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Frontispiece -- Sorrel-topped ponderosa pine killed by Black Hills beetles.

A STUDY OF
SOME ASPECTS OF SUSCEPTIBILITY OF PONDEROSA PINE TO ATTACK BY BLACK HILLS BEETLE

by

Edwin W. Mogren

A dissertation submitted in partial fulfillment
of the requirements for the degree of
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A Study of Some Aspects of Susceptibility of Ponderosa Pine to Attack by Black Hills Beetle

by Edwin ALFRED W. Mogren

Two problems are explored in this study: the first, an examination of ponderosa pine's susceptibility to attack by the Black Hills beetle; the second, an evaluation of pine's resistance to the beetle subsequent to its attack.

The observational design was based on both paired plots and paired trees. The standard error of the difference for paired data, and chi square were used to evaluate differences which resulted when infested and uninfested trees were compared.

Based on an analysis of differences in conditions and characteristics of infested and uninfested trees the following conclusions were reached concerning susceptibility of ponderosa pine to attack by the Black Hills beetle.

1. A difference does exist in susceptibility among ponderosa pine to Black Hills beetle attack under both endemic and epidemic levels of infestation.
2. Susceptibility of pine to beetle attack is a function of a tree's existing vigor. The more vigorous a tree is the less susceptible it is to beetle attack.
3. Vigor requirements associated with pine's susceptibility vary with the level of the beetle population.

4. Black Hills beetles, upon leaving the brood tree, do not fly great distances, but attack nearby susceptible pine.
5. A tree that has sustained current barking damage which is growing in an area of low beetle population is more subject to beetle attack than an unbarked tree.
6. Paired trees is the preferred sampling unit in the design of the experiment.
7. The differences that were found to exist between susceptible and less susceptible trees were of such a magnitude that they were not readily discernible in the field, but became evident only through a careful sampling procedure.

An analysis of the differences between resistant and non-resistant ponderosa pine constitutes the second portion of the study. Based on this analysis of tree conditions and characteristics the following conclusions were reached concerning resistance of ponderosa pine to attack by the Black Hills beetle.

1. There are ponderosa pine that are truly resistant to Black Hills beetle attack.
2. Resistance in ponderosa pine is a reflection of good vigor or health.
3. The occurrence of resistance in ponderosa pine can be traced back to earlier establishment in a group. By gaining a time advantage on its associates, the resistant ponderosa pine achieves dominance early in

its life, and if growing conditions are good is able to broaden the difference in size and vigor which occurs between it and the other trees in the group. Consequently, resistant trees are the largest, have the best crown development, and occupy the best position in the forest canopy.

4. Resistant trees appear to have a greater number of resin ducts with which to move resin and "pitch out" the attacking beetles.
5. The number of resistant trees is relatively small. Only about five per cent of trees attacked by the beetle are able to successfully resist attack.

FOREWORD

I wish first to express my gratitude to Professor Samuel A. Graham who directed my doctoral research, for his interest as a friend and his wise counsel as a teacher. I thank the other members of my committee, Professors Davis, La Rue, Rogers, and Spurr, for their help and guidance.

I am indebted to the Forest Insect and Disease Laboratory of the Rocky Mountain Forest and Range Experiment Station of the United States Forest Service for both financial and technical assistance. I wish to express appreciation to Dr. Noel D. Wygant and his staff for their numerous suggestions and cooperation.

To my wife, Arle Mae, I am especially indebted, for her help in the preparation of the manuscript and for her faith and encouragement. I extend to her my gratitude and affection.

Fort Collins, Colorado
March, 1955.

E.W.M.

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INTRODUCTION

Status of the Problem

Loss caused by the Black Hills beetle (Dendroctonus ponderosae Hopkins) is a serious problem in the management of ponderosa pine (Pinus ponderosa Laws) on the Front Range of the Rocky Mountains in Colorado. The beetle is an ever present part of the forest environment, always persisting in the forest and at frequent intervals bursting into epidemic numbers. On the Roosevelt National Forest in Colorado, where the study reported herein was conducted, outbreaks have occurred in different parts of the forest during the following periods: 1920-1930; 1933-1939; 1946-1948; and 1950-1953. These epidemics were localized, involving only part of the entire pine type. Losses to the beetle include both direct destruction of timber volume and the indirectly deleterious effect that the removal of forest cover has on the watershed.

Foresters and entomologists alike have directed their efforts chiefly toward mechanical and chemical control practices. These practices have been costly and are only effective in temporarily ameliorating the effects of the beetles. When judged on the basis of the recurrent outbreaks, direct control practices seem to have had little effect. A lack of basic information about the insect and its host relations is obvious and has handicapped those responsible for its control. The studies that have been published have dealt only briefly with its relations

to its host. Since Hopkins (1902) described and named the insect only three other workers have investigated and published their findings on the host -- Black Hills beetle coactions (Blackman, 1925; Craighead, 1925; Beal, 1939, 1943). The work of these investigators concerning the host susceptibility and resistance to the insect was not intensive, and the conclusions reached were supplementary to their primary investigation of the characteristics and habits of the beetle. In general, all are in agreement concerning the beetles' reactions to its host. They conclude that under endemic conditions the beetle prefers to attack weakened, slow growing, over-mature trees; but when epidemic populations of beetles develop the beetle appears to show no observable selectivity.

A number of observations, made prior to this present investigation, raised doubt as to the validity of these conclusions. It was noticed that under endemic conditions the beetle attacked young immature pines as frequently as it did older trees, thus raising the question of the relationship of tree age and susceptibility to beetle attack. It was also noticed that following severe epidemics and within large groups of killed trees there remained some that had either not been attacked or had successfully resisted the attack. This resulted in the hypothesis that certain trees even under epidemic conditions are less susceptible or perhaps resistant to beetle attack. Thus the present study has been undertaken to determine whether

ponderosa pine trees with certain characteristics, or growing under specific site conditions are especially susceptible or resistant to attack by the Black Hills beetle. The investigation was conducted during the period from 1952 to 1954 inclusive. The intensive work done on the Roosevelt National Forest was supplemented by a reconnaissance trip, to observe the Black Hills beetle in the Harney and Black Hills National Forests during the summer of 1952. This study is a silvical evaluation and is not concerned with the entomological aspects of the problem. Since little work has been done on the relation of the insect to its host, the approach to the problem has been through rudimentary and basic considerations. Therefore, every observable tree characteristic or site condition that might influence the susceptibility of trees to beetle attack was considered. Naturally, many of the comparisons proved to have no significance in determining susceptibility or resistance of the trees. However, this negative information was suggestive and in its way as valuable as the positive evidence.

Description of Areas Studied

The ponderosa pine type occupies approximately four million acres in Colorado. Economically this type is of value both as a source of timber and for game and livestock forage. On the Front Range in Colorado, where this study was made, ponderosa pine grows at elevations between 5500 to 8500 feet. It grows on both ridges and slopes. On the north exposures it is frequently mixed with Douglas-fir.

The ponderosa pine types can be classified into four aspects, namely: a.) relatively evenly spaced open stands, where sunlight reaches the ground, and herbaceous cover grows on the forest floor; b.) groups of timber interspersed with open grassy parks; c.) wet meadows and stream banks; and d.) closed forest which may be pure, or at higher elevations, and on north exposures, mixed with Douglas-fir. At drier, lower elevations the pine is mixed with juniper and species of the mountain brush type. The stands are often patchy and may occur as isolated groups of trees in mixture with other types. Along streams the pine type becomes associated with various plant communities, varying from grassy meadows, through willow thickets to stands of mountain maple, alder, cottonwood and sometimes aspen.

Each plant community in the pine zone represents a stage in the ecological succession of the area. Barring disturbance, the end of the primary succession in this zone is climax pine or pine-fir forests. However, throughout most of the pine type the primary succession has been interrupted and secondary successions are most common. Fire and grazing are the principal disturbance factors. The end result of secondary successions is, of course, the climax pine or pine-fir forest.

