit size relationships on Figure 9 were well described by the following linear regression equations:

$$\log_{10} s^2/\text{sq.ft.} = 4.4104 - 1.1700 \log_{10} x, \quad r^2 = 0.99,$$

$s_{\bar{x}} = 0.0208$ (rectangular units, V orientation)

$$\log_{10} s^2/\text{sq.ft.} = 4.0010 - 1.0967 \log_{10} x, \quad r^2 = 0.97,$$

$s_{\bar{x}} = 0.2680$ (rectangular units, H orientation)

$$\log_{10} s^2/\text{sq.ft.} = 4.0324 - 0.9725 \log_{10} x, \quad r^2 = 0.98,$$

$s_{\bar{x}} = 0.1650$ (square units)

$$\log_{10} s^2/\text{sq.ft.} = 4.0779 - 1.0409 \log_{10} x, \quad r^2 = 0.98,$$

$s_{\bar{x}} = 0.2222$ (circular units)

Where, s^2 = variance, x = sampling unit size in sq. in. units, r = simple correlation coefficient and $s_{\bar{x}}$ = standard error of estimate on logarithmic scale.

These sampling variance formulae were used, in conjuction with the population mean of the spatial pattern map (118.77 larvae/sq. ft.), for calculating sample size needed to establish the population mean with a half confidence belt equal to 0.1$\bar{x}$ and a probability level, p = 0.99 (section 4.2.1., Materials and Methods). The graphical form of the sample size vs. sampling unit size relationship is shown on Figure 10.

The sample size-sampling unit size graphs show that, for any fixed unit size, rectangular units of H orientation were superior to square and circular units and to rectangular units of V orientation, for the entire sampling unit size-range investigated.

Comparison to the relative efficiencies (section 4.2.2., Materials and Methods) of various sampling unit shapes and orientations on two population maps confirmed these findings (Table V).

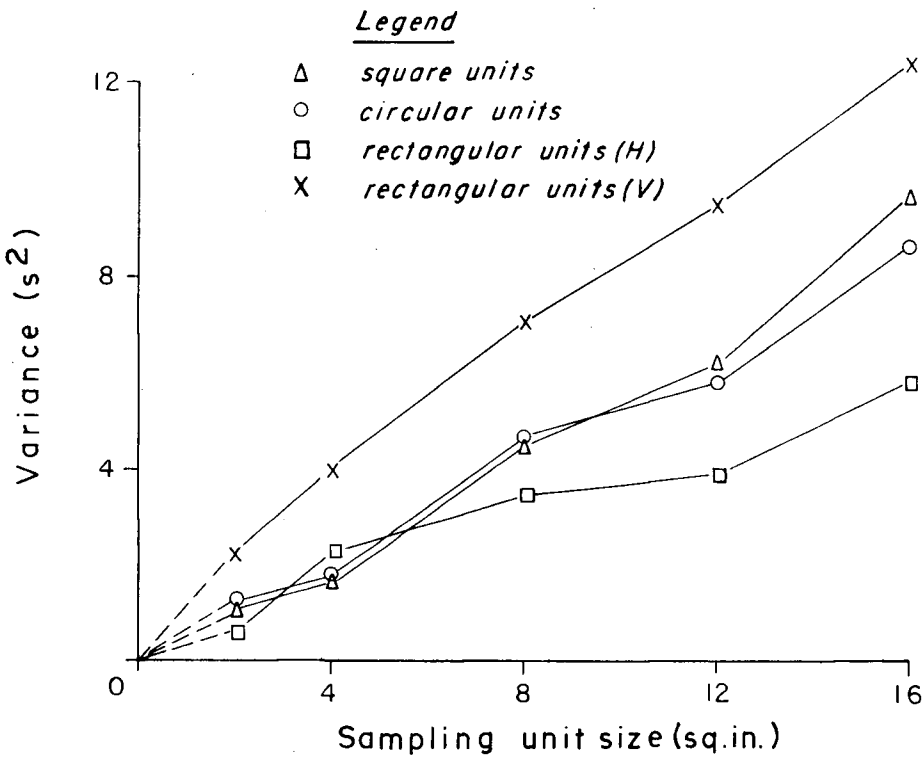
The relative efficiency of the 1 x 32, 1 x 16, and 1 x 8 inch units, when oriented with long sides perpendicular to the egg galleries, were consistently higher than that of any other unit, in their respective groups. The lowest relative efficiencies were given by the 2 x 16, 2 x 8, 2 x 4 and 4 x 8 inch units (long sides oriented parallel to egg galleries) posibly because clumping was present in the population on several scales. Moreover, at the higher brood density level (Map No. 1) there was considerably less difference between the relative efficiencies of the different sampling unit shapes and orientations than at low density level (columns 4 and 6, Table V).

Figure 9.

Relationship between precision of mean brood density estimates and sampling unit size for various sampling unit shapes.

Figures 10.

Relationship between sample size needed to establish the mean with a half confidence belt of $0.1\bar{x}$ and a probability level, $p = 0.01$, and sampling unit size for various sampling unit shapes.


Legend
square units
circular units
rectangular units (H)
rectangular units (V)
Variance (s2)
12
8
4
0
4
8
12
16
Sampling unit size (sq.in.)

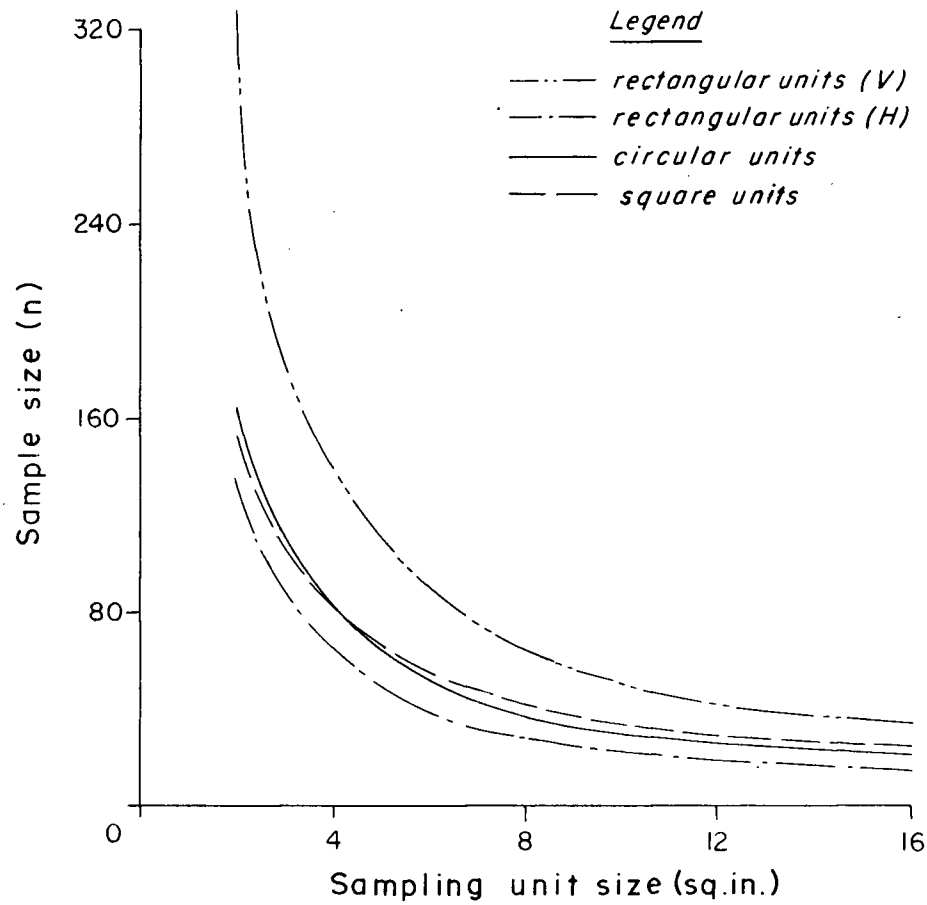

Legend
rectangular units (V)
rectangular units (H)
circular units
square units
Sample size (n)
320
240
160
80
0
4
8
12
16
Sampling unit size (sq.in.)

TABLE V. EFFECT OF SAMPLING UNIT SHAPE AND ORIENTATION ON RELATIVE EFFICIENCY

Sampling unit dimensions (in.)	Orientation	Map No.1*		Map No.2*	
		S^2	RE(%)**	S^2	RE(%)**
(1)	(2)	(3)	(4)	(5)	(6)
	32 square inch sampling units				
1 x 32	Long sides parallel	180.96	100	44.06	100
2 x 16	to egg galleries	264.36	72	56.73	78
4 x 8		275.23	69	47.81	94
$\sqrt{32}$ x $\sqrt{32}$		248.89	76	34.33	128
4 x 8	Long sides perpen-	242.60	78	31.75	139
2 x 16	dicular to egg	191.98	99	16.30	271
1 x 32	galleries	129.16	147	13.18	338
	16 square inch sampling units				
1 x 16	Long sides parallel	79.10	100	24.67	100
2 x 8	to egg galleries	105.96	75	24.69	100
4 x 4		89.42	89	21.27	114
2 x 8	Long sides perpendi-	77.70	102	14.88	166
1 x 16	cular to egg galleries	63.30	125	6.60	374
	8 square inch sampling units				
1 x 8	Long sides parallel	38.72	100	11.31	100
2 x 4	to egg galleries	45.56	84	9.68	117
$\sqrt{8}$ x $\sqrt{8}$		34.86	111	8.48	134
2 x 4	Long sides perpendi-	31.83	121	6.64	173
1 x 8	cular to egg galleries	25.64	150	3.99	284

* Maps No.s 1 and 2 had 1.21 and 0.27 larvae per square inch, respectively. ** The relative efficiencies (RE) of the 32, 16 and 8 square inch units were calculated relative to the 1 x 32, 1 x 16 and 1 x 8 inch units (long sides parallel to egg galleries), respectively. S^2 = variance.

These results, in general, are in agreement with those of the previous study, namely, that long, narrow rectangular units, when oriented with long sides perpendicular to the egg galleries, are superior to square and circular units and to rectangular units oriented with long sides parallel to egg galleries and the efficiency of the former units increases with decreasing w/l ratio.

The conclusions reached in this section regarding the importance of orientation, when sampling with rectangular units, were also supported by field data. The coefficient of variation (CV), on square foot basis, of the sampling units which were used for studies of accuracy in section 1.3., are given in Table VI.

TABLE VI. EFFECT OF SAMPLING UNIT SIZE AND ORIENTATION ON COEFFICIENT OF VARIATION (FIELD SAMPLE. ELK CREEK, 1964).

Sampling unit size (sq.in.)	Sampling unit shape	Number of units	CV%(north side)	CV%(south side)
(1)	(2)	(3)	(4)	(5)
6.25	square (S1)	45	61.56	92.10
20.10	circular (C1)	45	59.44	76.62
36.00	square (S2)	45	51.17	71.41
56.45	circular (C2)	45	51.32	64.29
72.00	rectangular (H)	45	50.04	59.30
86.40	rectangular (V)	45	52.46	68.23
14.4 inches x half circumference	rectangular(cyl)	45	50.61	54.34

CV decreased on both the north and the south sides, with increasing sampling unit size for all unit shapes up to 86.4 square inches. The coefficient of variation of the 86.4 square inch rectangular unit (w/l = 0.5), with long sides oriented parallel to the egg galleries, was considerably higher than that of the 72.0 square

inch unit (w/l = 0.5) with long sides oriented perpendicular to the egg galleries, in spite of the greater size of the former unit (52.46 vs. 50.04 in column 4 and 68.23 vs. 59.30 in column 5, Table VI). (Note: As the effects of shape and size were confounded in this study, the CV figures in Table VI contain a "shape" component which cannot be separated from the "size" component).

1.5. Analysis of the distributional pattern of attacks and late larval stages of the mountain pine beetle with Morrisita's Id index of dispersion. (Note: The spatial pattern of attacks and broods were analysed on the same sampling units (and on the same field samples) which were used for studying sampling accuracy in section 1.3. of the Experimental Results.)

The Id vs. sampling unit graphs for attacks and brood are shown on Figures 11 and 12, respectively. The significance of the departure from randomness of the Id values (which were tested as in equations 6 and 7, of the Materials and Methods) are given in Table VII.

TABLE VII. TESTS OF RANDOMNESS OF ATTACKS AND BROOD BY MORISITA'S Id INDEX OF DISPERSION.

Sampling unit size (sq. in.)	Sampling unit shape	Attacks		Brood	
		Id	Remark	Id	Remark
(1)	(2)	(3)	(4)	(5)	(6)
6.25	square (S1)	.3845	**	1.2600	**
20.10	circular (C1)	.8348	**	1.3480	**
36.00	square (S2)	.9982	ns	1.3457	**
56.45	circular (C2)	1.0364	ns	1.3079	**
72.00	rectangular (r_h)	1.0278	ns	1.2724	**
86.40	rectangular (r_v)	1.0944	**	1.3367	**
(14.4 inch x half circumference)	(rectangular (cyl))	(1.0693)	(**)	(1.2579)	(**)

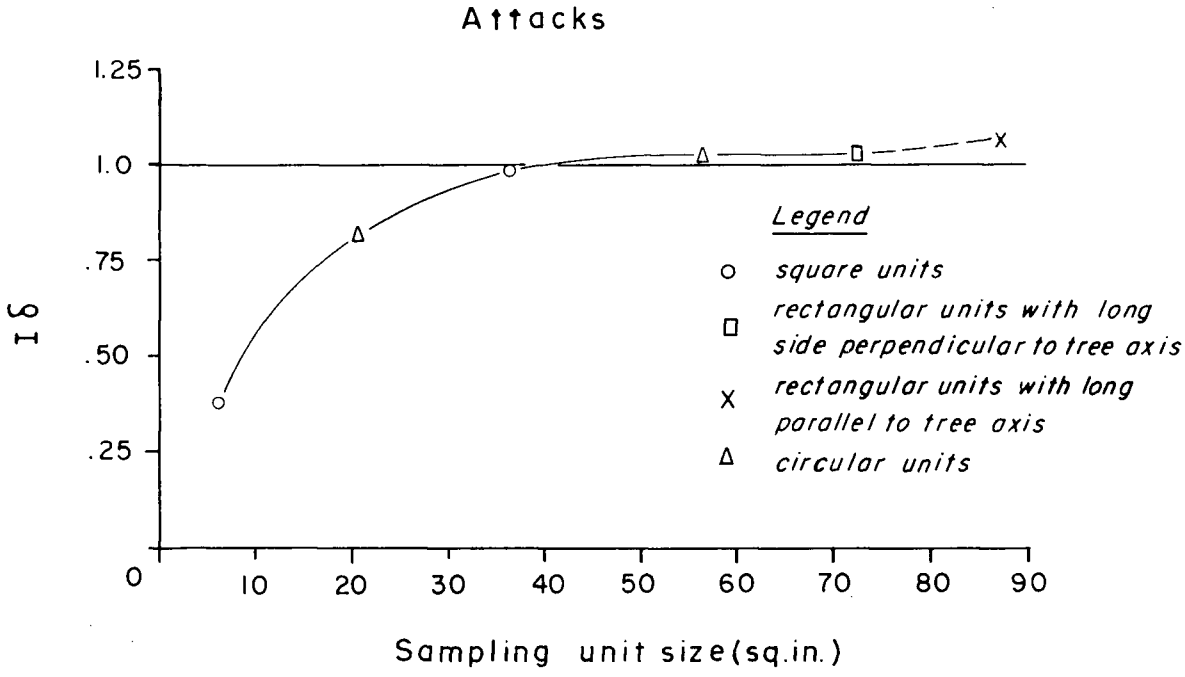
** = significant at p = 0.01 probability level, ns = not significant

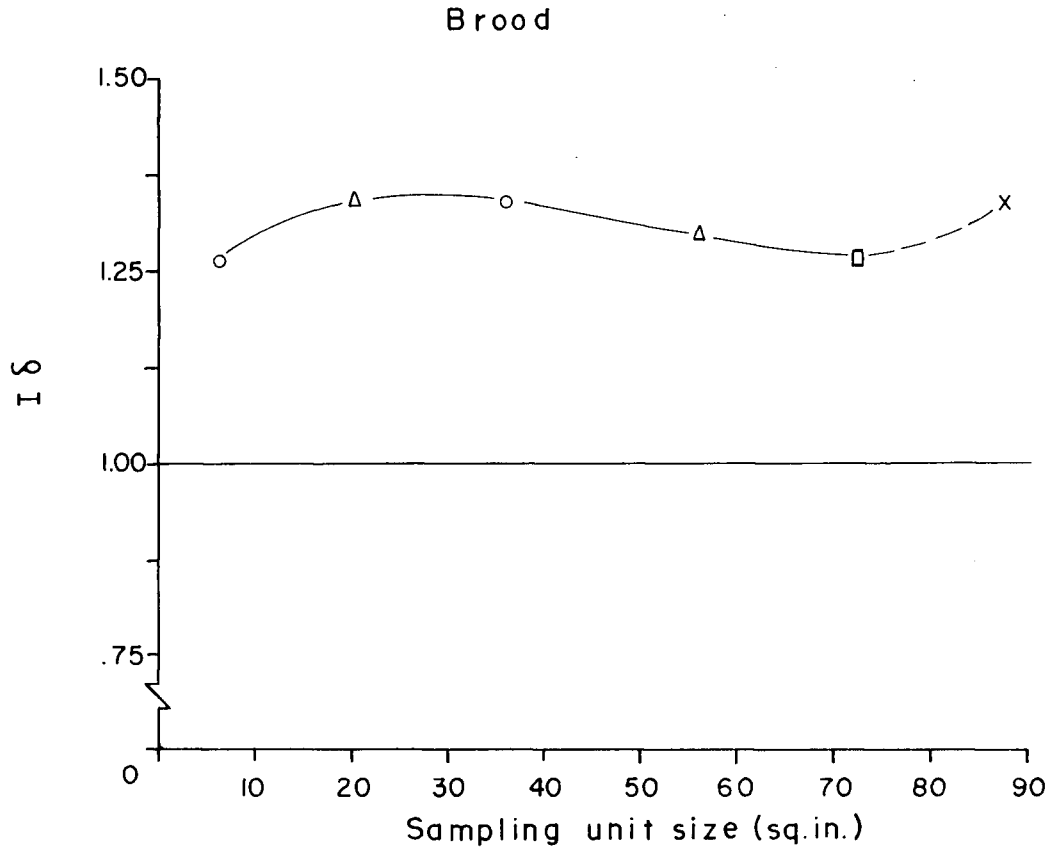
Figures 11.

Relationship between Morisita's index of dispersion and sampling unit shape and size for attacks of the mountain pine beetle.

Figure 12.

Relationship between Morisita's index of dispersion and sampling unit shape and size for mountain pine beetle brood in late larval stages of development.


Attacks
1.25
1.0
.75
.50
.25
0
10
20
30
40
50
60
70
80
90
SI
Sampling unit size(sq.in.)
Legend
square units
rectangular units with long side perpendicular to tree axis
rectangular units with long parallel to tree axis
circular units


Brood
1.50
1.25
1.00
.75
0
10
20
30
40
50
60
70
80
90
SI
Sampling unit size (sq.in.)

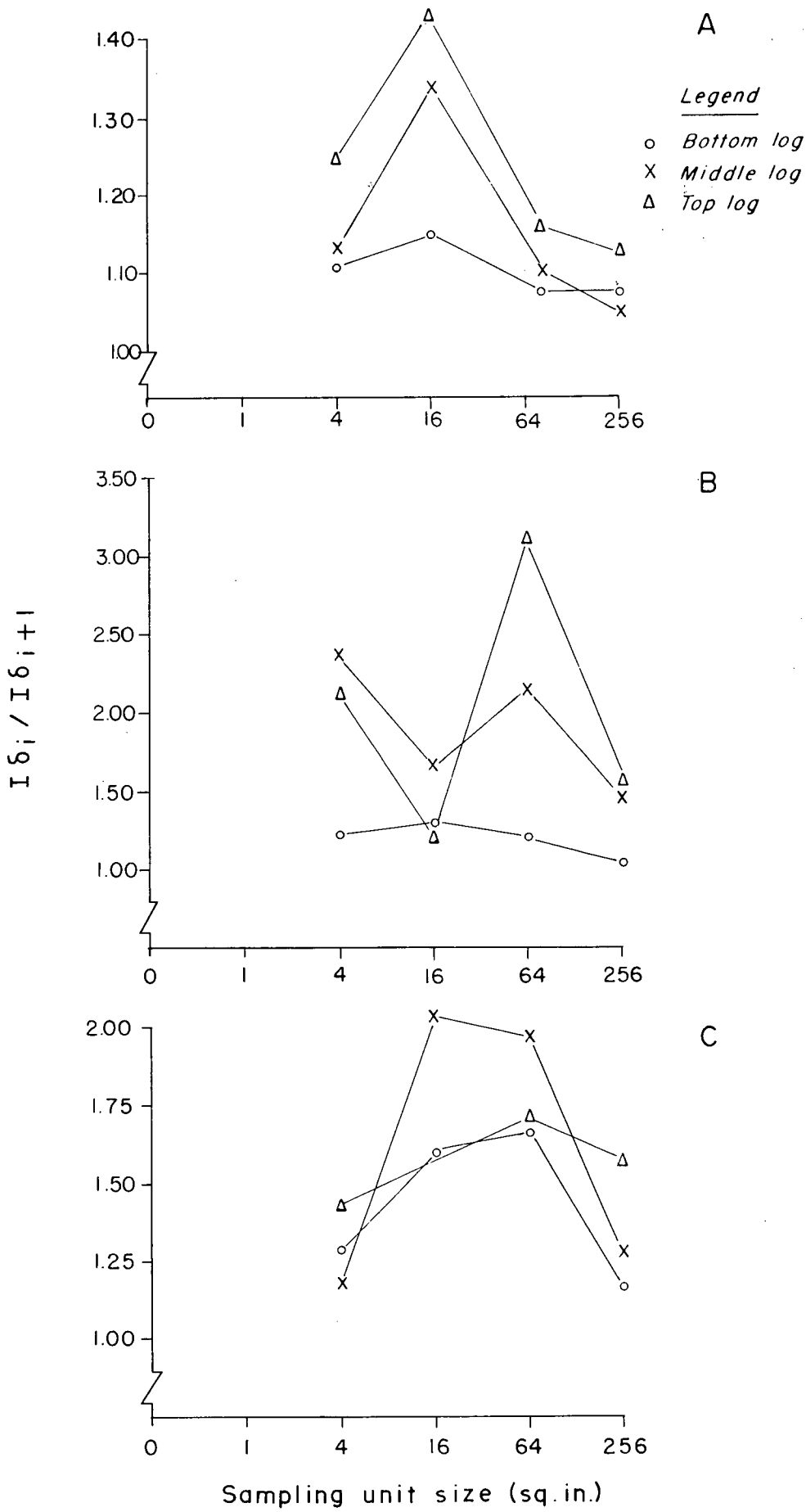
For attacks, the Id vs. sampling unit size graphs increased to unity with increasing sampling unit size (Fig. 11). The dispersion indices of the two smallest units were significantly smaller, while those of the two biggest units were significantly greater than unity (columns 3 and 4, Table VII). These findings indicate that attacks tend to form regular spatial arrangements on the bark surface of infested trees at fixed height levels. On the other hand, the distribution of larvae appeared contagious and these spatial pattern clumped, for all sampling unit shape-size combinations investigated (column 5 and 6, Table VII). The Id vs. sampling unit size curve for brood had a peak between 20.1 and 36.0 square inches suggesting that the average size of the clumps was within this range (Fig. 12).

1.6. Determination of mean larval clumps size and clump dimensions with Morisita's Id_i/Id_{i+1} method (section 4.2.3., Materials and Methods). The Id_i/Id_{i+1} vs. sampling unit size graphs, for the nine population maps used in the study (section 4.1., Materials and Methods), are shown on Figure 13. These graphs indicate that clump size varied from 4 to 64 square inches within a single tree (Fig. 13B) and that the tree to tree clump size variation was also of the same magnitude. The most frequently indicated clump sizes were 16 and 64 square inches. The prominence of peaks on each of the three sets of graphs (A, B and C, Fig. 13) were inversely proportional to mean density suggesting that the spatial pattern of larvae became more regular with increasing mean larval density.

Studies of clump dimensions, using Morisita's Id_i/Id_{i+1} method on two population maps (which were totally sampled with a series of

Figure 13.

Determination of mean larval clump size. (Graphs A, B, and C represent mean larval clump size determinations from three different trees).

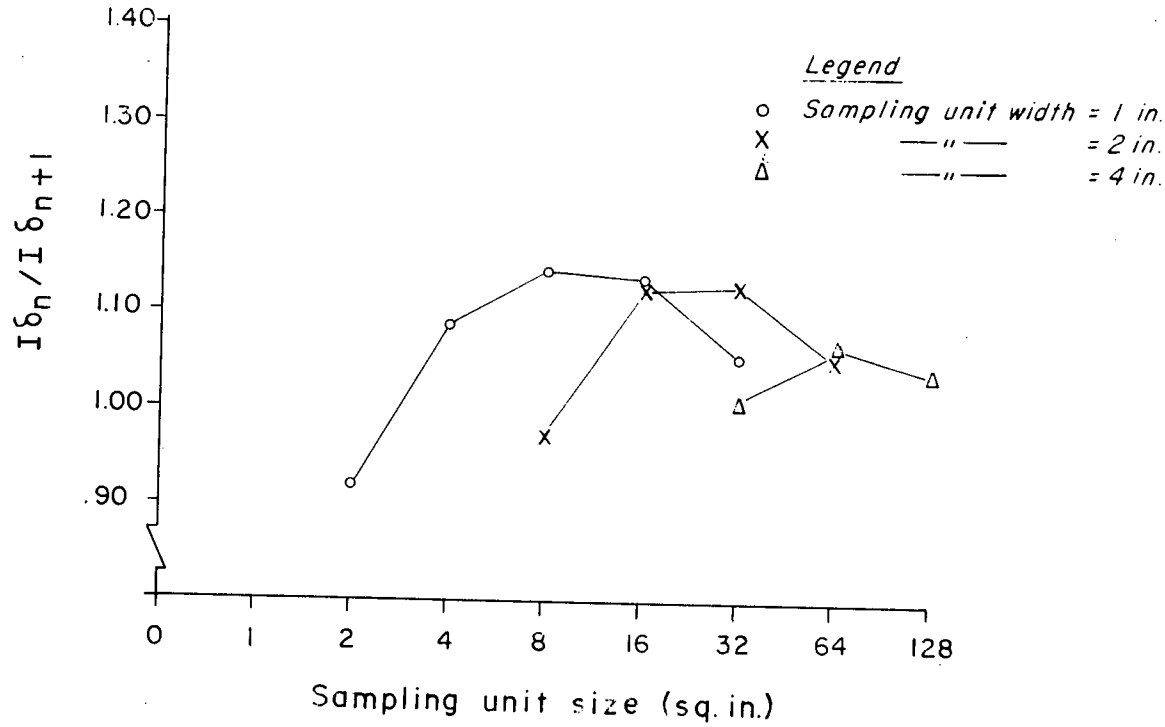

A
B
C
Legend
Bottom log
Middle log
Top log
1.40
1.30
1.20
1.10
1.00
3.50
3.00
2.50
2.00
1.50
1.00
2.00
1.75
1.50
1.25
1.00
0
1
4
16
64
256
I6i / I6i+1
Sampling unit size (sq. in.)

rectangular units with long sides oriented parallel to egg galleries. Section 4.1., Materials and Methods), showed that the most prominent peaks on the $\underline{Id_i/Id_{i+1}}$ vs. unit size graphs were obtained with sampling units having 1 or 2 inch short sides (Fig. 14). This suggests that the average length of the short axis of larval clumps was between 1 and 2 inches. As the peaks were located at the 8 and 16 square inch points for units with 1 inch short sides, and at the 16 and 32 square inch points for units with 2 inch short sides, the average long axis of the larval clumps was between 8 and 16 inches. Several clump sizes (peaks) were indicated on the $\underline{Id_i/Id_{i+1}}$- sampling unit size graphs because clumping occured on several scales. For example, on Map No.1, in addition to the basic clump size (1 by 8 inches), larger clumps with the following dimensions were also present: 1 x 16, 2 x 8, 2 x 16 and 4 by 16 inches.

1.7. Studies of the relationship between sampling time and sampling unit size and determination of optimum sampling unit size for rectangular units (w/l = 0.5 and long sides oriented perpendicular to egg galleries). The relationship between the various components of total sampling time (section 4.1., Materials and Methods) and sampling unit size are shown on Figure 15. The graphs show total sampling time broken down into components dictated by the sampling operation. At both height levels the most time consuming operations were de-barking and brood counting, and sampling unit delineating and cutting. Up to about 26 square inches, sampling unit delineation and cutting required more time than de-barking and subsequent counting of mountain pine beetle brood. The relationship between sampling time and sampling unit size was curvi-

Figure 14.

Determination of the average width and length of larval clumps. (Top and bottom graphs represent larval densities of 1.21 and 0.27 per sq. in., respectively.)


Legend
Sampling unit width = 1 in.
" = 2 in.
" = 4 in.
1.40
1.30
1.20
1.10
1.00
.90
$I\delta_n / I\delta_{n+1}$
0
1
2
4
8
16
32
64
128
Sampling unit size (sq. in.)

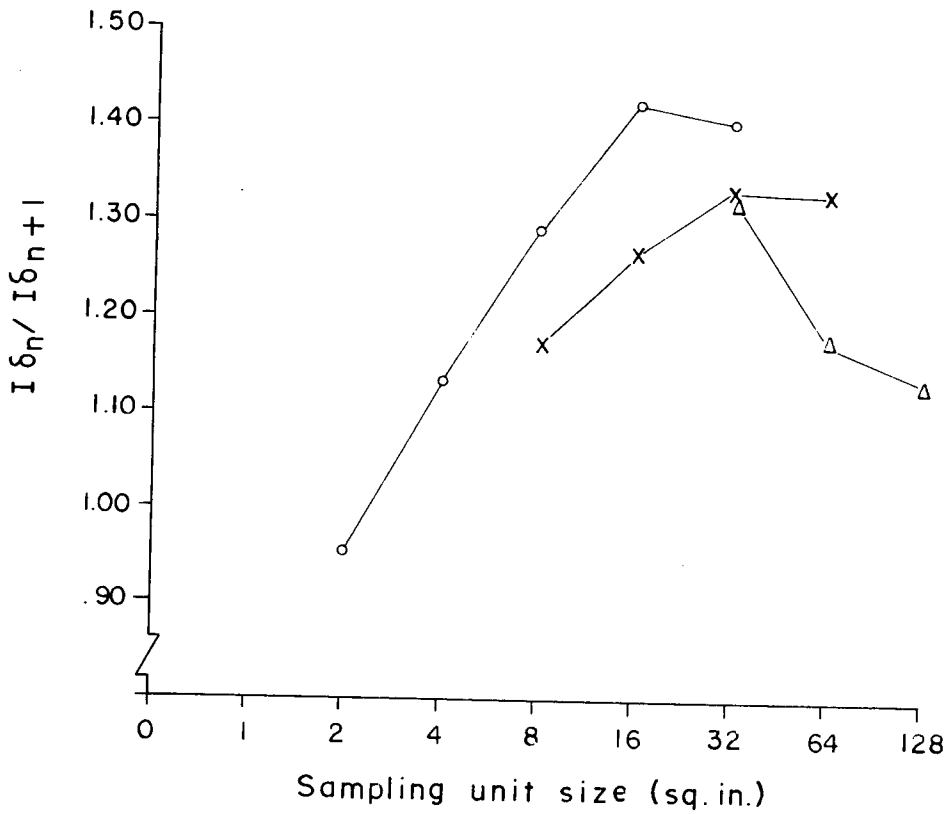
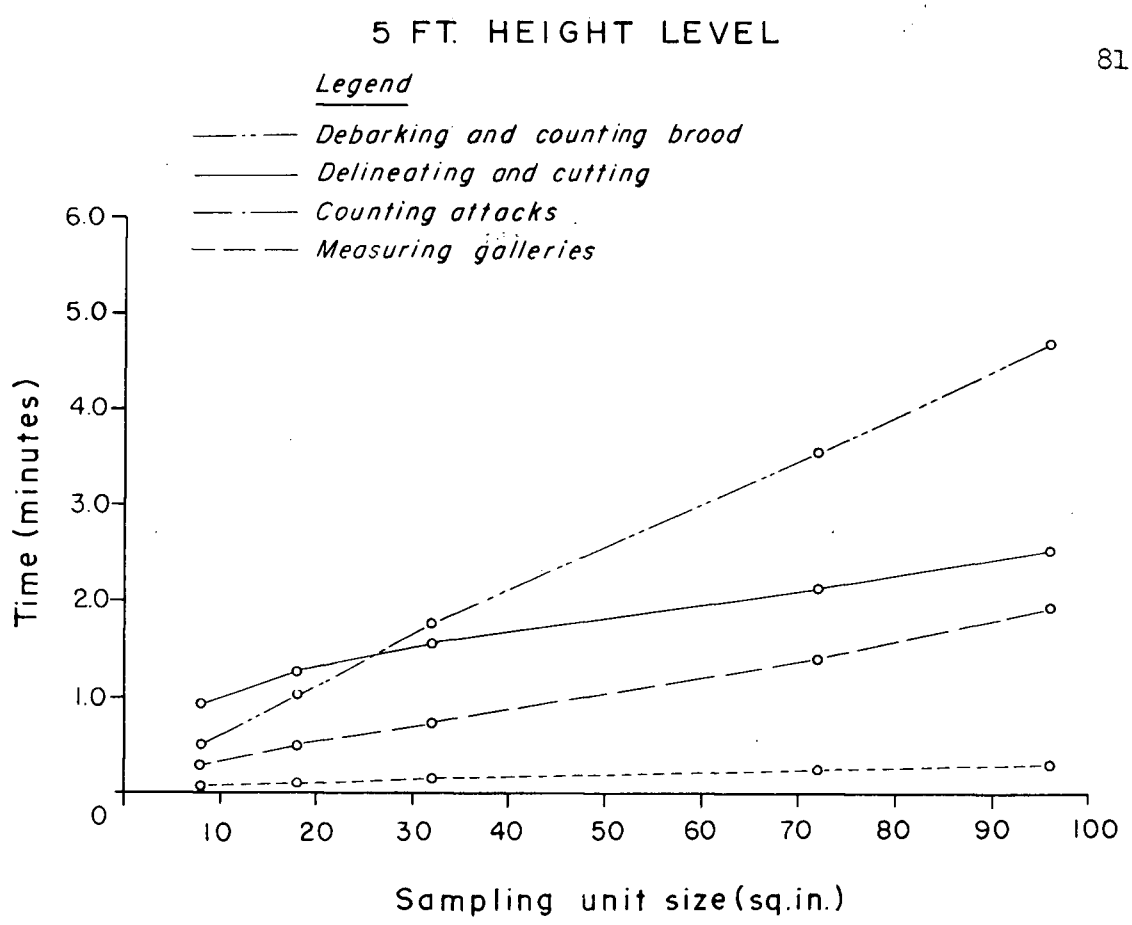
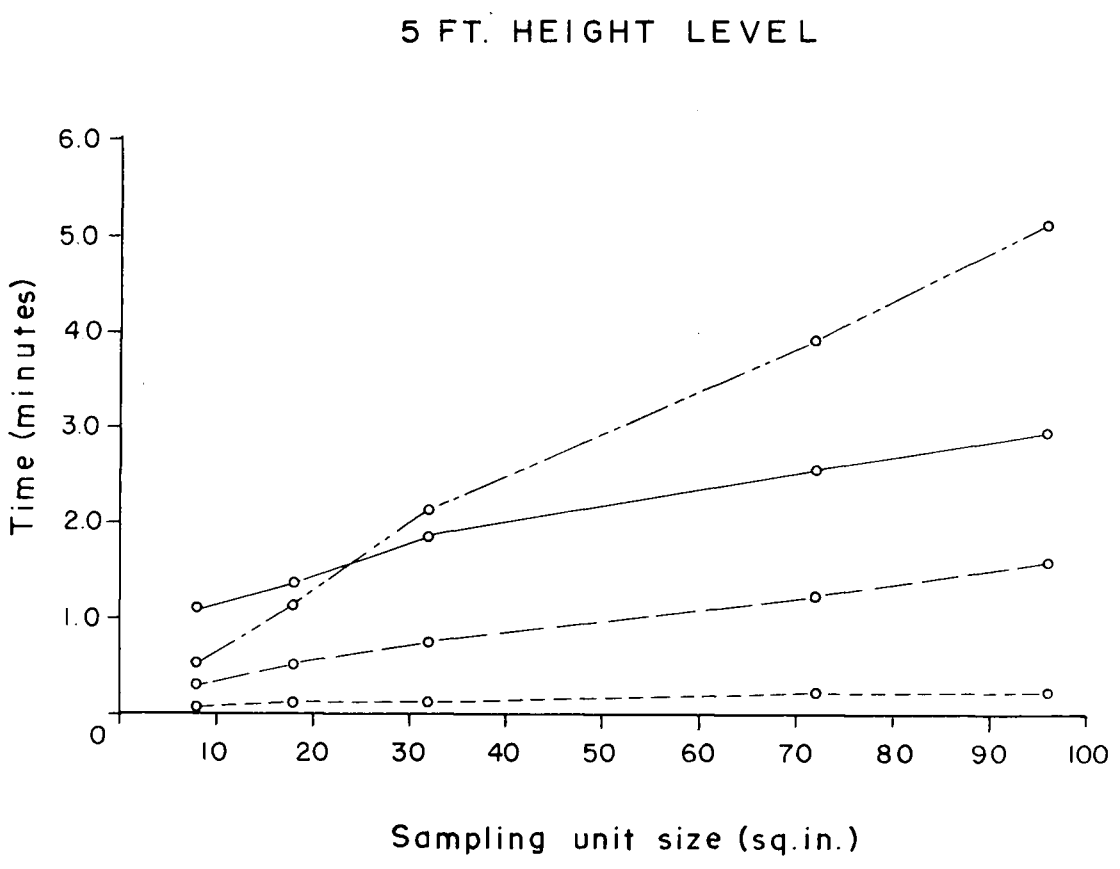

1.50
1.40
1.30
1.20
1.10
1.00
.90
$I\delta_n / I\delta_{n+1}$
0
1
2
4
8
16
32
64
128
Sampling unit size (sq. in.)

Figure 15.

Time needed to carry out various components of the sampling operation versus sampling unit size relationship.


5 FT. HEIGHT LEVEL
Legend
Debarking and counting brood
Delineating and cutting
Counting attacks
Measuring galleries
Time (minutes)
6.0
5.0
4.0
3.0
2.0
1.0
0
10
20
30
40
50
60
70
80
90
100
Sampling unit size (sq.in.)


5 FT. HEIGHT LEVEL
Time (minutes)
6.0
5.0
4.0
3.0
2.0
1.0
0
10
20
30
40
50
60
70
80
90
100
Sampling unit size (sq.in.)

linear for all four components of the total sampling operation. Surprisingly, it took less time to sample a unit area of larger units than that of smaller units. Time "wasted" on tool handling and data recording is not shown on Figure 15. Averages of 2.700 and 4.157 minutes were spent on these "non-sampling" operations at the 5, 15 foot levels, respectively.

The regressions of total sampling time (including "time wasted") on sampling unit size was linear at both height levels (Fig. 16). Sample size, mean sampling time and its standard error for the sampling units are summarized in Table VIII.

TABLE VIII. STATISTICS FOR THE SAMPLING TIME VS. SAMPLING UNIT SIZE RELATIONSHIP

Sampling unit size (sq. in.)	Numbers of observations (n)	Mean sampling time ($\bar{x}$) in minutes	$S_{\bar{x}}$(min.)
	5 foot height level		
(1)	(2)	(3)	(4)
8	20	4.247	0.057
18	20	5.579	0.077
32	20	6.894	0.125
72	20	10.066	0.276
98	12	12.256	0.723
	15 foot height level		
8	12	6.677	0.113
18	12	7.128	0.178
32	12	9.398	0.280
72	12	12.050	0.401
98	12	14.599	0.402

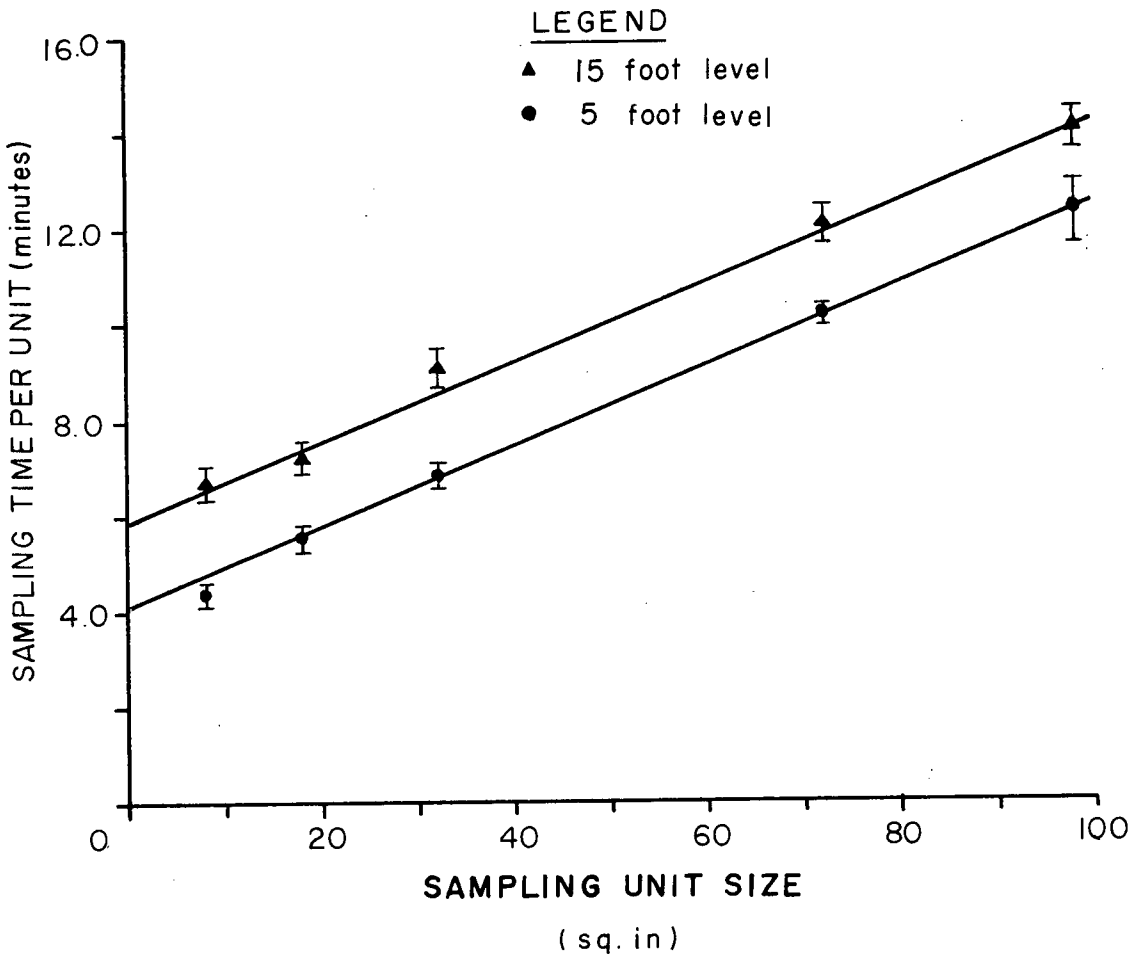
The least squares regression equations of total sampling time/unit on sampling unit size had the following form:

$$T = 4.032 + 0.084A_s,\ r = .93,\ n = 92,\ S_{\bar{x}} = 1.095$$

for the 5 foot level and

Figure 16.

Relationship between sampling time and sampling unit size at two height levels on the infested stem. (The vertical lines represent the size of the following expression: $\bar{x} \pm 1s_{\bar{x}}$)


LEGEND
15 foot level
5 foot level
16.0
12.0
8.0
4.0
0
20
40
60
80
100
SAMPLING TIME PER UNIT (minutes)
SAMPLING UNIT SIZE
(sq. in)

$$T = 5.794 + 0.084A_s,\ r = .94,\ n = 60,\ S_{\bar{x}} = 1.020$$

for the 15 foot level, where, T = total sampling time/unit in minutes, A_s = sampling unit size in square inches and r = simple correlation coefficient (on Figure 16, only the mean total times were plotted over sampling unit size (column 3, Table VIII) but the equations were fitted to the individual observations). The equations had identical slopes but different intercepts because at the 15 foot level more time was needed for non-sampling operations than at the 5 foot level.

The mean and variance estimates and sample sizes, to establish the population mean of brood counts with a half confidence belt equal to $0.1\bar{x}$ and a probability level of 0.99, are given in Table IX for each sampling unit at both height levels. Reference to Table IX indicates that the variability of brood counts was greater at the 5 foot level than at the 15 foot level and consequently a larger sample size was needed at the former height level, for all considered sampling unit sizes, than at the 15 foot height level (columns 4 and 7, Table IX).

TABLE IX. MEAN AND VARIANCE ESTIMATES AND SAMPLE SIZE FOR LATE LARVAL STAGE BROOD AT TWO HEIGHT LEVELS BY FIVE SAMPLING UNITS.

	5 foot level			15 foot level		
Sampling unit size (sq. in.)	$\bar{x}$*	s^2	n	$\bar{x}$*	s^2	n
(1)	(2)	(3)	(4)	(5)	(6)	(7)
8	3.700	12.326	360	1.583	4.265	676
18	7.050	29.629	239	4.166	8.697	200
32	16.200	158.589	242	5.583	15.356	196
72	28.400	421.300	210	18.833	157.605	176
98	34.916	663.174	215	26.083	258.811	153

$\bar{x}$ = mean, s^2 = variance, n = sample size

* Mean density per square foot was 56.80 at the five foot level and 37.66 at the 15 foot level.

The relationship between the product T x n (T = average sampling time/unit (column 3, Table VIII) and n = sample size (column 4 and 7, Table IX)) and sampling unit size is shown on Figure 17. The T x n vs. sampling unit size free-hand curves indicate that at both height levels, optimum sampling unit size was approximately 18 square inches (that is the T x n vs. unit size curves had minima corresponding to 18 square inches on the x-axis of Figure 17).

2. Studies of the distribution of attacks and late stage larvae over the host tree.

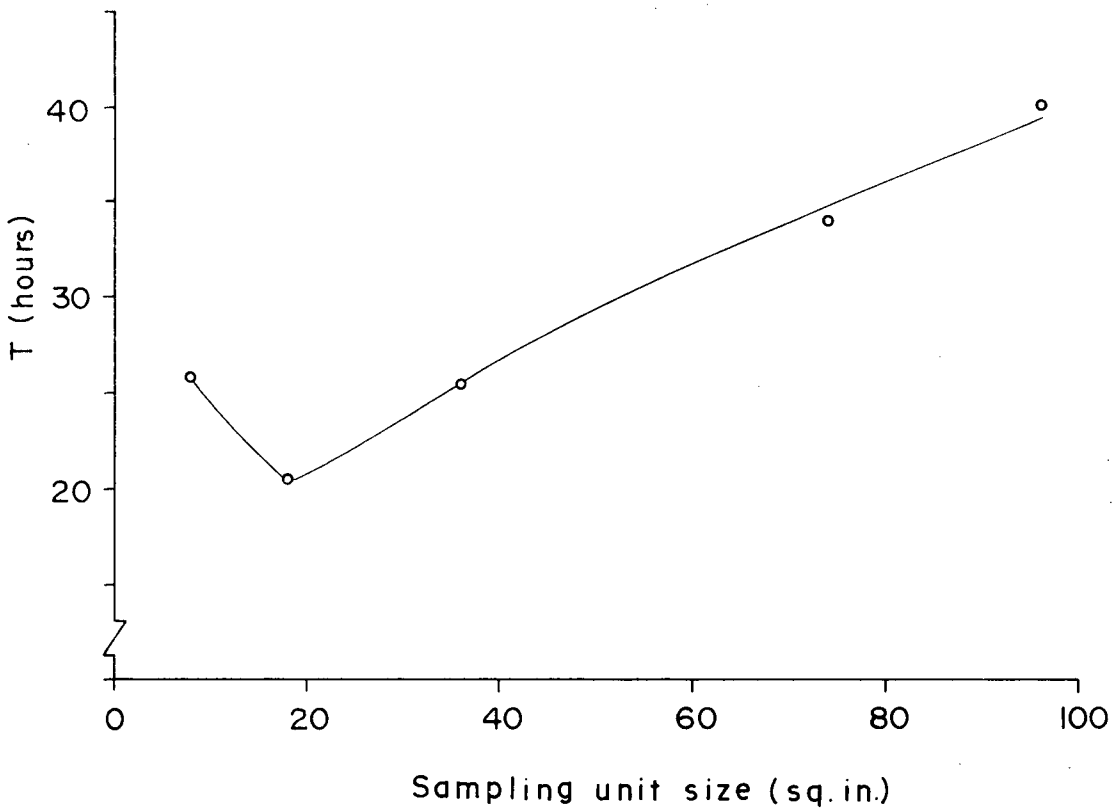
2.1. The distribution of attacks and late stage larvae around the stem circumference. The circular distributions of attacks and late stage larvae around the stem circumference at three height levels (section 4.1., Materials and Methods), by 20° class intervals taking the due S direction as zero point, are shown on Figures 18 and 19, respectively. The corresponding statistics are given in Table X.

The circular distribution of attacks, for logs cut from the lower and middle sections of the clear stem, were significantly different from the uniform distribution but the attacks were uniformly distributed around the circumference of logs cut from the stem in the mid crown region (column 3, Table X). The mean angles, $\underline{\lambda_1}$ when corrected for declination, were N 23.2°E and N 17.3°E for attacks on the bottom and middle logs, respectively. These mean angle values are in excellent agreement with the direction of the shady side of the stem at the time of peak flight activity of the emerging beetles. Reid (1960) reported that the peak of flight activity occurs at close to

Figure 17.

Total sampling time (to establish mean brood counts with a half confidence belt = $0.1\bar{x}$) versus sampling unit size relationship at two height levels.

5 FT. HEIGHT LEVEL



15 FT. HEIGHT LEVEL

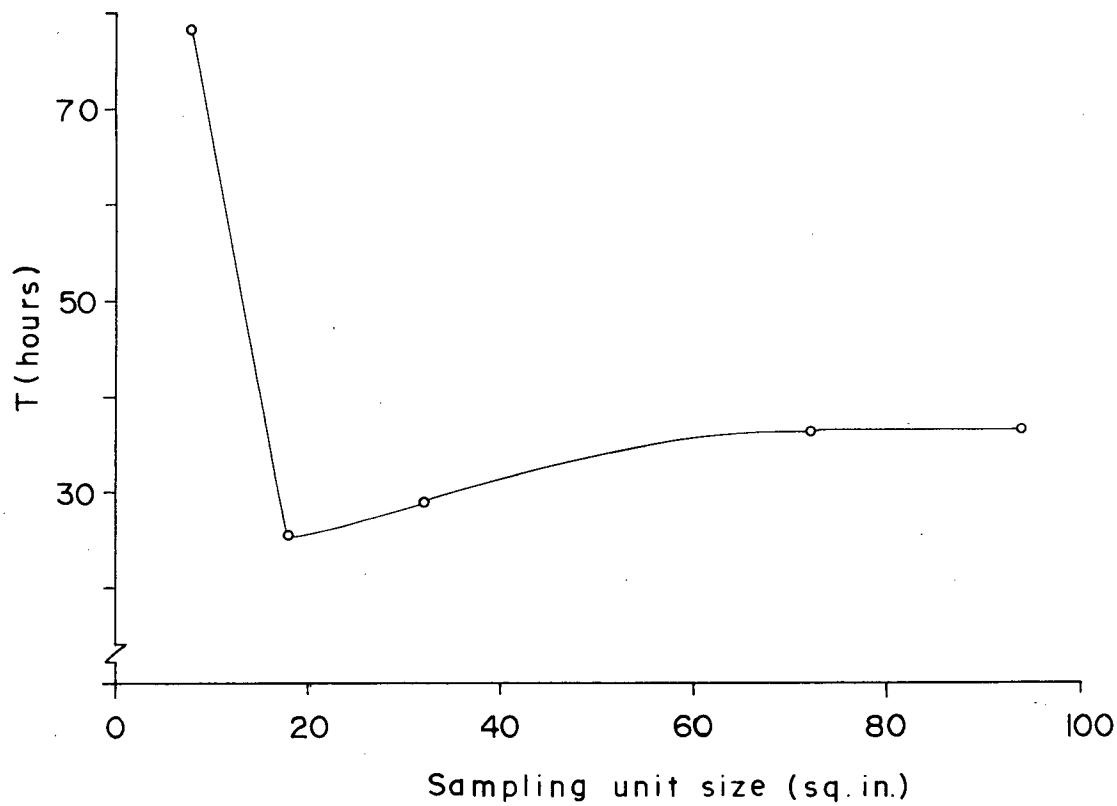
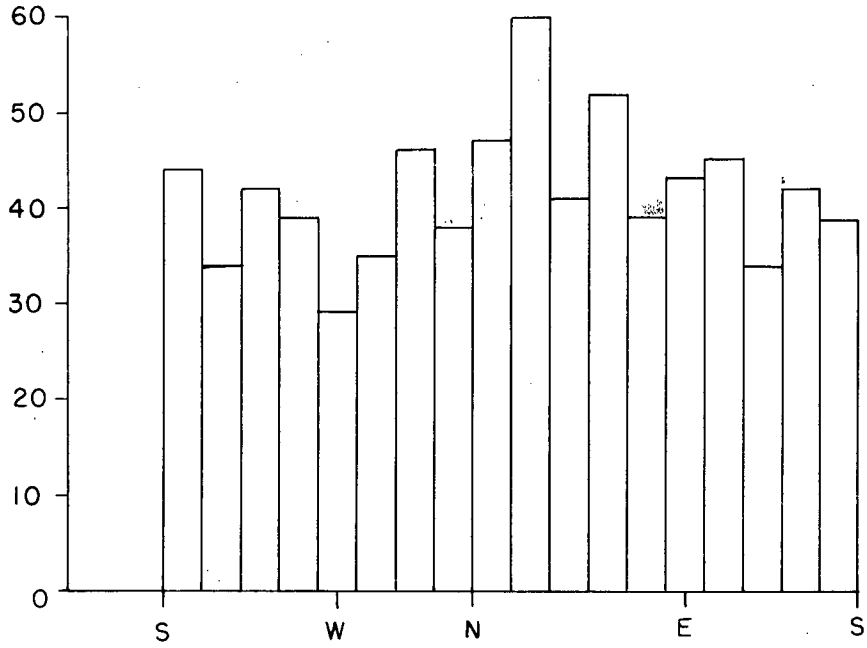


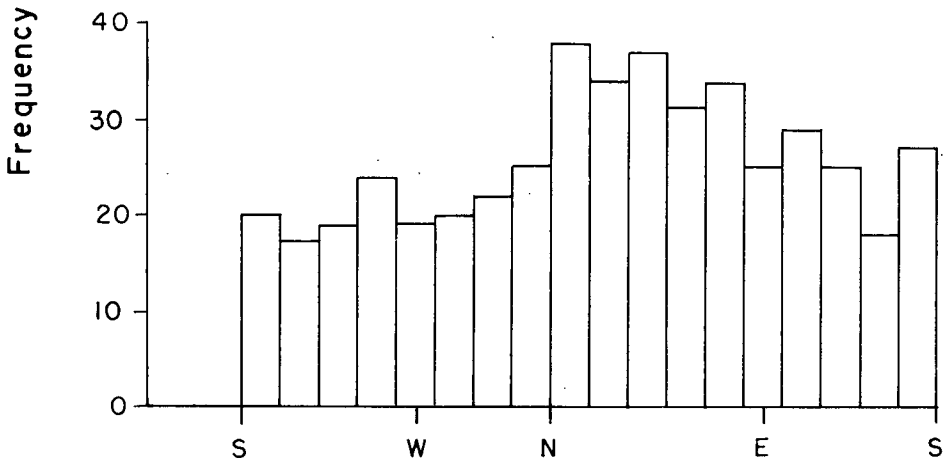
Figure 18.

Circular distribution of mountain pine beetle attacks at three height levels.

BOTTOM 3 FT. SECTION



MIDDLE 3 FT. SECTION



TOP 3 FT. SECTION

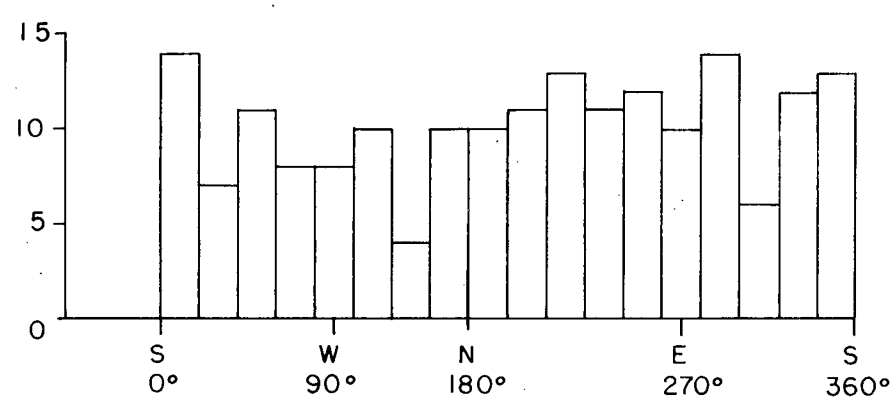


Figure 19.

Circular distribution of late stage mountain pine beetle larvae at three height levels. (On the top graph the curved line represents the theoretical frequency curve for the circular normal distribution).

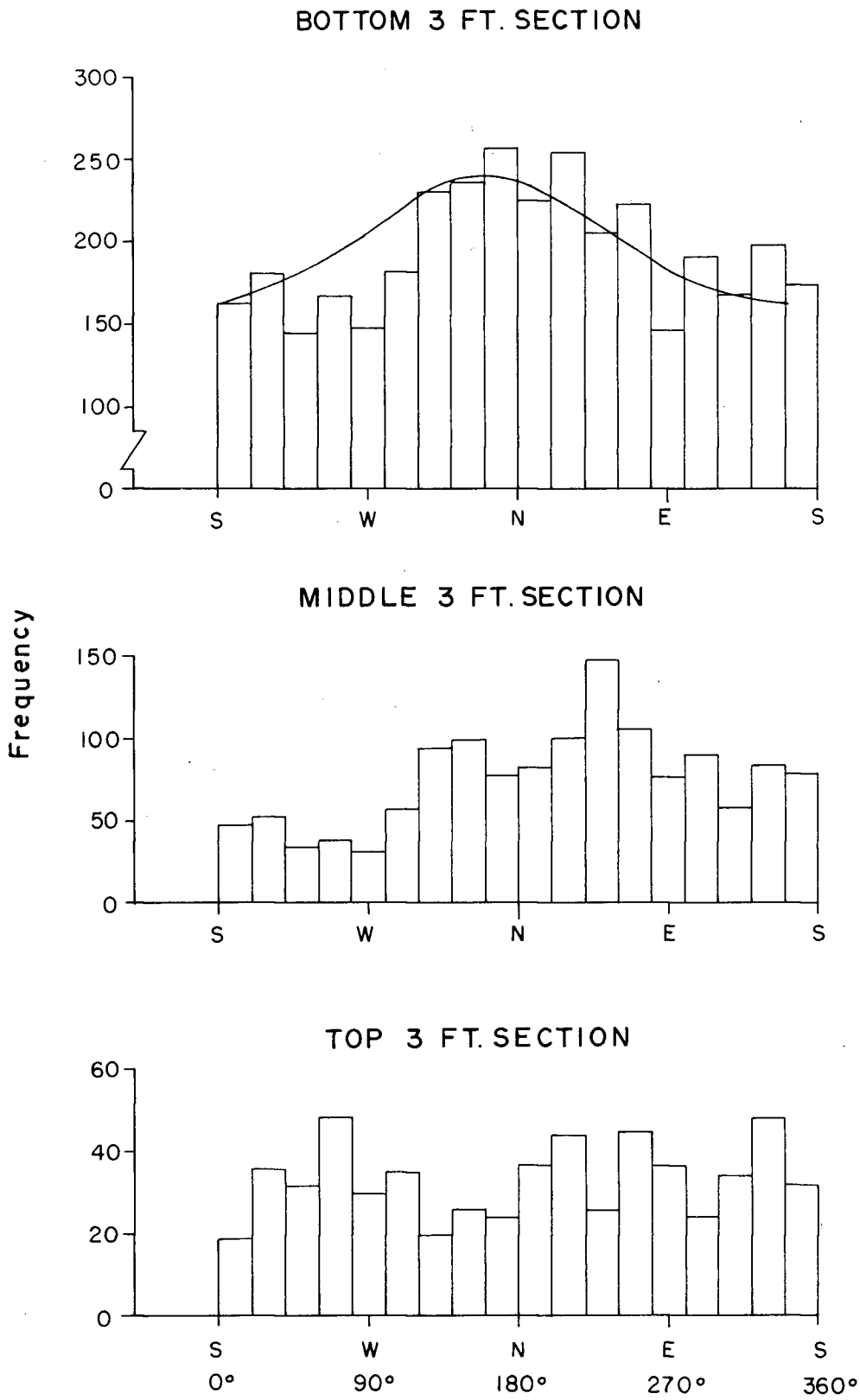

BOTTOM 3 FT. SECTION
300
250
200
150
100
0
S
W
N
E
S
MIDDLE 3 FT. SECTION
Frequency
150
100
50
0
S
W
N
E
S
TOP 3 FT. SECTION
60
40
20
0
S
0°
W
90°
N
180°
E
270°
S
360°

TABLE X. STATISTICS FOR THE CIRCULAR DISTRIBUTION OF ATTACKS AND LATE STAGE LARVAE

Position	r_1	z	$z_{.05}$	$z_{.01}$	λ_1	s	$c_{0.01}$	g	n
				Attacks					
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
Bottom logs	.0628	2.995*	2.995	4.605	N45.0°E	79.0°	54.0°	.0408	765
Middle logs	.1447	9.729**	"	"	N39.1°E	75.1°	34.9°	.0499	466
Top logs	.0843	1.308ns	"	"	------	----	----	-----	184
				Larvae					
Bottom logs	.0889	27.710**	"	"	N20.2°E	79.8°	20.3°	.0222	3544
Middle logs	.2337	43.670**	"	"	N24.0°E	71.5°	15.4°	.0277	808
Top logs	(.0903)	(4.807**)	"	"	(N19.3°E)	(77.5°)	(56.1°)	(.0251)	594

r_1 = mean vector length, z = test statistics for r_1, λ_1 = mean angle, s = mean angular deviation, g = skewness, c = half confidence belt for mean angle, n = number of observations, ns = not significant, * = significant at the 5% probability level and ** = significant at the 1% probability level. (Note: λ_1 has been measured without correction for magnetic declination and, therefore, 21.8° should be subtracted from the recorded values to obtain the corrected mean angles.)

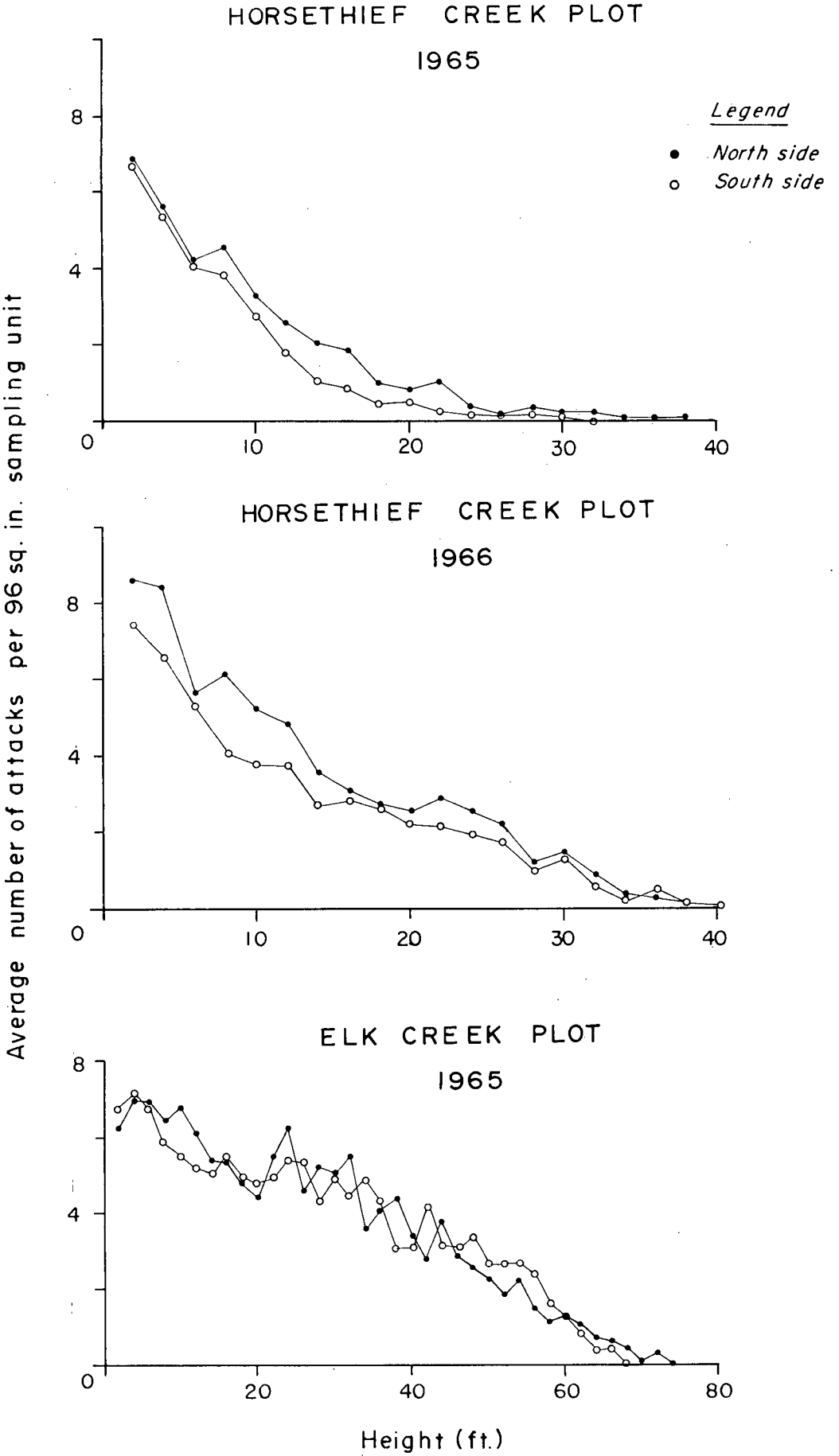
1:00 PM (MST). In 1965, when the survey was carried out, flight took place within the period from July 20 to August 10. During this period, at 1:00 PM, (MST) the shadow was centered on the N 18.75°E aspect of the stem in the study area.

The circular distribution of late-stage larvae for the bottom and middle logs were significantly different from the uniform circular distribution (the distribution of the larvae for the top logs was also significantly different from the uniform distribution, but the significance of $\underline{r}_2$ was, most likely, due to the fact that this distribution was considerably bi-modal and the z-statistic is valid to test only uni-modal circular-normal distributions - column 3, Table X). The corrected mean angles, N 1.6°W and N 2.2°E, respectively, for the bottom and middle logs, were approximately 20° closer to the due N direction than those of the attacks (column 6, Table X). This finding, in addition to experimental error, is probably due to the fact that at the point of highest attack intensity, the larvae are apt to suffer higher mortality from competition than at less crowded locations. Also, as the larvae mine perpendicularly to the egg galleries, this circumferential "advance" of the larvae could in time cause a shift in the concentration of larvae relative to that of the attacks. This last supposition seems to be supported by the finding that the circular distribution of the larvae were considerably more symmetric than that of the attacks (column 9, Table X).

2.2. The vertical density gradients of attacks and brood over the infested stem. The vertical density gradients of attacks and late stage brood, on two plots and at two aspects on the sample trees (section 4.1., Materials and Methods), are shown on Figures 20 and 21, res-

Figure 20.

Vertical gradients of attack density on two experimental plots in two successive years. (The vertical attack density gradient graph for the Elk Creek plot trees, in 1966, is shown on the following page.)


HORSETHIEF CREEK PLOT
1965
Legend
North side
South side
HORSETHIEF CREEK PLOT
1966
ELK CREEK PLOT
1965
Average number of attacks per 96 sq. in. sampling unit
Height (ft.)
0
4
8
10
20
30
40
60
80

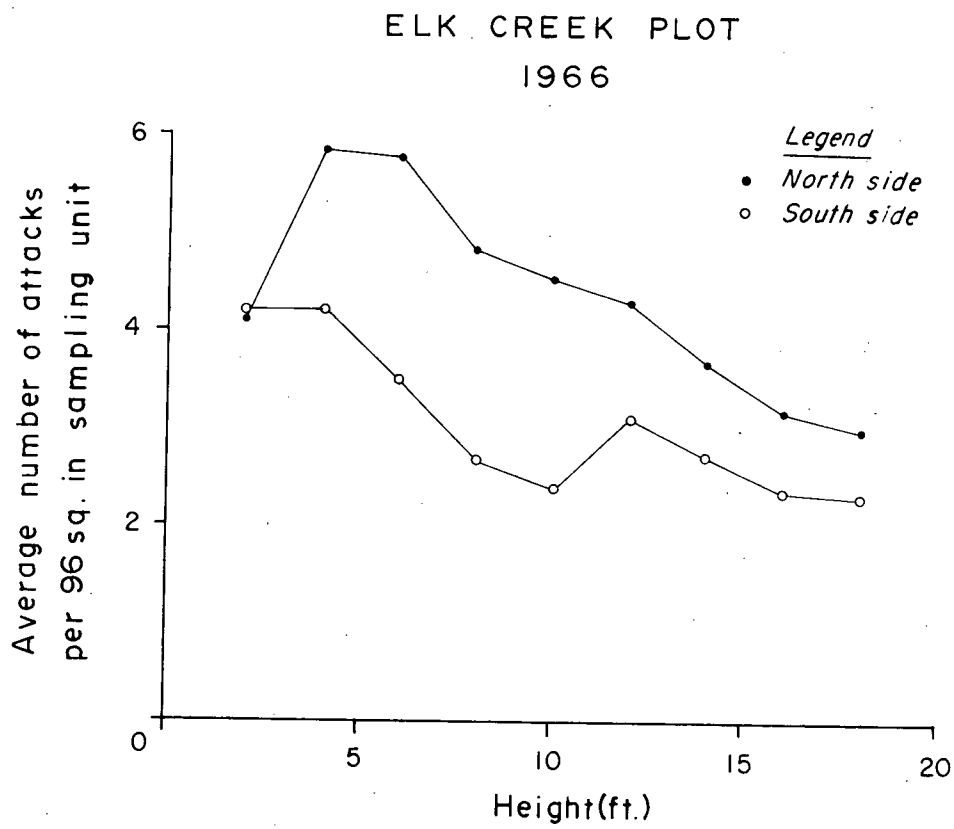
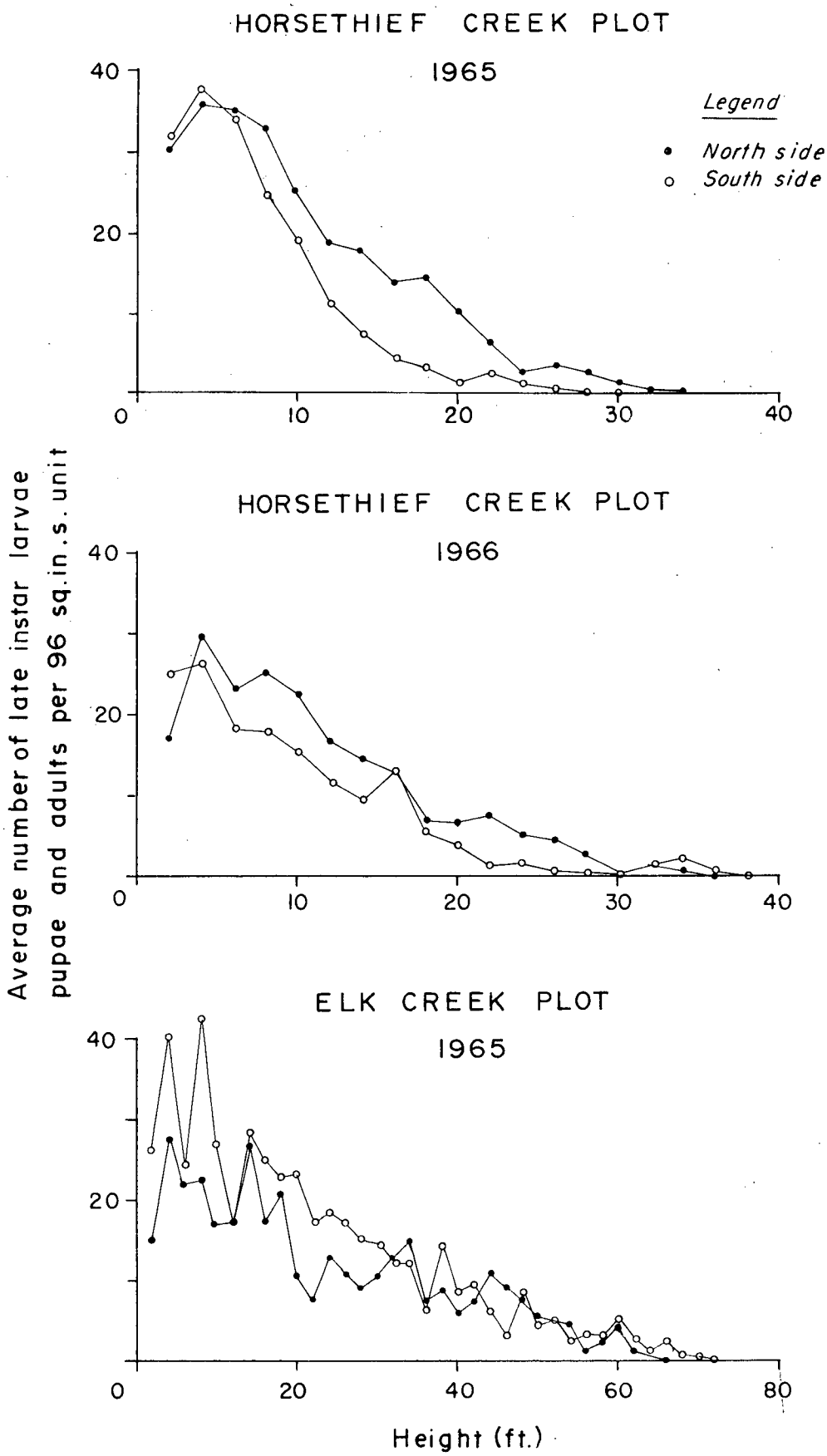

ELK CREEK PLOT
1966
Legend
North side
South side
Average number of attacks per 96 sq. in sampling unit
0
2
4
6
5
10
15
20
Height(ft.)

Figure 21.

Vertical gradients of brood density on two experimental plots.


HORSETHIEF CREEK PLOT
1965
Legend
North side
South side
HORSETHIEF CREEK PLOT
1966
ELK CREEK PLOT
1965
Average number of late instar larvae pupae and adults per 96 sq.in.s.unit
Height (ft.)
0
10
20
30
40
60
80

pectively. (Note: For Figures 20 and 21 mean attack and brood density were calculated by dividing the total number of observations with the total number of sample trees, not the total number of sampling units, at each height level.)

The gradient of attack density for the Horsethief Creek sample trees was steeper in 1965 than in 1966. Also, in both years the intensity of attacks was consistently higher on the northern than on the southern aspect, at all height levels, with the exception of the upper twenty percent of the infested stem. On the other hand, the gradient of attack density on height was only gradual for the Elk Creek sample trees in 1965 but in 1966 (data are available only from the lower eighteen foot of the infested stems) the slope of the gradient was similar to that of the 1966 Horsethief Creek data. The attack density gradient for the Elk Creek sample trees had its highest point at the four foot height level, in both years. Further, it is apparent that in 1965 there was no difference between the attack density gradient of the northern and southern aspects of the Elk Creek sample trees but in 1966 attack density was considerably higher on the northern aspect, at all height levels investigated.

The analysis of eighty-two infested trees indicated that maximum attack height (Y) was linearly related to total tree height (H) and logarithmicly related to d.b.h. (D). The regression equations had the following form:

$$Y = -41.511 + 1.024H, \quad r = 0.943, \quad n = 82$$

and

$$\log_{10}Y = -0.212 + 1.632(\log_{10}D), \quad r = 0.783, \quad n = 82$$

The logarithmic $\underline{Y}$ vs. $\underline{H}$ and the arithmetic $\underline{Y}$ vs. $\underline{D}$ relationships had smaller correlation coefficients than those of the above given equations ($r = 0.779$ for the former and $r = 0.748$ for the latter relationship).

The gradients of late stage brood (fourth instar larvae, pupae and adults) density generally followed those of the corresponding attack densities (Fig. 21). However, the highest mean brood density corresponded to the four foot region of the Horsethief Creek trees, in both years, and that of the Elk Creek trees was located between the four and six foot levels in 1965. (Similar data were not available from 1966 on latter plot). The rate of change of brood density with height was somewhat greater than that of attack density. The rate of change of the brood/attack ratio on height, however, was considerably less than that of attack or brood density (Fig. 22).

The brood density vs. height level relationship, when expressed in terms of cumulative number of broods and cumulative infested height (Fig. 23), indicate that only about 2% or less of the brood is found above the 0.80 (80%) point of the infested height. No insects were found above the 0.85 and 0.90 points of infested height on the Horsethief and Elk Creek plots, respectively. The cumulative numbers of brood vs. cumulative height relationships were decidedly sigmoid on both plots, and in both years, on the Horsethief Creek plot. The inflection point corresponded to approximately the 0.10 point of the "x"-axis, for all three curves. (Note: On Figure 23 the cumulative brood counts vs. cumulative infested height relationships were "smoothed" over by free-hand curves.)