The area studied, as delineated in Figure 1, includes the northern-most extension of the ponderosa pine type on the Front Range in Colorado. It encompasses an area of

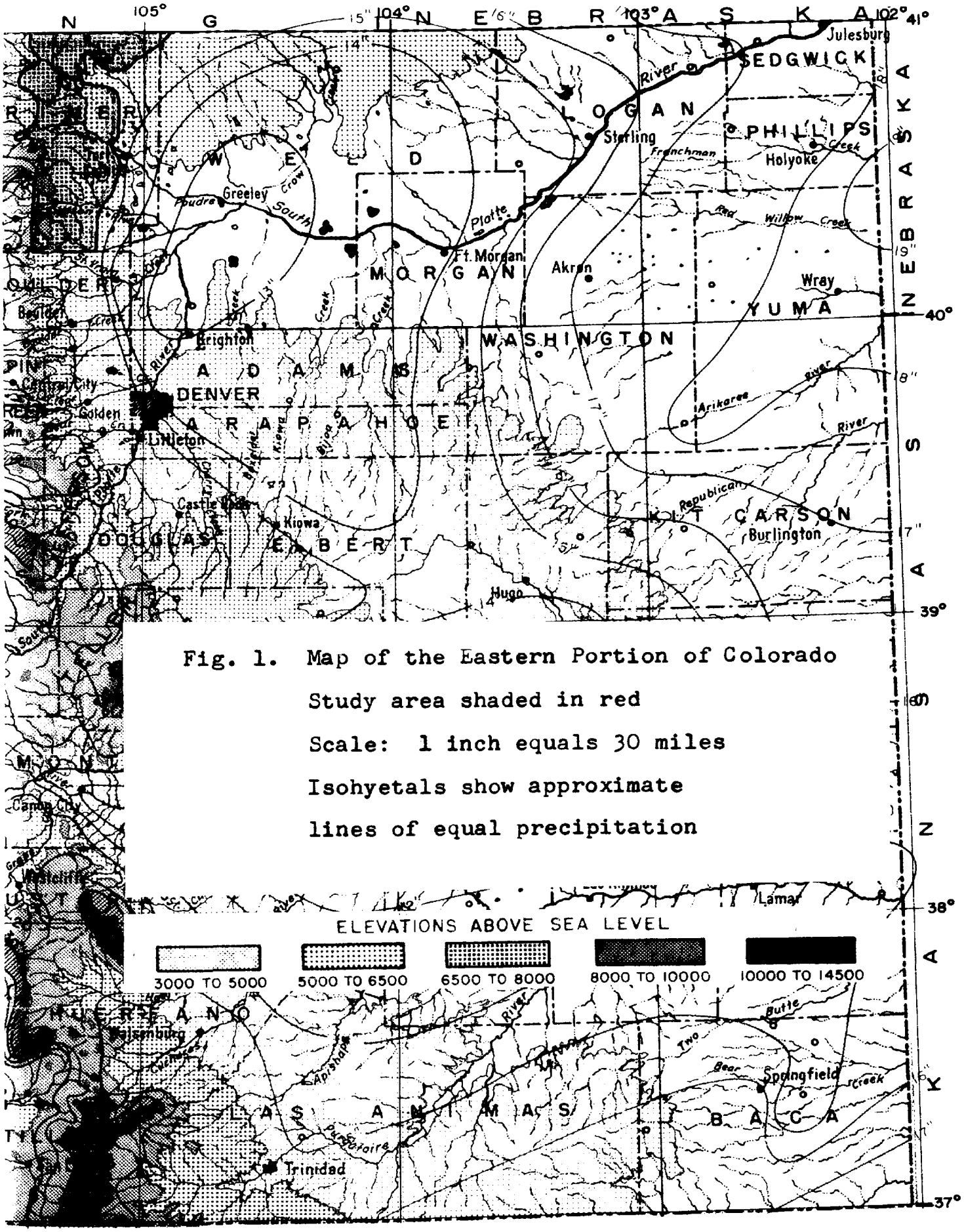


Fig. 1. Map of the Eastern Portion of Colorado

Study area shaded in red

Scale: 1 inch equals 30 miles

Isohyetals show approximate lines of equal precipitation

about forty miles long and fifteen miles wide.

Geologically, it is part of a great uplift which exposed granite and granite schists of the Archean period. Pikes Peak granite underlays the entire area and is the parent soil material. The soil consists of disintegrated granite, over solid granite. Loose rocks are scattered throughout, and rock-out-crops, some of considerable size, are frequently encountered. The soil, for the most part, is dry and gravelly, shallow, with weakly developed profile. No detailed soil classification has been made of the area, the soils being depicted on soil maps as Lithosols. However, along streams, in mountain parks, and in small valleys between rocky hills, small deposits of black sandy loam occur. Some of these tracts are very fertile, decaying organic matter, and fine materials having been washed from the slopes, mixed with decomposed granite, and deposited in these valley bottoms.

The topography of the area is rugged. Mountain streams cut the land into lateral ridges extending generally east and west. The elevation is relatively high; the lowest elevation, at the junction of Lewstone Creek and Cache la Poudre River, being 5200 feet. The highest elevation on the east face of White Pine mountain is 8400 feet.

Precipitation is low, varying with altitude from 15 to 20 inches annually, occurring mostly as late spring snow and early summer rain. The balance of the year is dry.

MATERIALS AND METHODS

A preliminary reconnaissance preceded the field measurements. The purpose was to locate infested trees and also to determine the extent of infestations. This work was greatly aided by personnel of the U. S. Forest Service Insect and Disease Laboratory, formerly of the Bureau of Entomology and Plant Quarantine. Results of surveys by the Laboratory were made available that delineated these infested areas and showed existing degrees of infestation. In the spring of 1952 when the study began all levels of infestation were present, from severe epidemic conditions in the northern end of the area, to low endemic conditions in the south.

The field work was conducted in three phases each emphasizing a different approach. Each will be discussed separately.

INFLUENCES RELATED TO SUSCEPTIBILITY

Infested Compared with Uninfested Paired Plots

Since most forest management practices are evaluated in terms of volume and area it was natural that the first attempts to test the significance of various factors upon susceptibility and resistance of ponderosa pine to bark-beetle attack should rest upon an area basis.

The experimental design of this phase of the study was based upon the use of paired plots. One plot of each pair was located in a group of ponderosa pine that had been infested by Black Hills beetle, whereas the second was

located in adjacent uninfested green timber and served as the check.

The first step was to designate areas according to levels of beetle infestation. In order to express quantitatively the intensity of infestation, the number of infested trees per acre was used. Two levels were recognized. Areas that averaged less than 0.2 of an infested tree per acre were considered to be in endemic condition, and those with a greater infestation than this were considered to contain epidemic beetle population. Following recognition and delineation of these infestation levels the actual field measurements were undertaken.

The sampling procedure employed paired one-twentieth acre rectangular plots. The study being "post mortem" did not follow the normal statistical pairing procedures. Instead of selecting the pair of plots, randomly choosing one for treatment and allowing the remaining one to serve as a check, the "treated", or infested plot was of necessity chosen, and the check plot used for comparison was selected randomly from the adjacent population of uninfested trees. Specifically, the procedure was as follows:

1. A group of infested trees was selected and the center and corners of the plot were established. The plots measured 46.67 feet on a side and were laid out with the aid of a steel tape.
2. From the adjacent population of green uninfested trees a check plot was randomly selected as follows:

a. One of sixteen possible compass directions was randomly chosen by drawing a card containing directions from a pack of shuffled cards. The directions indicated on the cards differed by 22.5°, reading true north, N22.5°E, N45°E, N67.5°E, true east, etc.

b. Along this randomly selected direction 89 feet was measured along a line and then the center of the check plot set. This distance insured a buffer zone of at least one-half the plot depth between plots, regardless of compass direction. If this procedure resulted in the selection of a plot in a location in a different tree population from the infested plot, a second drawing was made from the direction cards. Failure to maintain similar aspect, or slope, as well as type composition, were possible criteria for disqualifying check plots.

c. The check plot was laid out and staked.

This procedure results in as much randomization of pairs as the study allowed. Data were recorded on three field forms from each of the plots. The first, tree data; the second, general information; and the last, ground cover information.

On the plot tree data sheet the following observations

and measurements were recorded for each tree:

1. Tree diameter at b.h., measured with a steel diameter tape, recorded to the nearest one-tenth inch.
2. Total tree height, measured with abney hand level and recorded to the nearest foot.
3. Bark thickness, measured at b.h. by cutting through the bark with a hand ax and measuring with a small ruler, recorded to the nearest one-tenth inch.
4. Needle length measured from branches clipped from the upper one-third of the crown. Measurements were taken from four sides of the tree and averaged. The needle lengths were grouped into seven classes ranging from very short (less than 2½ inches) to very long (over 6 inches).
5. Twig growth determined from the branches clipped from the upper one-third of the crown. The past year's growth was measured and recorded to the nearest 1/10 inch.
6. Length of lateral shoot in relation to leading shoot determined by measurements of the true leader if it could be reached. However, in some cases it was necessary to determine the leader-lateral ratio from branches immediately below the top. These measurements were recorded in tenths of inches.