Figure 22.

Relationship between brood/attack ratio and height above ground level.

ELK CREEK PLOT

1965

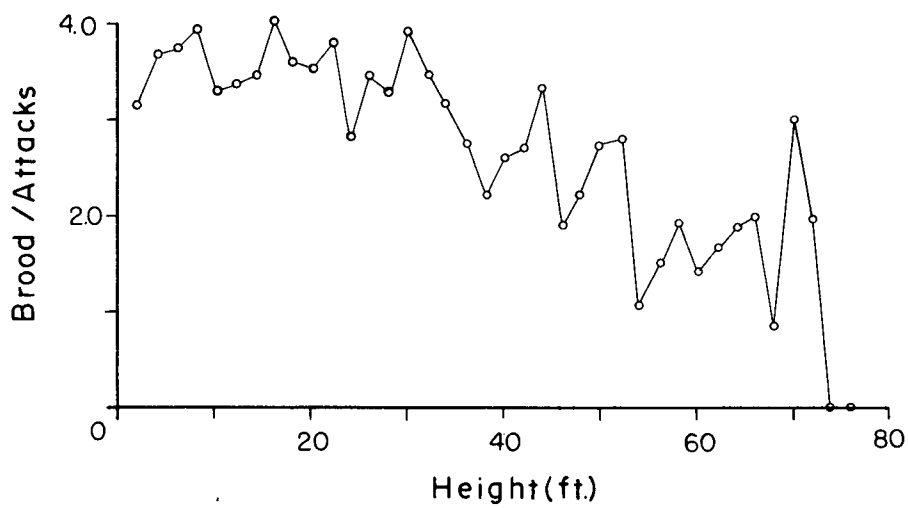
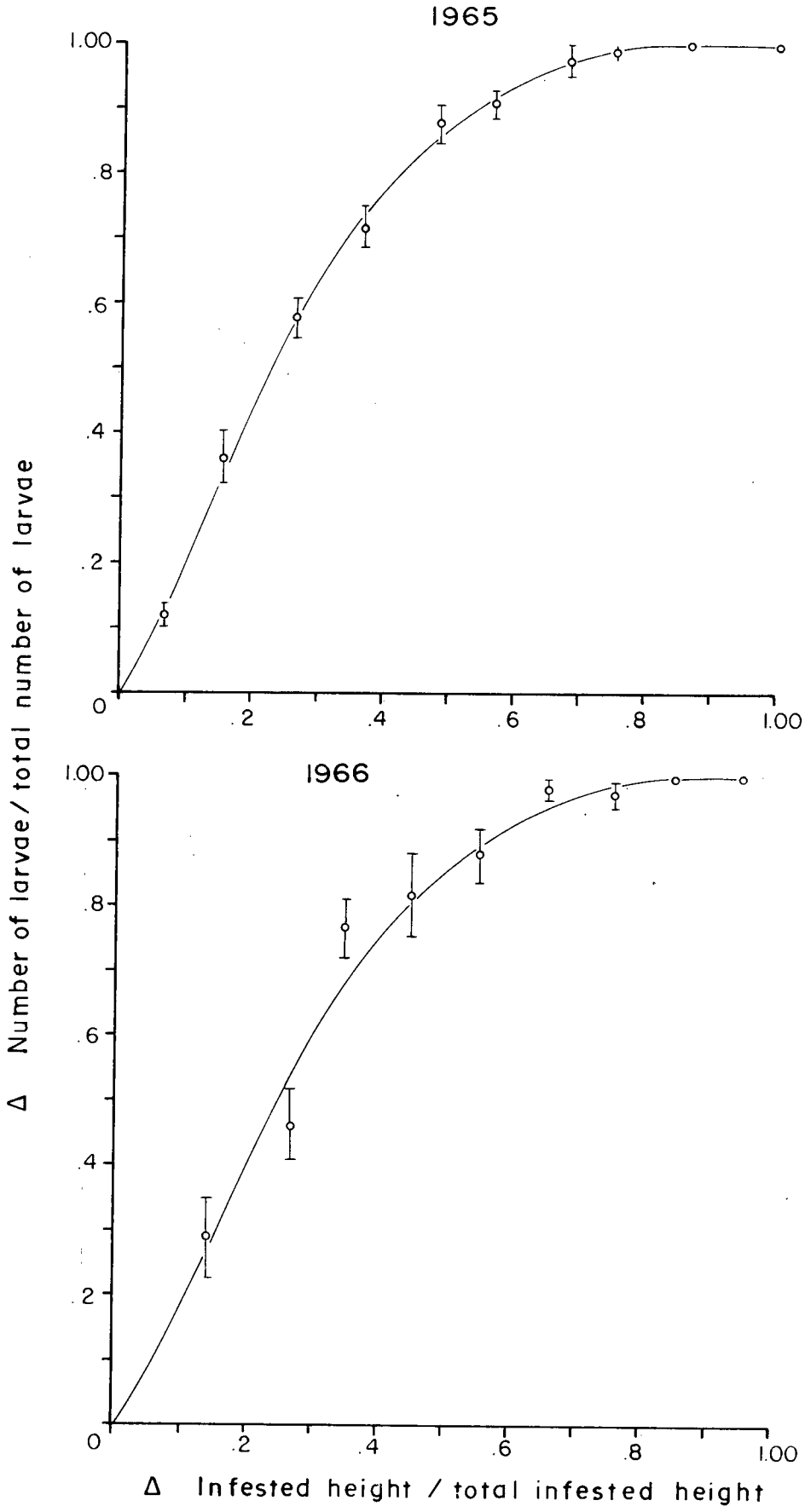


Figure 23.

Cumulative total late stage mountain pine beetle brood versus cumulative total height relationship. The vertical lines represent $\bar{y} \pm 1\ s_{\bar{y}}$. (The cumulative no. of late stage mountain pine beetle brood versus cumulative infested height relationship for the Elk Creek sample trees, in 1965, is shown on the following page.)

HORSETHIEF CREEK PLOT



2.3. The relationship between attack intensity and bark thickness. (The development of a mathematical model.) The least squares equations for the mathematical model $Y = Ymax\ (1 - 10^{-b'X_1})$ of the attack intensity vs. bark thickness relationship (equations 49 and 50 in section 4.3.3., Materials and Methods), on transformed and arithmetic scale, and their correlation coefficients are given in Table XI. The graphical form of these equations, on an arithmetic scale, is shown on Figure 24.

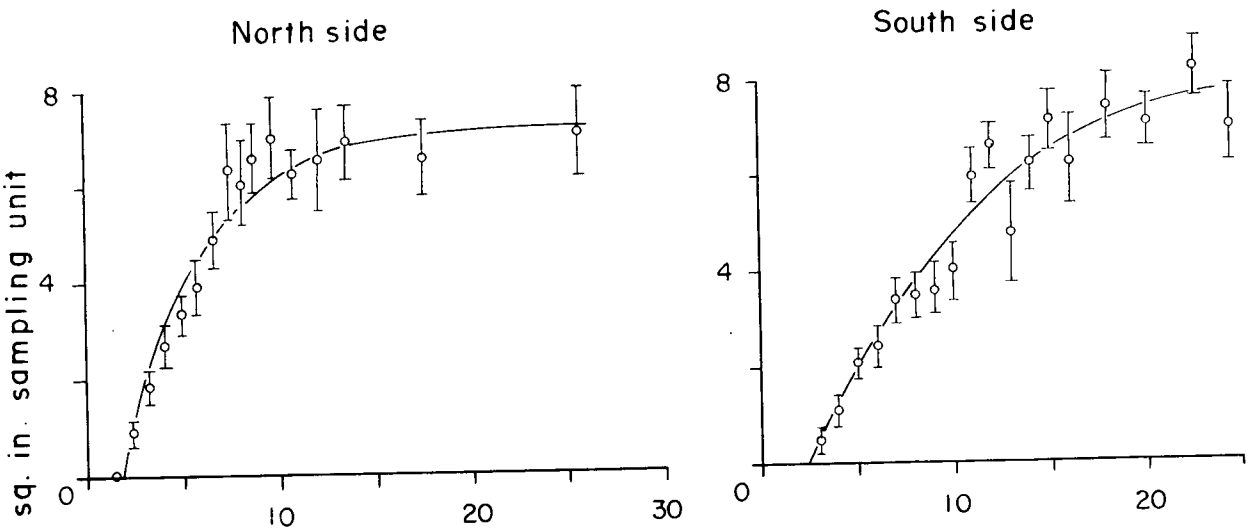
The attack density vs. bark thickness relationships were satisfactorily linear on transformed scale (i.e. the last squares transformed regression equations had high linear correlation coefficients - columns 3 and 5 in Table XI) and had negative Y intercepts. The average X_1 intercept on the two sample plots was 1.57 millimeters indicating that, on the average, no attack were initiated on bark surfaces less than this "threshold" bark thickness. The covariance analysis of the slopes and intercepts of the transformed equations for the southern and northern aspects (columns 6 and 7 in Table XI) showed that none of the slopes was significantly different but the intercepts of the equations for the Horsethief Creek plot, in both years, were different at the 1% probability level.

When the data were re-sorted on the proportion of unsuccessful egg galleries (X_2) and height level (X_3) and the "b" values (calculated as in equation (51), Materials and Methods) were plotted against these independent variates, a straight line was obtained, in both cases, which ran parallel to the X-axis. Thus, equation (49) (Materials and Methods) alone is adequate to describe the effect of bark

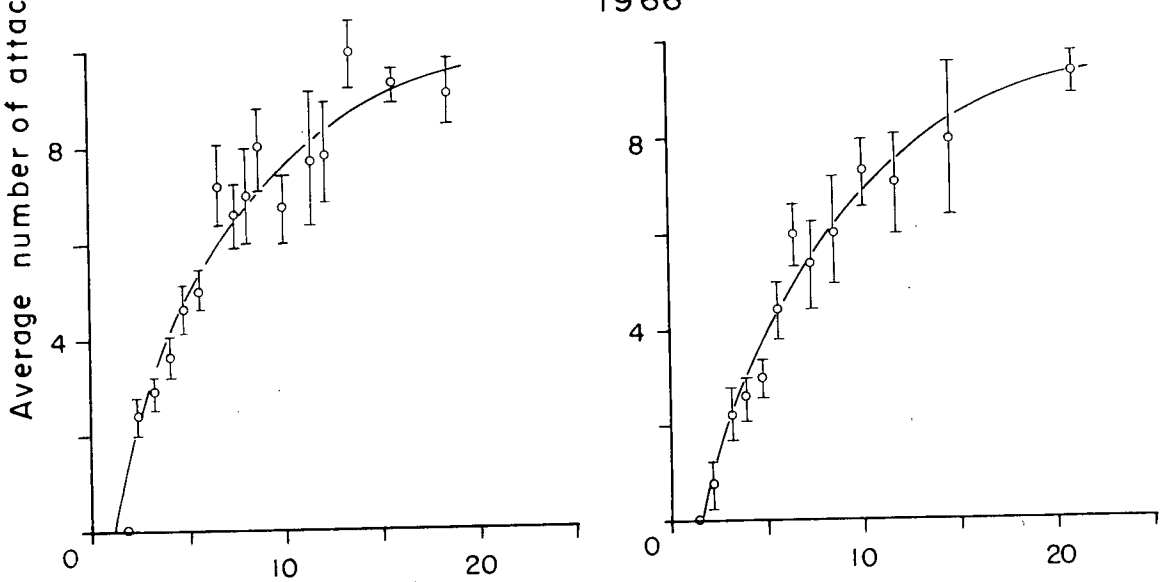
Figure 24.

Relationship between attack density and the combined thickness of outer and inner bark. The vertical lines represent $\bar{y} \pm 1s_{\bar{y}}$. (The attack density versus bark thickness relationship for the Elk Creek trees, in 1966, is shown on the following page.)

HORSETHIEF CREEK PLOT
1965



HORSETHIEF CREEK PLOT
1966



Average number of attacks per 96 sq. in. sampling unit

Bark thickness (millimeters)

TABLE XI. THE MATHEMATICAL FORM AND DEGREE OF FIT OF THE THEORETICAL MODEL $Y = Ymax(1 - 10^{-b' X_1})$ TO EXPERIMENTAL DATA.

	Horsethief Creek, 1965 (28 trees)					
	North side		South side		Comparison	
Scale	Equation	r	Equation	r	b	a
(1)	(2)	(3)	(4)	(5)	(6)	(7)
Transformed	$LOG_{10}(7.25/(7.25-Y)) = .1053X_1 - .1726$	.948	$LOG_{10}(8.50/(8.50-Y)) = .0664 - .1580$	.969	ns	**
Arithmetic	$Y = 7.25(1-10^{-.1053X_1+.1726})$	----	$Y = 8.50(1-10^{-.0664X_1+.1580})$	----	--	--
	Horsethief Creek, 1966 (15 trees)					
Transformed	$LOG_{10}(10.00/(10.00-Y)) = .0703X_1 - .0618$	.983	$LOG_{10}(10.00/(10.00-Y)) = .0609X_1 - .0944$	.989	ns	**
Arithmetic	$Y = 10.00(1-10.00^{-.0703X_1+.0618})$		$Y = 10.00(1-10^{-.0609X_1+.0944})$	----	--	--
	Elk Creek, 1965 (10 trees)					
Transformed	$LOG_{10}(10.00/(10.00-Y)) = .0973X_1 - .1550$	.760	$LOG_{10}(10.30/(10.30-Y)) = .0883X_1 - .1117$	.954	ns	ns
Arithmetic	$Y = 10.00(1-10^{-.0973X_1+.1550})$	----	$Y = 10.30(1-10^{-.0883X_1+.1117})$	----	--	--

r = simple correlation coefficient, b = slope, a = intercept, ns = not significant, ** = significant at the 1% probability level, Y = mean attack density per 96 sq. in. bark area, X_1 = combined thickness of the inner and outer bark (m.m.)

thickness on attack density.

In a separate study (Appendix F) it was found that bark thickness, from the base of the trees to the uppermost point of infestation, was well fitted by equations having the following form:

$$X_1 = A/H^{C/D}$$

Where, X_1 = bark thickness, H = height above ground level, D = diameter at breast height, A and C are constants.

Further, the average bark thickness over all trees, at any height level up to the highest point of infestation, was also well fitted by an equation of the same form. Consequently, the density gradient of attacks on height for a group of infested trees can be described by the following general equation:

$$Y = Ymax(1 - 10^{-A'/H^{C/D} + a})$$

Where, A' = constant and Y, Ymax, H, C and a are as before.

2.4. The relationship between brood density and bark thickness. The graphic plots of brood density on bark thickness are shown on Figure 25. The brood density vs. bark thickness relationship was decidedly sigmoid on both sample plots and in both years on the Horsethief Creek plot. It was noticeable, especially on the Elk Creek plot, that brood density increased to a maximum and then declined with increasing bark thickness. The greatest rate of change in brood density with respect to bark thickness occurred approximately at the x = 7/32 in. (5.5 m.m.) point on both plots and in both years on the Horsethief Creek plot.

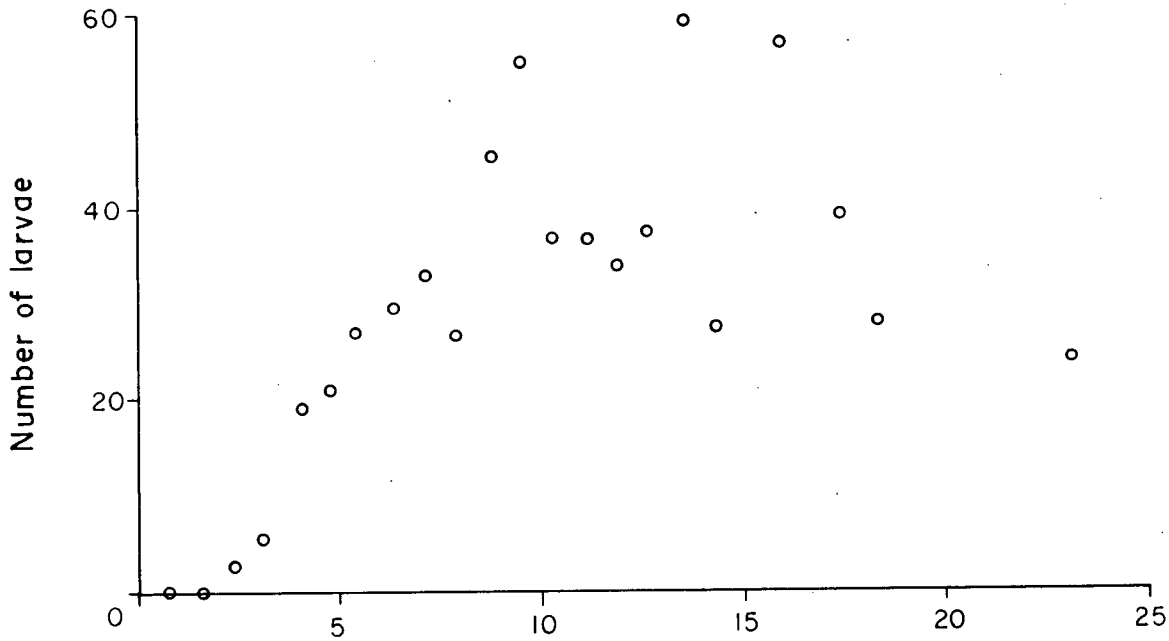
3. Analysis of some factors influencing the total number of attacks

Figure 25.

Relationship between brood density per 96 sq. in. unit and the combined thickness of inner and outer bark. (The brood density versus bark thickness relationship for the Elk Creek trees, in 1966, is shown on the following page.)

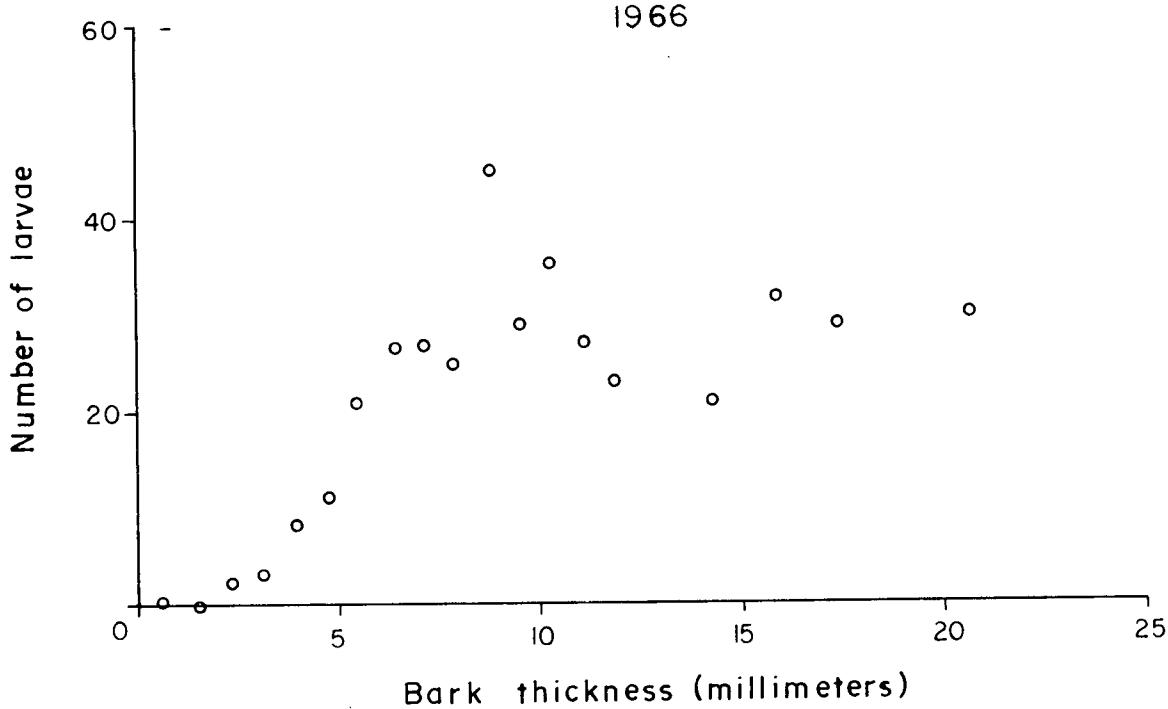
HORSETHIEF CREEK PLOT

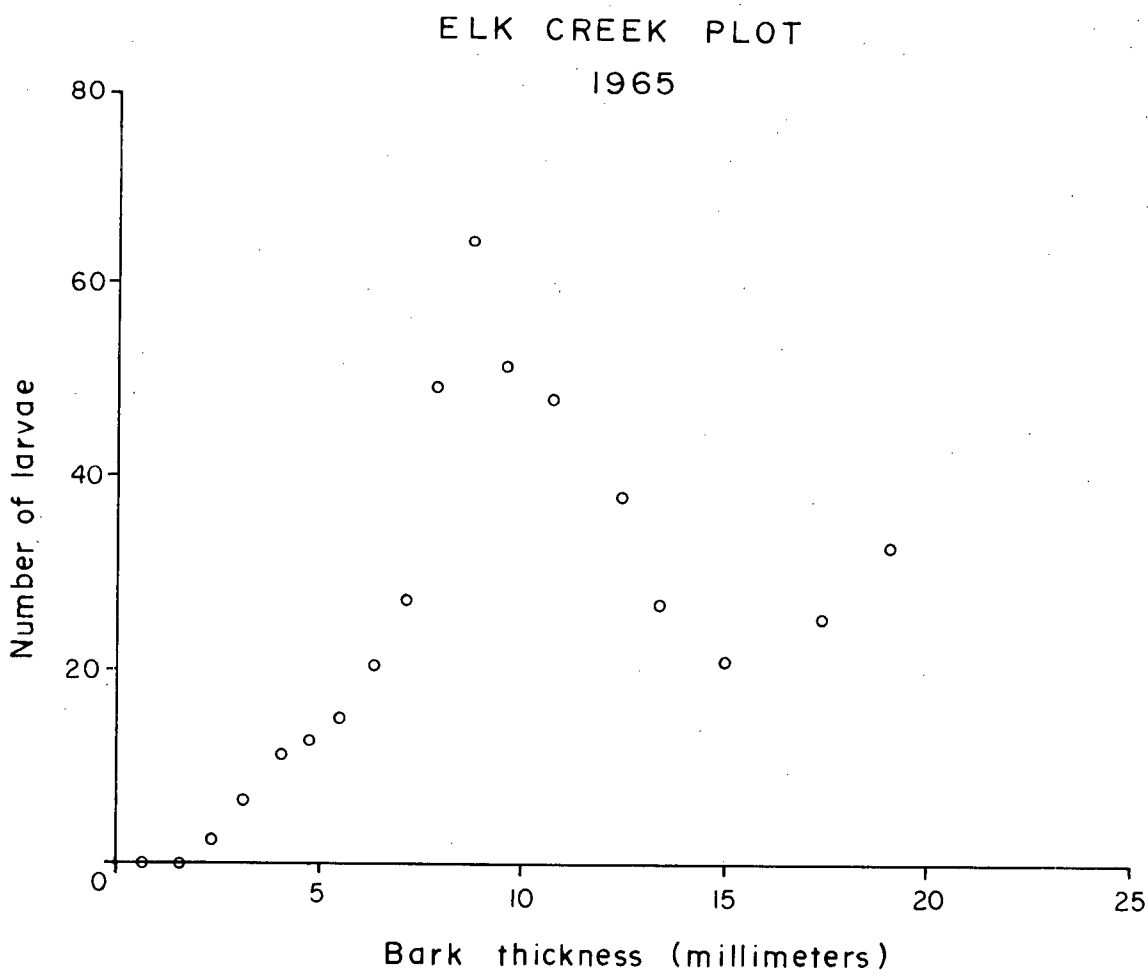
1965



HORSETHIEF CREEK PLOT

1966




ELK CREEK PLOT
1965
Number of larvae
80
60
40
20
0
5
10
15
20
25
Bark thickness (millimeters)

and broods in individual trees. The statistics of the variables used in this analysis are summarized in Table XII. In this table the variables are designated by the following symbols:

Y_1 = total numbers of attacks/tree, Y_2 = total numbers of broods/tree, X_1 = (growth increment at the 1 foot height level for the last 10 years) 32 in., X_2 = total tree age (yrs.), X_3 = sum of the distances from the three nearest neighbours over 4 inches in d.b.h. (ft.), X_4 = (combined thicknesses of the inner and outer bark at the d.b.h. level) x 32 (in.), X_5 = DH (D = d.b.h. (ft.) and H = total tree height (ft.)), X_6 = 1/D, X_7 = (crown width)^2(crown height) = CW^2CH(cu. ft.), X_8 = CW^2CH/D^2H.

The number of attacks/tree (Y_1) was found to be highly significantly correlated with DH_1, $1/D$ (a simplified expression of the D^2H/DH ratio) and CW^2CH. The simple correlation coefficients of the Y_1 vs. X_4 (bark thickness at d.b.h. level) and Y_1 vs. X_3 (sum of the distances from the three nearest neighbours) relationships were significantly different from zero at the 5% probability level and those of the Y_1 vs. X_1 (growth increment for the last 10 years) and Y_1 vs. X_8 (CW^2CH/D^2H) relationships were not significantly different from zero. The number of broods/tree (Y_2) was correlated with Y_1, X_2, X_6 and X_7 at the 99% probability level, and with X_3 and X_4 at the 95% probability level. The correlation coefficients between Y_2, X_1 and X_8 were not significantly different from zero.

3.1. Multiple regression analysis of the relationship between total number of attacks/tree and some host tree characteristics (combined Horsethief and Elk Creek data, 1965). The regression coeffici-

TABLE XII. STATISTICS FOR THE VARIABLES USED IN THE MULTIPLE REGRESSION EQUATIONS Y_1 AND Y_2 VS. $X_{(1-8)}$ (COMBINED HORSETHIEF CREEK AND ELK CREEK DATA, 1965)

Statistics	Variables									
	Y_1	Y_2	X_1	X_2	X_3	X_4	X_5	X_6	X_7	X_8
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)
Mean	559.18	2,701.50	13.66	72.94	37.18	10.45	69.97	1.19	19,665.70	233.26
Standard Deviation	573.48	2,796.83	5.84	22.56	14.26	3.39	34.61	0.42	24,694.10	138.18
Minimum	35.00	60.00	5.00	40.00	14.00	6.00	24.00	0.62	750.00	28.00
Maximum	1,912.00	12,000.00	30.00	115.00	65.00	19.00	162.00	2.40	130,207.00	640.00
Coefficient of Variation (%)	102.56	103.53	42.77	30.93	38.35	32.43	49.48	35.60	125.57	59.24
Numbers of Observations	38	38	38	38	38	38	38	38	38	38
$r(Y_2$ on $X_i)$	0.65**	-------	0.30^{ns}	0.48**	0.32*	0.35*	0.66**	-0.56**	0.67**	0.21^{ns}
$r(Y_1$ on $X_i)$	-------	0.65**	0.16^{ns}	0.82**	0.39*	0.33*	0.87**	-0.69**	0.65**	0.20^{ns}

r = simple correlation coefficient, * = significant at the 5% probability level, ** = significant at the 1% probability level, ns = not significant.

ents for the multiple regression equation of $\underline{Y_1}$ on $\underline{X_1}$ to $\underline{X_8}$, the significance of the contribution of each of the independent variates to the regression sum squares and the order of elimination of the variables are given in Table XIII.

TABLE XIII. REGRESSION COEFFICIENTS, TESTS OF SIGNIFICANCE AND ORDER OF ELIMINATION OF THE INDEPENDENT VARIATES (COMBINED ELK AND HORSETHIEF CREEK DATA, 1965)

Independent Variable (X_i)	Regression Coefficient	Variance Ratio	Order of Elimination of X_i
(1)	(2)	(3)	(4)
X_1	-14.499	2.436^{*}	6
X_2	- 1.777	0.093^{ns}	2
X_3	0.627	0.019^{ns}	1
X_4	32.487	4.723^{**}	7
X_5	22.686	10.915^{**}	8
X_6	329.871	2.168^{ns}	3
X_7	-77.038	2.217^{ns}	5
X_8	0.606	1.144^{ns}	4

ns = not significant, * = significant (the probability of a greater F-ratio = 0.05), ** = highly significant (the probability of a greater F-ratio = 0.01).

Constant term = -1,447.250, standard error of estimate = 266.682, R = 0.910**, sample size = 38, variance ratio for regression line = 17.763** with 8 and 29 degrees of freedom.

The multiple regression equation of $\underline{Y_1}$ on $\underline{X_1}$ to $\underline{X_8}$ accounted for 83% of the variability in $\underline{Y_1}$. Only three of the eight independent variates used contributed significantly to the regression sum squares. These variates were $\underline{X_1}$ (width of the last ten year rings at the 1 foot height level), $\underline{X_4}$ (bark thickness at d.b.h. level and $\underline{X_5}$(DH)). The

multiple regression equation of Y_1 on X_1, X_4 and X_5 had the following form:

$$Y_1 = - 554.247 - 14.771X_1 + 27.135X_4 + 14.743X_5$$

Standard error of estimate = 262.619 and R = .899**.

This multiple regression equation accounted for 80.9% of the variability in Y_1. The best independent variable was X_5(DH), an index of the total surface area for individual trees, Y_1 decreased with increasing radial tree growth (X_1) and increased with increasing bark thickness (X_4) and DH(X_5).

3.2. Multiple regression analysis of the relationship between total number of broods/tree (Y_2), total number of attacks/tree (Y_1) and some host tree characteristics on the Horsethief and Elk Creek sample plots in 1965. The regression coefficients for the multiple regression equation of Y_2 on Y_1, X_1, X_2, X_5, X_6, X_7 and X_8, the significance of the contribution of the independent variates to the regression sum squares and the order of elimination of independent variables are given in Table XIV for the Elk Creek sample trees.

TABLE XIV. REGRESSION COEFFICIENTS, TESTS OF SIGNIFICANCE AND ORDER OF ELIMINATION OF THE INDEPENDENT VARIATES (ELK CREEK DATA, 1965)

Independent Variable (X_i)	Regression Coefficient	Variance Ratio	Order of Elimination of X_i
(1)	(2)	(3)	(4)
Y_1	6.615	0.816^{ns}	6
X_1	92.088	0.126^{ns}	4
X_2	90.729	0.014^{ns}	3
X_5	25.031	0.005^{ns}	2
X_6	23,150.300	0.237^{ns}	5
X_7	9.092	0.151^{ns}	7
X_8	0.186	0.000^{ns}	1

ns = not significant.

Constant term = -40,885.700, $\bar{Y}_2$ = 4,847.100, standard error of estimate = 3,669.550, R = 0.893^{ns}, variance ratio = 1.131^{ns} with 7 and 2 degrees of freedom and sample size = 10.

The multiple regression equation accounted for 79.8% of the variability in Y_2 but the regression line was not significant, possibly because data was available only from ten sample trees. The three best variables were $X_7(CW^2CH)$, Y_1 (total number of attacks/tree) and $X_6(1/D)$, in that order. The regression equation of Y_2 on Y_1, X_6 and X_7 had the following form:

$$Y_2 = -1,823.670 + 5.271Y_1 + 1,437.950X_6 + 0.0982X_7$$

Standard error of estimate = 2,294.100 and R = 0.874*.

This multiple regression equation had a significant correlation coefficient and accounted for 76.3% of the variation in Y_2. Of the three independent variates, X_7 and Y_1 contributed significantly to the regression sum squares. The contribution of X_6 to the regression sum squares was not significant.

The regression coefficients for the multiple regression equation of Y_2 on Y_1, X_1, X_2, X_5, X_6, X_7 and X_8, the significance of the contribution of the independent variates to the regression sum squares and the order of elimination of the variables for the Horsethief Creek data are given in Table XV.

The multiple regression equation had a highly significant correlation coefficient but only two of the seven independent variables used (Y_1 and X_7) contributed significantly to the regressions sum squares. The best three independent variables were Y_1(total number of attacks/tree), X_2 (tree age) and $X_7(CW^2CH)$, in that order. The multiple

regression equation of $\underline{Y_2}$ on $\underline{Y_1}$, $\underline{X_2}$ and $\underline{X_7}$ had the following form:

$$Y_2 = -3,193.860 + 9.313Y_1 + 61.594X_2 - 0.102X_7$$

Standard error of estimate = 1,249.470 and R = 0.793**.

Thus, on the Horsethief Creek sample plot in 1965, total number of broods/tree in late stages of development increased with both, increasing tree age and total number of attacks/tree and decreased with increasing crown volume (CW^2CH).

TABLE XV. REGRESSION COEFFICIENTS, TESTS OF SIGNIFICANCE AND ORDER OF ELIMINATION OF THE INDEPENDENT VARIATES (HORSETHIEF CREEK DATA, 1965)

Independent Variable (X_i)	Regression Coefficient	Variance Ratio	Order of Elimination of X_i
(1)	(2)	(3)	(4)
Y_1	7.918	11.330**	7
X_1	-18.760	0.084^{ns}	1
X_2	48.010	1.334^{ns}	6
X_5	44.748	0.830^{ns}	4
X_6	-1,033.160	0.443^{ns}	2
X_7	-0.208	6.298*	5
X_8	5.773	1.924^{ns}	3

** = highly significant (the probability of a greater F-ratio = 0.01), * = significant (the probability of a greater F-ratio = 0.05).

Constant term = -2,857.570, $\bar{Y}_2$ = 1,935.250, standard error of estimate = 1,241.130, R = 0.818**, variance ratio = 5.806** with 7 and 20 degrees of freedom, and sample size = 28.

4. Development of total and partial surface area equations for lodgepole pine.

4.1. Total surface area equations. The pertinent statistics for the sample survey data, which was used for developing total bark area equations are summarized in Table XVI.

The least squares fit of the general combined variable surface area function (equation 54, Materials and Methods) to the sample survey data had the following form:

$$S_t = 1.9708DH + 3.7196, \text{ (trees without fork)}$$

$r = 0.9883$, $s_{y.x} = 6.5809$ ($s_{y.x}$ = standard error of estimate)

$$S_t = 2.3086DH + 2.6761, \text{ (forked trees)}$$

$r = 0.9900$, $s_{y.x} = 10.1447$

The least squares fit of the "transformed variable" surface area function (equation 56, Materials and Methods) to the sample survey data yielded the following equations:

$$D/S_t = 5.4187(1/H) + 0.000516, \text{ (trees without fork)}$$

$r = 0.9658$, $s_{y.x} = 0.00440$

and

$$D/S_t = 4.5424(1/H) + 0.000623, \text{ (forked trees)}$$

$r = 0.9511$, $s_{y.x} = 0.00623$

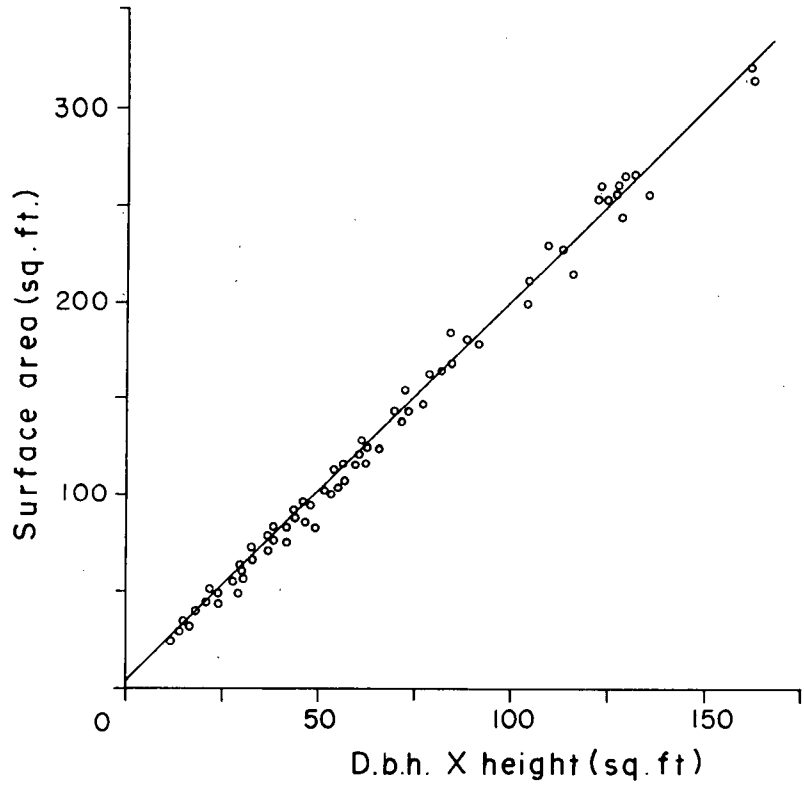
The graphical form of these surface area equations are shown on Figures 26 and 27.

The sample survey data were well fitted by both functions, but the least squares equations of the general "combined variable" function had higher correlation coefficients than those of the "transformed variable" function. Further, the scatter about the regression line of the former function was considerably more uniform than that of the latter function, for both forked and forkless trees. The scatter about the regression lines for the "transformed variable" function increased with increasing values of the independent variable (1/H). The regression equations of the two surface area functions had com-

Figure 26.

Graphical form of the total surface area versus (d.b.h.)(total height) relationship for lodgepole pine.

TREES WITHOUT FORKS



FORKED TREES

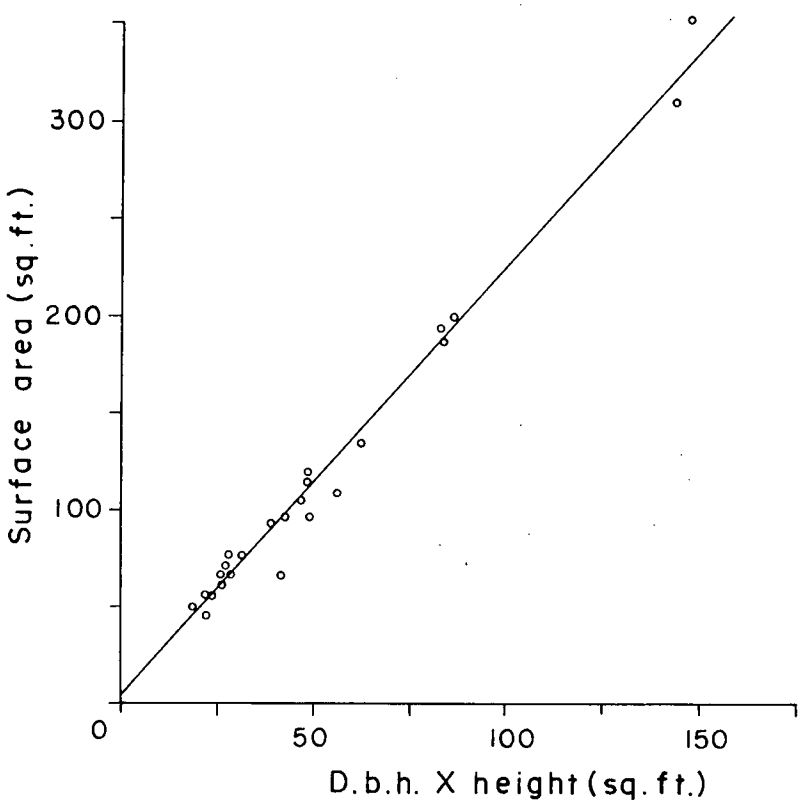
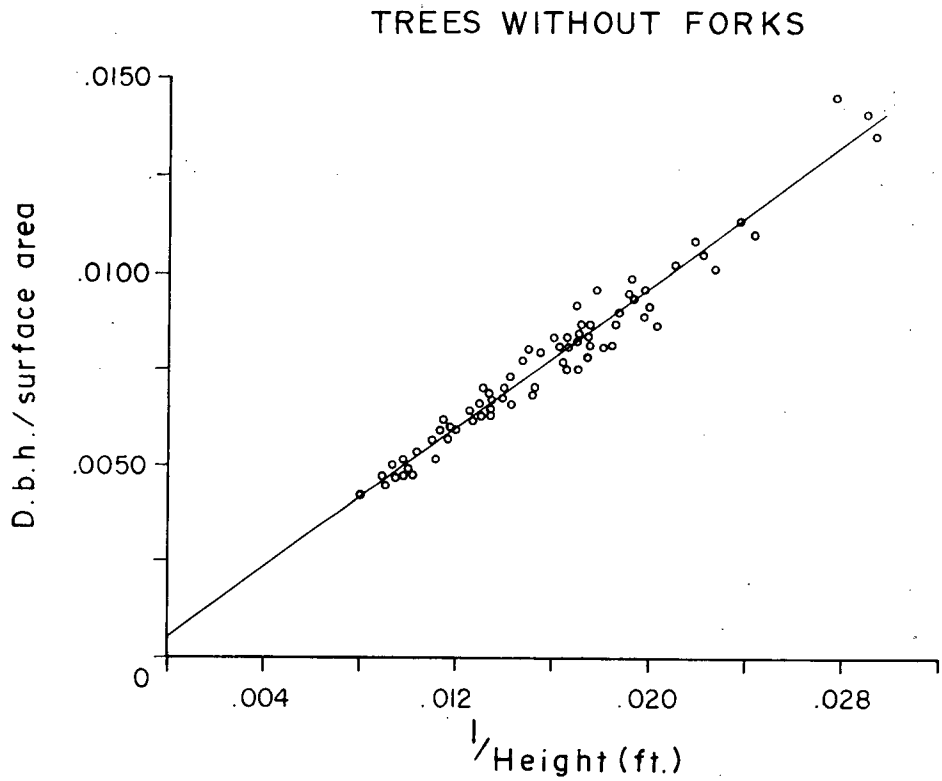
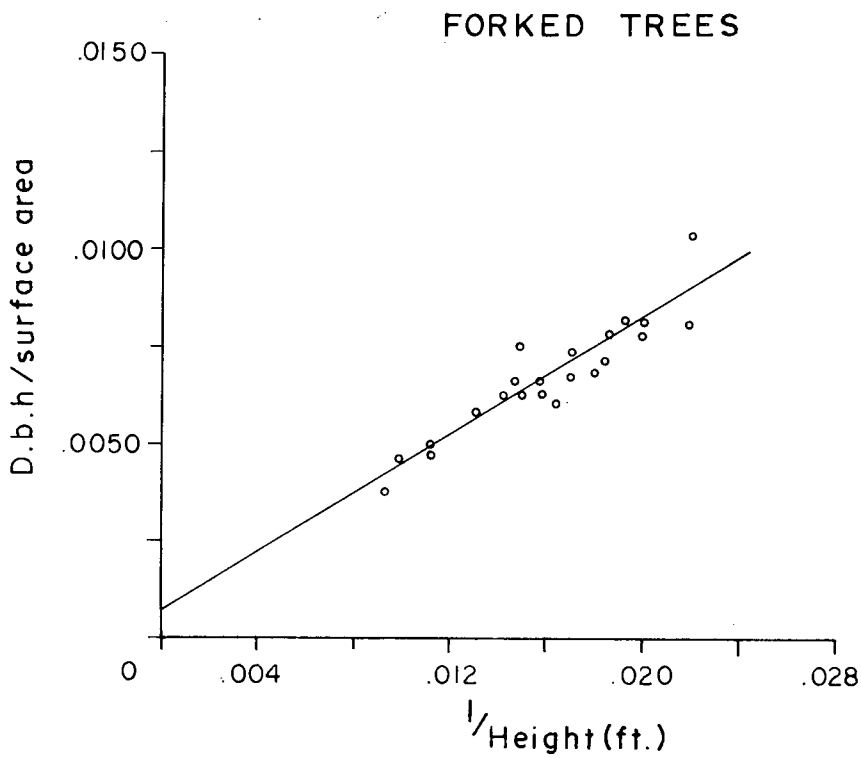


Figure 27.

Graphical form of the (d.b.h.)/total surface area versus (1/total height) relationship for lodgepole pine.


TREES WITHOUT FORKS
.0150
.0100
.0050
0
D.b.h./surface area
.004
.012
.020
.028
1/Height (ft.)


FORKED TREES
.0150
.0100
.0050
0
D.b.h/surface area
.004
.012
.020
.028
1/Height (ft.)

parable precision. For forkless trees, the standard error of estimate was 4.7% and 5.0% for the "combined variable" and "transformed variable" regression equation, respectively. For forked trees, these figures were 8.5% and 7.9% for the former and latter regression equation, in that order. The slopes and intercepts of the regression equations fitted to sample survey data on forkless trees differed considerably from those fitted to data on forked trees. Further, the relative standard error of estimates (i.e. $100s_{y.x}/\bar{y}$) were almost twice as high for the latter group of trees than those for trees without forks. Therefore, the precision of surface area estimation was considerably increased by developing separate predicting equations for these two groups of trees.

TABLE XVI. STATISTICS FOR DATA USED IN DEVELOPING TOTAL SURFACE AREA EQUATIONS FOR LODGEPOLE PINE

Variable	Max.	Min.	Mean	SD	CV	n
			Trees without fork			
H (ft.)	124.0	34.0	69.50	23.09	33.23	73
D (in.)	19.0	4.3	9.77	3.07	31.40	"
DH (sq. ft.)	167.4	12.2	64.51	42.71	69.19	"
S_t (sq. ft.)	318.5	26.4	130.86	78.59	62.94	"
D/S_t(1/ft.)	0.9664	0.0237	0.0885	0.1290	117.27	"
1/H (1/ft.)	0.0294	0.0080	0.0155	0.0588	37.93	"
			Forked trees			
H (ft.)	106.0	45.0	66.34	13.98	21.07	23[1]
D (in.)	17.0	5.1	8.37	2.92	34.86	"
DH (sq. in.)	145.7	13.1	51.14	35.98	70.35	"
S_t (sq. ft.)	367.6	48.3	119.53	45.15	37.77	"
D/S_t(1/ft.)	0.1242	0.0449	0.0799	0.0930	111.29	"
1/H (1/ft.)	0.0222	0.0094	0.0159	0.0036	22.43	"
Fork height (ft.)	71.7	19.2	35.82	11.21	31.29	"

SD = Standard deviation, CV = coefficient of variation, n = number of

[1] Of the thirty trees sampled by the author only three trees had forks. Data on the rest of the twenty forked trees were obtained from the B.C. Forest Service, Victoria, British Columbia.

observations, H = total tree height, D = d.b.h. and S_t = total bark area.

4.2. Studies of the relationship between cumulative surface area and cumulative height and the estimation of partial surface area. The statistics for the data used in these studies are summarized in Table XVII. In Table XVII, the variables are designated by the following symbols:

ΔH = bole section height, H = total tree height,

ΔS_t = bole section surface area and S_t = total surface area.

TABLE XVII. STATISTICS FOR DATA USED IN STUDIES OF THE RELATIONSHIP BETWEEN CUMULATIVE BOLE AREA AND CUMULATIVE HEIGHT

Statistic	Variable			
	$\Delta H/H$	$(\Delta H/H)^2$	$(\Delta H/H)^3$	$\Delta S_t/S_t$
Forked trees				
Mean	0.4581	0.3162	0.2472	0.5289
Standard deviation	0.3269	0.3268	0.3151	0.3455
Minimum	0.0094	0.889×10^{-4}	0.838×10^{-6}	0.0138
Maximum	1.0000	1.0000	1.0000	1.0000
Coefficient of variation (%)	71.37	103.35	127.43	64.95
Number of observations	195	195	195	195
$r(\Delta S_t/S_t$ vs. $(\Delta H/H)^i$	0.9912	0.9263	0.8526	--------
Trees without forks				
Mean	0.4914	0.3405	0.2657	0.6029
Standard deviation	0.3150	0.3242	0.3148	0.3271
Minimum	0.0095	0.906×10^{-4}	0.863×10^{-6}	0.0192
Maximum	1.0000	1.0000	1.0000	1.0000
Coefficient of variation (%)	64.10	95.20	118.45	54.26
Number of observations	565	565	565	565
$r(\Delta S_t/S_t$ vs. $(\Delta H/H)^i$	0.9771	0.8982	0.8202	--------

r = simple correlation coefficient

The $\Delta S_t/S_t$ vs. $\Delta H/H$ relationship was well described by third

degree multiple curvilinear regression equations (section 4.3.4., Materials and Methods) for both forked and forkless trees. These regression equations had the following form:

$$\Delta S_t/S_t = 0.0179 + 0.0150\Delta H/H - 0.2108(\Delta H/H)^2 - 0.3027(\Delta H/H)^3,$$

(forkless trees) $R = 0.9921$, $s_{y.x} = 0.04045$.

and $$\Delta S_t/S_t = 0.0150 + 0.0118\Delta H/H - 0.2819(\Delta H/H)^2 - 0.4692(\Delta H/H)^3,$$

(forked trees) $R = 0.9974$, $s_{y.x} = 0.02474$.

Where, R = multiple correlation coefficient, and the other notations are as defined previously.

When multiple regression equations of $\underline{\Delta S_t/S_t}$ on all three combinations of two independent variables were calculated, the regressions on the $\underline{\Delta H/H}$, $(\underline{\Delta H/H})^2$ and $(\underline{\Delta H/H})$, $(\underline{\Delta H/H})^3$ combinations of the independent variables had close to equal R-values. The R-value of the regression on the third combination of the independent variables: $(\underline{\Delta H/H})^2$ and $(\underline{\Delta H/H})^3$, was significantly smaller than that of the former two regression equations. The best two of the multiple curvilinear equations had the following form:

$$\Delta S_t/S_t = 0.0059 + 1.6761\Delta H/H - 0.6657\ (\Delta H/H)^2$$

Forkless trees: $R = 0.9921$, $s_{y.x} = 0.04097$

$$\Delta S_t/S_t = 0.0242 + 1.4150\Delta H/H - 0.4391(\Delta H/H)^3$$

and $R = 0.9923$, $s_{y.x} = 0.04052$

$$\Delta S_t/S_t = 0.00062 + 1.4452\Delta H/H - 0.4191(\Delta H/H)^2$$

$R = 0.9970$, $s_{y.x} = 0.02675$

Forked trees:

$$\Delta S_t/S_t = 0.0079 + 1.2914\Delta H/H - 0.2857\ (\Delta H/H)^3$$

$R = 0.9974$, $s_{y.x} = 0.02499$

The third degree multiple curvilinear regression equations had

greater R-values and smaller $s_{y.x}$-values, for both forked and forkless trees, than those of the corresponding second degree multiple curvilinear equations. Therefore, the former equations were retained for the development of a partial surface area table for lodgepole pine. The graphical form of the third degree multiple curvilinear equations is shown on Figure 28.

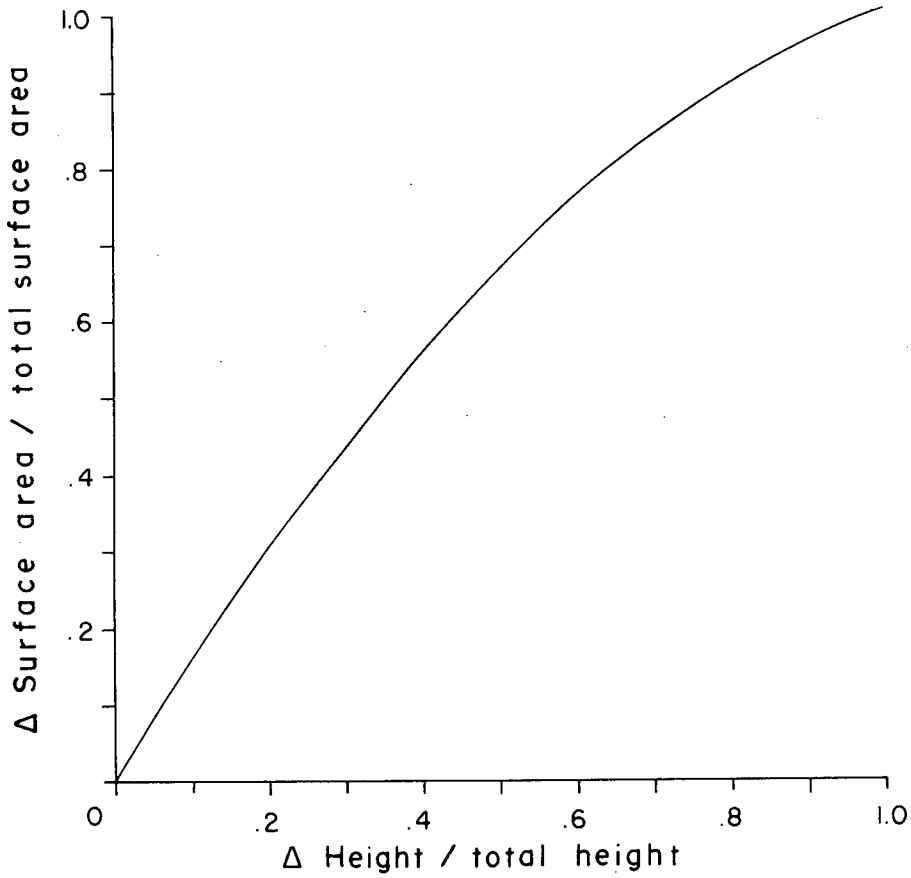
The least squares multiple curvilinear regression equations had an intercept and did not pass through the coordinate point (x,y) = (1,1) as required when $\underline{\Delta H} = \underline{H}$ amd $\underline{\Delta S_t} = \underline{S_t}$. This discrepancy was "corrected" by imposing the following restrictions upon the least squares solutions of the normal equations: The regression line must pass through the coordinate points (x,y) = (0,0) and (x,y) = (1,1). When these restrictions were applied to the least squares solutions of the third degree multiple curvilinear equations, the partial regression coefficients were found to be nearly of the same magnitude as those of the unrestricted least squares equations (Appendix A). Further, the scatter about the above defined multiple curvilinear equation of $\underline{\Delta S_t / S_t}$ on $\underline{\Delta H/H}$ was found to be the greatest at the coordinate point (x,y) = (0.5, f(x)) and it decreased from this point with both increasing and decreasing values of the independent variable (Appendix G). The standard deviation of the y-observations was found to be approximately proportional to x(1 - x)(Appendix H). Therefore, new variance formulas were proposed to estimate the variability about the regression line and that of an individual observation (Appendix B).

The partial surface area table for forkless trees was developed by substituting the appropriate expressions for $\underline{S_t}$ and $\underline{f(\Delta H/H)}$ into

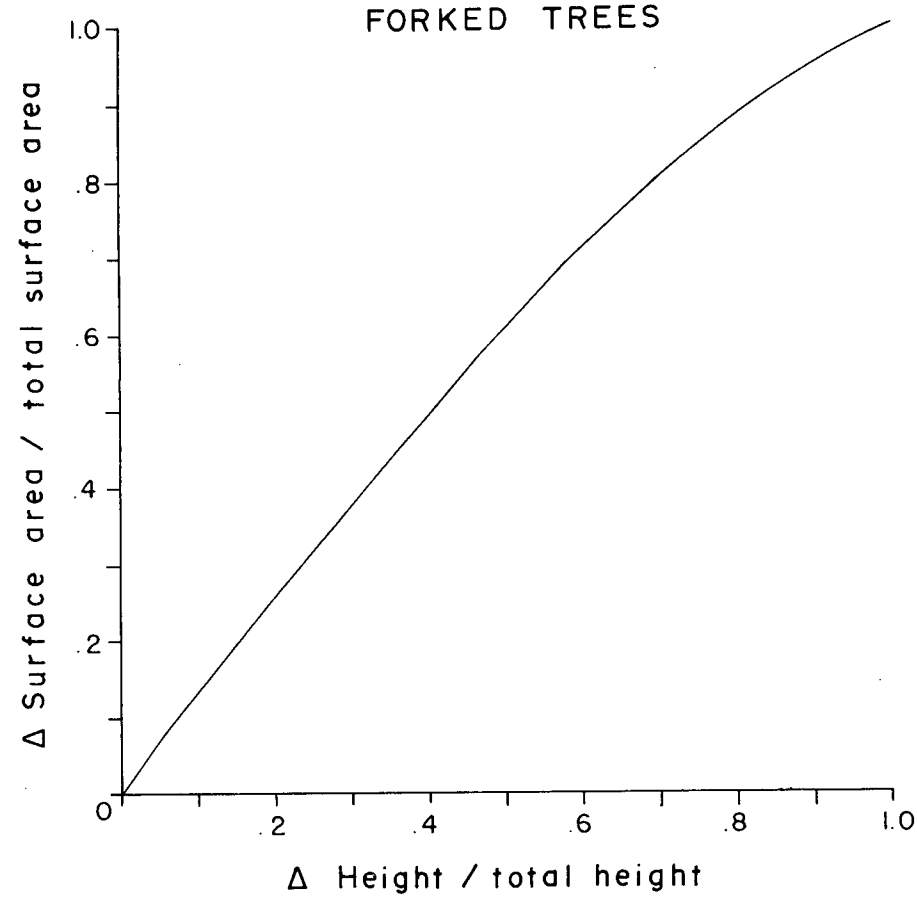
Figure 28.

Graphical form of the infested surface area/total surface area versus height/total height relationship for lodgepole pine.

TREES WITHOUT FORKS



FORKED TREES



equation 57 of the Materials and Methods section. That is:

$$S_p = (1.9708DH + 3.7196)(0.0242 + 1.4150(\Delta H/H) - 0.4391(\Delta H/H)^3)$$

Where, S_p = partial surface area in sq. ft. units and the other symbols are as defined earlier.

This equation was programmed on an electronic computer to produce a partial surface area table covering the 6.0 - 15.8 inch d.b.h. range at 0.2 inch intervals and the 32 - 124 foot total height and 4 - 84 foot infested height ranges at 4 foot intervals. A sample of the partial surface area table is given in Appendix C.

5. Studies of the frequency distribution of attacks and late stage progeny of the mountain pine beetle and studies of transformations.

5.1. The frequency distribution of attacks and late stage progeny of the mountain pine beetle. The means, variances, k-values (the index of dispersion of the negative binomial distribution) and numbers of observations for late stage progeny and attacks on the Horsethief and Elk Creek plots in 1965 are given in Table XVIII. The frequency histograms are shown on Figures 29 and 30, respectively, for the former and latter variable.

TABLE XVIII. MEANS, VARIANCES AND DISPERSION INDICES OF BROOD AND ATTACK COUNTS OF THE MOUNTAIN PINE BEETLE (COMBINED DATA FROM THE NORTHERN AND SOUTHERN ASPECTS OF INFESTED TREES)

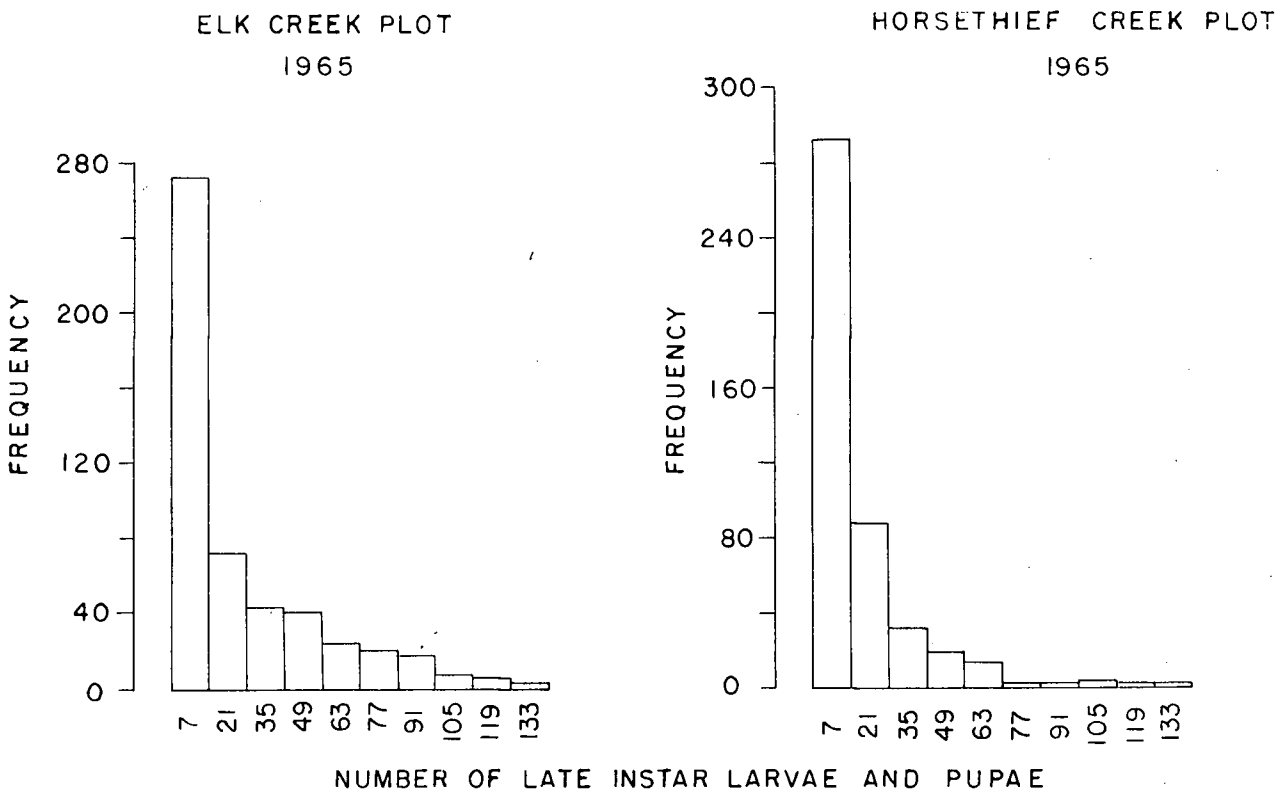
Horsethief Creek plot - 1965				Elk Creek plot - 1965			
Mountain pine beetle brood in fourth larval, pupal and teneral adult stages.							
n	Mean($\bar{Y}$)	Variance(S^2)	k	n	Mean($\bar{Y}$)	Variance(S^2)	k
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
542	22.839	889.500	0.602	604	16.331	628.600	0.436
Attacks							
542	3.310	8.100	2.280	604	4.542	8.400	5.355

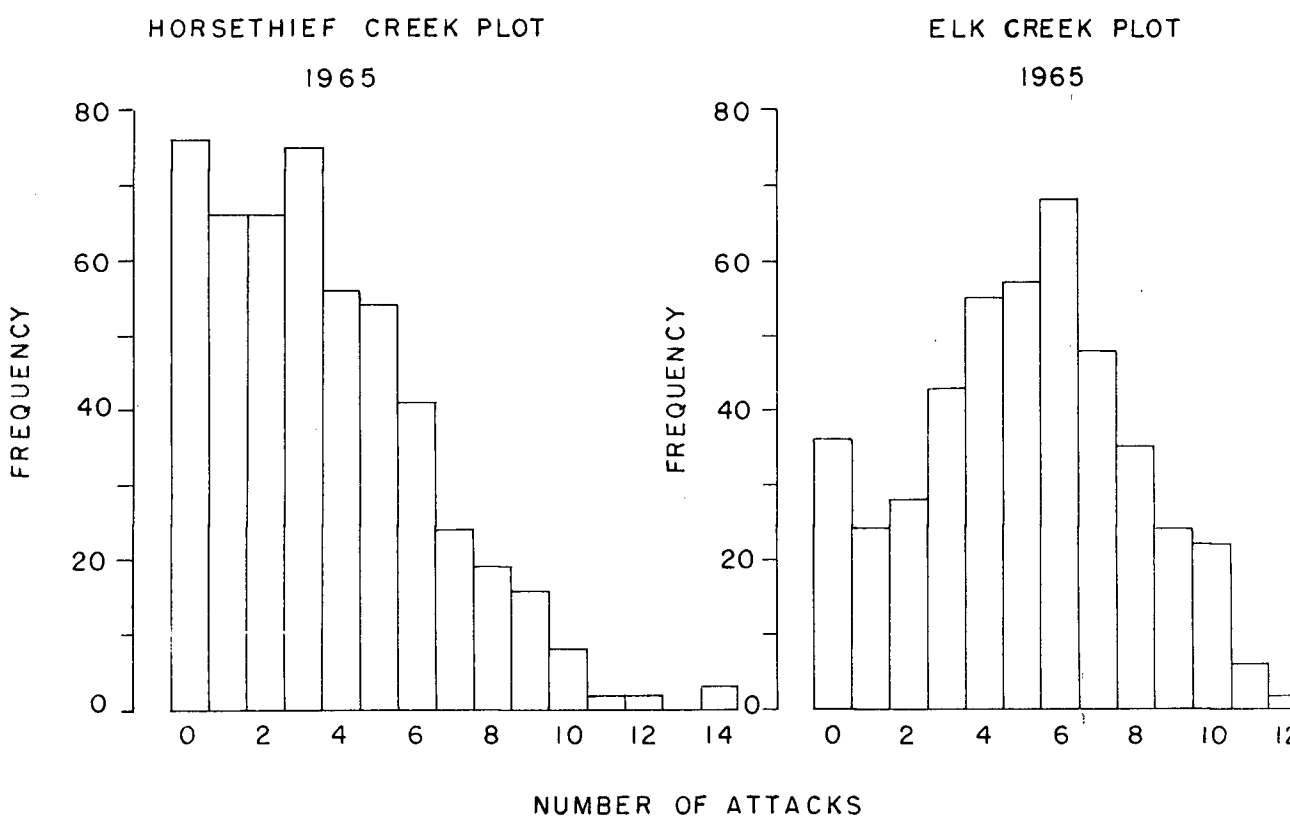
Figure 29.

The frequency distribution of late stage mountain pine beetle larvae and pupae per 96 sq. in. sampling unit.

Figure 30.

Frequency distribution of the number of attacks per 96 sq. in. sampling unit.


ELK CREEK PLOT
1965
HORSETHIEF CREEK PLOT
1965
FREQUENCY
280
200
120
40
0
300
240
160
80
0
7
21
35
49
63
77
91
105
119
133
NUMBER OF LATE INSTAR LARVAE AND PUPAE


HORSETHIEF CREEK PLOT
1965
ELK CREEK PLOT
1965
FREQUENCY
80
60
40
20
0
0
2
4
6
8
10
12
14
NUMBER OF ATTACKS

n = number of observations, k = dispersion index of the negative binomial distribution.

The distribution of attacks on both the Horsethief and Elk Creek plots were decidedly skewed. Although sampling continued only to the upper most point of attack, approximately one fourth of the sampling units produced zero counts. On the Horsethief Creek plot, at the time of sampling when the broods were mainly in the fourth larval stage, they suffered close to 100% mortality in the upper 15% of the infested stems while on the Elk Creek plot only a few live beetles were found in the upper 7% of the infested stems. Therefore, since the infested stems were systematically sampled, at two foot intervals on the due N and due S aspects, approximately 15% and 7%, respectively, of the sampling units on the Horsethief and Elk Creek plots produced zero counts. The zero counts, in excess of the above cited percentages were caused by tree resistance and wood pecker predation on the Elk Creek plot and by tree resistance on the Horsethief Creek plot.

The frequency distributions of attacks were less skewed than those of the brood counts. The distribution of attacks on the Elk Creek plot was more symmetric than that on the Horsethief Creek plot. The skewness of both of these distributions would have been somewhat reduced if the sampling units were drawn with equal probability. However, Shepherd (1960) found that, when taking a 100% tally of 60 infested trees, the distribution of attacks was definitely more skewed than that of the present studies. His results point to the fact that the frequency distribution is a function of both the size of the attacking population and tree characteristics such as bark roughness,

branchiness or resin-producing ability.

5.2. The relationship between variance and mean. The relationship between sampling variance (within-tree variance) and mean was well fitted by Taylor's power law (equation 15, section 4.2.6., Materials and Methods) for both late stage mountain pine beetle broods and attacks. The equations on transformed scale and their graphical forms and correlation coefficients are shown on Figures 31 and 32. The slopes of the S^2 vs. $\bar{y}$ relationships were considerably higher for the brood data than those for attack density data indicating that the former variable was more aggregated than attack counts per sampling unit. There was an excellent correspondance between the slopes of S^2 vs. $\bar{y}$ relationships for brood and attack counts on the Horsethief and Elk Creek plots in spite of the differences between the average diameter and average height of the sample trees and the density gradients of mean attack and brood density. Therefore, it appears that the coefficient of aggregation (the power of Taylor's equation) for attacks and for brood in a certain developmental stage, will stay fairly constant with varying host conditions and characteristics and with changing mean densities of the two variables.

5.3. Transformation. The variance vs. mean relationships of brood counts, after Taylor's Z (section 4.2.7., Materials and Methods) and $\log_{10}(y + k)$ transformations, are shown on Figures 33 and 34, respectively. (Note: These Figures are the transformed equivalents of Figure 31.)

Both transformations sufficiently stabilized the variance, although, for the $\log_{10}(y + k)$ transformation of the Horsethief Creek

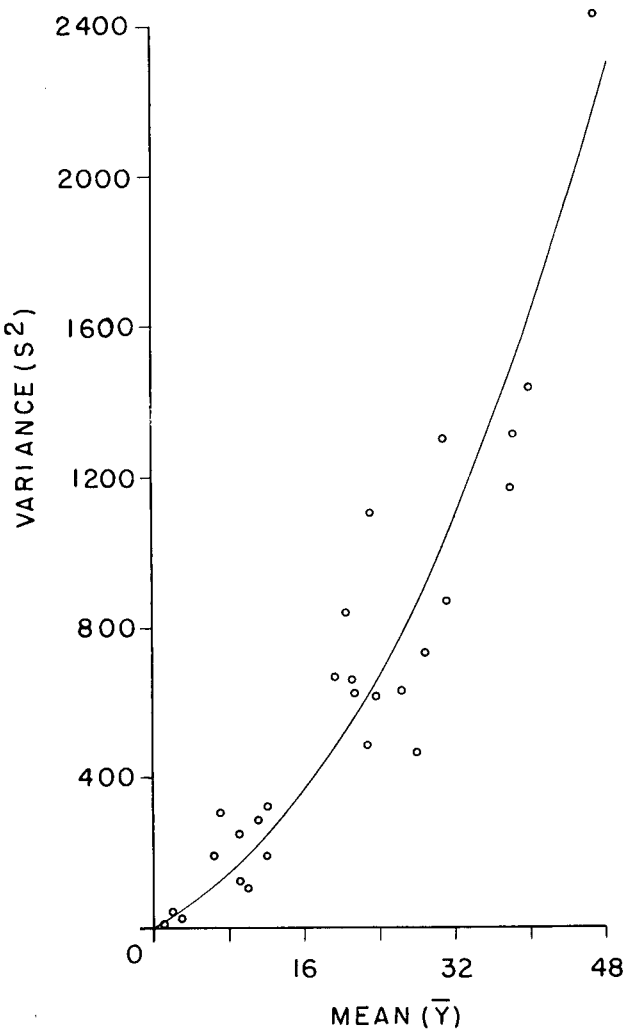
Figure 31.

Relationship between within-tree variance and mean brood density per 96 sq. in. sampling unit. (Combined data from the N and S aspects.)
Equations:

$$\log_{10} S^2 = 0.6637 + 1.5789 \log_{10} \bar{y},\ r = 0.901 \text{ (Elk Creek, 1965)}$$

$$\log_{10} S^2 = 0.6892 + 1.5693 \log_{10} \bar{y},\ r = 0.947 \text{ (Horsethief Creek, 1965)}$$

HORSETHIEF CREEK PLOT
1965



ELK CREEK PLOT
1965

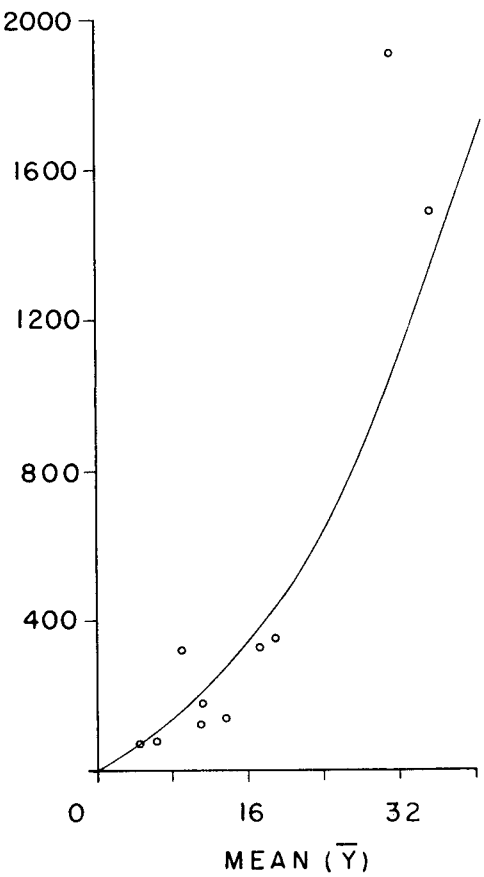


Figure 32.

Relationship between within-tree variance and mean attack density per 96 sq. in. sampling unit. (Combined data from the N and S aspects)

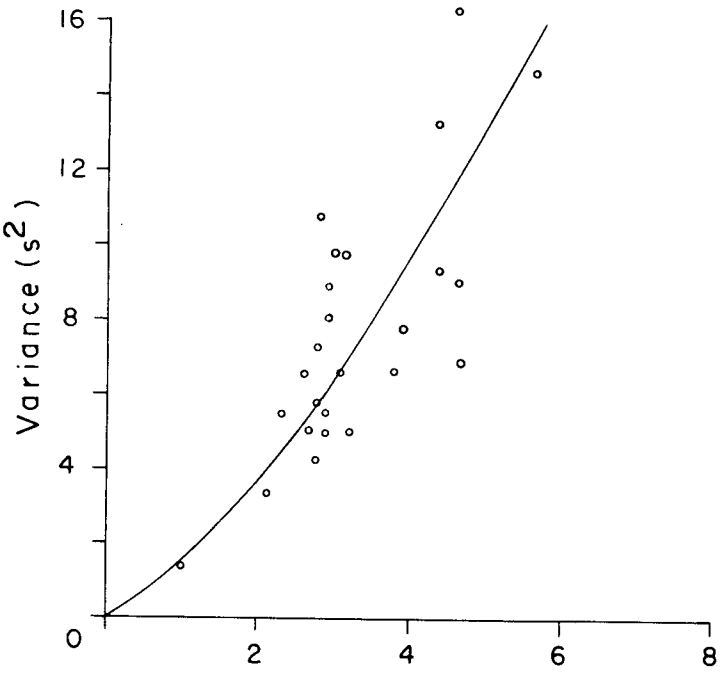
Equations:

$\log_{10} S^2 = -0.0465 + 1.3007 \log_{10} \bar{y}$, $r = 0.768$ (Elk Creek, 1965)

$\log_{10} S^2 = 0.1992 + 1.2998 \log_{10} \bar{y}$, $r = 0.849$ (Horsethief Creek, 1965)

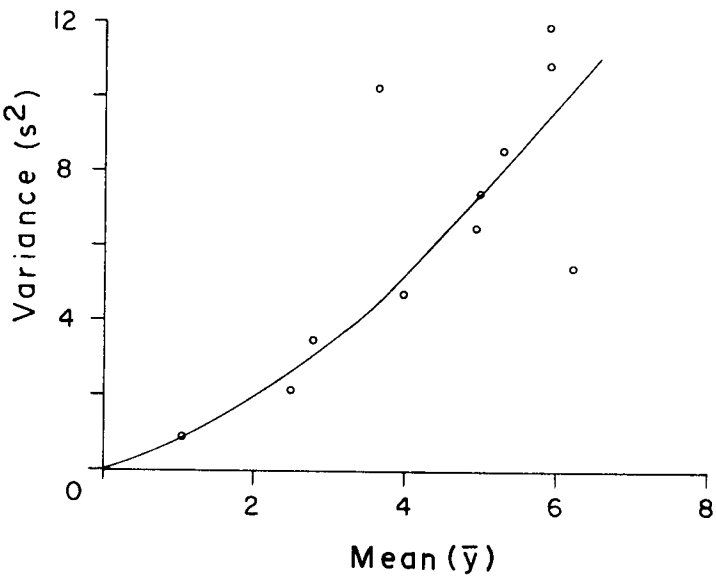
HORSETHIEF CREEK PLOT

1965



ELK CREEK PLOT

1965



data the variance noticeably increased with increasing mean. In addition to its excellent performance in stabilizing the variance, a further advantage of the Z over the logarithmic transformation is that the former eliminates the necessity of finding, by trial and error, an "appropriate" constant to be added to the individual observations in order to stabilize the variance as it is often done with the square root and logarithmic transformations. On the other hand, the logarithmic transformation is easier to carry out when there is no access to computer facilities.

The relationship between the mean and variance of attack counts after Taylor's Z transformation is shown on Figure 35. (Note: This Figure is the transformed equivalent of Figure 32.) It is evident that the variance was not related to the mean on the transformed scale.

6. The sampling design.

6.1. Estimation of the gain in precision due to intra-primary unit stratification of brood counts/secondary unit (Elk Creek plot data, 1965). The statistics and variables needed for estimating the intra-primary unit component of the sampling variance of brood population total from five secondary unit strata, and that from unstratified systematic sampling of the primary units, are given in Table XIX. (Note: The five within-primary unit strata were established by forming "horizontal" stratum boundaries at height levels coinciding with the position of 5.5 m.m. thick bark on the stem (Fig. 25) and with the 80% of infested height (Fig. 23) and by dividing the lowest two "horizontal" strata into due N and S aspects.)