7. Crown Class of each tree in the stand recorded conventionally as dominant, co-dominant, intermediate, or suppressed.
8. Tree Class according to Keen's Tree Classification for ponderosa pine.
9. Lightning damage, wind damage, mechanical barking, and evidence of recent burns recorded individually for each tree.

Two increment borings, reaching to the center, were taken from each tree, from opposite sides at the average diameter, 4½ feet above the ground. Cores were placed in a container and subsequently measured in the laboratory.

In addition, on the tree record sheet were recorded any comments that seemed pertinent but did not fit any of the specified categories.

On a general plot information form were recorded the following:

1. More detailed information on several entries on the tree record form -- particularly:
   a. Lightning
   b. Wind throw
   c. Mechanical barking
2. Direction of prevailing winds and local air currents. In the study area it should be noted that the prevailing summer winds were from the southwest quadrant and local air currents were usually masked by prevailing winds. On the few

windless days during the field season the local air currents appeared to move perpendicular to the slope, upward during the day and downward during the night.

3. Evidence of earlier insect attacks, particularly the closest possible source of infestation of infested group. This distance was measured to the nearest chain by pacing up to a distance of five chains. Infestation sources beyond that distance were tallied as being over five chains.
4. Direction of spread of the infestation, by determining location of earlier infested groups and tracing probable routes of movement of the beetles.
5. Soil origin. This proved to be the same throughout the area, namely -- Pikes Peak granite.
6. Aspect recorded for each plot according to the cardinal directions.

The extent and composition of woody ground cover were recorded on the "Ground Cover Tally" form. The first entry made on this form was an estimate of per cent of area covered by vegetation of all forms. The second entry was the type and frequency of woody vegetation occurring on five milacre sub-plots. These sub-plots were located in the four corners and one in the center of the one-twentieth acre plot. The following were recorded for each:

1. A list of all woody plants found on the sub-plot.
2. Per cent of occurrence of each woody species.
3. The per cent of possible shade. This was determined by observing the density of the tree canopy over each sub-plot.

Infested Compared With Uninfested Paired Trees

In the second phase of the study, paired trees form the basis for the design. One tree of each pair had been infested by the Black Hills beetle, whereas the other was a similar but uninfested nearby tree which served as a check. The trees were located in areas of very low endemic beetle populations. This phase was included to supplement the paired plot series. Two purposes were served by this series of paired tree measurements. First, it allowed the Black Hills beetle the greatest play of selectivity of the host that it was able to demonstrate; and secondly, any masking influence that resulted by averaging plot data was eliminated.

As in the first phase the design was one of paired items, the "treated" member of each pair being selected by the insect and the "untreated" member, or the green tree, was selected randomly from the adjacent uninfested tree population. To insure the greatest similarity in microsite conditions the nearest uninfested tree of comparable size was chosen as the check tree. Due to uniformity of trees within stands there were few occasions

when the nearest tree did not qualify, and only on rare occasions was the check tree located more than one-half chain from its infested mate.

The measurements taken on the paired trees were the same as those for each of the trees in the paired plot phase of the study, and records were made on the same type of forms.

INFLUENCES RELATED TO RESISTANCE

Resistant Compared With Non-resistant Paired Trees

This phase was undertaken in an attempt to evaluate differences existing between beetle attacked ponderosa pine that had demonstrated resistance to Black Hills beetle and those which had been killed by the beetle. Paired trees were again used as an observational design. One member of each pair was a tree that had been successful in coping with the beetle attack and had survived, while the other member of each pair had been killed. The proportion of trees able to "pitch out" the beetle is comparatively low; therefore, to ensure encountering in the field a sufficient number to yield an adequate sample, trees were searched out in the most severe epidemic infestations that existed on the study area. Pines that had been attacked by only a few beetles were often able to "pitch out" the beetle, but doubt existed as to their ability to resist a heavy insect attack. Therefore, these were not selected for study. Only trees that had been heavily attacked and had been able to "pitch out" a number of beetles equivalent in number to

the infestation on trees that had been killed were selected.

The procedure used for pairing trees was the same as for the second phase. This time, however, the "pitch-out" tree was selected and the nearest killed tree of comparable size was chosen to complete the pair. Again, little difficulty was encountered in obtaining an infested tree close to the "pitch-out" trees. As was mentioned, these trees were located in epidemic areas, usually in or near large groups of infested trees. Consequently trees that had been killed were immediately available to complete each pair.

The tree measurements made on these pairs were the same as in the second phase of the study. In addition, however, an estimate of the intensity of the insect attack was made for the members of each pair. The first attempted to determine the number of insect attacks on the lower ten feet of the bole of the tree. This was done by counting the number of pitch-tubes and entrance holes in so far as they could be seen on this portion of the tree bole. To insure greater accuracy of the estimate a second sampling procedure was employed. Two one-half foot squares were cut from the tree at breast height and the number of entrance holes was counted.

INCREMENT CORE ANALYSIS:

Following the field work the increment cores previously mentioned were measured and the results analyzed in the laboratory. Each core was processed in the following fashion:

1. The core was secured in a wooden clamp, and with a razor blade a flat smooth surface was cut on one side of the core.
2. The core, in the clamp, was placed under a binocular microscope and the rings counted and marked as follows:
   a. The first five rings from the cambium were counted and marked with a very hard and very sharp pencil.
   b. The second five ring group were counted and marked.
   c. The remaining rings were counted and marked in groups of ten until the pith of the tree was reached.
3. The age of the tree was determined by counting the number of decadal groups plus the additional rings to the pith.
4. The core was adjusted against a scale on the clamp and the length of each group of rings previously marked was measured to the nearest one-hundredth of an inch, measurements being made from the cambium to the pith.

Two cores had been extracted from each tree. Consequently two measurements resulted for each growth period, and two age determinations were made for each tree. The age determinations on opposite sides of the tree were

not always the same due in part to unavoidable inaccuracy in counting very fine rings and in part to the fact that in injured trees wood may be laid down on only a part of the trunk circumference in a certain year. In each case the two measurements were averaged for individual trees.

INFLUENCE OF ENVIRONMENT FACTORS AFFECTING SUSCEPTIBILITY TO ATTACK

The results of the analysis of data obtained in this study will be presented in two separate sections. The first will deal with susceptibility of ponderosa pine to Black Hills beetle attack, the second with appraising tree characteristics and conditions which influence their resistance to beetle attack. The first is influenced by beetle preference, the second by tree resistance. Thus, although the field work was conducted in three phases, the problem is actually two-fold; namely, the evaluation of susceptibility and the evaluation of resistance subsequent to beetle attack.

The meaning of the terms "susceptible" and "resistant" as used in this dissertation should be made clear. As used here one is not the antonym of the other. The word "susceptible" will be used to convey the idea of probability. For example, if a tree is susceptible to attack there is a high probability that it may be attacked. The term "low susceptibility" means low probability, and is not synonomous with the term "resistant" as used in this study. That term will be associated with the ability of a tree to defend itself against the beetle when attacked. The question arises then, what is the relationship between susceptible and resistant trees? Resistant ponderosa pine, under most conditions would demonstrate low susceptibility to beetle attack. This immediately poses a second question. Why were they then attacked? The

best explanation that can be made assumes that high populations of beetles are relatively less selective than are sparser populations. This assumption is supported by the fact that ponderosa pine that have been able to resist attack successfully by "pitching out" the beetle are rarely discovered under endemic or low epidemic conditions, but only in areas of very high beetle populations. Under such conditions the beetles are attracted to a group of trees already under attack by other beetles. In such infested groups all susceptible trees in the group are attacked and as more and more beetles are attracted to the group the later arrivals attack the less desirable living trees. If one of these trees is a resistant individual it will still be attacked, but because of its special characteristics it will be able to resist successfully and will "pitch out" the beetles.

Thus, the concepts of resistance and susceptibility are indeed related, each being a segment of the same total concept, but each emphasizing a different aspect of a situation.

The procedure employed for appraising the validity of the differences that resulted when the paired plots and paired trees were compared was the standard error of the difference method for paired data. The chi square test was also used in certain instances. The mechanics of the two procedures are outlined in detail on page 95 of the Appendix. A statistical probability of 95 per cent

was assumed as the standard before differences between infested and uninfested plots or trees were accepted as significantly different. This allowed only one chance in twenty that a difference would be accepted which was the result of the sampling process and therefore not significant.

Susceptibility of ponderosa pine to Black Hills beetle attack seemed to be linked to the level of the beetle population in the area in which the tree was growing. This concept has been accepted for other Dendroctonus beetles, but in order to determine its applicability to D. ponderosae the paired plots under epidemic conditions were analyzed separately from those under endemic population levels. The plots were grouped according to the level of the local beetle population, since the number of currently infested trees per acre is considered to indicate the level of the existing beetle population. The upper limit of an endemic infestation was set at 0.20 infested trees per acre whereas any infestation exceeding this amount was classified as an epidemic. The limit of 0.20 infested trees per acre was selected as the upper index of endemic beetle populations, because it has been observed that above this level of infestation the insects begin to attack groups of trees rather than individuals and the epidemic stage is then reached. Actually the highest endemic level of infestation observed was 0.15 infested trees per acre, the lowest, 0.02. In contrast,

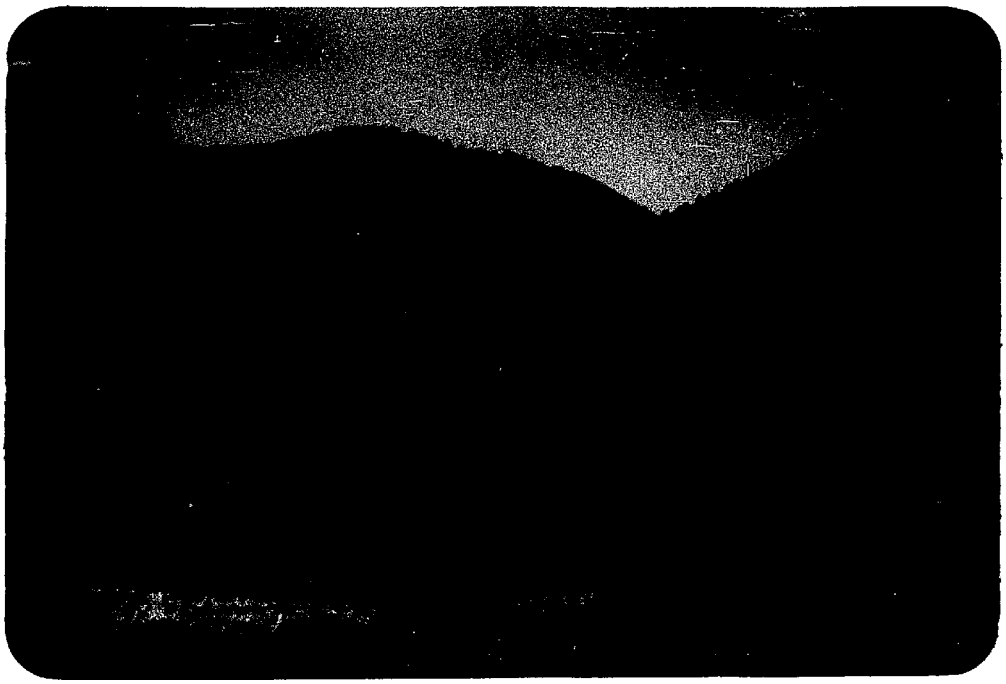


Fig. 2 -- Large group of beetle killed pine under epidemic conditions.

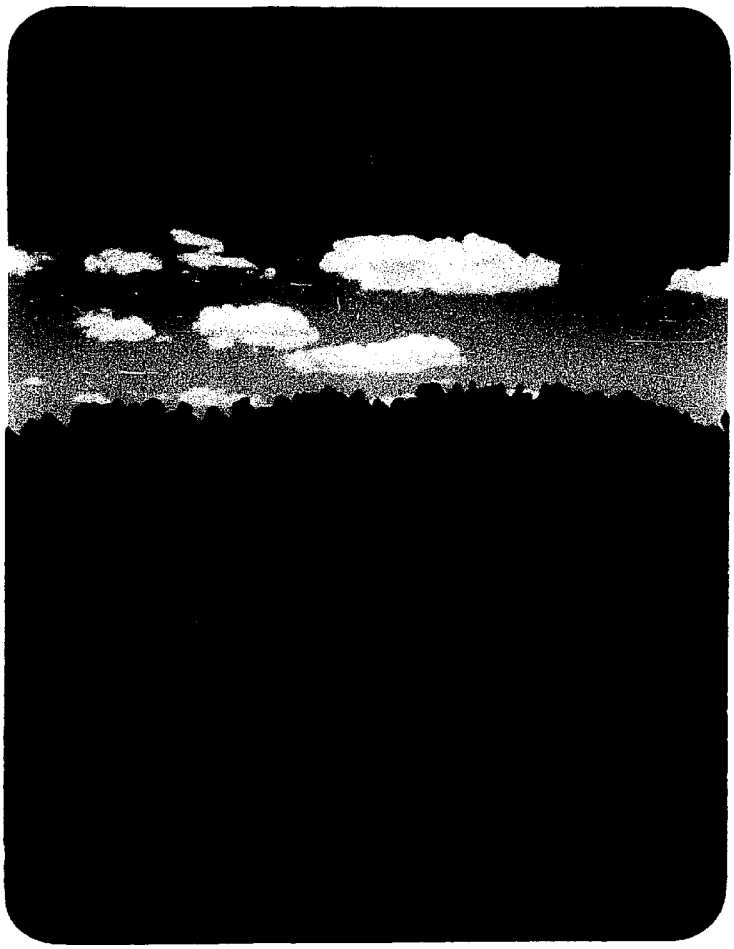


Fig. 3 -- Isolated pine killed by beetles under endemic conditions.

in locations classified as having epidemic infestations the beetle attacked trees numbered from 0.23 to 0.75 per acre.

The beetles appear to be relatively less selective under epidemic conditions than when they are present in smaller numbers. Therefore, observations made on plots placed in groups of infested trees and compared with nearby uninfested spots might not show clearly the true host selection reactions of the beetle. Thus, the study of paired trees, one infested and one uninfested seemed desirable. These pairs were located in areas of low endemic infestation where only isolated infested trees occurred. The study of susceptibility was thus divided into two phases, the first paired plots, the second the paired tree series. Together these two phases constitute the first part of the study, namely, the evaluation of ponderosa pines' susceptibility to Black Hills beetle attack.

On discovering and learning the identity of any harmful forest insect the forest manager immediately needs to know what injury to the forest it is likely to cause and under what conditions it is likely to become epidemic in numbers. In other words he is concerned with its host relations. This is particularly pertinent if its activities are seriously detrimental to man's interest. Hopkins (1902) described the Black Hills beetle and gave it the name Dendroctonus ponderosae. Since that time,

only three investigators have published results of studies concerned with the relation of this insect to its host (Blackman, 1925; Craighead, 1925; Beal, 1939, 1943). The reason for this dearth of published information is threefold. First, a major part of that portion of the ponderosa pine type which is coincident with the range of the Black Hills beetle is of low economic value. Second, no obvious, easily discernible relation appeared to exist between the insect and its host promising a simple solution of the problem. Third, there has been a tendency to accept as applicable to this insect comparable work on related beetles in other areas. For example, research on the western pine beetle, in its relation to ponderosa pine, has been assumed by some to be similar to the relationship existing between the Black Hills beetle and its host. In some respects this has proved to be correct, but in other instances marked differences are evident. As an example, in their host relations both beetles show varying levels of both susceptibility and resistance to attack. However, the degree of susceptibility is not the same. Keen (1936, 1943) demonstrated a close relationship between age and crown vigor of the host, and the incidence of attack by the western pine beetle under endemic beetle populations. His work resulted in a tree classification which is used to evaluate the probability of beetle attack in ponderosa pine stands subject to the attack of the western pine

beetle, and this classification becomes the first factor in the analysis of the host relations of the Black Hills beetle.

Keen's Tree Classes

Keen's tree classification is based on tree age and crown vigor, and is applicable only to ponderosa pine. The age and crown vigor classes are as follows:

Age Classes

Class 1. - Young trees less than 75 years old. Bark dark and crown pointed.

Class 2. - Immature trees 75 to 150 years old. Bark reddish brown with narrow or incompletely formed plates. Crown pointed and branches in whorls.

Class 3. - Mature trees 150 to 300 years old. Bark light reddish brown with moderately large plates. Usually round topped. Incomplete whorls with nodes indistinct. Branches horizontal or drooping.

Class 4. - Overmature trees over 300 years old. Bark light yellow. Plates large and smooth. Crown flat. Branches drooping, gnarled, and crooked.