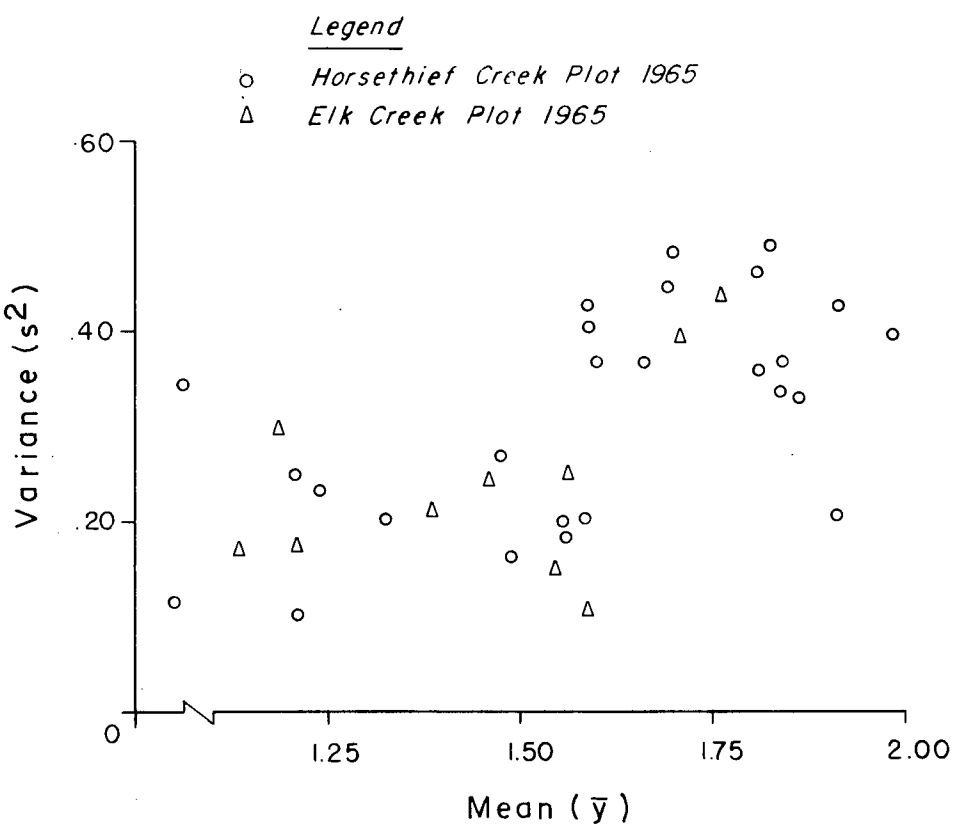
In Table XIX the statistics and variables are represented by the

Figure 33.

Relationship between within-tree variance and mean brood density per 96 sq. in. unit after Taylor's Z- transformation.

Figure 34.

Relationship between within-tree variance and mean brood density after $\log_{10}(y + k)$ transformation.


Legend
Horsethief Creek Plot 1965
Elk Creek Plot 1965
.60
.40
.20
0
Variance (s^2)
1.25
1.50
1.75
2.00
Mean ($\bar{y}$)

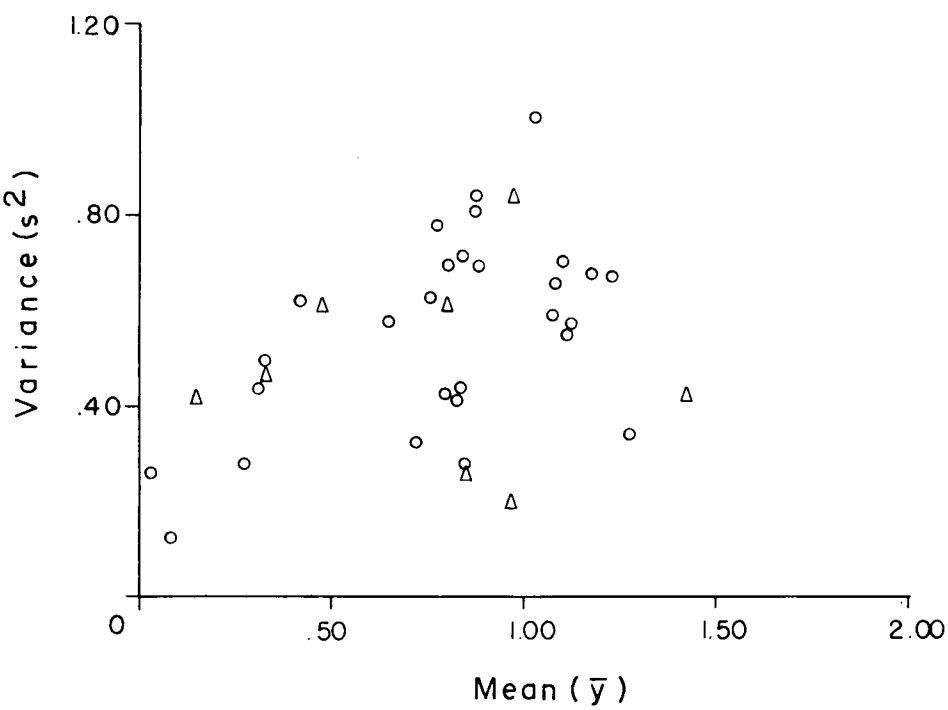
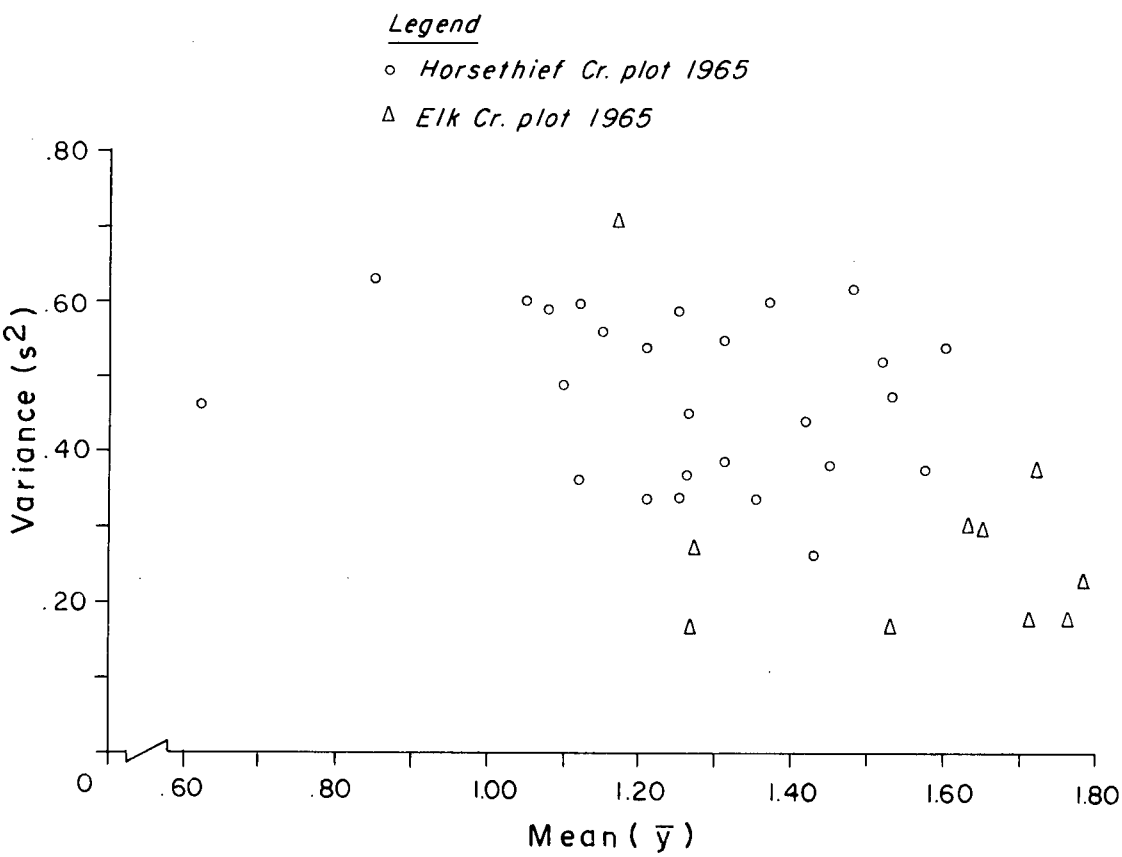

1.20
.80
.40
0
Variance (s^2)
.50
1.00
1.50
2.00
Mean ($\bar{y}$)

Figure 35.

Relationship between within-tree variance and mean attack counts per 96 sq. in. unit after Taylor'S Z-transformation.


Legend
Horsethief Cr. plot 1965
Elk Cr. plot 1965
.80
.60
.40
.20
0
Variance (s^2)
.60
.80
1.00
1.20
1.40
1.60
1.80
Mean ($\bar{y}$)

following symbols: M_j = size of the j-th primary unit in 0.66 sq. ft. units, m_j = second-stage unit sample size in primary unit j, $\bar{y}_{mj}$ = sample mean in the j-th primary units based on m numbers of observations, s_j^2 = within-primary unit sampling variance in the j-th primary unit, m_{ij} = number of secondary units drawn from the i-th stratum of the j-th primary unit, s_{ij}^2 = sampling variance in the i-th stratum of the j-th primary unit.

TABLE XIX. SUMMARY OF STATISTICS NEEDED FOR ESTIMATING THE INTRA-PRIMARY UNIT COMPONENT OF THE POPULATION TOTAL OF MOUNTAIN PINE BEETLE BROODS ON THE ELK CREEK PLOT IN 1965 (THE DATA WAS TRANSFORMED BY TAYLOR'S "Z" TRANSFORMATION)

Tree number	M_j	y_{mj}	m_j	s_j^2/m_j	$M_j^2 s_j^2/m_j$	$M_{ij}^2 s_{ij}^2/m_{ij}$*
(1)	(2)	(3)	(4)	(5)	(6)	(7)
744	222.59	1.4699	68	0.003583	177.524	77.9369
740	219.58	1.2521	40	0.004022	193.870	101.1004
743	278.09	1.5478	61	0.002484	192.320	114.1590
747	216.29	1.1399	31	0.004175	195.310	180.9737
747	284.41	1.6124	52	0.004984	403.150	142.9989
745	292.77	1.7674	58	0.007461	639.514	250.1817
742	299.10	1.3902	69	0.003143	281.264	141.8186
746	317.69	1.6344	64	0.001741	175.713	220.1540
809	351.45	1.1913	74	0.005220	644.759	194.1629
802	382.24	1.7162	77	0.003907	571.140	567.7067
Total			604		3,474.564	1,988.1920

* = column (6) is a summary of the last column of Appendix D.

The within-tree variance component of the population total, on the basis of systematic sampling within primary units, s_{ws}^2 (second term on the right hand side of formula (19), Materials and Methods, but finite population correction ignored), appears in Table XIX as the sum of column (6). The within-tree variance component for stratified sampling of the secondary units, s_{wst}^2 (formula (21), Materials

and Methods, but finite population correction ignored), is given as the sum of column (7) in Table XIX. Thus

$$s^2_{ws} = 3,474.564$$

and

$$s^2_{wst} = 1,988.192$$

The stratified systematic sampling of the second stage units had the following efficiency over systematic sampling without stratification (formula 22, Materials and Methods):

$$E = (s^2_{ws}/s^2_{wst})100 = 174.8\% \text{ (on transformed scale)}$$

Thus the size of the intra-primary unit variance component of the population total was substantially reduced by constructing five secondary unit strata.

6.2. Estimation of the gain in precision of the inter-primary units variance estimate of brood population total due to stratification and regression sampling (Elk Creek plot data, 1965). The summarized data for estimating the intra-primary unit component of brood population total with and without stratification, and with regression sampling of the primary units, is given in Table XX. The relative index of abundance for individual trees (I_j) and the population total estimates/primary unit from an unstratified systematic second-stage sample (Y_j) and from a stratified systematic second-stage sample (Y_{mj}) are given in columns (4), (7) and (8) of Table XX, respectively. The primary units strata were formed by arbitrarily grouping primary units which had I_j index values greater than 20,000, between 20,000 and 2,000 and less than 2,000 (column 5, Table XX).

The possibility of regression sampling of the primary units on

their infested surface areas was suggested by the tendency of the total number of insects/tree, Y, to increase with increasing infested surface area, M. When Y was plotted over M for the Elk Creek and Horsethief Creek plot samples from 1965 and linear regression lines were fitted to the (M,Y) pairs of observations, the equations had the following form:

$$Y_h = -847.87 + 52.96M_h,\ r = 0.79^{**},\ s_{y.x} = 145.79,\ n = 28$$

$$Y_e = -8{,}100.08 + 45.20M_e,\ r = 0.66^{*},\ s_{y.x} = 2{,}688.30,\ n = 10$$

Where the subscripts h and e designate the Horsethief and Elk Creek plots, respectively, $s_{y.x}$ = standard error of estimate, n = sample size, r = simple correlation coefficient, ** and * respectively = significant at the 1% and 5% probability level, M = number of 0.66 sq. ft. units/primary unit and Y = estimated total number of late stage larvae/primary unit.

After the individual counts on the secondary units were transformed by Taylor's Z transformation the least squares equations had the following form:

$$Y_h = -11.3728 + 1.866M_h,\ r = 0.96^{**},\ s_{y.x} = 158.58,\ n = 28$$

$$Y_e = -117.334 + 1.9344M_e,\ r = 0.88^{**},\ s_{y.x} = 208.80,\ n = 10$$

The notation is the same as above. For the Elk Creek equation, on the transformed scale, the M and Y values are recorded in columns (2) and (8) of Table XX, respectively.

The between-tree variance estimates of the brood population total on transformed scale for random (s^2_{br}), stratified random (s^2_{bst}) and regression sampling (s^2_{bre}) of the primary units were calculated as in equation 20, 23 and 24, respectively, and the numerical values

are as follows:

s^2_{br} = 43,792.864 (columns 2 and 7, Table XX)

s^2_{bst} = 29,510.050 (columns 2 and 8, Table XX)

s^2_{bre} = 13,548.417 (columns 2 and 8, Table XX)

Hence, the efficiency of regression and stratified sampling over simple random sampling of the primary units (E_1 and E_2) was calculated as follows:

$$E_1 = (s^2_{br}/s^2_{bst})100 = 148.5\%$$

and

$$E_2 = (s^2_{br}/s^2_{bst})100 = 323.0\%$$

Thus, of the three sampling methods compared, regression sampling of primary unit totals on primary unit size provided the smallest between-primary unit variance estimate of the population total. The between-primary unit component of the sampling variance was more than six times as large as the within-primary unit variance component (s^2_{bre} = 13,548.417 vs. s^2_{wst} = 1,988.192). Consequently, the bias of sampling variance estimates from systematic second-stage samples (but random first stage samples) will be small and the precision of population total estimates can be greatly increased by regression and stratified sampling of the primary and secondary units, respectively.

TABLE XX. SUMMARIZED DATA FOR INTER-PRIMARY UNIT STATIFICATION AND REGRESSION SAMPLING OF LATE STAGE MOUNTAIN PINE BEETLE BROOD (ELK CREEK PLOT, 1965)

Tree Number	M_j	D_j	$I_j=D_j xM_j$	Strata	$\bar{y}_{mj}$	$Y_j=M_j\bar{y}_{mj}$	$Y_{mj}=M_j\bar{y}_{wmj}$
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
745	292.77	105.5	30,887.2	I	1.7674	517.4358	545.6376
802	382.34	85.0	32,498.9	I	1.7162	656.1680	657.9382
809	351.45	39.0	13,706.5	II	1.1913	418.6894	435.4165
746	317.69	25.0	7,942.2	II	1.6344	519.2335	525.5671
742	299.10	48.5	14,506.6	II	1.3902	415.8237	425.5424

Table XX continued

TABLE XX. SUMMARIZED DATA FOR INTER-PRIMARY UNIT STRATIFICATION AND REGRESSION SAMPLING OF LATE STAGE MOUNTAIN PINE BEETLE BROOD (ELK CREEK PLOT, 1965)

Tree Number	M_j	D_j	$I_j=D_j \times M_j$	Strata	$\bar{y}_{mj}$	$Y_j=M_j\bar{y}_{mj}$	$Y_{mj}=M_j\bar{y}_{wmj}$
(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
741	284.41	26.5	7,536.9	II	1.6124	458.5997	467.4887
743	278.09	12.5	3,476.1	II	1.5478	430.4277	444.6110
740	219.58	25.0	5,489.5	II	1.2521	274.9492	281.4684
744	222.59	2.5	556.5	III	1.4699	327.2006	334.7584
747	216.29	6.5	1,405.9	III	1.1399	246.5597	247.7057
	2,864.31					4,265.0868	4,366.2291

$\bar{\bar{y}} = \frac{4,265.087}{2,864.31} = 1.48904$, $\bar{\bar{y}}_w = \frac{4,366.2291}{2,864.31} = 1.52431$, $\bar{M} = \frac{2,864.31}{10} = 286.431$

$N = 10$, M_j = number of 0.66 sq. ft. secondary units in the j-th primary unit, D_j = density/0.66 sq. ft. secondary unit at the 6 foot level of the j-th primary unit (arithmetic scale), I_j = index value of the j-th primary unit for stratification, $\bar{y}_{mj}$ = mean for a secondary sample size "m" in the j-th primary unit based on systematic samples and Taylor's Z transformation, Y_j = total brood for the j-th primary unit based on systematic second stage sampling, Y_{wj} = total brood for the j-th primary unit based on stratification of the second stage units into five strata, $\bar{\bar{y}}$ = overall secondary-unit mean based on systematic second stage sampling and Taylor's Z transformation, $\bar{\bar{y}}_w$ = weighted secondary unit mean based on the grouping of second-stage units into five strata and on Taylor's Z transformation and $\bar{M}$ = average number of secondary units/primary unit for the population (assuming that population size, N, was equal to ten).

6.3. Estimation of sample size needed to establish the population mean of brood counts/secondary unit with a standard error = 0.1 of the sample mean (Elk Creek plot sample, 1965). As the sampling variance was estimated from transformed data and the sampling mean from

the original observations (section 3.2.4., Materials and Methods), the transformation of the required standard error to transformed scale involved the computation of the following statistics:

$\bar{\bar{y}}_w$ = population mean on transformed scale = 1.5243 (Table XX)

$\bar{x}_w$ = "back transformed" population mean (antilog (log. 1.5243/0.211)= 7.273

$\bar{x}$ = population mean on original scale = 16.922 (Table XXI)

$s_{\bar{x}}$ = required standard error on original scale = 10% of $\bar{x}$ = 1.692

$s_{\bar{\bar{y}}}$ = required standard error on transformed scale

$\bar{x} + s_{\bar{x}} = 17.614$

$\bar{x} - s_{\bar{x}} = 15.230$

$p = (\bar{x}_w/\bar{x}) = 0.4298$

$c = (1 - b/2) = 0.211$ (Taylor's Z transformation constant)

s_p^2 = pooled within-primary unit variance component (equation (28), Materials and Methods) = $\frac{80.3184}{554} = 0.1449$ (Appendix D)

f_2 = second-stage sampling fraction = 2% (section 3.2.5., Materials and Methods)

$\bar{M}$ = mean infested surface area in 0.66 sq. ft. units = 286.431 (Table XX)

$s_p^2 \left(\frac{1}{f_2 \bar{M}} - \frac{1}{\bar{M}}\right) = 0.02478$ (formula 28, Materials and Methods)

$$S_b^2 = s_{bre}^2/n\bar{M}^2 - s_p^2/nS_n \frac{1 - f_{2j}}{m_j} = \frac{13,548.4170}{(10)(286.431)^2} - \frac{0.1449}{10}\ 0.0791 = 0.01536$$

In the equation above the value of s_{bre}^2 was calculated in section 6.2., n and $\bar{M}$ in Table XX and $S_n(1 - f_{2j})/m_j$ in Appendix D. Then, by substituting the appropriate values into equation (29), Materials and Methods, the following value is obtained for $s_{\bar{\bar{y}}}$:

$$s_{\bar{\bar{y}}} = \frac{((16.922)0.4298)^{0.211} - ((1 - 0.1)(16.922)0.4298)^{0.211}}{2} +$$

$$\frac{((1 + 0.1)(16.922)0.4298)^{0.211} - ((16.922)0.4298)^{0.211}}{2} = 0.0322$$

Thus, the standard error on transformed scale, $s_{\bar{\bar{y}}}$, is equal to 0.0322 when the required standard error on original scale is $0.1\bar{x}$ (1.6922).

The estimate of the standard error for the Elk Creek sample on transformed scale, $S_{\bar{\bar{y}}w}$, is calculated from equation (25), Materials and Methods, as follows:

$$S_{\bar{\bar{y}}w} = \sqrt{\frac{0.01536 + 0.02478}{n} - \frac{0.01536}{N}}$$

By ignoring the negative term (finite population correction) in this equation and substituting $s_{\bar{\bar{y}}}$ for $S_{\bar{\bar{y}}w}$, the equation can be solved for n = primary unit size. That is

$$0.0322 = \sqrt{(0.01536 + 0.02478)/n}, \text{ and } n = 39.$$

Therefore, it may be concluded that for a desired precision of $s_{\bar{x}} = 10\% \bar{x}$ on the original scale and for a second-stage sampling fraction of $f_{2j} = 2\%$, 39 primary units should be sampled on the Elk Creek experimental area when the mean per secondary unit is close to 17 insects (provided that first-stage sampling is with regression on primary unit size and second-stage sampling is stratified systematic as defined in section 6.1., of the Experimental Results).

TABLE XXI. SUMMARIZED DATA FOR CALCULATING THE MEAN NUMBER OF BROOD PER SECONDARY UNIT FOR THE ELK CREEK, 1965, SAMPLE (UNTRANSFORMED DATA)

Tree Number	Brood		
	M_j	Mean ($\bar{x}_j$)	$\bar{x}_j M_j$
(1)	(2)	(3)	(4)
744	222.59	11.8477	2,637.2007
740	219.58	6.6306	1,455.9662
743	278.09	12.7149	3,355.6334
747	216.29	4.3378	938.2225
741	284.41	18.5254	5,268.8193
745	292.77	39.2010	11,476.9406
742	299.10	9.9717	2,982.5365
746	317.69	13.9138	4,420.2841
809	351.45	10.6830	3,754.5743
802	382.34	31.3860	12,000.3906
	2,864.31		48,470.5582

$$\bar{x} = \frac{48,470.5582}{2,864.3100} = 16.922$$

$\bar{x}_j$ = mean number of brood per secondary unit for the j-th primary unit (tree), $\bar{x}_j M_j$ = total number of brood for the j-th primary unit, $\bar{x}$ = brood sample mean of the secondary units.

6.4. Estimation of brood population total and its variance (Elk Creek sample, 1965). The brood population total (Y) is estimated from equation 34, Materials and Methods, as the product of the total number of primary units in the population (N), the average primary unit size ($\bar{M}$) and the average number of broods/secondary unit ($\bar{x}$). By substituting the appropriate numerical values for $\bar{x}$, $\bar{M}$ and N, into equation 34, the following estimate of Y was obtained:

$$Y = N(\bar{M})\bar{x} = 10(2,864.31)16.922 = 48,471$$

Thus, on the Elk Creek plot in 1965, the estimate of brood population total was 48,471 beetles in late larval, pupal and teneral adult stages of development.

The estimation of the variance of $\bar{x}(s^2_{\bar{x}})$ in equation 34 involves the conversion of the variance on transformed scale ($s^2_{\bar{\bar{y}}}$) to arithmetic scale and requires the computation of the following statistics:

$s^2_{\bar{\bar{y}}}$ = variance of $\bar{\bar{x}}$ on transformed scale (equation 32, Materials and Methods) = $1,569.0811/10^2(286.431)^2 = 0.0001912$ (columns 6 and 10, Appendix D).

(Note: As all primary units were sampled in the population $f_1 = 1$, and the first term on the right hand side, after the equal sign, of equation 32, Materials and Methods, becomes zero).

$s_{\bar{\bar{y}}} = 0.01383$

$\bar{\bar{y}}_w = 1.52431$ (Table XX)

$\bar{\bar{y}}_w + s_{\bar{\bar{y}}} = 1.53813$

$\bar{\bar{y}} - s_{\bar{\bar{y}}} = 1.51047$

$\bar{x}_w = 7.273$ (section 6.3., Experimental Results)

$\bar{x} = 16.922$ (Table XXI)

$p = (\bar{x}/\bar{x}_w) = 2.3267$

$s_{\bar{x}w}$ = standard error of $\bar{x}_w$, the "back transformed" mean = 0.3155 (from formula, 30, Materials and Methods)

$s^2_{\bar{x}w} = 0.3155^2 = 0.09954$

From $s^2_{\bar{x}w}$, $s^2_{\bar{x}}$ is calculated as $s^2_{\bar{x}} = p \times s^2_{\bar{x}w} = 2.3267^2(0.09954) = 0.53886$. Thus, the mean number of beetles/0.66 sq. ft. unit (secondary unit) and its variance were 16.922 and 0.53886 on the Elk Creek plot in 1965. On square foot basis these values become $\bar{x} = 1.5\ (16.922) = 25.383$ and $s^2_{\bar{x}} = 1.5^2(0.53886) = 1.21243$, respectively.

$\bar{M}$, the mean primary unit surface area is estimated as a product

of $\bar{a}$ = mean surface area of infested trees and $\bar{p}$ = the mean proportion of the total surface area/tree occupied by insects. Consequently, the variance of M, $s^2_{\underline{M}}$, is estimated from the variance of p, $s^2_{\underline{p}}$, and the variance of a, $s^2_{\underline{a}}$ by the variance of product formula (formula 36, Materials and Methods).

The statistics required for the estimation of $s^2_{\underline{a}}$ (formula 38, Materials and Methods) are as follows:

$n = 73$ (sample size for the surface area vs. (D.b.h.) (Ht.) regression equation,

$s^2_{y.x} = 43.3035$, $n_1 = 10$ (sample size for the Elk Creek plot in 1965), $x^2 = (64.510 - 119.055)^2$ = the square of the difference between the regression mean of (D.b.h.) (Ht.) and that of the Elk Creek sample mean (D.b.h.) (Ht.) (Table XXII), and $S_n x^2 = 40{,}113.6734$ = sum squares of the (D.b.h.)(Ht.) values for the regression equation.

By substituting the appropriate values into formula 38 (Materials and Methods), $s^2_{\underline{a}}$ is calculated as:

$$s^2_{\underline{a}} = 43.3035\left(\frac{1}{10} + \frac{1}{73} + \frac{(119.055 - 64.510)^2}{40{,}113.6734}\right) = 8.13456$$

TABLE XXII. STATISTICS FOR THE CALCULATION OF THE AVERAGE INFESTED BARK SURFACE AREA PER TREE (SQ. FT.) AND ITS VARIANCE

Tree Number	D.b.h. (ft.)	Ht. (ft.)	$\frac{Ht_f}{Ht.}$	(Ht.)(D.b.h.) (sq.ft.)
(1)	(2)	(3)	(4)	(5)
746	1.333	93.0	.688	123.97
742	1.208	91.0	.729	109.93
743	1.225	85.0	.441	104.12
744	0.900	88.0	.705	79.20
740	1.266	94.0	.425	119.04
741	1.483	94.0	.553	139.40
745	1.291	86.5	.769	111.67
747	1.316	86.0	.795	123.17
809	1.316	97.0	.748	127.65
802	1.600	101.5	.773	162.40
				1,190.55

$\overline{(D.b.h.)(Ht.)}$ = 1,190.55/10 = 119.055 sq. ft.

Ht_f = infested height and Ht. total height.

The numerical value of $\bar{a}$ is obtained by substituting (D.b.h.)(Ht.) = 119.055 sq. ft. in the following equation:

$$a = 1.9078(D.b.h.)(Ht.) + 3.7196$$

Where, a = surface area per tree in sq. ft. and (D.b.h.)(Ht.) = product of total height (ft.) and diameter at breast height (ft.). Thus, the solution for $\bar{a}$:

$$\bar{a} = 1.9708(119.055) + 3.7196 = 238.3531 \text{ sq. ft.}$$

Thus, the ten sample trees on the Elk Creek plot in 1965 had a mean totals surface area of 238.3531 sq. ft. and this estimate had a variance, $s^2_{\bar{a}} = 8.13465$ ft.^{4}.

The statistics required for the estimation of the variance of $\bar{p}$, the average infested proportion of the total surface area/tree (formula 37, Materials and Methods) are as follows:

$s^2_{y.x}$ = the variance about the regression of p on x_p = 0.001642

n = 565 (number of observations for the regression equation of p on x_p)

n_1 = 10 (number of observations on the Elk Creek plot in 1965)

$x_p = Ht_f/Ht$ (column 4, Table XXII)

$p = 0.0242 + 1.4150\ x_p^3$ (Fig. 28)

$\bar{x}_p = 0.500$

$\underline{x}_p = 0.660$ (calculated from column 4, Table XXII as in section 4.2.12., Materials and Methods)

Thus, the solution for $s^2_{\underline{p}}$:

$$s^2_{\underline{p}} = 0.001642\left(\frac{1}{10} + \frac{1}{565}\right)\left(\frac{0.660 \times 0.340}{0.250}\right) = 0.0001589$$

The numerical value of $\underline{\bar{p}}$ is obtained by substituting $x_{\underline{p}}$ for $x_{\underline{p}}$ in the equation

$$p = 0.0242 + 1.4150x_{\underline{p}} - 0.4191x^3_{\underline{p}}$$

Thus,

$$\underline{\bar{p}} = 0.0242 + 1.4150(0.660) - 0.4191(0.660)^3 = 0.80114$$

On the Elk Creek plot in 1965, on the average, 80.1% of the total surface area of the ten sample trees was infested and this estimate had a variance, $s^2_{\underline{p}} = 0.0001589$. (Note: The technique for the calculation of the total infested surface area involves the formation of separate "pa" products for individual infested trees and the summing of these products over all infested trees (and not the formation of a single mean "pa" product involving all infested trees.) It is for this reason that the weighted mean of the $x_{\underline{p}}$ values, $x_{\underline{p}}$, rather than their arithmetic mean had to be substituted in the previous equation to estimate the appropriate $\underline{\bar{p}}$ value.)

The variance of $(\bar{p} \times \bar{a})$, $s^2_{\underline{M}}$ is calculated by the variance of product formula (equation 36, Materials and Methods in the following manner:

$$s^2_{\underline{M}} = (0.80114 \times 238.3531)^2\left(\frac{0.0001589}{0.80114^2} + \frac{8.13456}{238.3531^2}\right) = 14.14782$$

Thus, the average infested surface area of the ten sample trees was $\bar{M}$ = 190.9542 sq. ft. and it had a variance estimate of $s^2_{\underline{M}} = 14.14782$ ft.^{4}.

The variance of the product $\underline{\bar{x} \times \bar{M}}$ is calculated in the same manner as the variance of $\underline{\bar{M}}$. That is:

$$s^2_{\overline{xM}} = 48{,}470.5582^2\left(\frac{14.14782}{190.9540^2} + \frac{1.21440}{25.3830^2}\right) = 53{,}343.9954$$

Finally, the variance of $\underline{Y} = N(\overline{M})\overline{x}$ (the population total) is calculated as follows:

$$s^2_{N(\overline{M})\overline{x}} = N^2(s^2_{\overline{Mx}}) = 5{,}334{,}399$$

and, therefore:

$$s_{N(\overline{M})\overline{x}} = 2{,}309 \text{ insects.}$$

Thus, on the Elk Creek experimental plot, in 1965, the estimate of the population total of late stage mountain pine beetle brood, $\underline{Y}$, was 48,471 and had a standard deviation of 2,309 insects.

7. Estimation of population trend for insect surveys.

7.1. Studies of the relationship between average and maximum brood density in individual trees. The relationship between average and maximum brood density (i.e. brood density at the four and six foot height levels for the Horsethief and Elk Creek sample trees, respectively) is shown in Figure 36. All three regression equations had significant correlation between the dependent and independent variables.

The slopes and intercepts of the three regression equations on Figure 36 were compared by covariance analysis and the results are given in Table XXIII.

No significant differences were found between the slopes of the three regression equations. The intercepts, however, were different at the 1% probability level. The significance of the difference between intercepts was caused by the higher intercept (a = 5.590) of the regression equation for the Horsethief Creek sample in 1965 than that of either the Horsethief Creek sample in 1966 (a = 2.050) or the Elk Creek sample in 1965 (a = 3.767). The Horsethief Creek sample

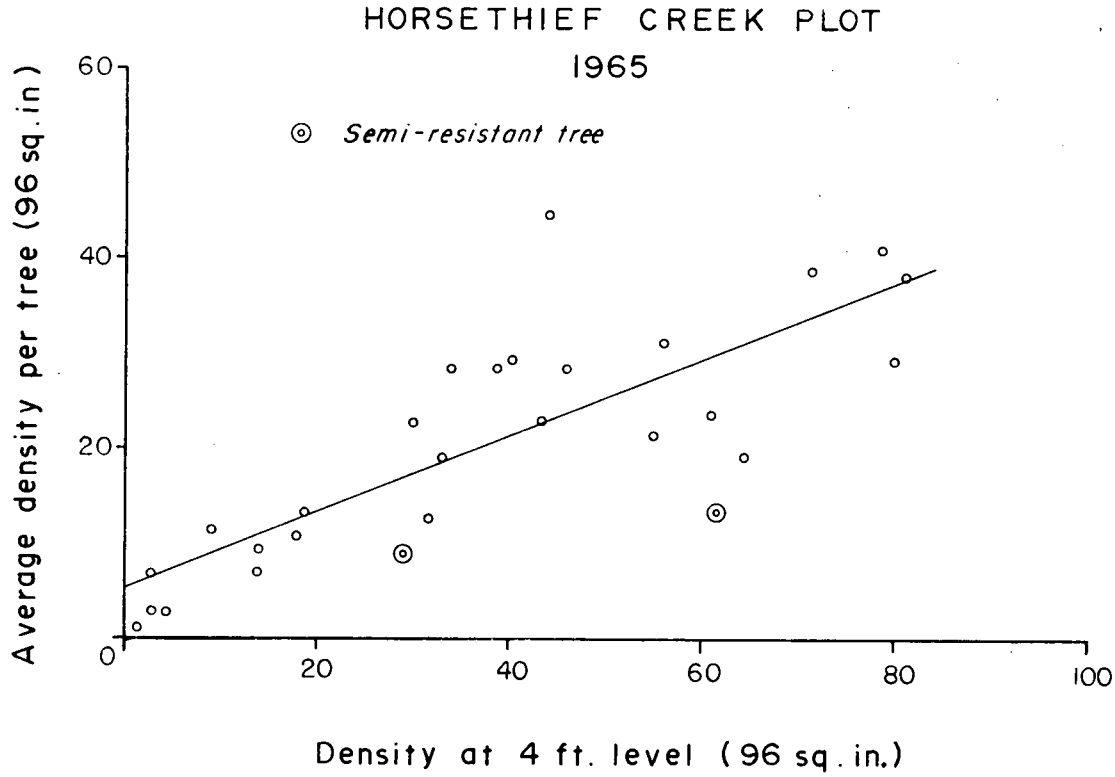
Figure 36

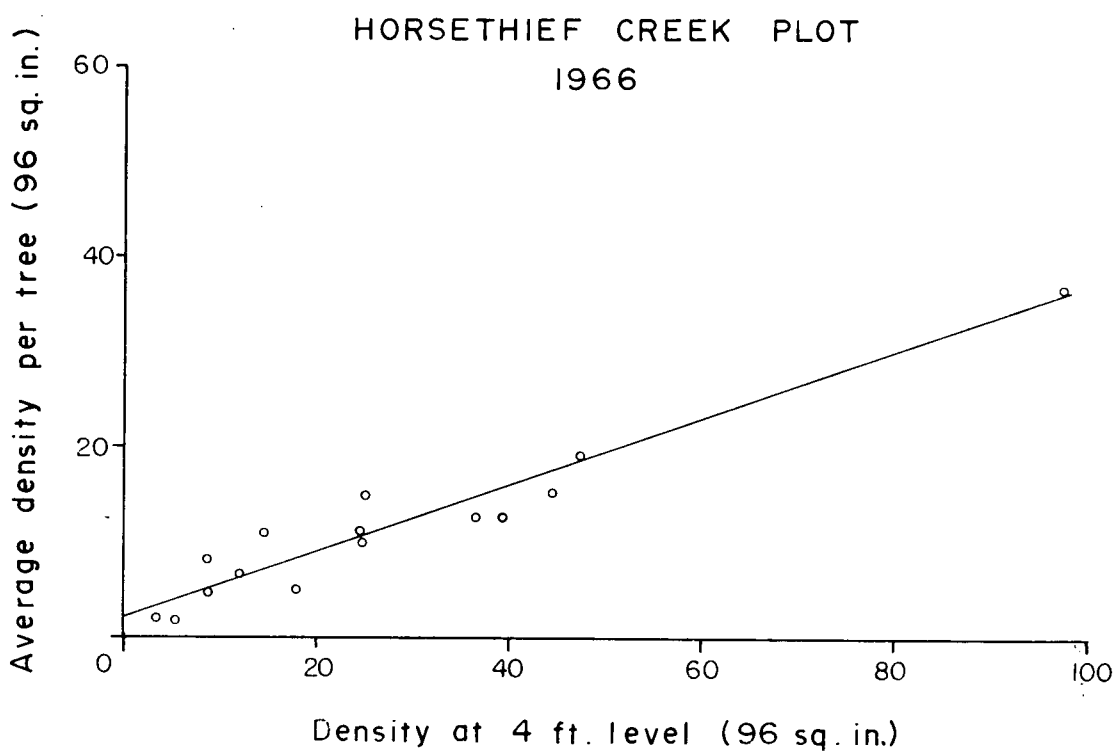
Relationship between within-tree average and "maximum" brood density. (The within-tree average vs. maximum brood density relationship for the Elk Creek trees in 1965 is shown on the following page).
Equations:

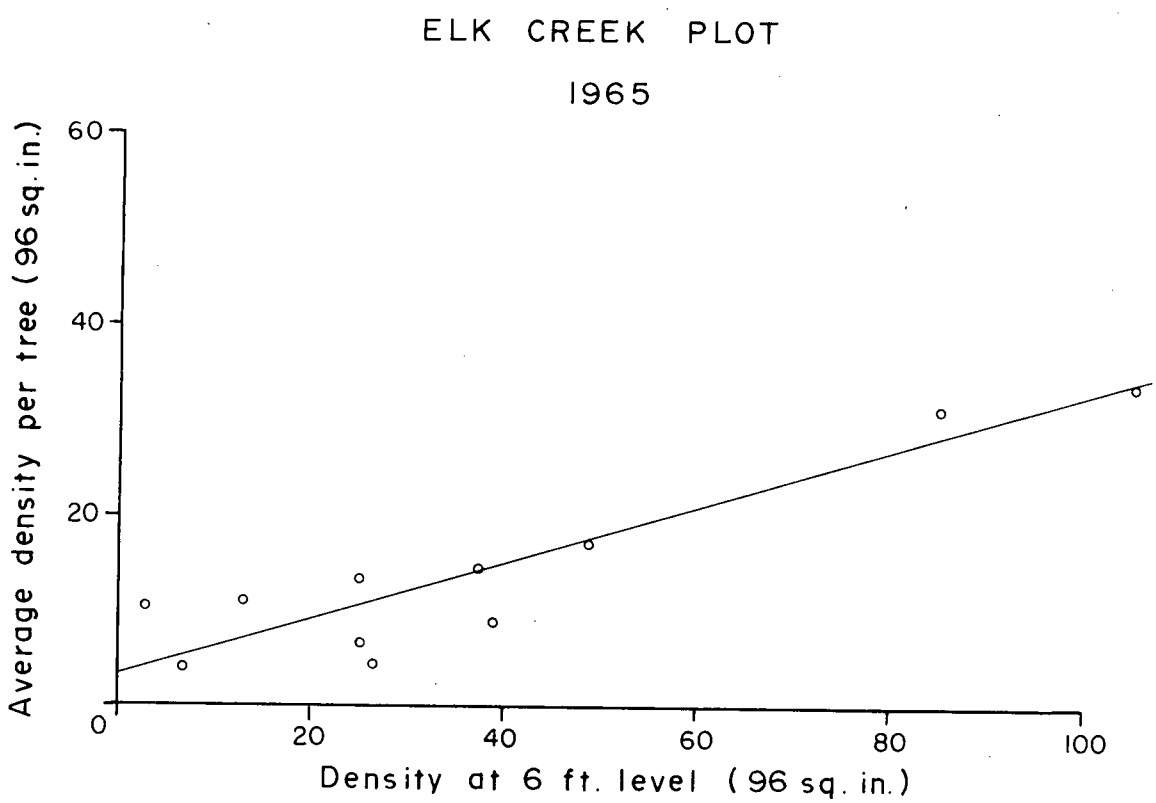
$y = 5.590 + 0.385\ x$, $r = 0.776$, $s_{y.x} = 7.980$ (Horsethief Creek, 1965)

$y = 2.050 + 0.340\ x$, $r = 0.980$, $s_{y.x} = 1.495$ (Horsethief Creek, 1966)

$y = 3.767 + 0.278\ x$, $r = 0.896$, $s_{y.x} = 4.830$ (Elk Creek, 1965)


HORSETHIEF CREEK PLOT
1965
◎ Semi-resistant tree
Average density per tree (96 sq. in.)
0
20
40
60
0
20
40
60
80
100
Density at 4 ft. level (96 sq. in.)