Crown Vigor Classes

A. Full crown 55 per cent of tree height. Average width or wider. Foliage dense, long, dark green.

B. Fair crown. Less than 55 per cent of tree height and less than average width. Foliage not sparse.

C. Fair to poor crowns. Brush top narrow and thin. Foliage short and thin.

D. Crown poor. Diameter subnormal. Foliage sparse and thin.

Figure 4 depicts diagramatically this system of classification. The tabulation in Table 1 indicates relative susceptibility of each subdivision of the system.

The statistical analysis of this comparison presented a problem. Although Keen's tree classes are fully described, the classes are nevertheless qualitative in character. A quantitative relationship between classes had to be found. On the suggestion of F. P. Keen, the demonstrated periodic diameter growth of trees of different classes, when growing under average site conditions was used as a measure of health. These values were worked out by Briegleb (1945) and are presented in Table 2.

The growth values in Table 2 for Keen's tree classes do not represent the actual growth of ponderosa pine on the study area, but are used merely to give numerical weights to each of Keen's age and vigor classes. Keen's tree classification is based on a combination of age and vigor. However, in this study in Colorado, the average age of both the infested and uninfested trees was the same, namely, Age Class 2. Since the age class is the same, any differences observed in this study must be the result of vigor. The Keen tree classes for ponderosa pine are grouped according to infestation probability for the western pine beetle. It appears, based on the statistical significance of the differences between infested and uninfested trees in Table 3, that the classification holds good, also, as a measure of the susceptibility of the host of the Black Hills beetle.

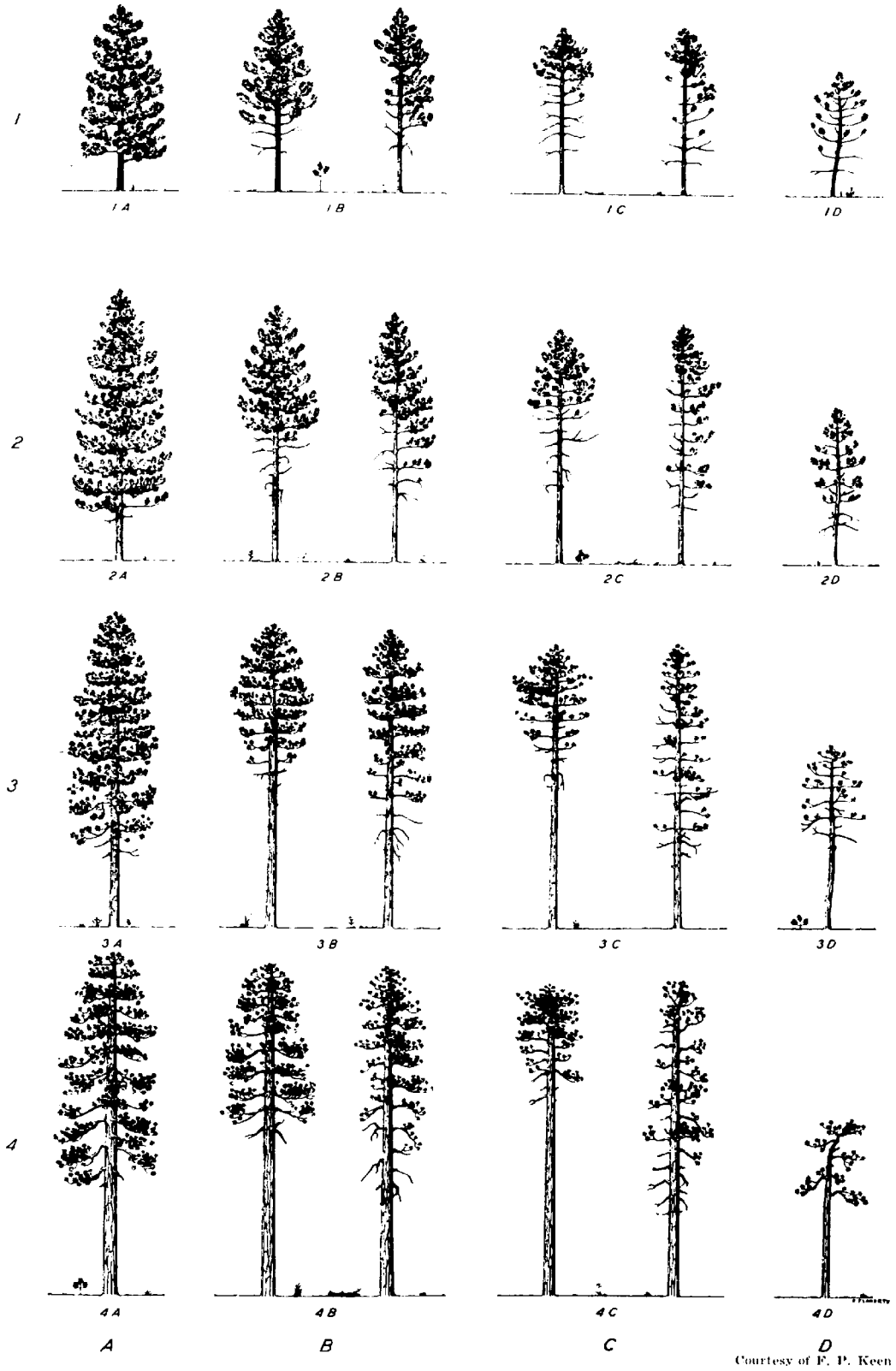


Fig. 4 -- A ponderosa pine tree classification chart for determining relative growth capacity based on age and vigor.

Table 1

Probability of Attack of Ponderosa Pine by Western Pine Beetle According to Keen's Tree Classes

Age Class	CROWN VIGOR CLASSES			
	A	B	C	D
1	Risk very low	Risk slight	Risk very high	Risk very high
2	Risk very low	Risk slight	Risk very high	Risk very high
3	Risk low	Risk medium	Risk medium	Risk highest
4	Risk high	Risk high	Risk high	Risk highest

Table 2

Normal 10-year Growth in Diameter at Breast Height Outside Bark; by Tree Class in Virgin Forest

Age Class	Vigor Class				Unweighted ave.
	A inches	B inches	C inches	D inches	inches
1	1.56	1.21	.92	.66	1.09
2	1.21	.97	.71	.49	.84
3	.90	.71	.50	.37	.62
4	.55	.46	.37	.27	.41
Unweighted average	1.06	.84	.62	.45	.74

(According to Briegleb, 1945)

Table 3

Influence of Keen's Tree Class on Susceptibility
(Values expressed in inches of decadal diameter growth)

Breigleb Class Weights			Stand.	Stand.	Deg.	Value	Value	Level
Ave. inf. trees	Ave. uninf trees	Diff.	dev. of diff.	error mean diff.	of free- dom	5% -t-	com- puted -t-	of sig.
EPIDEMIC PAIRED PLOTS								
0.81	0.90	0.09	0.14	0.03	21	2.08	2.90	99%
ENDEMIC PAIRED PLOTS								
0.73	0.82	0.09	0.12	0.03	19	2.09	3.35	99%
ENDEMIC PAIRED TREES								
0.76	0.84	0.08	0.21	0.02	115	1.98	3.98	99%

The analysis reveals that the infested trees under both endemic and epidemic conditions were of lower relative vigor than the uninfested trees. When the indices were reconverted to tree classes the infested trees from endemic areas fell in Keen's Tree Class 2C, whereas the uninfested trees were midway between classes 2C and 2B. Infested trees occurring in areas of epidemic beetle populations, appeared midway between classes 2C and 2B; the uninfested trees almost in the 2B class. The interpretation then, of this comparison is that of the ponderosa pines studied, those of lower relative vigor were more susceptible to Black Hills beetle attack under both endemic and epidemic conditions.

As a result of this study in Colorado it has been suggested that susceptibility of ponderosa pine to

Black Hills beetle attack is a function of tree vigor. However, the relationship is not as clear cut as in the case of the western pine beetle. The differences between susceptible and less susceptible trees, under both endemic and epidemic levels of infestation, are small and consequently not easily discernible in the field. This possibly accounts for Blackman's (1925) observation in which he indicates that the beetle shows no discrimination in selecting trees to attack. He based his conclusion on the general appearance of the increment growth in a small sample of two groups of five increment cores each. Craighead (1925) and Beal (1939) also conclude that under epidemic conditions the beetle attacks trees in all vigor groups and prefers if anything the more vigorous second growth pine. It is quite true that under epidemic conditions trees of relatively higher vigor are attacked, but there still exists a vigor differential between susceptible and less susceptible trees. This can be observed, as we have seen, when the trees are grouped according to Keen's Tree Classification. However, in Colorado the average age of both infested and uninfested trees under both levels of infestation proved to be in a common age class--Keen's class two; and thus the differences observed were limited to differences in crown vigor. Under endemic conditions, as mentioned previously, susceptible trees were in Keen's 2C class; whereas the less susceptible trees were midway between the 2C and 2B classes. Under epidemic conditions

the susceptible trees fell midway between the 2C and 2B classes, whereas the average of the less susceptible trees was almost in the 2P class. From this it can be seen that levels of susceptibility in ponderosa pine do exist; that susceptibility is related to tree vigor; and that degree of susceptibility of a tree at any specific time is a function of the level of the beetle population at that time.

When dealing with a single age class as was the case in this study, Keen's Tree Classification is reduced to a complex of crown characteristics which reflect tree vigor. The total of all factors making up the complex has a positive influence on the susceptibility of pine to beetle attack. However, in an effort to isolate, if possible, the individual components of the complex that influences pine susceptibility, each factor was considered separately.

Leader-Lateral Ratio

Crown condition is an integral part of the Keen classification, and thus may be expected to reflect the vigor of a tree. In order to analyze the crown complex several of its components were measured individually and tested statistically. A vigorous, rapidly growing ponderosa pine will have a pointed crown; a slow growing, less vigorous tree, a relatively round or flat-topped crown. The pointed crown of the more vigorous tree results from rapid growth of the crown's leader in comparison to that of the associated laterals. If the average length of the laterals is divided into that of the leader, a leader-lateral ratio results. The higher the ratio, the greater would be the

leader length in relation to its associated laterals, and more pointed the crown of the tree. The leader-lateral ratio was computed for each tree, and the averages and statistical analysis appear in Table 4.

Table 4

Analysis of Leader-Lateral Ratio
(Values in leader-lateral ratio units)

Ave. of inf. trees	Ave. of uninf. trees	Diff.	Stand. dev. of diff.	Stand. error mean diff.	Deg. of free-dom	Value 5% -t-	Value com-puted -t-	Level of sig.
EPIDEMIC PAIRED PLOTS								
1.49	1.45	0.04	0.25	0.06	17	2.11	0.74	60%
ENDEMIC PAIRED PLOTS								
1.37	1.37	0.00	0.15	0.04	12	2.18	0.13	50%
ENDEMIC PAIRED TREES								
1.46	1.52	0.06	0.75	0.07	102	1.98	0.85	60%

The results of the tests fail to indicate any significant relation between leader-lateral ratios and susceptibility. The ratio under endemic conditions was somewhat higher in the case of the uninfested trees, but under epidemic conditions the reverse was true. However, the statistical analysis leads to the conclusion that no difference exists between infested and uninfested trees, and that the leader-lateral ratio cannot be used as a measure of ponderosa pine's susceptibility to Black Hills beetle attack.

Twig Growth

Another characteristic of ponderosa pine included as a component in Keen's tree classes that indicates low vigor is the bunching of needles near the ends of branches. Slow twig growth combined with the pattern of needle growth results in this phenomenon. Thus, twig growth is a measure of tree vigor, and is considered as a possible measure of susceptibility in Table 5.

Table 5

Analysis of Twig Growth in Inches

Ave. of inf. trees	Ave. of uninf. trees	Diff.	Stand. dev. of diff.	Stand. error mean diff.	Deg. of free-dom	Value 5% -t-	Value com-puted -t-	Level of sig.
EPIDEMIC PAIRED PLOTS								
1.222	1.048	0.174	0.423	0.113	13	2.16	1.54	85%
ENDEMIC PAIRED PLOTS								
0.976	0.883	0.093	0.371	0.124	8	2.13	0.010	50%

Although the averages indicate that length of twig growth on infested trees in both levels of infestation is greater than on uninfested trees, statistical tests showed differences to be without significance.

Needle Length

Still another indication of tree vigor is the length of needles in the upper portion of the crown -- longer needles indicating greater vigor. Needles were clipped from branches in the upper one-third of the crown of the

tree, and average length of the needles from the four sides of the crown was determined. The results of these measurements and a summary of the statistical evaluation appear in Table 6.

Table 6

Analysis of Needle Length in Inches

Ave. needle length of inf. trees, inches	Ave. needle length of uninf. trees, inches	Diff.	Stand. dev. of diff.	Stand. error mean diff.	Deg. of freedom	Value 5% -t-	Value computed -t-	Level of sig.
EPIDEMIC PAIRED PLOTS								
4.19	4.25	0.06	0.56	0.14	16	2.12	0.412	50%
ENDEMIC PAIRED PLOTS								
4.15	4.15	0.00	0.43	0.12	12	2.18	0.022	50%
ENDEMIC PAIRED TREES								
4.10	4.30	0.20	0.70	0.10	72	1.99	3.26	99%

Differences between the endemic paired plot series were not statistically significant, the average needle length being very nearly the same on both infested and uninfested pines in that series. However, when paired trees were compared there proved to be a significant difference, as shown in Table 6. The difference in results of the two sampling procedures under endemic conditions can probably be explained. The paired trees were selected only from areas of very low endemic beetle populations, whereas the

paired plots, although they were in areas that would fall in the endemic class, were located where populations approached epidemic numbers on certain plots. As a result the paired trees were located where the beetles could exhibit their maximum selectivity, whereas in the paired plots the higher population level led to the attack of more vigorous trees, thus masking the effects of selectivity.

Also differences in the design of the experiments may have influenced the significance of the results since in the endemic paired plot series there were twelve degrees of freedom, whereas, in the paired tree series there were seventy-two. The greater number of entities compared in the paired tree series thus allowed a more accurate appraisal of the difference which existed between the infested and uninfested trees. Therefore, we may logically conclude that under endemic conditions trees of lower vigor, showing shorter needle length, are more susceptible to beetle attack than are those possessing longer needles. Under epidemic conditions, however, the infested trees appeared to have shorter needles but when tested statistically the difference was not significant. Therefore, length of leaf, taken alone, cannot safely be used as a measure of susceptibility after an outbreak has reached epidemic proportions.

Before continuing the discussion of the crown conditions it would be well to deviate a moment and explore this rather

interesting situation that was noticed concerning the design of experiment. When needle length of infested and uninfested trees was compared in the endemic paired plot series, no difference was demonstrated. However, when compared in the endemic paired tree series a highly significant difference was shown to exist. An explanation for this variation in results has already been presented.

However, the portion ascribed to the masking influence of the plot measurements warrants further elaboration. It is the opinion of the writer that when individual tree characteristics are to be analyzed or compared as they are in this study, the single tree as a sampling unit is preferable to the plot. In this type of data, variance among the mean differences of a series of plots is not reduced in the same proportion as it is when we are concerned primarily with areas and volumes standing on such areas. For example, the standard error of the mean difference in needle length for the endemic paired plot series was 0.12 inches, whereas that for the endemic paired tree series was 0.10 inches. This relationship was also noted in a number of other comparisons that were made in the study. In addition to the failure of the plots to reduce the variance among the plot means, the use of the plots reduced the number of degrees of freedom available in the design and consequently reduced the sensitivity of the design itself. Also, the tree differences with which the study was primarily concerned are masked by averaging plot measurements.

An explanation of this can be more clearly developed

if we leave the present study and set up a simple hypothetical proposition. Assume that a study is being made of the relation of tree diameter growth and precipitation in a northern hardwood forest. Within the stand concerned, some trees are growing on level ground, others in small depressions and still others on small knolls. In years of deficient rainfall the trees in small depressions will be favored by drainage of water from the surrounding area and will show relatively greater growth than trees growing on the knolls. The converse would be true in years of abundant precipitation. Trees growing in depressions would undoubtedly show a reduced growth rate when compared with those growing on the well drained knolls. If sample plots were employed to measure tree diameter growth, it is possible that within a single plot both growing conditions described could exist, and when growth was averaged the effect of precipitation on the individual would be masked. The resultant average for the area would not be the desired result, for it was the effect of precipitation on the growth of the tree rather than the stand that was sought. Thus it is suggested for further studies such as this, that paired trees rather than paired plots be used as the sampling units in the experimental design.