HORSETHIEF CREEK PLOT
1966
Average density per tree (96 sq. in.)
0
20
40
60
0
20
40
60
80
100
Density at 4 ft. level (96 sq. in.)


ELK CREEK PLOT
1965
Average density per tree (96 sq. in.)
60
40
20
0
20
40
60
80
100
Density at 6 ft. level (96 sq. in.)

in 1965 contained several trees which had high brood density at the four foot level but low average density because of tree resistance (resinosis) in the higher portions of the stem. These trees were probably responsible for the high intercept of the average vs. maximum brood density relationship of the Horsethief Creek sample in 1965.

It should be noted that when brood density at the point of maximum is zero, average brood density should also be zero. Thus, the regression equations on Figure 36 could have been conditioned to pass through the origin.

7.2. Development of the population trend index. In the preceding section it was found that average brood density within individual trees (y) is related to brood density at a predetermined height level by the equation: $y = bx + a$. The linear regression equations of $\underline{y}$ on $\underline{x}$, on two different plots and in two different years on one of these plots, had identical slopes and small but significantly different intercepts. Therefore, in an outbreak area, average brood density for a sample of infested trees ($\bar{y}$) will be related to average brood density at a predetermined height level ($\bar{x}$) as: $y = b\bar{x} + a$. Further, as the regression lines on Figure 36 could have been forced through the origin (because they had small intercepts), the relationship between $\bar{y}$ and $\bar{x}$ can be rewritten as: $\bar{y} = b'\bar{x}$. Therefore, if we let:

a_i = estimate of the surface area of the i-th tree,

$S_N a_i$ = estimate of the total surface area of all infested trees in any one year,

$(S_N a_i)\bar{y}$ = estimate of brood population total in any one year,

$(S_N a_i)\bar{x}$ = index of brood population total in any one year,

than the $(S_N a_i)\bar{y}$ vs. $(S_N a_i)\bar{x}$ relationship within a given infested area is described by the following equation:

$$(S_N a_i)\bar{y} = b'(S_N a_i)\bar{x} \qquad \text{(XIII)}$$

Therefore, population trend may be expressed as the ratio of the estimates of total population in years N and N + 1. That is:

$$I = \frac{((S_N a_i)\bar{y})_N}{((S_N a_i)\bar{y})_{N+1}}, \qquad \text{(XIV)}$$

Where, I = index of population trend. (Note: A more meaningful expression of population trend is the ratio of the population of reproducing individuals in successive years. $\underline{I}$ in equation (XIV), will estimate this ratio only if we assume a stable generation to generation sex ratio). In accordance with equation (XIII) an estimate of $\underline{I}$ can be calculated as follows:

$$I' = \frac{b'((S_N a_i)\bar{x})_N}{b'((S_N a_i)\bar{x})_{N+1}} = \frac{((S_N a_i)\bar{x})_N}{((S_N a_i)\bar{x})_{N+1}} \qquad \text{(XV)}$$

If equation (XIII) has an intercept other than zero, $\underline{I'}$ will be a biased estimator of the true population ratio. Therefore, the use of $\underline{I'}$ is recommended only for general insect survey work, at least until more is known concerning the relationship between $(S_N a_i)\bar{y}$ and $(S_N a_i)\bar{x}$.

TABLE XXIII. ANALYSIS OF COVARIANCE TO COMPARE THE SLOPES AND INTERCEPTS OF THE THREE LINEAR REGRESSION EQUATIONS OF AVERAGE BROOD DENSITY ON MAXIMUM BROOD DENSITY PER TREE, FOR THE ELK AND HORSETHIEF CREEK SAMPLES.

						Residuals						
Line	Group	Df	$S_n y^2$	$S_n yx$	$S_n x^2$	Df	Sum squares	Mean square	F	$F_{.05}$	$F_{.01}$	Remark
1	A	9	989.675	2,854.900	10,247.900	8	194.3459					
2	B	27	4,150.000	6,497.300	16,872.900	26	1,648.0650					
3	C	14	975.260	2,751.120	8,074.870	13	37.9500					
4					Total	47	1,880.3609	40.0076				
5					Difference for testing slopes	2	72.4140	36.2070	0.905	3.20	5.10	ns
6		50	6,114.935	12,103.320	35,195.670	49	1,952.7750	39.8525				
7					Difference for testing levels	2	420.2900	210.1500	5.273	3.19	5.08	**
8		52	6,974.690	12,936.400	36,367.690	51	2,373.0700					

A = Elk Creek, 1965, sample, B = Horsethief Creek, 1965, sample, C = Horsethief Creek, 1966, sample,

ns = not significant, ** = significant at the 1% probability level.

DISCUSSION

The variance and edge effect bias of sample estimates of mean brood density in late larval stages of development were related to the shape, size and orientation of the sampling unit. Edge effect bias, a result of the inclusion or exclusion of most individuals from sampling unit boundaries, was directly proportional to the circumference area ratio of the units. Consequently, for any fixed sampling unit size, edge effect bias decreased from rectangular through square to circular units. The edge effect of long, narrow rectangular units increased with decreasing width per length ratio (w/l) because the circumference per area ratio is inversely related to w/l. Rectangular sampling units, when orientated with long sides parallel to the egg galleries, had greater edge effect bias than rectangular units of the same w/l ratio but rotated by 90°. This difference can be explained on the basis of the spatial arrangement of mountain pine beetle larvae. When the long sides of the units are parallel to the egg galleries they will also lie approximately parallel to the long axes of larval clumps. Thus, the long sides of these units will, on the average, bisect more larvae than the long sides of the same units but rotated by 90°. This explanation implies that edge effect bias, in addition to the w/l ratio of the unit, is a function of the spatial arrangement of the organisms. However, it has been shown that this bias was independent of mean density.

For any given sampling unit shape, edge effect bias was inversely proportional to the square root of sampling unit size and directly proportional to the square root of the cross-sectional area of an "average" larva. The rate of change of the edge effect bias ($L_c\%$) decreased rapidly with increasing sampling unit size up to about 12 square inches for all sampling unit shapes. For sampling units greater than 12 square inches the change in $L_c\%$ with respect to unit size became more gradual. These findings indicate that mean brood density, when estimated from sampling units smaller than about 12 square inches, will have considerable systematic bias resulting from edge effect (greater than 7%). Therefore, these units should not be considered for intensive population work, especially if edge effect cannot be controlled. For a fixed sampling unit size, circular units will give smaller $L_c\%$ values than square or rectangular units. As edge effect bias increases with decreasing w/l ratio, when a rectangular unit is used for sampling its w/l ratio should, if possible, be at least $\frac{1}{2}$ especially for small sampling units (i.e. close to 12 square inches). (Note: The edge effect bias of mean brood density can be minimized by X-raying infested slabs of wood and sampling the radiographs with a transparent overlay "sampling unit" over the light table. With this sampling technique it is possible to identify those insects which fall on the sampling unit boundaries.)

The sampling variance of mean brood counts per sampling unit was related to the size and shape of the sampling unit and to the orientation of long, narrow units. When the shape and size of the unit were approximately equal to the mean size of larval clumps, the va-

riance of the estimate of mean brood counts/unit was maximal. This result is supported by experimental evidence from vegetation studies. Greig-Smith (1957) and later Kershaw (1964) indicated that the same relationship holds for quadrat samples of many plant species which exhibit "patchy" spatial arrangement.

When sampling is done with rectangular units, the orientation of which are parallel to the egg galleries, these units will bisect fewer egg galleries (Appendix I) and include more "extreme" counts than units of any other shape and orientation. This is because the former units will approximate the shapes, sizes and orientations of larval clumps. Consequently, as a result of the comparatively high frequency of extreme brood counts, the estimated variance of the former units will be higher than that of any other unit, for any fixed sampling unit size. The effect of sampling unit orientation on sampling variance decreased with increasing brood density, possibly because at high densities the spatial arrangement of the larvae were more regular then at low densities. Of the three sampling unit shapes (circular, rectangular and square) and two orientations (long sides parallel and perpendicular to the egg galleries) considered, rectangular units oriented perpendicular to the egg galleries gave the smallest variance estimates (greatest precision) for all sampling unit sizes investigated. For these units the estimate of the sampling variance decreased with decreasing w/l ratio. Therefore, when there is access to radiographic facilities (so that edge effect can be controlled) the efficiency of the sampling design can considerably be increased by using long, narrow units the long sides of which are orientated perpendicular to the egg galleries.

Optimum sampling unit size, in terms of the least total time needed to establish mean brood density for a predetermined degree of precision, was determined separately at two height levels by assuming simple random sampling for multiple items (brood and attack density). At both height levels optimum unit size was found to be approximately eighteen square inches (w/l ratio = $\frac{1}{2}$, long sides perpendicular to egg galleries). However, this result has limited generality as it is applicable only to simple random sampling at fixed height levels. In addition to the technique of sampling, optimum unit size will be affected by the method of sampling unit delineation and enumeration, the work-speed of the sampler and by changes in brood density. For the two-stage sampling technique, which was developed for the mountain pine beetle, the definition of the optimum unit differs from the above given definition. As the second-stage sampling fraction was set at 2%, the optimum unit is that which gives the most efficient estimate of the within-primary unit component of the population total for a fixed second-stage sampling fraction, when the units are selected by within-primary unit stratification. The nature of the within-tree variance vs. mean relationship is such that the smallest units will give lower estimates of the within-tree variance component of the population total, of all units of optimum shape and orientation which do not have serious edge effect bias. This conclusion is valid only when variance is estimated from untransformed data.

Studies indicated that in the branch-free portions of infested stems the concentration of both attacks and brood were highest on

the north-eastern aspect and lowest on the south-western exposure. However, in the mid-crown region the circular distribution of both of these variables appeared uniform. These findings confirm those of Shepherd (1960) who reported highest attack densities from the northern aspects of infested lodgepole pine trees. Shepherd stated that aspect differences in attack density were due to the attacking female beetle's behaviour. The attacking beetles are stimulated to fly by high heat and light intensities and, therefore, the southern and western aspect of the clear bole will harbour lighter attacks than the more shaded northern and eastern aspects. This hypothesis was also supported by the finding that at 1:00 P.M. MST, when peak flight usually occurs within a day (Reid 1960), at the time of emergence the shadow was centered on those positions of the infested clear boles where the highest attack concentration was recorded. Brood density is related to attack density and, therefore, it was natural to expect the circular distribution of the former to be similar to that of attack density. However, this correlation is disturbed by competition, woodpecker predation, insect predation and parasitisim, resinosis and the differential rates of drying of the inner bark and outer sapwood on the various aspects of the stem. Therefore, the difference in the location of the highest incidence of attacks and brood counts in the lower and middle regions of the stems, was probably caused by the action of these mortality factors on brood density.

The difference, which was found between the vertical attack density gradients on the due N and S aspect of infested trees is the

result of the attacking female beetle's reaction to high heat and light intensity and it has been explained earlier. This hypothesis appears to be contradicted by the fact that, in 1965, the attack density gradients of the northern and southern aspects of the Elk Creek sample trees were identical. This apparent contradiction is due to the fact that, in 1965, on the Elk Creek experimental plot an early flight took place and the lightly infested southern aspects of most sample trees have been reattacked. Although this flight was not actually observed, indirect evidence supports this hypothesis. At the time of sampling, during the first half of July, on the southern aspects a considerable portion of the insects was in the egg, first and second larval stages, while the majority of the insects on the northern aspect was in late larval, pupal and teneral adult stages. The between-plot and between-years within plot differences in the rate of change of attack density with height is probably the result not only of tree resistance and size of the attacking population, but also of bark roughness. As bark roughness is a function of age and diameter (in addition to site, climatic and genetic factors) the older and bigger diameter trees of the Elk Creek plot had rougher bark and, consequently a greater number of suitable attack sites higher up the stem than the younger and smaller diameter trees of the Horsethief Creek plot. On the Elk Creek plot, in 1966, attack density decreased with height at a greater rate than the attack density in 1965. As the sample trees were of the same age and size in both years, this finding is probably the result of the lighter intensity of attacks at all levels on the sample trees in 1966 than that of the sample

trees in 1965. A strong contrast appears in the fact that in the Elk Creek samples the two foot level supported lower attack densities than those of the four foot region (in spite of the greater bark roughness at the former level), while on the Horsethief Creek plot, the highest mean attack density occurred at the two foot level. The reason probably lies in the fact that the high ground vegetation on the former plot prevented attack initiation close to the base of the infested trees.

These results generally are in good agreement with those of Shepherd (1960, 1965) who found differences in attack intensity between levels and aspects within trees, between areas, between diameter classes within areas and between trees within diameter classes. Also, the interaction of height with trees, diameters and areas proved to be significant. On any given location, the differences between height levels, diameter classes and trees and the significance of the interaction of these variables with height level can be explained on the basis of the relationship between bark roughness and number of suitable attack sites and resistance. The aspect difference is due to the female beetle's reaction to high light intensity and heat and the area difference is the result of the combined effects of bark roughness, resistance and the size of the attacking population.

The functional relationship between bark roughness and the number of available attack sites was shown indirectly by assuming that the number of suitable attack sites is an asymptotic function of the combined thicknesses of the inner and outer bark and that the intensity of attacks on the bark surface of a "non-resistant" tree will be approximately proportional to the number of suitable attack sites.

The mathematical model gave an excellent fit to the brood density vs. bark thickness relationship. The formulae had positive "x"-intercepts indicating that, at any level of the attacking population, the height level of attacks on a "non-resistant" host tree will coincide, on the average, with the location of a certain minimum bark thickness on the stem. The average value of this threshold bark thickness was found to be about 1.5 m.m. on the Horsethief and Elk Creek experimental plots. This result seems to suggest that bark surfaces thinner than the threshold thickness either did not support suitable attack sites or they proved to be too thin for egg gallery construction. The parameters of the brood density vs. bark thickness relationships were not influenced by either height level or resinosis within the limitations of the sample data. When tested at fixed height level over a large group of sample trees, the spatial pattern of attacks was regular. Shepherd (1965) arrived at the same conclusion on the basis of plotless sampling on a limited bark area and argued that the regularity of attack pattern was probably due to the regularity of suitable attack sites. Thus, when all of the findings are taken into consideration, it is suggested that at any fixed level of the attacking population, the intensity of attacks on "non-resistant" trees will be determined by the number of suitable attack sites per unit bark area of the host, lodgepole pine.

Although, the brood density vs. bark thickness graphs had a general resemblance to those of attack density, the relationship between brood density and bark thickness was decidedly sigmoid on

both experimental plots and in both years on the Horsethief Creek plot. The sigmoid brood density vs. bark thickness curves resulted from the inverse relationship between the brood/attack ratio and height (Fig. 22). It was noticeable, especially on the Elk Creek plot that brood density increased to a maximum and then declined with increasing bark thickness. This result is clearly not due to the action of bark thickness because in 1965, for the 15 m.m. bark thickness class, maximum and minimum brood densities were recorded on the Horsethief and Elk Creek plots, respectively. The most likely explanation, therefore, seems to be that at the bases of infested trees brood suffer excessive mortality from resinosis (Reid 1960).

Correlation analysis of 38 infested trees taken from two sampling localities indicated that total numbers of attacks/tree (Y_1) was significantly correlated with the following variables: d.b.h. x total tree height, 1/d.b.h., crown width^2 x crown length, tree age, sum of the distances from the three nearest trees larger than 4 inches in d.b.h. and bark thickness at d.b.h. level. The combined variable, d.b.h. x total height, had the highest correlation coefficient with Y_1 followed by tree age, 1/d.b.h., (crown width)^2 x crown length, in that order ($r = 0.87, 0.82, -0.69$ and 0.65). These results suggest that the attack harbouring potential of lodgepole pine trees is related to external tree characteristics and stand density. The combined variable d.b.h. x total tree height and 1/d.b.h. (d.b.h. x total tree height/d.b.h.^{2} x total tree height) are both expressions of the total bole area, therefore, Y_1 is rela-

ted to the total surface area available for attack in individual trees. Both tree age and (crown width)^2 x crown length are strongly correlated with d.b.h. x total tree height (r= 0.88 and 0.79 respectively) and, therefore, the high correlation of the former two variables with $\underline{Y_1}$ is probably due to their interrelationship with the latter variable. The combined variable (crown width)^2 x crown length, is an expression of crown volume and thus, to a degree, stand density or crowding. An other measure of crowding is the sum of the distances to the sample tree to its three nearest neighbours more than 4 inches in d.b.h. Both expressions of crowding were significantly correlated with $\underline{Y_1}$ indicating that relatively open-grown trees tend to harbour more attacks than trees which are crowded by their neighbours. Bark thickness is an index of bark roughness and, thus, the number of suitable attack sites/unit area of bark and, in addition to d.b.h. x total height, it is an important tree characteristic influencing the attack harbouring potential of individual trees.

In individual trees, the total number of attacks (Y_1) was predicted by a multiple regression equation of $\underline{Y_1}$ on bark thickness at d.b.h. level, d.b.h. x total tree height and radial stump height growth for the last ten years with high degree of accuracy (R^2 = 0.809). However, this result have limited generality because total number of attacks in individual trees depend, in addition to physical tree characteristics, on factors such as the size of the attacking beetle population, the number of susceptible host trees, climatic conditions at the time of beetle dispersion and localized resistance.

For the combined Elk and Horsethief samples in 1965, the brood total estimate/tree (Y_2) was significantly correlated with Y_1, the attack total estimate/tree, and with those tree characteristic variables which were also significantly correlated with Y_1. The four variables which had the highest correlation with Y_2 were (crown width)^2 x crown height, d.b.h. x total tree height, Y_1 and 1/d.b.h., in that order, ($r = 0.67, 0.66, 0.65$ and -0.56, respectively). These results indicate that the total number of broods surviving to late larval and pupal stages of development is related to indices of tree size such as d.b.h. x total tree height, 1/d.b.h. and an expression of total crown volume, in addition to the total number of attacks, in individual trees. The expression of crown volume, (crown width)^2 x crown length, may affect survival by controlling the rate of drying of the insects sub-cortical habitat and by affecting the nutritional quality of the inner bark. The variable 1/d.b.h., in addition to being an expression of tree size, is an index of the bole area/bole volume ratio and, therefore, this variable may also affect brood survival by controlling the moisture loss from the bole through the bark after the death of the infested tree.

For the Elk Creek sample trees, the total number of attacks/tree was estimated by a multiple regression equation of Y_2 on the total number of broods/tree, 1/d.b.h. and d.b.h. x total tree height ($R^2 = 0.763$). Similarly, for the Horsethief Creek sample, the multiple regression equation of Y_2 on the total numbers of brood/tree, tree age and on the combined variable d.b.h. x total tree height gave a moderately good fit to the sample data ($R^2 = 0.599$). The Elk Creek

plot sample trees were much older than the Horsethief Creek plot trees (107.6 vs. 60.6 years) and had a smaller age spread (12 vs. 40 years) and this may be the reason for age not being an important independent variable for the Elk Creek predictive equation. Although, these predictive equations have limited generality and are not suitable for sampling purposes because the estimation of attack totals in individual trees is a time consuming procedure, they are useful for indicating what combination of external tree characteristics have the greatest effect on brood survival. These external tree characteristics can be used for constructing strata to reduce the between-tree (primary unit) component of brood variance estimates.

The brood density vs. bark thickness relationship proved to be well adaptable to the construction of within-primary unit strata. The nature of this relationship is such that within-primary units variability can be substantially reduced by dividing the primary units into three or more strata, horizontally, at height levels corresponding to certain bark thickness values. However, the formation of much more than about three horizontal strata is not advisable for the following reasons: Firstly, the observations need to be transformed before analyses and within-primary unit variability of brood counts, on a transformed scale, will be substantially reduced. Secondly, for brood counts, first-stage variability is known to be considerably greater than second-stage variability, therefore, it will be more rewarding to concentrate efforts on reducing the former source of variation.

Experiments indicated that stratification by aspect will not

be as efficient as that by level, especially if the data is transformed prior to analysis. At height levels greater than about the 80% point of infested height, there is little or no difference between brood densities on the northern and southern aspects. Therefore, aspect stratification is needed only for the lower four-fifths of the infested stem. The aspect-stratum boundaries should coincide with the N 45°W and N 45°E compass directions. On the other hand, it was suggested by the brood density vs. bark thickness relationship that efficient horizontal stratification will be obtained by forming stratum boundaries at the height levels coinciding with the location of 5.5 m.m. thick bark (Appendix J) and with the 80% point of the infested stem (Fig. 24).

The cumulative brood total vs. cumulative infested height relationship on Figure 24 has another practical use beside stratification. Cahill (1960) reported that during chemical control of the mountain pine beetle a decision must be made on how much of the infested tree should be sprayed to effect satisfactory kill. He based this decision on the entire infested bole and stated that trees which are infested to greater heights than the effective spary height (27.5 ft.) should be felled to complete the treatment. Figure 24 indicates that, even if the total infested height was 55 feet (double of the effective spray height), approximately 85% of the brood would be killed without having to fall the infested tree. The percentage kill, in all probability, would be much higher than cited 85% because the cumulative brood curves were constructed on the basis of brood samples taken mainly in late larval and pupal

stages. There is strong evidence to indicate that between these stages and emergence the brood will suffer heavy mortality in the upper stem from excessive rates of drying of the inner bark and outer sapwood.

The density gradients of brood counts and attacks had the same general form, therefore, the within-tree stratification developed for the former variable will be reasonably efficient for attacks also.

The frequency distribution of attacks and brood of the mountain pine beetle had strong positive skewness and the variances were shown to be related to their respective means. The skewness of the frequency distributions of these variables is the result of within-tree density gradients and between-tree variability, due to tree resistance and differences in the density of suitable attack sites. In addition, between and within-tree differences in woodpecker predation, winter mortality and in mortality caused by drying of the inner bark, contribute significantly to the frequency of zero and low brood counts.

Although, no adequate transformation was found to normalize the frequency distribution of the data, both the $\log(x + k)$ transformation (k = index of dispersion for the negative binomial distribution), and Taylor's power transformation sufficiently stabalized the variance. However, as non-normality must be extreme to invalidate parametric tests (Hayman and Lowe, 1961), both transformations can be considered adequate for the purpose of sampling. Of the two transformations, the logarithmic is easier to calculate but, for intensive population work, Taylor's power transformation would be more

appropriate. This is because, when the observations are transformed in accordance with Taylor's power law, the number of insects per primary units will be highly correlated with primary unit size. This correlation can be utilized to reduce the variability of primary unit means by regression sampling on primary unit size.

The transformation of brood and attack counts raises the question of how should means and variances be expressed in the final presentation of the results? Morris (1955) pointed out that once the data have been transformed, and found appropriate, they can be best summarized as to central tendency and variance by giving the mean and variance of the transformed values. This will provide consistent and efficient estimates of the parameters (Finney, 1941) and will be satisfactory for most purposes. However, for the purposes of expressing rate of mortality and population total (or population per acre) the transformed mean would pose considerable difficulties. For these reasons the original mean per secondary unit, as determined from the original observations should be used to estimate within generation mortality or population trend. On the other hand, estimates of the sampling variance should be calculated from transformed data for the following reasons: Firstly, Finney (1941) demonstrated that for highly skewed distributions, when the distribution of the logarithmic values is normal, the variance of the original observations will be an unbiased but inefficient estimate of the population variance. Secondly, sample size, for a specified degree of precision of the standard error on the original scale, may be estimated even though the variance has been

calculated from transformed data.

As both, regression sampling of the primary units had the calculation of population totals require the knowledge or an estimate of primary unit size, a surface area equation was developed to predict total surface area of individual trees in terms of the combined variables; d.b.h. and total height. Separate equations were calculated for forked and forkless trees because it was noticed that, on the combined (x,y) plots of these two tree types, the greatest source of variability was caused by the forked trees. The "combined variable" linear surface area equations gave better fit to experimental data than surface area equations developed from Honer's (1965) "transformed variable" cubic volume function. Moreover, the variability of the dependent variable about the combined variable regression lines was remarkably uniform for all values of the independent variable, while the scatter about the regression line for the transformed variable function was noticably increasing with decreasing values of "x". Although, it is claimed (Golding and Hall, 1961; Honer, 1965) that the combined variable volume function gives poor estimates in the smaller $\underline{D^2H}$ classes while the medium to large classes are estimated with a high degree of accuracy, this shortcoming of the volume function does not apply to the surface area equation because trees smaller than about 4 inches in diameter are rarely infested by the mountain pine beetle. Therefore, on the basis of its simplicity, higher correlation coefficient and greater accuracy in the medium to high $\underline{DH}$ classes, the combined variable surface area function was used for developing partial surface area

equations and tables for lodgepole pine.

The surface area of trees is an important variable and has implications for respiration rate, energy exchange and water and mineral budget. Consequently, the surface area equations developed in this thesis may be used for ecological studies of the energetics of lodgepole pine stands.

In order to estimate primary unit size (the infested surface area of individual trees) an equation was developed to estimate the proportion of total surface area infested in terms of the infested height/total height ratio. It was found that the ratio infested surface area/total surface area can be predicted with high degree of accuracy by a multiple curvilinear equation involving the ratio; infested height/total height as independent variable. Therefore, a good estimate of primary unit size can be obtained by forming the product (total surface area of the i-th tree) x (infested surface area/total surface area ratio of the i-th tree). The within-primary unit stratum sizes can be calculated in similar manner. Since it would be difficult to calculate primary unit and within-primary unit stratum sizes by forming the above specified product, a "partial surface area table" was developed to simplify the estimation procedure.

Although, an excellent estimate of population total will be obtained by forming the product (estimate of total infested surface area in the population) x (estimate of mean number of brood (or attacks) per unit area), the estimation of the variance of the population total will pose some difficulties. The main source of this

difficulty is that no unbiased estimate of the variance of individual observations can be calculated for the regression of the ratio infested surface area/total surface area on the ratio: infested height/total height, without complicated weighting procedure. As the variance about this regression is approximately proportional to the product $(1 - x)x$, (Appendix H), where x = value of the independent variable, this difficulty could be over come by weighting the observations by $1/((1 - x)(x))^2$. However, the weighted regression would give poor estimates in the middle ranges of the independent variable ($\underline{x}$ varies from 0 to 1). Therefore, the best solution to this problem seems to be to redefine the primary unit. The primary unit may be redefined as the total surface area of infested trees. Then, on the basis of this definition, the population total can be calculated by forming the product: (estimate of total surface area of all infested trees in the population) x (estimate of brood (or attack) counts per unit area). As this estimate of population total does not require the knowledge of the proportion of infested surface area, a nearly unbiased estimate of its variance can be calculated.

As the size of the primary unit is expected to vary considerably, even if the redefined units are used (i.e. the total stem surface area of individual trees), the choice of the technique to estimate the sampling mean and variance has to be carefully considered. The choice of the appropriate formulae to estimate means and variances for the two-stage sampling design will depend on the manner in which the primary units are selected and on the relationship between primary unit size and the number of brood (or attack) counts on that

unit. The primary units may be selected at random, with equal probability and without replacement or at random, with probability of selection proportional to primary unit size and with replacement. When the primary units are selected in accordance with the former case, the available unbiased formula to estimate the sampling variance is of poor efficiency (Cochran, 1953; Samford, 1962) and, therefore, its use is not advisable. Moreover, the available biased formulas assume that the variable to be estimated is independent of the size of the primary unit. Obviously, this assumption is incorrect for mountain pine beetle broods and attacks, therefore, the primary units should be selected at random with replacement and with probability of selection proportional to primary unit size. The formulae available to estimate sample means and variances, when the selection of the primary units is proportional to unit size, are unbiased, easy to calculate and the variance formula will give an efficient estimate of the sampling variance.

The secondary units should be selected without replacement from all secondary units contained in stratum i of the j-th primary unit, each time this unit appears in the sample. The number of secondary units should not exceed about 2% of the total number of samples contained in the primary units, especially if the same primary units are used to estimate within-generation mortality by sampling several times during the life cycle of the insect. Excessive debarking of the sample trees can cause additional mortality by accelerating the drying rate of the inner-bark and outer-sapwood. Systematic selection of the secondary units is preferable to random allocation because the former is easier and its use leads to ac-

curate estimates of the population mean. However, systematic second-stage sampling will lead to an underestimate of the population variance. The underestimation of the population variance will likely be small because the within-primary unit component of the population total was less than 14% of the total variance for the Elk Creek sample in 1965. Random selection of the secondary units will pose some technical problems but within-primary unit stratification will considerably simplify the identification of these units in the field. However, completely random selection of the secondary units can never be achieved if fixed-sized units are used, because tree taper complicates the sub-division of primary units into secondary units. This problem will be more serious when sampling is done by circular second-stage units. The secondary units should be allocated in proportion to the size of within-primary unit strata. The efficiency of proportional allocation will probably be comparable to that of the optimal allocation because stratum to stratum variability of brood (or attacks) within-primary units is expected to be considerably reduced by transformation.

The sampling design, when modified as discussed in the preceding paragraphs, is adaptable to suit the purposes of intensive population work on the mountain pine beetle in lodgepole pine. It can be used for estimating population totals in a group infestation several times during the beetle's life-cycle. The differences between the population totals estimated from successive sample surveys will provide mortality estimates for the various stages of the beetle's development. Moreover, estimates of population totals at the

end of the life-cycle in two successive generations can be used for estimating population trend. Although, this sampling design was developed by studying mountain pine beetle broods in advanced stages of development, it will probably prove efficient in estimating mean brood densities in all developmental stages. It is because the basic within-tree population gradients prevail through the insects entire subcortical life. However, the efficiency of the design could probably be increased for sampling egg and first to second larval stages of the beetle, by substituting ratio sampling on egg gallery length for within-primary unit stratification.

Although this sampling technique was developed for sampling the mountain pine beetle in lodgepole pine, the principles underlying its development have wider generality. The same principles could be applied to the development of sampling techniques for all bark beetle species in the genus Dendroctonus.

D. valens? If so, nearly any scolytid?

When an approximate index of population trend is required, it can be obtained by sampling at a fixed height level. This method is based on the assumption that, at a fixed height level, brood density in advanced developmental stages is approximately proportional to average brood density. The average vs. "maximum" brood density relationships appeared to be linear and had zero intercepts. Thus, these two variables can be considered directly proportional. This last property of the average vs. maximum brood density relationship made possible the substitution of the former for the latter variable for expressing population trend. Population trend was defined as the ratio of the population totals of late stage (possibly adult) mountain pine beetle brood in successive years.

To obtain estimates of the quantity $(S_N a_i)\bar{x}$ in equation (XV), the surveyor should obtain an estimate of the mean of the product of d.b.h. and total height from a random sample of infested trees. The size of the sample should possibly be 20 or more trees and both d.b.h. and height should be measured on the same sample trees. The mean of the products, (d.b.h.)(ht.), is determined as:

$$\overline{(d.b.h.)(ht.)} = S_n((d.b.h.)(ht.)_i)/n$$

Where, i denotes the i-th sample tree and the other notations are the same as before. The mean, $\overline{(d.b.h.)(ht.)}$ is then converted to sq. ft. units and substituted into the equation a = 1.9708(d.b.h.)(ht.) + 3.7196 for the value of (d.b.h.)(ht.) to obtain $\bar{a}$, the estimate of the population mean of the surface area per tree in sq. ft. units. Then, the product $M\bar{a}$ will be an estimate of $S_N a_i$ in equation (XV), (M = total number of infested trees in the population). To secure an estimate of $\bar{x}$ in equation (XV) an independent sample of at least 20 trees should be selected at random and a sample of the brood taken from both the northern and southern aspects of the sample trees. Than, $\bar{x}$ can be calculated as the mean of the combined observations from the northern and southern aspects. For the purposes of the survey the shape of the sampling unit is not very important, but sampling unit size should possibly be greater than 36 sq. inches. The height level of sampling should be close to four feet above ground level for infested stands which measure less than about ten inches in mean d.b.h. and close to five feet above ground level for stands with average d.b.h. greater than ten inches. The position of

sampling units, on the northern and southern aspects of the bole, will probably not influence the results greatly, but the sampler should be consistent in allocating the sampling units to approximately the same compass directions for all trees within a single year and every year within a given infested area. The timing of sampling should be such that the mountain pine beetle brood is sampled in the fourth larval and pupal or more advanced developmental stages. As even teneral adults are known to suffer heavy mortalities up to the time of emergence (Reid, 1960) the most reliable results will be obtained by sampling the emerging population, at the specified level by "emergence traps". This approximate method of population trend prediction is considerably more complicated and difficult to use in the field than that developed by Knight (1959) for the Black Hills beetle. Knight predicted population trend by the ratio of the number of newly infested trees to the number of trees infested the previous year. However, the mountain pine beetle tends to kill the biggest diameter trees first in lodgepole pine stands (Hopping and Beall, 1948, Shepherd, 1960) and, thus, reduces the infested surface area of the average attacked tree each year compared with that of the previous year. This fact, coupled with the substantial year-to-year fluctuation of the attack/emergence ratio, tends to make Knight's population trend estimating technique less reliable than that proposed in this theses. Although several authors demonstrated that the population in the lower bole of the stem is comparable to that in the upper bole (Beal, 1939, Blackman, 1931, Hopkins, 1905, DeLeon, 1939, Knight, 1959), to this

author's knowledge, the actual relationship between maximum and overall mean brood density has not been demonstrated prior to the present study.

As the sample data for studying the maximum vs. overall mean brood density relationship was collected from only two localities in south-eastern British Columbia, the approximate method of population trend measurement should be used only for the mountain pine beetle and only in lodgepole pine stands similar to the ones studied for this thesis.

CONCLUSIONS

Edge effect bias is independent of mean brood density and is inversely proportional to the square root of sampling unit size and directly proportional to the circumference/area ratio of the unit and to the square root of the cross-sectional area of the "average insect". For any one fixed sampling unit size, circular units will have the smallest and rectangular units the greatest edge effect bias. Edge effect bias of the latter units increases with decreasing width/length ratio.

For mountain pine beetle broods in late larval stages of development, edge effect bias will be greater than about 7% of the mean when circular sampling units smaller than 12 square inches, are used in the sample survey. For a 12 square inch rectangular unit, this figure will be approximately 10%, when the width/length ratio is $\frac{1}{4}$. Consequently, if edge effect bias cannot be controlled, sampling units smaller than about 12 square inches should not be used for intensive population work on the mountain pine beetle.

For a fixed sampling unit size, rectangular units oriented perpendicular to the egg galleries will give the smallest, and the same units rotated by 90° the greatest variance estimate of the sampling mean. Circular and square units will give variance estimates intermediate between these two extremes. Thus, the shape of the "optimum" unit is rectangular and its orientation is with long sides perpendicular to the egg galleries. If edge effect cannot be cont-

rolled, the w/l ratio of the optimum unit should possibly be $\frac{1}{2}$ or more.

For simple random sampling of the brood at a fixed height level, "optimum" unit size will be approximately 18 square inches when sampling unit boundary delineation is done with a template and chisel and hammer and debarking with a wide blade hunting knife.

The circular distribution of attacks on the stem circumference is related to the attacking female beetles reaction to high heat and light intensity. These beetles are stimulated to fly by high temperatures and light intensity and, consequently, the highest and lowest concentration of attacks will occur on the north to-north-eastern and south to south-western aspects on the branch-free portion of the infested stem, respectively. In the crown region of the infested stems, branch-shading tends to reduce temperature and light intensity differences between northern and southern aspects and, therefore, the circular distribution of attacks will be rectangular.

At a fixed height level, the spatial arrangement of attacks appears to be uniform, possibly because suitable attacks sites are evenly distributed over the bark surface.

The distribution of brood around the stem circumference is similar to that of attacks. However, there is a tendency for maximum brood density to shift closer to the due N aspect than the position of maximum attack density on the branch-free portions of the infested stems. The difference between the locations of maximum brood and attack density is probably the result of the circumfer-

ential advance of the larvae and the effects of various mortality factors on the sub-cortical stages of the beetle.

Late stage mountain pine beetle broods form "clumped" spatial patterns, the long axes of which are oriented approximately parallel to the egg galleries. Clumping appears on several scales and variation in clump dimensions is the consequence of the spatial arrangement of attacks and the nature and intensity of action of various mortality factors on the sub-cortical stages of the beetle.

Attack intensity is a function of the combined thicknesses of the outer and inner-bark because the latter variable is an expression of bark roughness and thus, the density of suitable attack sites/unit area of bark. The attack density vs. bark thickness relationship is asymptotic as attack density approaches an upper limit with increasing bark thickness. This relationship has a positive "x"-intercept, which averaged 1.5 m.m. for the Horsethief and Elk Creek sample trees in 1965. This result indicates that bark surfaces thinner than the "threshold" bark thickness either do not support suitable attack sites or they are too thin for egg gallery construction. Thus, the upper-most limit of attacks on the stem and, therefore, the potential bark area available for infestation is determined by the position of the "threshold" bark thickness on the stem of lodgepole pine trees. Furthermore, the shape of the vertical attack gradient in infested stems appears to be a result of the attack density vs. bark thickness relationship, in addition to the size of the attacking population, host tree availability and tree resistance. The shape of vertical brood

density gradients is directly related to that of vertical attack density gradients but this relationship is disturbed by differential mortality due to factors such as intra-specific competition, insect parasitisim and predation, woodpecker predation and differences in the rate of drying of the insects sub-cortical habitat, vertically within the infested stem.