Crown Class

Because the position occupied by a tree crown in the forest canopy has a great influence on the growth capacity of the tree, it was speculated that perhaps trees growing

in a less desirable position would be more susceptible to beetle attack than those in a more favorable position. Therefore, the relative position of each tree was recorded in conventional crown classes as dominant, codominant, intermediate or suppressed. Crown classification is a qualitative grouping and to facilitate statistical analysis a quantitative expression was necessary. A straight arithmetic progression was first considered; dominant trees assigned the value four, codominants -- three, intermediates -- two, and suppressed trees -- one. This arrangement did not appear logical when considered in the light of the effect crown position has on tree growth and vigor. As a result the squares of these index values were selected as the quantitative expression of crown class. Crown classes of infested and uninfested pine were compared and a summary appears in Table 7.

Although susceptible trees in both levels of infestation appear to have poorer than average positions in the forest canopy, these apparent differences did not prove to be significant when analyzed statistically. Thus crown class alone cannot be relied upon to indicate ponderosa pine's susceptibility to beetle attack.

Thus we see that, in the analysis of Keen's crown-vigor complex as a whole, a strong relationship was shown between the health and susceptibility to beetle attack. When, however, the individual items comprising the complex were analyzed separately, only needle length was found to

be a statistically significant indicator of susceptibility. As a matter of fact, if the apparent trends of the data are considered, some items seem to contradict the conclusions drawn from analysis of Keen's tree classes. It must be remembered, however, that the tree classes include other unmeasured elements that convey to the observer the crown vigor of the tree. The density of the needle complement and branch structure are examples of these. Therefore, it must not be concluded that because the analysis of some of the factors that make up the complex do not result in significant differences between susceptible and less susceptible trees, that the tree classification is invalid as an indicator of tree vigor and the resulting degree of susceptibility of pines to beetle attack.

Table 7

Influence of Crown Class on Susceptibility
(Based on index values)

Ave. of inf. trees	Ave. of uninf. trees	Diff.	Stand. dev. of diff.	Stand. error of diff.	Deg. of freedom	Value 5% -t-	Value computed -t-	Level of sig.
EPIDEMIC PAIRED PLOTS								
10.95	11.11	0.16	2.86	0.61	21	2.08	0.27	50%
ENDEMIC PAIRED PLOTS								
10.68	11.34	0.66	2.77	0.65	17	2.11	1.01	70%
ENDEMIC PAIRED TREES								
13.27	13.28	0.01	3.60	0.34	113	1.98	0.03	50%

Keen's classification for ponderosa pine has been successfully used to measure the probability that trees of a certain age with certain crown characteristics will be attacked. Several other investigators, namely, Salman and Bongberg (1947) in California, Johnson (1949) in California, and the Inland Empire and Hornibrook (1939) in the Black Hills have approached the problem somewhat differently and rated trees according to current health. However, the underlying principle of Keen's classification has been proved to be statistically sound and stands today as the most widely accepted and used tree classification for ponderosa pine. Keen developed his classification for west coast ponderosa pine occurring on average or better than average sites. In comparison with the Black Hills beetle, the western pine beetle is less aggressive. This last fact is attested to be by both Hopkins and Craighead. Hopkins (1909) writes, "Dentroctonus ponderosae differs from other members of the genus by its decided preference for living timber, and therefore is a primary enemy of ponderosa pine." Craighead (1925), indicates that the Black Hills beetle is the most aggressive of all species of the genus. The pine sites on the study area, as will be demonstrated later, were very poor, the best site falling far below the average for west coast ponderosa pine. Nevertheless, Keen's classification held good as a basis for grouping trees according to their susceptibility. This is most remarkable. Apparently Keen's tree

classification provides a means of grouping trees through the complete series of pine site conditions, according to susceptibility to either a semi-aggressive or a very aggressive species of bark beetle.

Current Periodic Diameter Growth

Person (1928) in his writing on tree selection by the western pine beetle says, "Tree vigor is a more or less intangible character and difficult to indicate. However, the width of the annual ring is generally accepted as a good index of vigor. It is realized that width of the ring alone is not always a true index, but it is used because it is the character most easily determined and because it is considered to be the most reliable for the purpose. It is a definite character that can be readily compared in both insect-killed trees and living check trees." Following the same reasoning and for the same purpose, diameter increment was analyzed and utilized in this study.

Since rate of growth and vigor are closely correlated, an analysis was made of the relation existing between growth rate and susceptibility. For each tree, diameter growth for the current five year period was determined from two increment cores extracted from opposite sides of the tree at the height of 4½ feet above the ground. Averages were computed and tested statistically. The results appear in Table 8.

Table 8

Analysis of Current Five Year Diameter Growth
(Growth at breast height in inches)

Ave. of inf. trees	Ave. of uninf. trees	Diff.	Stand. dev. of diff.	Stand. error mean diff.	Deg. of free-dom	Value 5% -t-	Value com-puted -t-	Level of sig.
EPIDEMIC PAIRED PLOTS								
0.240	0.274	0.034	0.10	0.02	21	2.08	1.55	85%
ENDEMIC PAIRED PLOTS								
0.246	0.248	0.002	0.10	0.02	19	2.09	0.14	50%
ENDEMIC PAIRED TREES								
0.300	0.360	0.060	0.20	0.02	115	1.98	2.69	99%

Under both endemic and epidemic conditions the infested trees were growing more slowly than the uninfested ones. However, in the endemic paired plot series, when the differences were appraised statistically, they were found to lack significance. In other words, the differences could have been the result of sampling. In the paired tree series the differences were statistically significant. This variation in results is doubtless explained by differences in population level and the greater statistical strength of the paired tree data, as previously discussed in the section on needle length.

Thus, when periodic diameter growth was contrasted for infested and uninfested trees a significant difference was demonstrated under endemic conditions but not under

epidemic conditions. The trend, however, under epidemic conditions showed the susceptible tree to be growing slower, but the statistical probability of the difference (85 per cent) was not quite high enough to include the difference in the significant class. These findings, however, suggest that susceptible trees are slower growing under both levels of infestation, and the interpretation is that trees of relatively lower vigor are more susceptible to beetle attack.

Reduction of Diameter Growth

It was postulated that sudden slowdown in growth might be a possible cause of susceptibility to beetle attack. Beal (1943) believes that a decline in growth regardless of the cause may furnish favorable conditions for change from an endemic to an epidemic state. The results of the current analysis appear to bear out Beal's belief.

When current growth in diameter was compared with average growth over the life of the tree, current growth was the smaller almost without exception. Thus the problem became one of determining the amount of slowdown in diameter growth. From increment cores and other measurements, mean growth for the average five year period was computed for each tree. Outline of the procedure is found on page 97 of the Appendix. The difference between mean periodic diameter growth and current periodic growth was

determined for each tree, and these differences for infested and uninfested trees were compared. A summary of these average differences, and the result of the statistical analysis are presented in Table 9.

Table 9

Analysis of Difference Between Current and Mean Periodic Diameter Growth in Inches

Ave. diff. for inf. trees	Ave. diff. for uninf. trees	Diff.	Stand. dev. of diff.	Stand. error mean diff.	Deg. of free-dom	Value 5% -t-	Value com-puted -t-	Level of sig.
EPIDEMIC PAIRED PLOTS								
0.248	0.204	0.044	0.10	0.01	21	2.08	2.20	95%
ENDEMIC PAIRED PLOTS								
0.214	0.212	0.002	0.10	0.02	19	2.09	0.13	50%
ENDEMIC PAIRED TREES								
0.130	0.120	0.010	0.11	0.01	113	1.98	0.64	50%

In both endemic and epidemic areas the infested trees showed the greatest reduction in growth. However, when the differences were tested statistically, those under endemic conditions proved to have no significance, whereas the difference between infested and uninfested trees in epidemic areas was significant. This would indicate that in areas where endemic beetle population occurred in Colorado, a current slowing in diameter growth does not have a measurable effect on pine's susceptibility to beetle attack.

In epidemic areas, however, a greater reduction in current diameter growth does produce a measurable difference, and indicates a higher degree of susceptibility. These results indicate that in order to achieve the same degree of susceptibility, a tree growing in epidemic areas must be relatively more vigorous than one growing in an area where the beetle population is endemic. Thus the conclusion that under epidemic conditions the reduction in tree vigor associated with a current reduction in diameter growth caused trees to become susceptible to attack, whereas, under endemic conditions the vigor of a tree, as evidenced by current diameter increment, might be reduced without having an attack following such a reduction.

Age

Age is still another tree characteristic that has often been considered a factor influencing susceptibility of ponderosa pine to bark beetle attack, the older trees being the more susceptible. With this idea in mind, age for each tree examined was determined from increment cores taken at 4½ feet above the ground. The average ages and summary of statistical analysis are presented in Table 10.