The attack harbouring potential of non-resistant trees (total number of attacks/tree) is strongly related to the external tree characteristics d.b.h. and total tree height in their "combined variable" form; d.b.h. x total tree height. Although, other tree characteristics are also strongly correlated with total number of attacks/tree (i.e. 1/d.b.h., $(\text{crown width})^2$ x crown length and tree age), these correlations are probably indirect and are due to the interrelationships of these variables with d.b.h. x total tree height.

The total number of broods surviving to late larval, pupal and teneral adult stages of development in non-resistent trees is strongly correlated with the total number of attacks/tree, d.b.h. x total tree height, 1/d.b.h. and with $(\text{crown width})^2$ x crown length. The variable $(\text{crown width})^2$ x crown length, in addition to being an expression of crown volume, it is also related to stand density and probably to the nutritional quality of the inner bark. Consequently, the brood-producing potential of non-resistant host trees seems to be directly related to the nutritional quality of the inner bark and inversely related to stand density. The combined variable d.b.h. x total tree height and 1/d.b.h. are indices of bole area and the bole

area/bole volume ratio, respectively, and probably affect brood survival by controlling the rate of moisture loss from the stem after the death of the tree due to infestation by the mountain pine beetle and the associated blue stain fungi.

Total bole area of lodgepole pine trees can be predicted with high degree of accuracy with a linear regression equation of total bole area on the combined variable d.b.h. x total tree height. Bole area to a predetermined height level, on the other hand, is accurately predicted by a third degree multiple curvilinear equation of section bole area on section height. Consequently, partial surface area (or infested surface area) can be predicted as the product of these two equations.

The within-tree sampling variance estimates for brood and attack counts are strongly related to their respective means but this relationship can be removed by transforming the counts by Taylor's Z transformation.

The mean and variance of population total estimates (or estimates of the population mean/primary or secondary unit) will be efficiently estimated from a modified two-stage sampling design whereby the population mean is calculated from the original observations and its sampling variance from the dispersion of the transformed values. The modified two-stage sampling design involves regression and stratified sampling of the primary and secondary units, respectively. On transformed scale, brood totals/tree are strongly correlated with infested bole area and this relationship can be used for reducing the primary unit (between-tree) variability of brood popu-

lation total estimates. The within-primary unit variability of brood population total estimates can be successfully reduced by sub-dividing the primary unit population gradients into five secondary unit strata at critical points. This modified two stage-sampling design is especially suited for obtaining accurate estimates of population totals and population trend for studies of the population dynamics of the mountain pine beetle in lodgepole pine.

For the purposes of general insect surveys population trend can be estimated by sampling only at the d.b.h. region of infested trees. An index of the population total is calculated by multiplying the mean brood density estimate obtained from the d.b.h. level with an estimate of total infested surface area for the infestation. Population trend will be estimated by the ratio of two population total indeces in successive years.

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APPENDIX A

THE CALCULATION OF REGRESSION COEFFICIENTS FOR THE MULTIPLE REGRESSION EQUATION: $Y = a_o + a_1X + a_2X^3$ WHEN THE FOLLOWING CONDITIONS ARE GIVEN:

$a_o = 0$, and $f(X) = 1$ WHEN $X = 1$.

The second condition is identical to the following requirement: $a_1 + a_2 = 1$. Thus, the multiple regression equation will take the following general form:

$$Y = (1 - a_2') X + a_2'(X^3) \tag{1}$$

or

$$(Y - X) = a_2'(X^3 - X). \tag{2}$$

If we designate $Y' = Y - X$ and $X' = X^3 - X$, then equation (2) may be rewritten as:

$$Y' = a_2' X' \tag{3}$$

The appropriate normal equation for equation (3) is

$$a_2'(S_n X'^2) = S_n Y'X' \tag{4}$$

Where S_n = sum over n observations, $S_n X'^2$ and $S_n Y'X'$ are uncorrected sum of squares and products, respectively. Thus

$$a_2' = \frac{S_n Y'X'}{S_n X'^2} \tag{5}$$

therefore

$$a_1' = 1 - a_2'$$

In section 4.2. of the Experimental Results, the least squares regression coefficients of the $\Delta S_t/S_t$ vs. $\Delta H/H$ relationship were given

as; $a_1 = 1.4150$, and $a_2 = -0.4391$, for forkless trees. For the same relationship the least squares regression coefficients of the conditioned regression are; $a'_1 = 1.3758$ and $a'_2 = -0.3758$.

APPENDIX B.

AN APPROXIMATE FORMULA TO CALCULATE THE VARIANCE ABOUT THE REGRESSION OF $\Delta S_t/S_t$ VS. $\Delta H/H$ RELATIONSHIP.

In section 4.2. of the Experimental Results it was pointed out that the $\Delta S_t/S_t$ vs. $\Delta H/H$ relationship was well described by second and third degree curvilinear regression equations. In the same section it was said that the variability of the dependent variable about the regression surface is related to the independent variable and that the regression equation should pass through the coordinate points; (0,0) and (1,1).

The standard deviation of the dependent variable, for different values of the independent variable, was found to be approximately related to $(\Delta H/H)(1 - \Delta H/H)$. Therefore, in order to make the residual error mean square applicable to making valid probability inferences, each squared deviation from the regression surface have to be assigned a weight, $w_i = 1/((\Delta H/H)(1 - \Delta H/H))^2$. Moreover, to satisfy the restrictions; intercept = 0 and $a_1 + a_2 = 1$ (a_1 and a_2 are regression coefficients), the regression equation has to be conditioned simultaneously with weighting. That is, in mathematical terms, this problem for the second degree curvilinear regression can be writted as:

$$\sqrt{w_i}Y = (1 - a_2)\sqrt{w_i}X + a_2\sqrt{w_i}X^2 \qquad (1)$$

w_i = weight of the i-th unit, $Y = \Delta S_t/S_t$, a_2 = regression coefficient and $X = \Delta H/H$. The normal equation for (1) will be:

$$S_n w_i(Y')(X') = a_2 S_n w_i(X')^2 \qquad (2)$$

S_n = sum over n observations: $Y' = Y - X$ and $X' = X^2 - X$.

Then

$$a_2 = \frac{S_n w_i (Y')(X')}{S_n w_i (X')^2} = S_n (\frac{Y'}{X'})/n \qquad (3)$$

Therefore, the variance of $\bar{Y}'$, $S^2_{\bar{y}'}$, can be calculated as that of a "mean-of-ratios estimator" (Freese, 1962). That is

$$S^2_{\bar{y}'} = \bar{X}'^2 (S_n (\frac{Y'}{X'})^2 - (S_n \frac{Y'}{X'})^2/n)/n(n-1) \qquad (4)$$

The variance of $\bar{Y}$ may then be obtained from equation (4) by substituting $Y - X$ for Y' and $X^2 - X$ for X'. Thus

$$S^2_{\bar{y}} = \bar{X}'^2 (S_n (\frac{Y}{X^2 - X})^2 - (S_n \frac{Y}{X^2 - X})^2/n)/n(n-1) \qquad (5)$$

Where $S^2_{\bar{y}}$ = the variance of $\bar{Y}$ and the other symbols are defined as earlier. Equation (5) may be adopted to calculate the variance of individual observations about the conditioned and weighted second degree curvilinear regression of $\Delta S_t/S_t$ on $\Delta H/H$. However, both the weighting and conditioning of the regression (as defined above) would tend to increase the reliability of the prediction toward the extreme values of $\Delta H/H$ (the range of this variable is bounded by the values of 0 and 1). On the other hand, the regression equation will be used most frequently close to the middle of the range of $\Delta H/H$. Therefore, the accuracy of the predictions by the unweighted and conditioned regression in the mid-range of the independent variable may be as good or better than that of the weighted (or weighted and conditioned) regression. Further, the unweighted least squares regression equations give unbiased estimates of the regression coefficients, whether the variances are homogenious or not. For these

reasons the prediction of $\Delta S_t/S_t$ on $\Delta H/H$ was based on untransformed and unconditioned least squares curvilinear multiple regression. The variance about this regression, $S^2_{y.x}$, was used to predict the variance of individual observations, S^2_p. The following approximate formula was used to estimate S^2_p:

$$S^2_p = S^2_{y.x}\,(1 + \frac{1}{n})\,(\frac{\bar{x}_p(1 - \bar{x}_p)}{x_p(1 - x_p)}),$$

Where, $\bar{x}_p$ = the midpoint of the range of $\Delta H/H(0.5)$, $x_p = \Delta H/H$, n, $S^2_{y.x}$ and S^2_p are defined as earlier. The ratio on the right hand size of this equation is a "correction factor" for the relationship between the variance of individual observations and the independent variable. The approximate expression for S^2_p does not contain the familiar term:

$$c_{ij} \sum_{i=1}^{k} \sum_{j=1}^{k} x_i x_j,$$

c_{ij} = coefficient of the i-th row and j-th column of the inverse matrix, $x_i x_j$ = corrected sum of products of the independent variables, and S = sum. This term has been excluded from the formula because it would be difficult to compute. However, the exclusion of this term makes the approximate formula unreliable for predicting $\Delta S_t/S_t$ values outside the mid-range (0.3, - 0.7) of the independent variable.

APPENDIX C

A SAMPLE FROM THE PARTIAL SURFACE AREA TABLE FOR INDIVIDUAL LODGEPOLE PINE TREES.

DIAMETER 6.0 INCHES

TOTAL HEIGHT (FT)

INFESTED HEIGHT	84	80	76	72	68	64	60	56	52	48	44	40	36	32
4	7.9	7.8	7.8	7.7	7.6	7.5	7.4	7.4	7.3	7.2	7.2	7.1	7.1	7.1
8	13.7	13.6	13.6	13.5	13.4	13.4	13.3	13.3	13.2	13.2	13.1	13.1	13.1	13.1
12	19.5	19.4	19.3	19.3	19.2	19.1	19.1	19.0	19.0	18.9	18.9	18.8	18.8	18.7
16	25.1	25.1	25.0	24.9	24.9	24.8	24.7	24.6	24.6	24.5	24.4	24.2	24.1	23.9
20	30.7	30.6	30.6	30.5	30.4	30.3	30.1	30.0	29.9	29.7	29.5	29.2	28.8	28.3
24	36.2	36.1	35.9	35.8	35.7	35.5	35.3	35.1	34.9	34.5	34.1	33.6	32.8	31.7
28	41.5	41.3	41.2	41.0	40.8	40.5	40.2	39.9	39.4	38.9	38.2	37.3	36.0	34.1
32	46.6	46.4	46.2	45.9	45.6	45.2	44.8	44.2	43.6	42.7	41.6	40.2	38.2	35.3
36	51.6	51.3	50.9	50.5	50.1	49.6	48.9	48.1	47.2	45.9	44.3	42.2	39.2	
40	56.3	55.9	55.4	54.9	54.3	53.5	52.6	51.5	50.2	48.4	46.2	43.1		
44	60.8	60.2	59.6	58.9	58.1	57.1	55.9	54.4	52.5	50.2	47.1			
48	65.0	64.3	63.5	62.5	61.4	60.1	58.5	56.6	54.1	51.0				
52	68.9	68.0	67.0	65.8	64.4	62.7	60.6	58.1	55.0					
56	72.4	71.3	70.1	68.6	66.8	64.7	62.1	58.9						
60	75.7	74.3	72.7	70.9	68.7	66.1	62.9							
64	78.6	76.9	75.0	72.7	70.0	66.8								
68	81.0	79.0	76.7	74.0	70.7									
72	83.1	80.7	77.9	74.7										
76	84.7	81.9	78.6											
80	85.9	82.6												
84	86.5													

DIAMETER 6.2 INCHES

TOTAL HEIGHT (FT)

INFESTED HEIGHT	84	80	76	72	68	64	60	56	52	48	44	40	36	32
4	8.2	8.1	8.0	7.9	7.8	7.8	7.7	7.6	7.5	7.5	7.4	7.3	7.3	7.3
8	14.2	14.1	14.0	13.9	13.9	13.8	13.7	13.7	13.6	13.6	13.5	13.5	13.5	13.5
12	20.1	20.0	19.9	19.9	19.8	19.7	19.7	19.6	19.6	19.5	19.5	19.4	19.4	19.3
16	25.9	25.9	25.8	25.7	25.6	25.6	25.5	25.4	25.3	25.2	25.1	25.0	24.8	24.6
20	31.7	31.6	31.5	31.4	31.3	31.2	31.1	31.0	30.8	30.6	30.4	30.1	29.7	29.1
24	37.3	37.2	37.1	37.0	36.8	36.6	36.4	36.2	35.9	35.6	35.2	34.6	33.8	32.7
28	42.8	42.6	42.5	42.3	42.0	41.8	41.5	41.1	40.7	40.1	39.4	38.4	37.1	35.2
32	48.1	47.9	47.6	47.3	47.0	46.6	46.2	45.6	44.9	44.0	42.9	41.4	39.3	36.3
36	53.2	52.9	52.5	52.1	51.7	51.1	50.5	49.6	48.6	47.4	45.7	43.5	40.4	
40	58.1	57.7	57.2	56.6	56.0	55.2	54.3	53.1	51.7	49.9	47.6	44.5		
44	62.7	62.1	61.5	60.8	59.9	58.9	57.6	56.1	54.2	51.7	48.5			
48	67.0	66.3	65.5	64.5	63.4	62.0	60.4	58.4	55.8	52.6				
52	71.1	70.1	69.1	67.9	66.4	64.6	62.5	59.9	56.7					
56	74.8	73.6	72.3	70.7	68.9	66.7	64.0	60.8						
60	78.1	76.7	75.1	73.1	70.9	68.1	64.8							
64	81.1	79.3	77.3	75.0	72.2	68.9								
68	83.6	81.5	79.1	76.3	73.0									
72	85.7	83.3	80.4	77.0										
76	87.4	84.5	81.1											
80	88.6	85.2												
84	89.3													

APPENDIX D

STATISTICS FOR THE CALCULATION OF WITHIN-PRIMARY UNITS VARIANCE OF BROOD COUNTS (TRANSFORMED DATA)

Tree Number	Stratum*	M_{ij} **	$\bar{y}_{ij}$	m_{ij}	$(m_{ij}-1)$	$(1-f_{2ij})/m_{ij}$	$(m_{ij}-1)s^2_{ij}$	s^2_{ij}	$M^2_{ij}s^2_{ij}/m_{ij}$
	1	33.15	0.9718	14	13	.04126	.0169	.0013	.1099
	2	72.60	1.6955	22	21	.03169	4.0845	.1945	46.5900
744	3	72.60	1.6998	22	21	.03169	1.5978	.0760	18.2295
	4	22.12	1.5506	5	4	.15479	.4484	.1121	10.9699
	5	22.12	1.3783	5	4	.15479	.0792	.0198	1.9376
	1	36.30	.8696	8	7	.09745	.0497	.0071	1.1694
	2	55.27	1.0264	11	10	.09072	.9640	.0964	26.7709
740	3	55.27	1.2196	11	10	.09072	.6720	.0672	18.6618
	4	36.37	1.6508	6	5	.13917	.9640	.1928	42.5050
	5	36.37	1.8069	6	5	.13917	.2720	.0544	11.9933
	1	29.85	1.0173	11	10	.05740	1.0330	.1033	8.3690
	2	83.92	1.5905	18	17	.04364	1.5861	.0933	36.5038
743	3	83.92	1.6855	18	17	.04364	1.7527	.1031	40.3377
	4	40.20	1.7854	7	6	.14179	.2370	.0395	9.1185
	5	40.20	1.6802	7	6	.14179	.5154	.0859	19.8300
	1	37.35	.8397	7	6	.11608	.0000	.0000	.0000
	2	41.55	.9825	8	7	.10093	.5166	.0738	15.9250
747	3	41.55	1.3330	8	7	.10093	1.8158	.2594	55.9750
	4	47.92	1.1771	8	7	.10413	1.0766	.1538	44.1462
	5	47.92	1.3297	8	7	.10413	1.5834	.2262	64.9275
	1	47.85	0.8876	11	10	.07001	.0910	.0091	1.8536
	2	51.98	1.6059	11	10	.07167	1.9310	.1931	47.4227
741	3	51.98	1.6330	10	9	.08076	1.0035	.1115	30.1226
	4	66.30	2.1817	10	9	.08491	.7585	.0842	37.0100
	5	66.30	1.6893	10	9	.08491	.5442	.0604	26.5500
	1	31.35	.8397	10	9	.06810	.0000	.0000	.0000
	2	82.95	1.8179	16	15	.05044	4.8840	.3256	140.0187
745	3	82.95	1.5662	16	15	.05044	3.3075	.2205	94.8243
	4	47.76	2.6320	8	7	.10406	.2058	.0294	8.3825
	5	47.76	2.3638	8	7	.10406	.1708	.0244	6.9562

APPENDIX D (cont.)

	1	37.50	.9363	13	12	.05025	.7500	.0625	6.7615
	2	101.10	1.4114	21	20	.03772	4.2240	.2112	102.8047
742	3	101.10	1.5931	21	20	.03772	1.1640	.0582	28.3238
	4	29.70	.8739	7	6	.10918	.0492	.0082	1.0286
	5	29.70	2.0388	7	6	.10918	.1380	.0230	2.9000
	1	52.65	1.3941	14	13	.05243	1.6900	.1300	25.7428
	2	83.62	1.5612	17	16	.04686	4.2288	.2643	108.7058
746	3	83.62	1.7861	17	16	.04686	1.5168	.0948	38.9882
	4	48.90	1.7436	8	7	.10455	.4781	.0683	20.4139
	5	48.90	1.7789	8	7	.10455	.6160	.0880	26.3033
	1	46.95	1.1999	8	7	.10370	.8890	.1270	34.9925
	2	103.95	.8682	24	23	.03204	.2461	.0107	4.8175
809	3	103.95	1.0359	26	25	.02884	7.5850	.3034	12.6092
	4	48.30	1.7144	8	7	.10429	2.1448	.3064	89.3412
	5	48.30	2.0362	8	7	.10429	1.2579	.1797	52.4025
	1	62.40	1.3866	13	12	.06089	2.9448	.2454	73.5023
	2	99.30	1.6583	20	19	.03993	2.1660	.1140	56.2045
802	3	99.30	1.3962	20	19	.03993	4.7595	.2505	123.5025
	4	60.67	2.1644	12	11	.06685	5.0017	.4547	139.4738
	5	60.67	2.2544	12	11	.06885	6.2766	.5706	175.0241
Total				604	554	3.9558	80.3184		1,988.1920

$$\overline{(1 - \frac{f_{2j}}{m_j})} = 0.0791$$

* 1 = upper 20% of the infested surface area

2 = middle-stratum, south side

3 = middle-stratum, north side

4 = bottom-stratum, south side

5 = bottom-stratum, north side

** measured in 0.66 sq. ft. units

APPENDIX E

THE FREQUENCY DISTRIBUTION OF BROOD COUNTS/SQ. FT. TAKEN BY SAMPLING UNITS OF VARIOUS SHAPES AND SIZES ON THE N AND S ASPECTS, AT THE D.B.H. REGION, OF FORTY-FIVE TREES. (THE EXPECTED FREQUENCIES WERE CALCULATED ASSUMING NEGATIVE BINOMIAL PARENT DISTRIBUTION.)

Class limits	Observed frequency	Expected frequency *
0 - 24	76	24
25 - 49	54	62
50 - 74	93	92
75 - 99	86	98
100 - 124	95	94
125 - 149	77	79
150 - 174	50	60
175 - 199	32	43
200 - 224	32	29
225 - 249	15	19
250 - 274	9	12
275 - 299	8	8
300 +	3	3
Total	630	630

$k = 5.40$
$p = 0.7954$
$q = 1.7954$
$R = 0.4146$

* The observed distribution is decidedly bi-modal and this is the reason why the negative binomial distribution gave poor fit to the first two frequency classes.

APPENDIX F

SLOPES, INTERCEPTS AND CORRELATION COEFFICIENTS FOR THE EQUATION $(\log_e B)/D.b.h. = a + \log_e H$ IN THE INFESTED BOLE SECTIONS OF THIRTY-FIVE LODGEPOLE PINE TREES.

Tree Number	D.b.h. (in.)	a	b	r	n*
(1)	(2)	(3)	(4)	(5)	(6)
Horsethief Creek plot, 1965					
706	5.0	0.8069	-0.1786	0.981	5
719	5.2	0.8474	-0.1966	0.987	8
704	7.4	0.6372	-0.1215	0.929	9
709	8.9	0.4405	-0.0718	0.948	9
713	6.8	0.5340	-0.0970	0.987	5
714	8.2	0.3839	-0.0574	0.938	7
718	8.0	0.5625	-0.1132	0.975	7
724	7.0	0.5985	-0.1075	0.958	11
716	7.7	0.5445	-0.9090	0.984	12
705	6.0	0.6655	-0.1504	0.977	5
702	10.8	0.3060	-0.0403	0.860	11
707	9.5	0.4160	-0.0781	0.930	7
711	10.5	0.3448	-0.0394	0.930	13
712	9.2	0.3441	-0.0421	0.982	8
720	9.8	0.3945	-0.0520	0.937	7
722	11.2	0.3945	-0.0520	0.915	11
723	9.2	0.5342	-0.1209	0.984	7
728	10.5	0.3278	-0.0348	0.892	9
708	9.9	0.3546	-0.0504	0.955	15
727	12.0	0.2708	-0.0336	0.836	18
729	12.2	0.3590	-0.0548	0.956	12
717	10.0	0.3211	-0.0274	0.819	6
701	13.1	0.2859	-0.0404	0.914	13
710	13.0	0.2649	-0.0333	0.971	14
725	14.1	0.2943	-0.0369	0.894	11
726	14.6	0.2432	-0.0171	0.951	13
703	12.2	0.3170	-0.0361	0.898	20
Elk Creek plot, 1965					
740	15.2	0.2011	-0.0164	0.886	21
741	17.8	0.1909	-0.0168	0.919	26
742	14.5	0.2299	-0.0423	0.935	35
743	14.7	0.3040	-0.0393	0.918	31
745	15.5	0.2667	-0.0264	0.736	31
746	16.0	0.2165	-0.0217	0.947	32
747	15.8	0.2223	-0.0183	0.859	20
744	10.8	0.2942	-0.0251	0.795	35

* The first sample was taken at the two ft. height level and sampling continued at two ft. intervals up to the uppermost point of infestation on each sample tree. The symbols a, b and r, respectively, represent intercept, slope and simple correlation coefficient for the regression equation of $\log_e \frac{B}{\text{D.b.h.}}$ on $\log_e H$.

B = combined thicknesses of the inner and outer bark in 1/32 in. units.

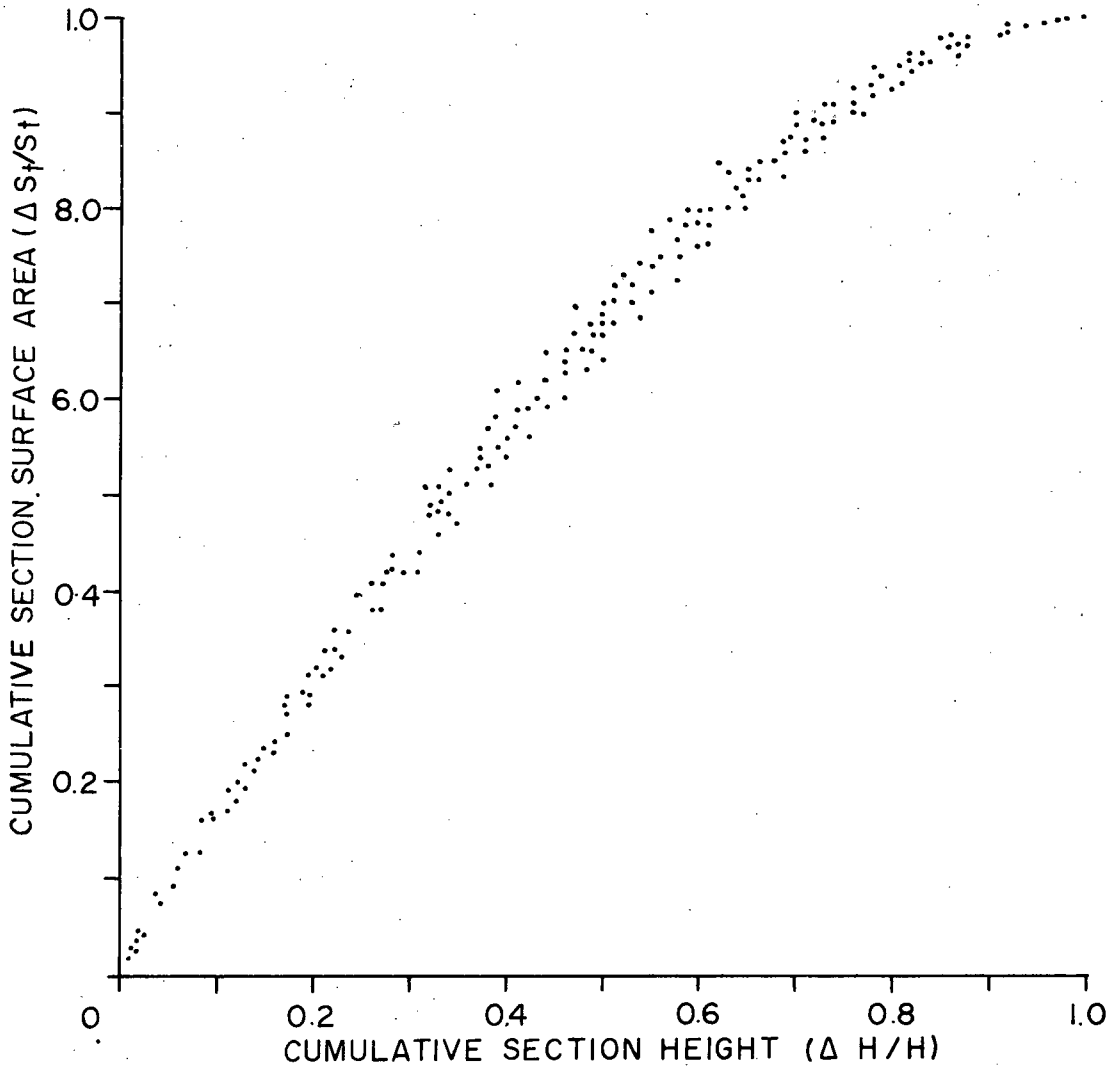
H = height level above ground in ft. units.

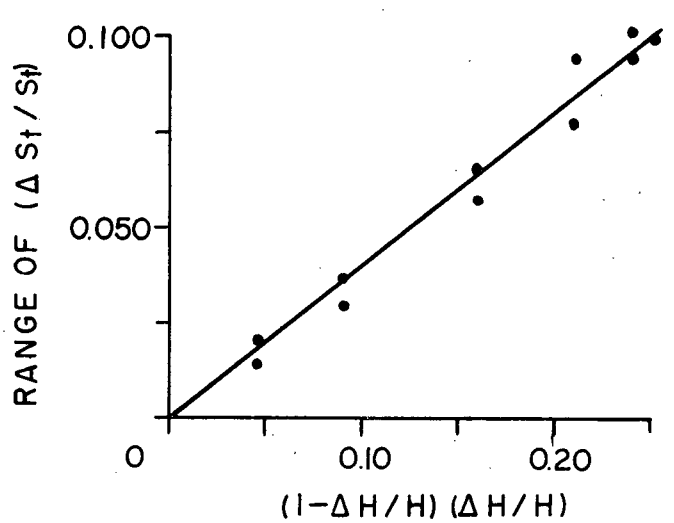
APPENDIX G

SCATTER DIAGRAM OF THE CUMULATIVE SECTION SURFACE AREA VS. CUMULATIVE SECTION HEIGHT RELATIONSHIP FOR FORKLESS TREES.

APPENDIX H

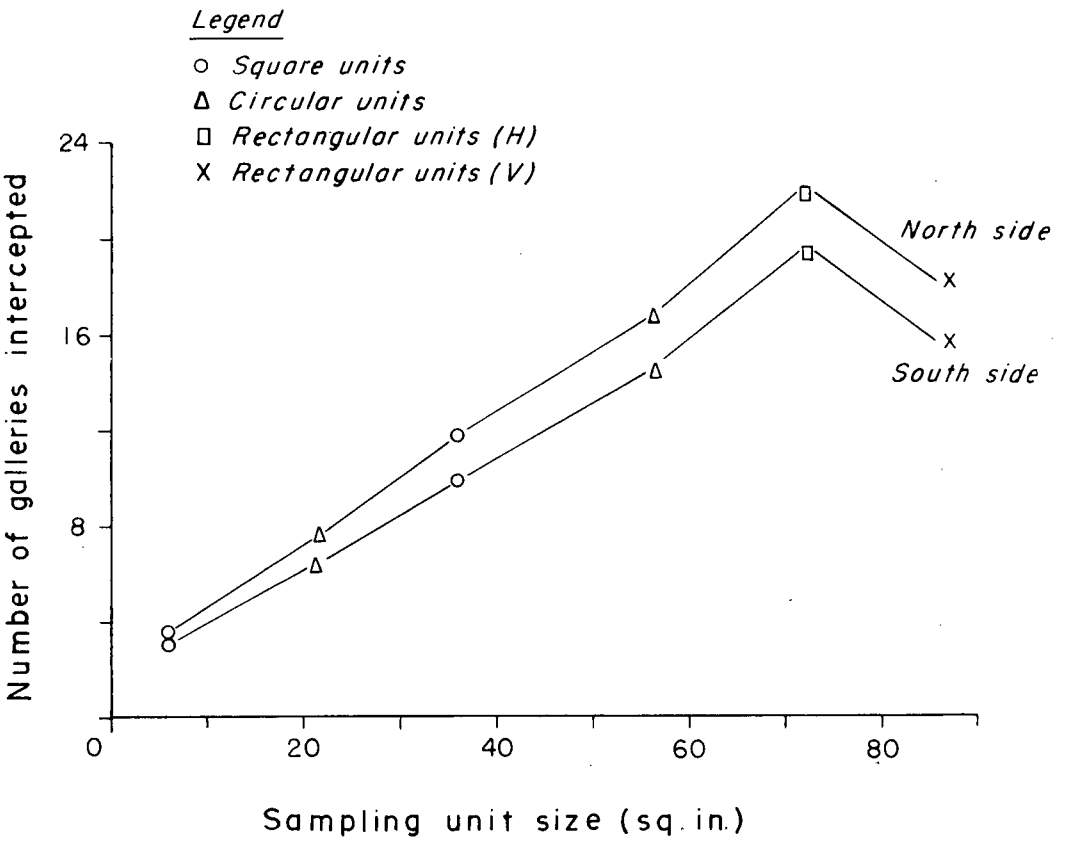
RELATIONSHIP BETWEEN THE RANGE OF CUMULATIVE SECTION SURFACE AREA AND $(1 - \Delta H/H)(\Delta H/H)$ FOR FORKLESS TREES. (THE STRAIGHT LINE DRAWN THROUGH THE ORIGIN IS THE FREE-HAND APPROXIMATION OF THE RELATIONSHIP)


1.0
8.0
6.0
0.4
0.2
0
0.2
0.4
0.6
0.8
1.0
CUMULATIVE SECTION SURFACE AREA (Δ St/St)
CUMULATIVE SECTION HEIGHT (Δ H/H)


0.100
0.050
0
0.10
0.20
RANGE OF (Δ St / St)
(1−Δ H/H) (Δ H/H)

APPENDIX I

NUMBER OF EGG GALLERIES INTERCEPTED BY SAMPLING UNITS OF VARIOUS SHAPES AND SIZES (EACH POINT REPRESENTS THE AVERAGE OF 45 OBSERVATIONS. THE SAMPLES WERE TAKEN FROM THE 4 FOOT HEIGHT LEVEL).


Legend
Square units
Circular units
Rectangular units (H)
Rectangular units (V)
North side
South side
Number of galleries intercepted
24
16
8
0
20
40
60
80
Sampling unit size (sq. in.)

APPENDIX J

HEIGHT LEVEL OF 5.5 M.M. BARK VS. D.B.H. RELATIONSHIP FOR LODGEPOLE PINE.

$LOG_{10} Y = 0.0507D + 0.4032$, $r = 0.80^{**}$, $n = 57$

(Y = Position of 5.5 m.m. bark on the stem (ft.), D = d.b.h. (in.), r = simple correlation coefficient, n = number of observations and ** = significant at the 1% probability level.)

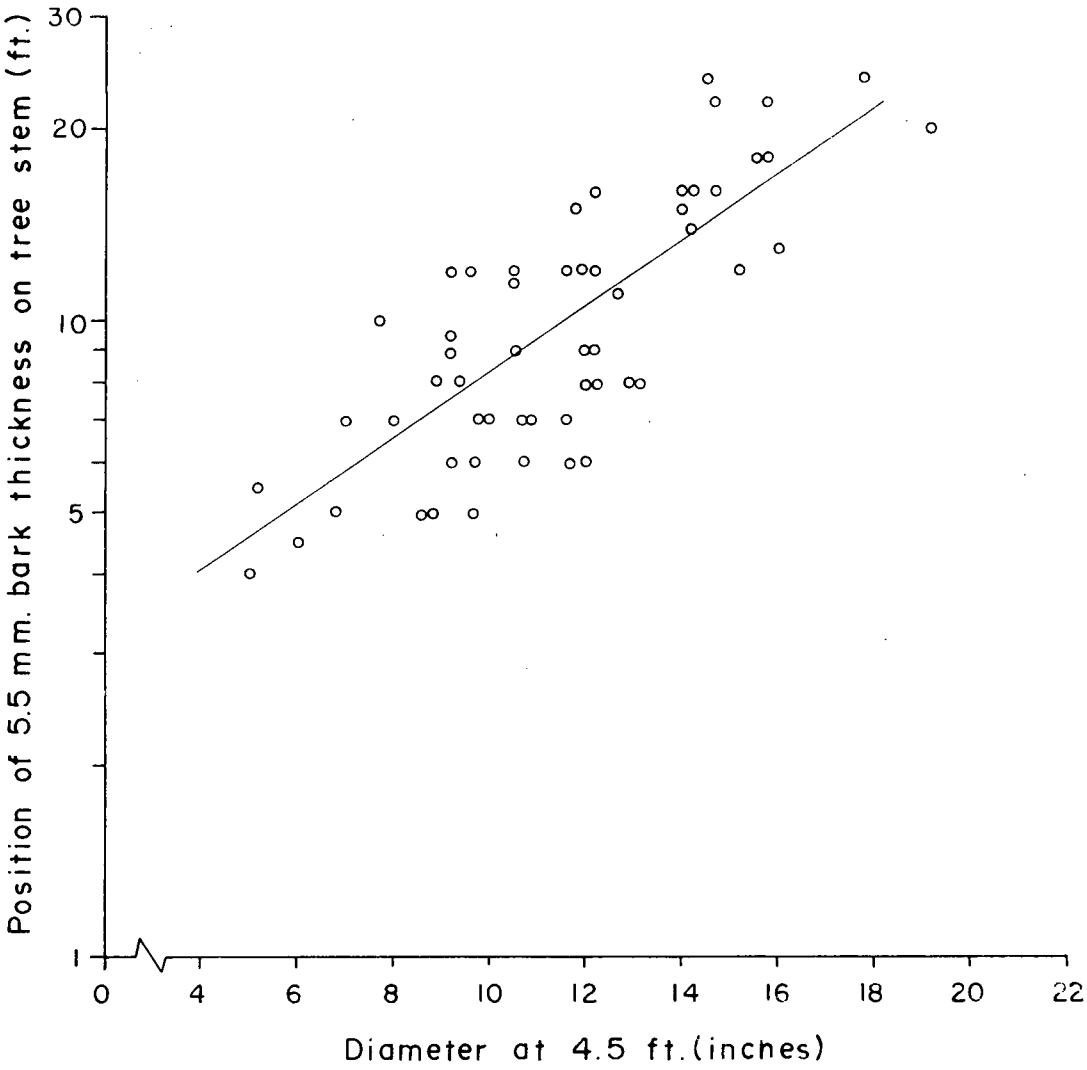

Position of 5.5 mm. bark thickness on tree stem (ft.)
30
20
10
5
1
0
4
6
8
10
12
14
16
18
20
22
Diameter at 4.5 ft. (inches)

Figure 12. Trend in maximum, minimum, and average infestation heights of S.lapathi(L.) with changing d.b.h.

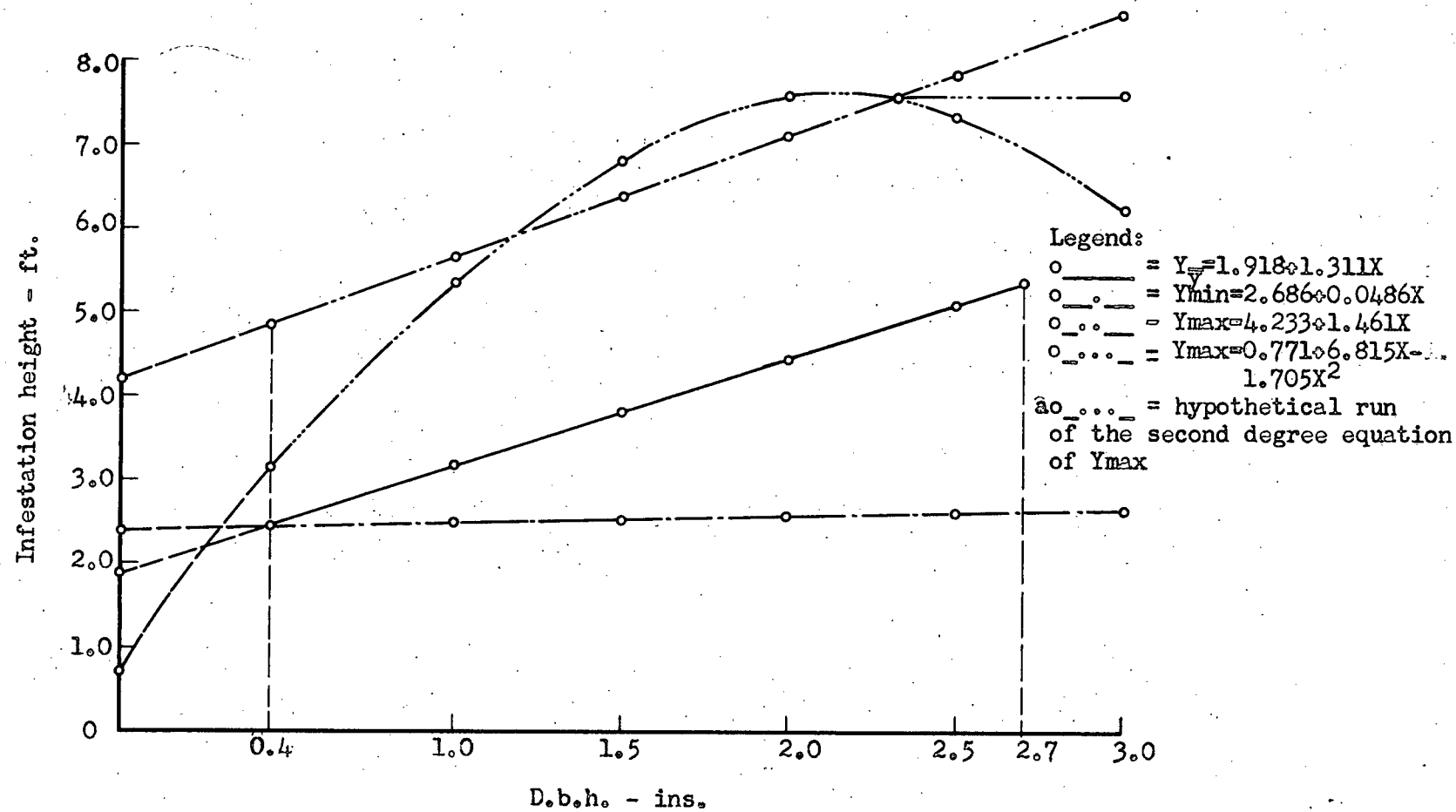
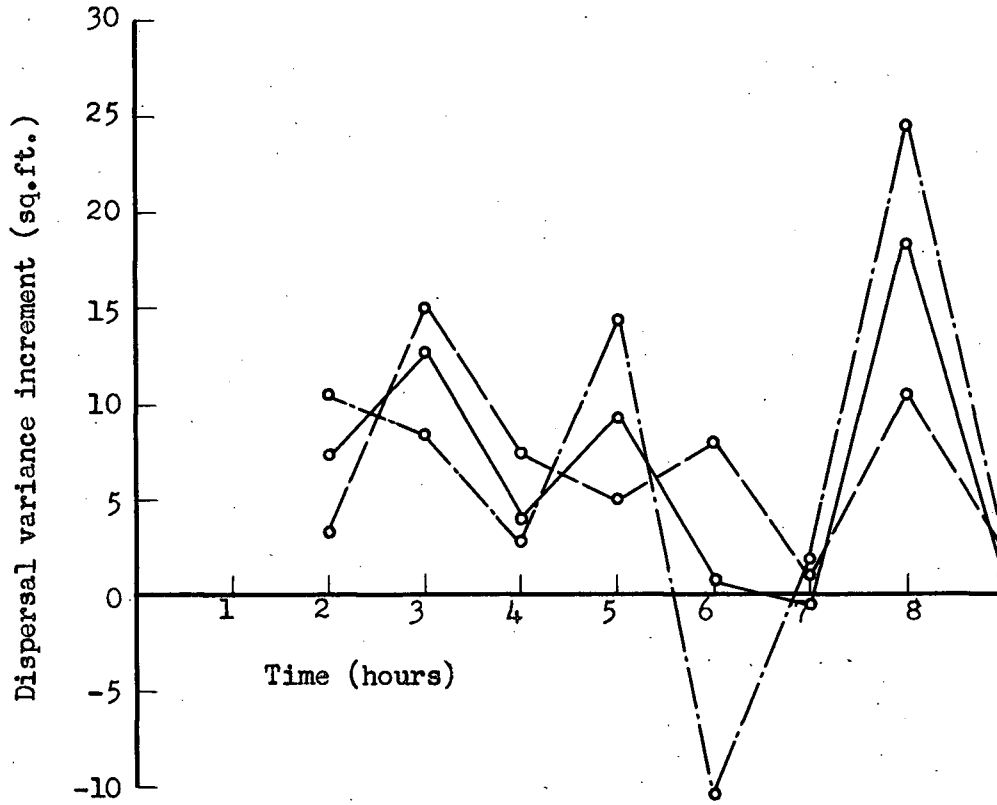


Figure 11. Hourly increments in variance of dispersing fed, starved, and combined populations of S. lapathi(L.).



Legend:
o___ = combined (fed+starved) variance increment
o- - = variance increment of fed population
o-.- = variance increment of starved population

Figure 10. Differences between observed and expected mortality ratios of I+II instar, III+IV+V instar larvae, and pupal+adult stages of S. lapathi(L.) at three different height levels of 20 trees.

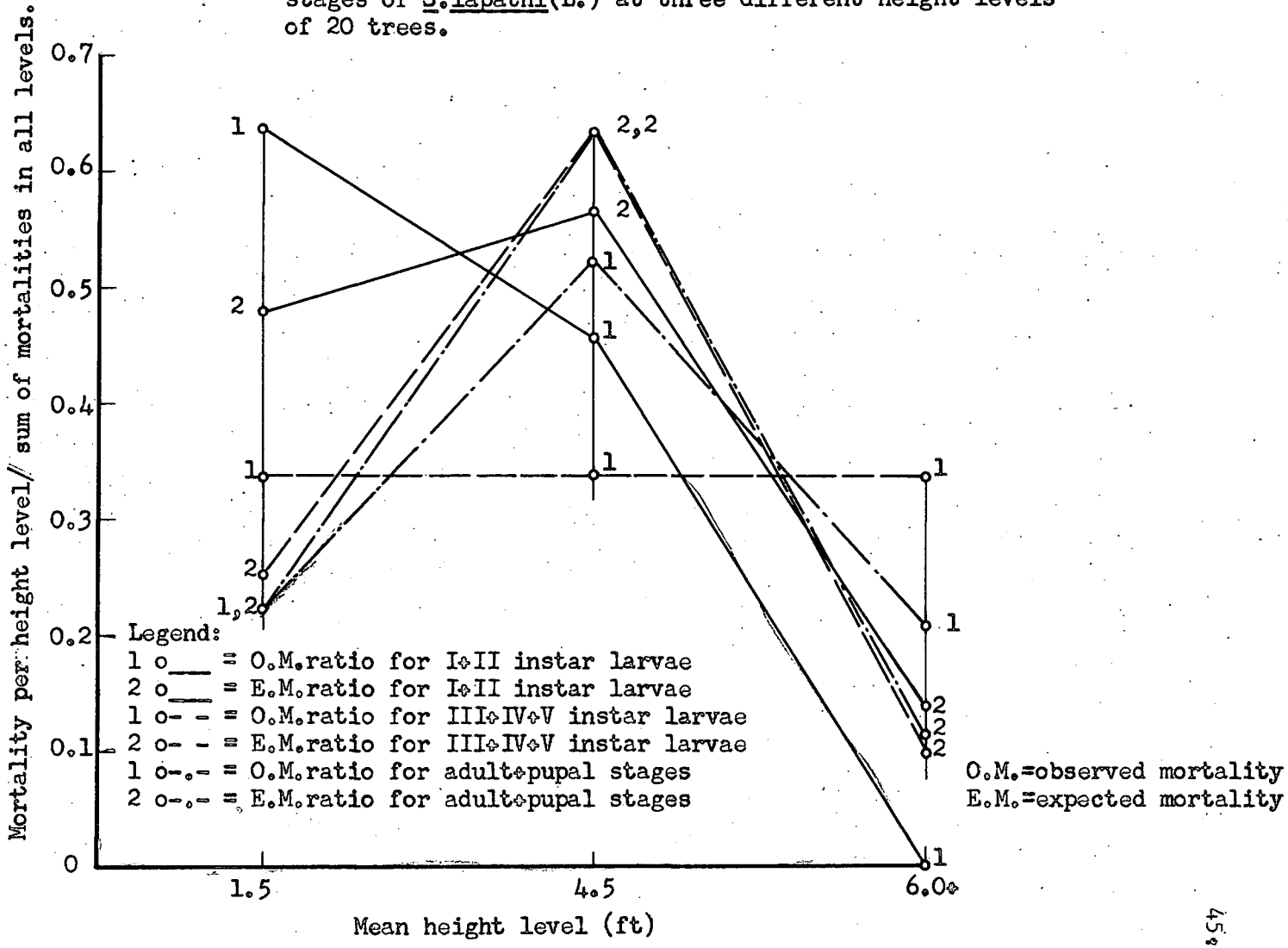


Figure 9. Differences between observed and expected mortality ratios at three different height levels of 20 trees for all stages of S.lapathi(L.) combined.

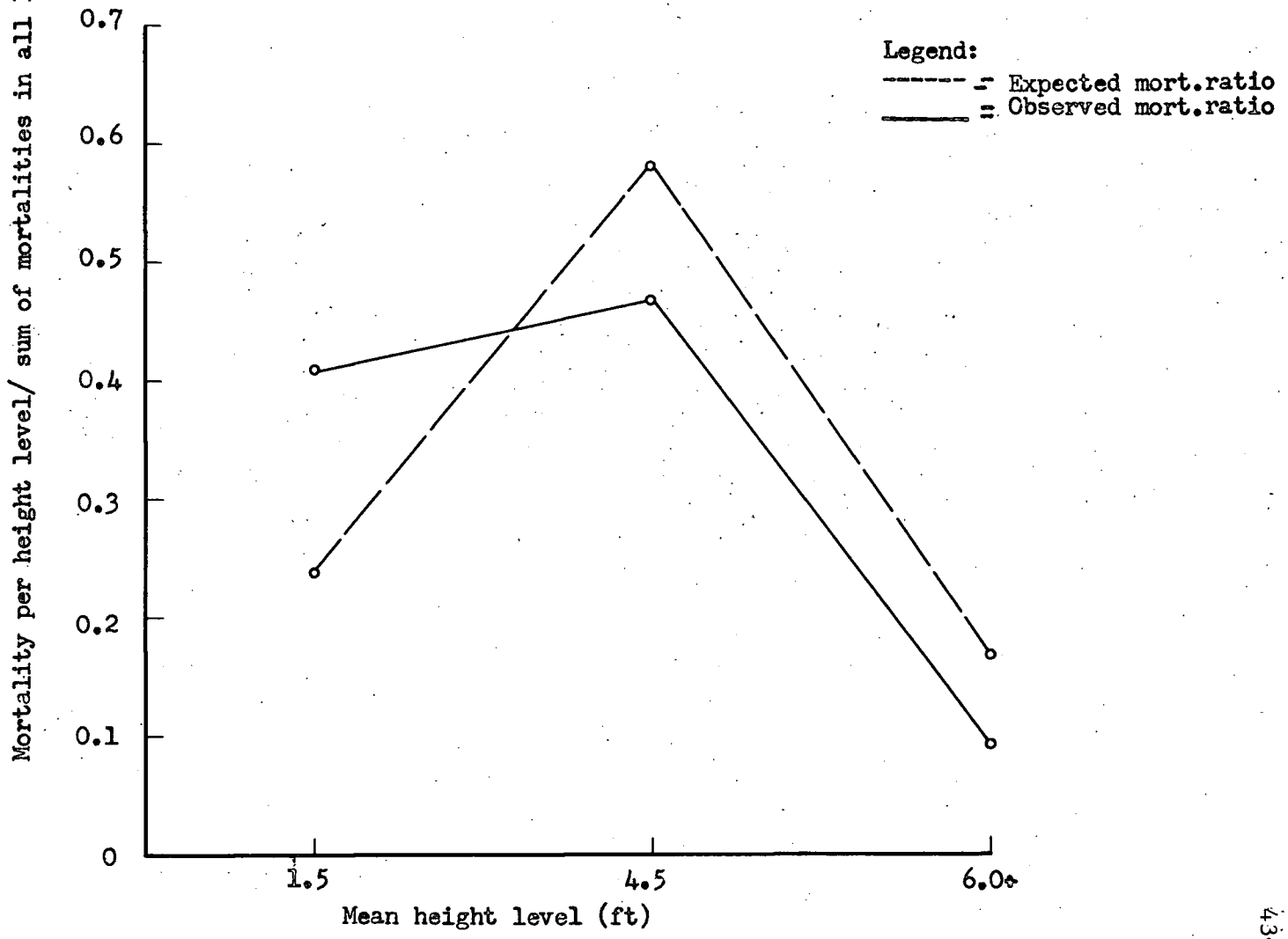


Figure 8. Simple and cumulative percentage mortality in different stages of S. lapathi(L.)

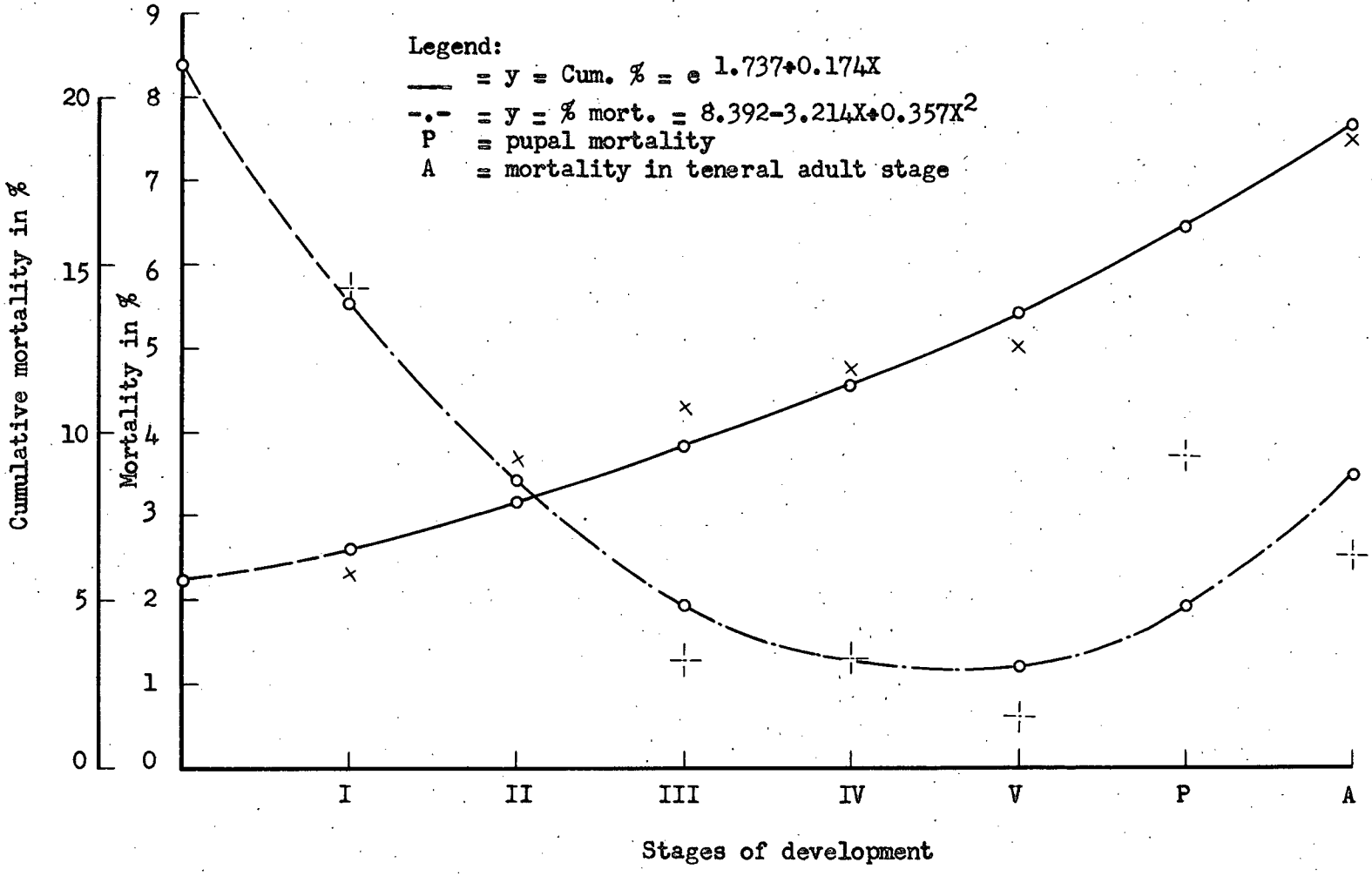
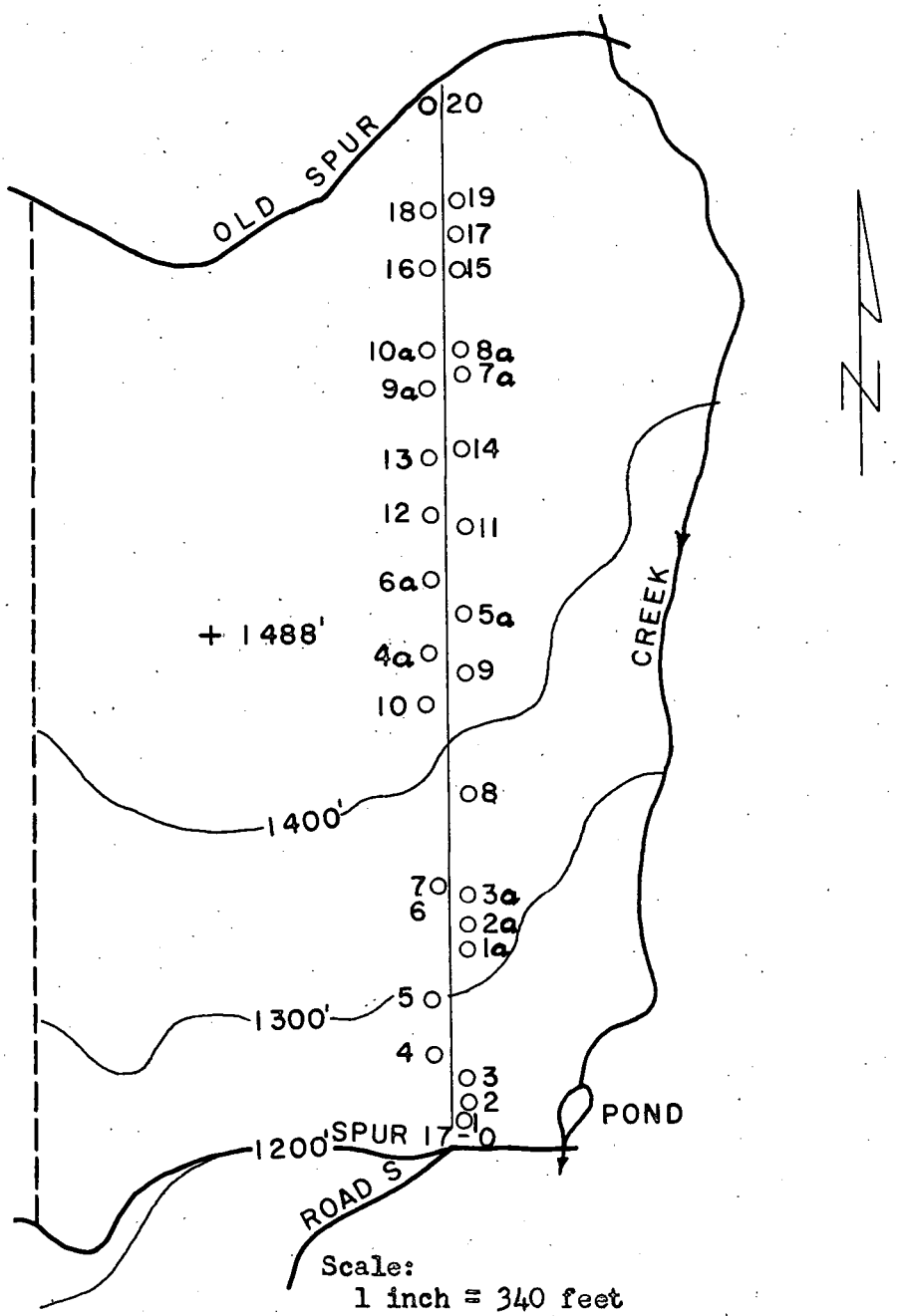


Figure 7. Location of sample trees on the experimental area.



Legend

1. Numbers from 1 to 20 are designating trees numbered on April 20, 1963 to study mortality and differential development in vertical direction in the tree trunks.
2. Numbers from 1a to 10a are designating trees established to study dispersal by flight.

Figure 6. Occurrence of larval instars of S. lapathi(L.) in the field

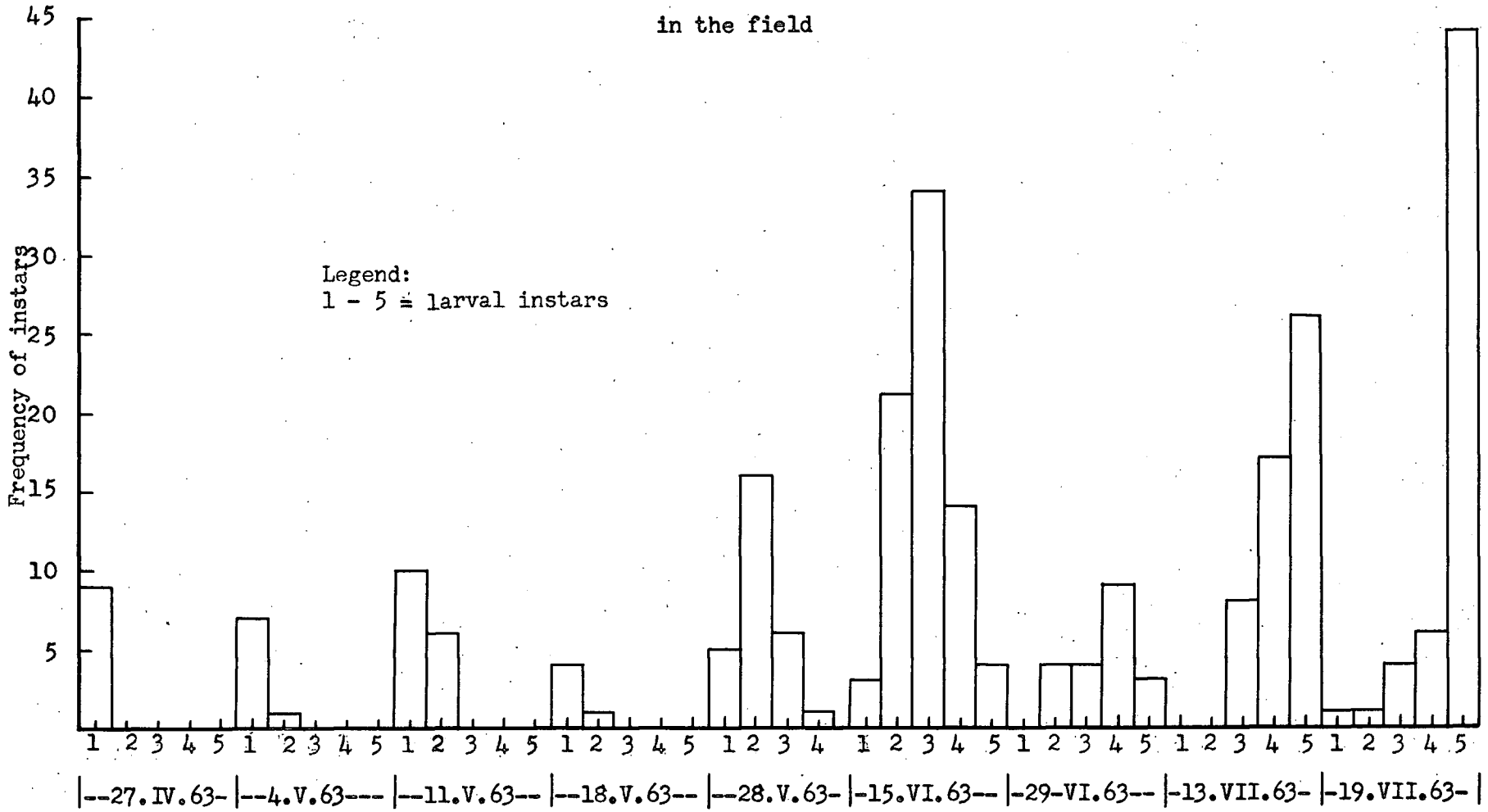


Figure 5. Mean width of head capsule per instar, S. lapathi(L.).

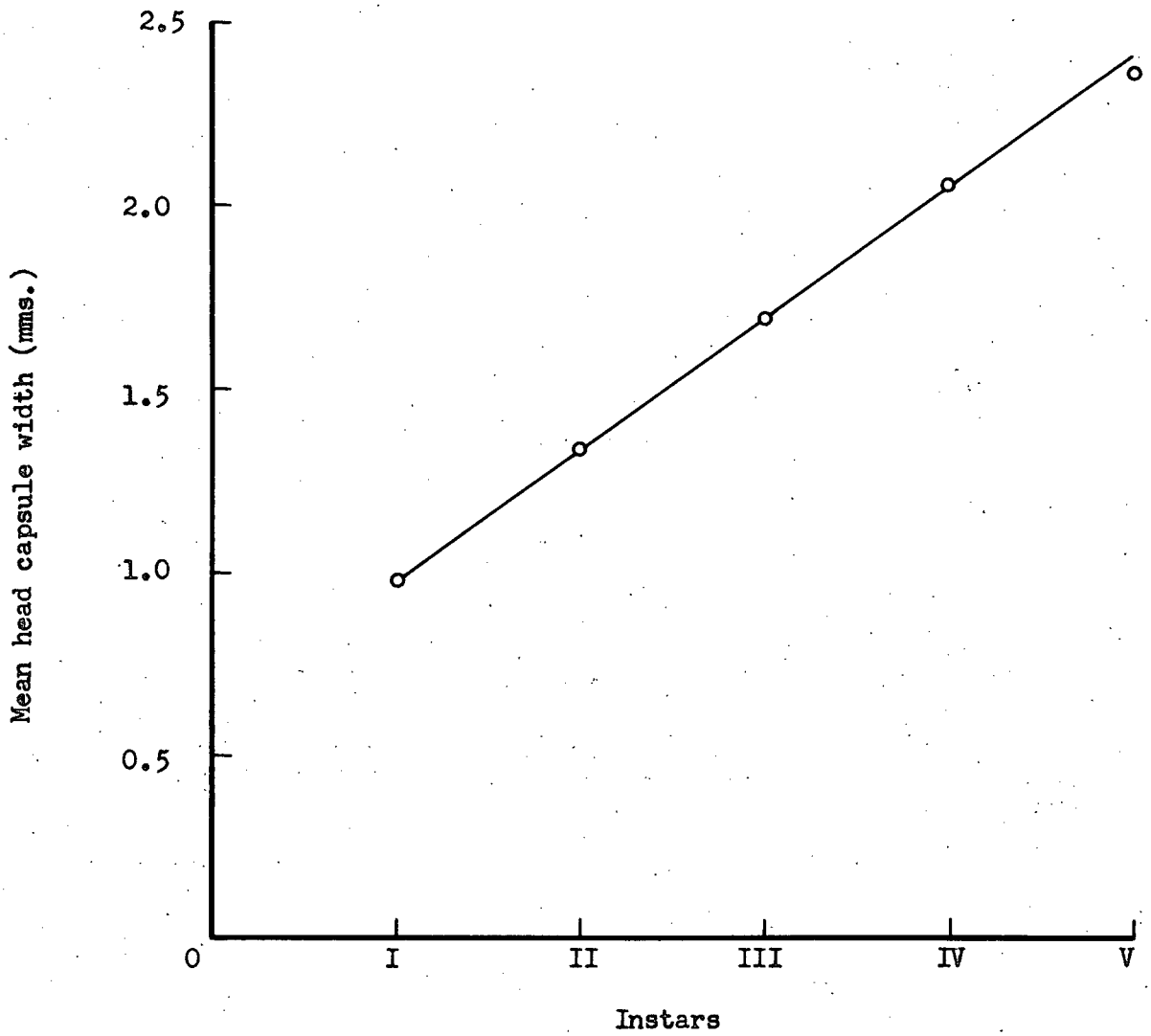


Figure 4. Frequency histogram of head capsule widths of S. lapathi(L.).

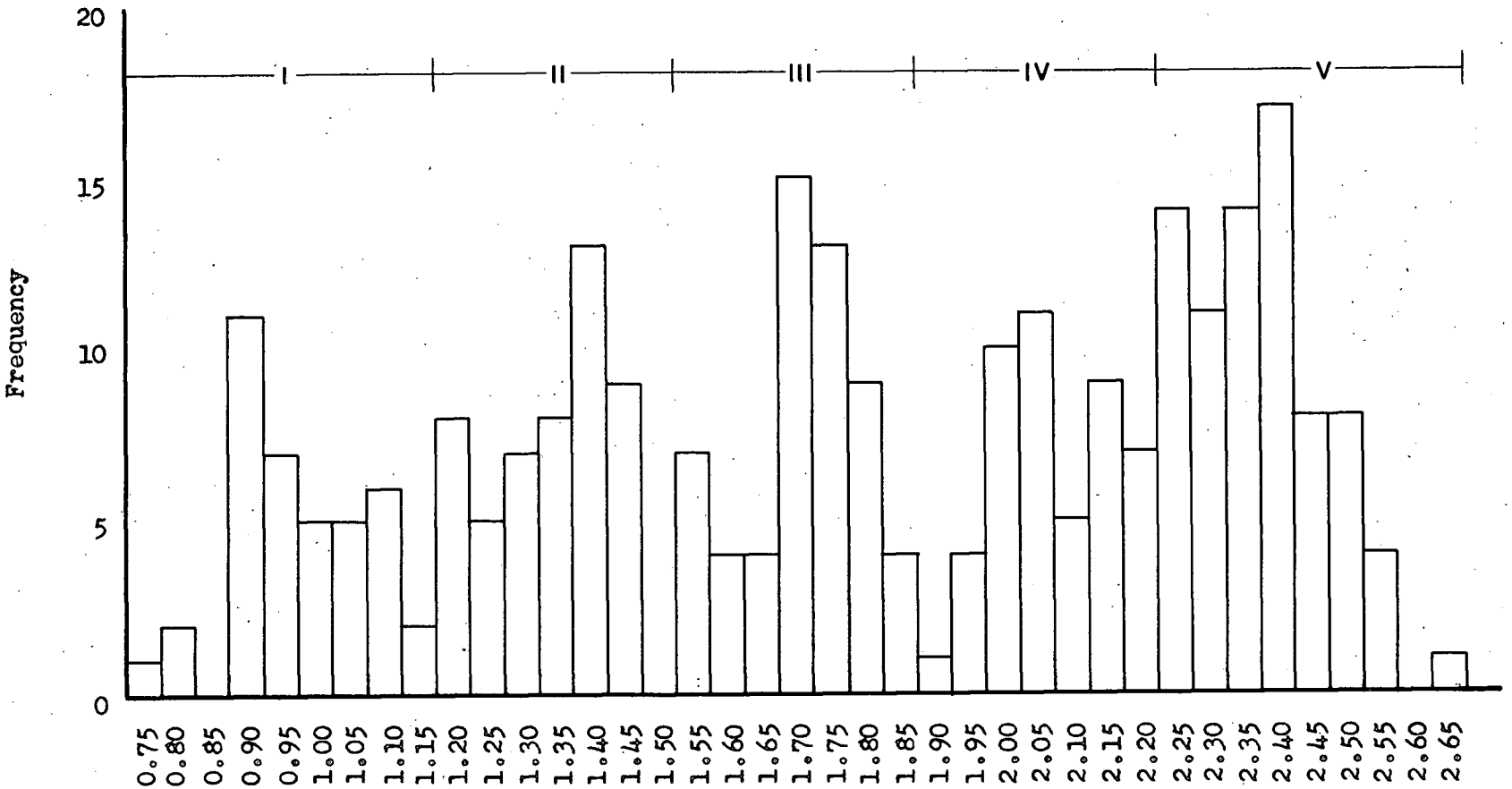
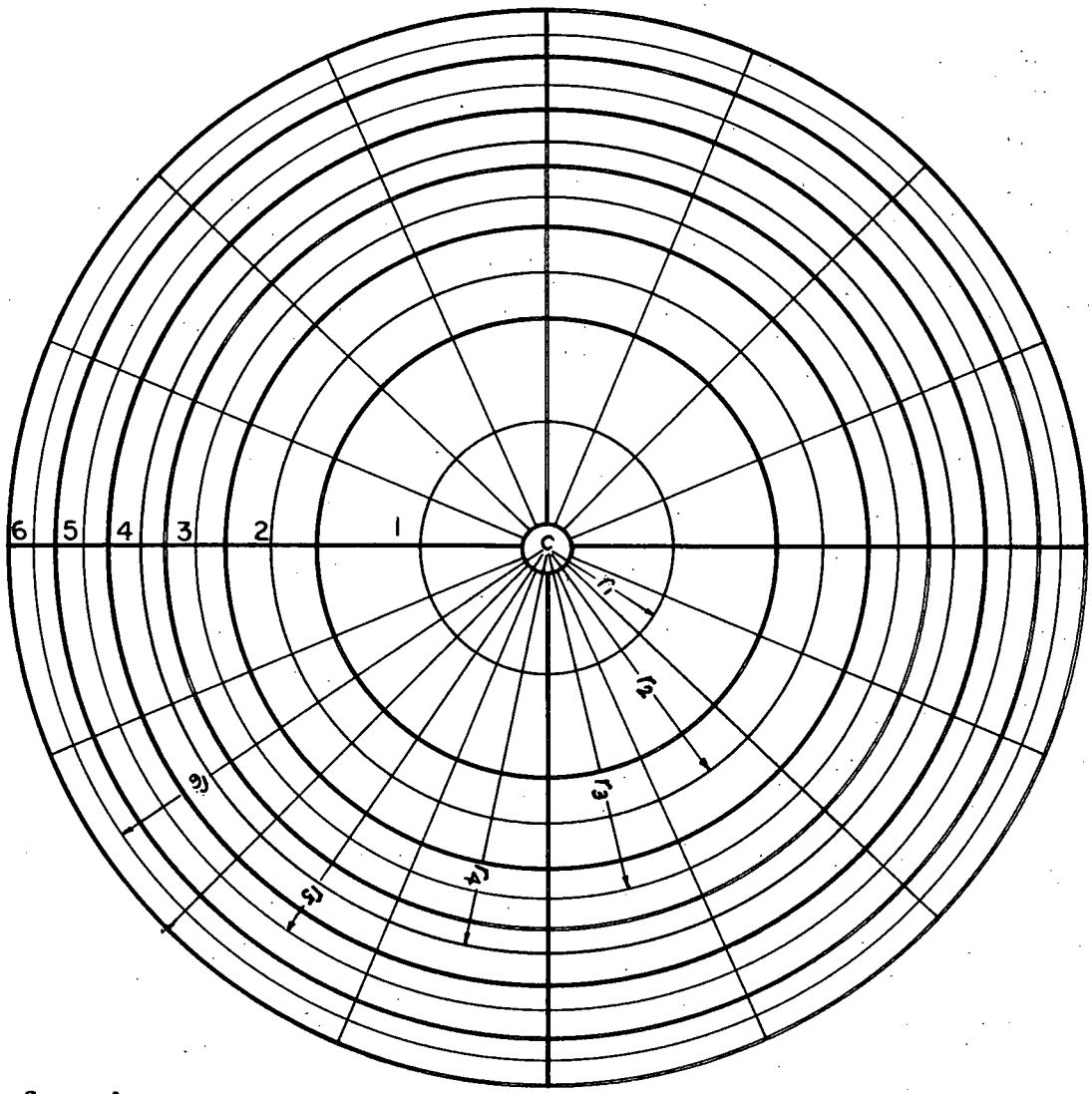
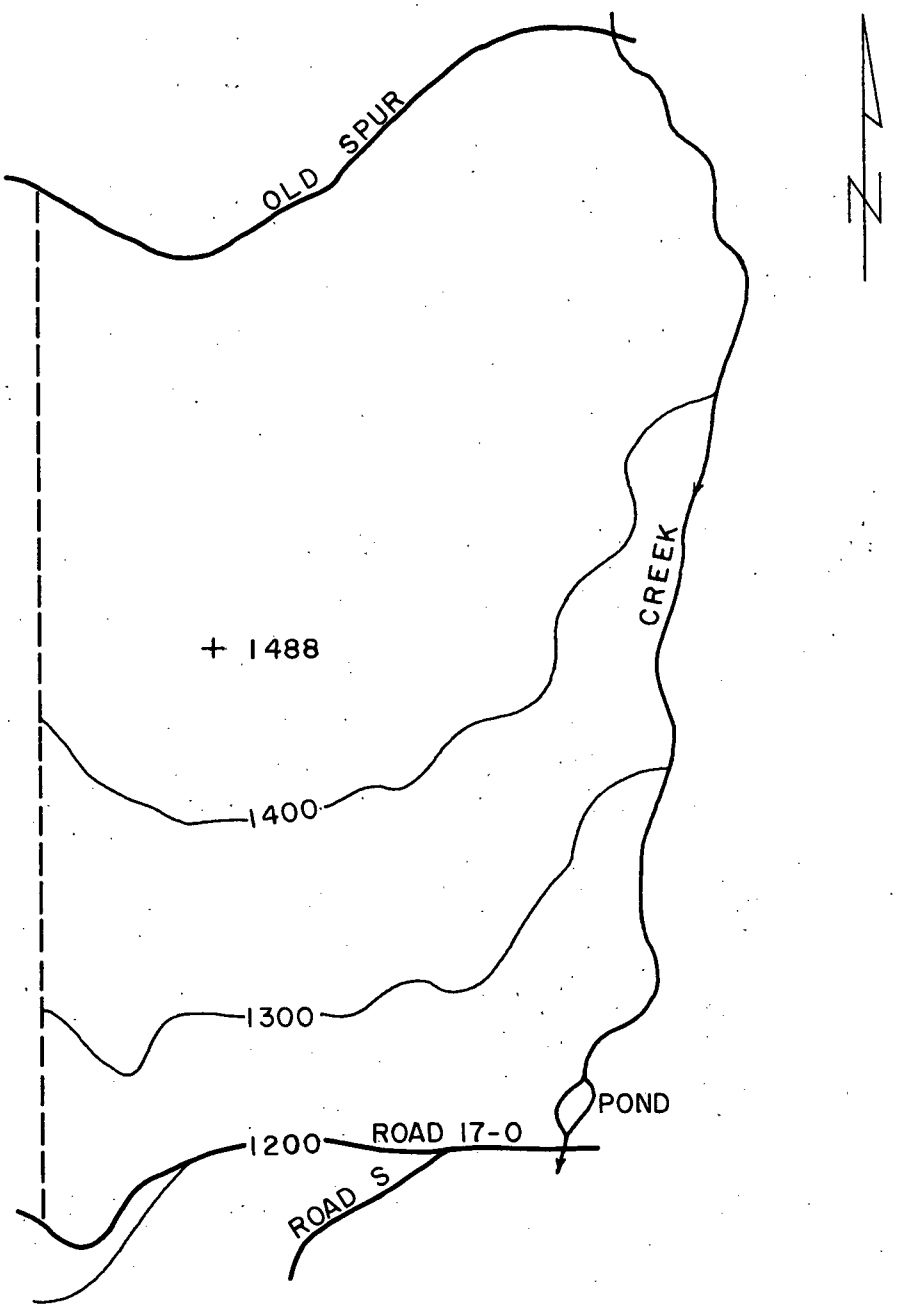


Figure 3. Design to measure the rate of dispersal of S.lapathi(L.)



Legend
Area of an annulus = 50'40 sq.ft.
Area of central circle = 0.78 sq.ft.
r_1 = 2.27 ft.
r_2 = 4.86 ft.
r_3 = 6.33 ft.
r_4 = 7.48 ft.
r_5 = 8.48 ft.
r_6 = 9.38 ft.
r_c circle = 0.50 ft.

Figure 2. Map of the experimental area
(Area = 36·88 acres)



Scale:
1 inch = 340 feet.

Figure I. Development of S. lapathi(L.) in different host trees at different temperatures.

(Redrawn from Szalay-Marzso, 1959)