Uninfested trees under endemic conditions appear on the average to be older, whereas under epidemic conditions the infested trees are older. Actually the differences in age are not great and when analyzed statistically neither difference is significant. This finding would indicate that age alone has no influence on susceptibility of pine

to beetle attack.

Table 10

Influence of Tree Age on Susceptibility
(Age in years measured at 4½ feet from ground)

Ave. of inf. trees	Ave. of uninf. trees	Diff.	Stand. dev. of diff.	Stand. error mean diff.	Deg. of free-dom	Value 5% -t-	Value com-puted -t-	Level of sig.
EPIDEMIC PAIRED PLOTS								
84.8	76.1	8.7	19.8	4.2	21	2.08	2.04	90%
ENDEMIC PAIRED PLOTS								
92.9	93.6	0.7	15.9	3.5	19	2.09	0.18	50%
ENDEMIC PAIRED TREES								
91.5	91.9	0.4	17.3	1.6	115	1.98	0.25	50%

Many of the bark beetles, the western pine beetles included, show preference for mature and over mature trees in times of endemic numbers. Keen's (1936) work brings out this relationship sharply. This study, however, within the range of ages dealt with did not find that the susceptibility of pine is associated with age of the tree. It was true that the averages of the stands involved in the study were the same for both infested and uninfested trees. However, there were present old veterans as well as very young groups of trees which appeared to be attacked with about the same intensity. The corollary of this then must be true -- trees of all ages are equally susceptible to beetle attack. This is felt to be true. Any tree that for some reason has low vigor becomes susceptible to beetle attack. Beal (1943)

hints at this when he writes, "It is the opinion of the writer that a decline in growth rate of pine, whether it is the result of drought, age, or stagnation of the stand through crowding or other causes, may furnish favorable conditions for the change from an endemic to an epidemic state." Thus, as age influences tree vigor it may be a factor of pine's susceptibility to beetle attack; independently it is not.

Tree Diameter, Height and Bark Thickness

Person (1928) in his work with the western pine beetle found that ponderosa pine in certain diameter classes were more subject to attack than others. In order to determine whether this held true for the Black Hills beetle in Colorado, records were made of current diameter measurements of all trees. In addition total height and bark thickness were measured and the averages together with the statistical analysis of each are shown in Table 11.

The results of these analyses indicate that tree diameter as well as tree height and bark thickness has no influence on susceptibility of pine to beetle attack. However, there appeared to be a minimum diameter below which trees were not attacked by the beetle. In the study

Table 11

Analysis of Tree Diameter, Height, and Bark Thickness

Ave. of inf. trees	Ave. of uninf. trees	Diff.	Stand. dev. of diff.	Stand. error mean diff.	Deg. of free-dom	Value 5% -t-	Value com-puted -t-	Level of sig.
DIAMETER B.H. IN INCHES								
EPIDEMIC PAIRED PLOTS								
10.01	9.27	0.74	1.70	0.37	21	2.08	1.89	90%
ENDEMIC PAIRED PLOTS								
9.52	9.51	0.01	1.70	0.38	19	2.09	0.01	50%
ENDEMIC PAIRED TREES								
11.0	11.3	0.3	2.5	0.2	113	1.98	1.33	80%
TOTAL HEIGHT IN FEET								
EPIDEMIC PAIRED PLOTS								
33.9	32.2	1.7	6.9	1.5	21	2.08	1.17	90%
ENDEMIC PAIRED PLOTS								
35.9	35.0	0.9	5.2	1.2	19	2.09	0.75	50%
ENDEMIC PAIRED TREES								
37.0	37.8	0.8	6.6	0.6	114	1.98	1.38	80%
BARK THICKNESS IN INCHES								
EPIDEMIC PAIRED PLOTS								
0.70	0.70	0.00	0.14	0.03	21	2.08	0.12	50%
ENDEMIC PAIRED PLOTS								
0.65	0.63	0.02	0.11	0.03	19	2.09	0.67	50%
ENDEMIC PAIRED TREES								
0.78	0.76	0.02	0.22	0.02	114	1.98	1.03	70%

area this minimum diameter was in the neighborhood of three inches. However, this minimum diameter seemed to vary with the level of infestation. Under high population levels smaller trees were attacked than under lower levels. Except for this, diameter appeared to have no influence on susceptibility of pine to beetle attack.

Tree Injury

When beetles attack a pine other beetles are attracted to that tree. It is not known what the attractive agency is, but some investigators believe it is the odor of resin exuding from the entrance tunnels. If it is a resinous odor, trees that have been recently barked by porcupine should be more susceptible than unbarked trees. In order to determine the validity of this hypothesis, records were kept of the incidence of recent barking by porcupines. An analysis of these records is found in Table 12.

Table 12

Influence of Barking by Porcupine upon Susceptibility (Based on number of trees observed)

Total barked trees inf.	Total barked trees uninf.	Diff.	Value 5% chi square	Value computed chi square	Level of sig.
EPIDEMIC PAIRED PLOTS					
9	26	17	3.84	1.60	78%
ENDEMIC PAIRED PLOTS					
53	44	9	3.84	1.34	70%
ENDEMIC PAIRED TREES					
22	11	11	3.84	3.83	95%

Under epidemic conditions barking was more common on uninfested trees than on those infested by bark beetles. However, the chi square test failed to indicate any significant relationship. In the endemic plot series the trend was reversed, but still no significant relationship could be demonstrated. However, when the paired trees from areas of low levels of infestation were considered, barking and infestation were strongly related. Therefore, one is led to the conclusion that barked trees are more susceptible to attack than those that have not been barked. Once again a variation in results is almost certainly the result of differences in the beetle populations. At very low population levels the recently exposed resin surfaces attract the beetles to attack the injured trees, but as the beetle population increases, the influence of the freshly barked trees is offset by the presence of resin exudation on trees currently being attacked by beetles. Thus the influence of barked trees is cancelled.

As indicated above, the data collected in this study indicate that under epidemic conditions injury to the bark had no discernible influence on susceptibility. This is in harmony with Blackman's (1925) findings when he hack-girdled pine and concluded that those trees offered no more attraction to the beetle than untreated trees. The present study conflicts with Blackman's findings in areas of endemic beetle populations where a very strong relationship was evident between barking by porcupines and incidence

of infestation. It is believed that the failure of this relationship to be apparent also in epidemic conditions can be explained, as above, by the fact that in epidemic areas there is a pronounced increase in the number of trees undergoing attack, and these trees serve to draw the beetles even more strongly than the barked trees. Thus the influence of the barked trees is masked. However, it appears that any injury to the bark that results in exudation of resin must be very recent to have an influence on susceptibility. To exert the greatest influence upon susceptibility the injury should occur during or immediately prior to the beetle flight. Otherwise the attractive substance in the resin may be lost before the beetles are ready to attack. Beal (1939) stated that pine odor was an attractor to the beetle. This present study gives limited confirmation of his findings.

In 1905 Hopkins stated that, "Trees struck by lightning are usually attacked by beetles and such trees serve to perpetuate the species at times when it does not occur in sufficient numbers to kill trees on its own accord." This statement was based upon an examination of a ponderosa pine stand attacked by Black Hills beetles, located about one hundred miles south of the study area. This belief is also held by many workers in the field. To test its validity, records were kept of all lightning struck trees and whether or not each was infested. The results of their analysis are found in Table 13.

Table 13

Influence of Lightning Damage upon Susceptibility
(Based on total number of trees)

Total inf. trees struck	Total uninf. trees struck	Diff.	Value 5% chi square	Value computed chi square	Level of sig.
		EPIDEMIC PAIRED PLOTS			
0	1	1	3.84	0.56	60%
		ENDEMIC PAIRED PLOTS			
7	1	6	3.84	2.40	85%
		ENDEMIC PAIRED TREES			
4	3	1	3.83	0.15	50%

The trend of the data seems to support Hopkins' idea, but the statistical analysis failed to show a significant relation. However, it is felt that the number of trees encountered in the study was too small to permit arriving at safe conclusions.

Site Quality

In addition to the individual tree characteristics thus far discussed, stand and site conditions certainly influence tree growth and vigor. Therefore, it seemed likely that site quality might influence susceptibility. A measure of site quality employing the heights of the average dominant trees at a selected age was first considered. Meyer (1934) developed site index curves for ponderosa pine that have been used throughout the ponderosa

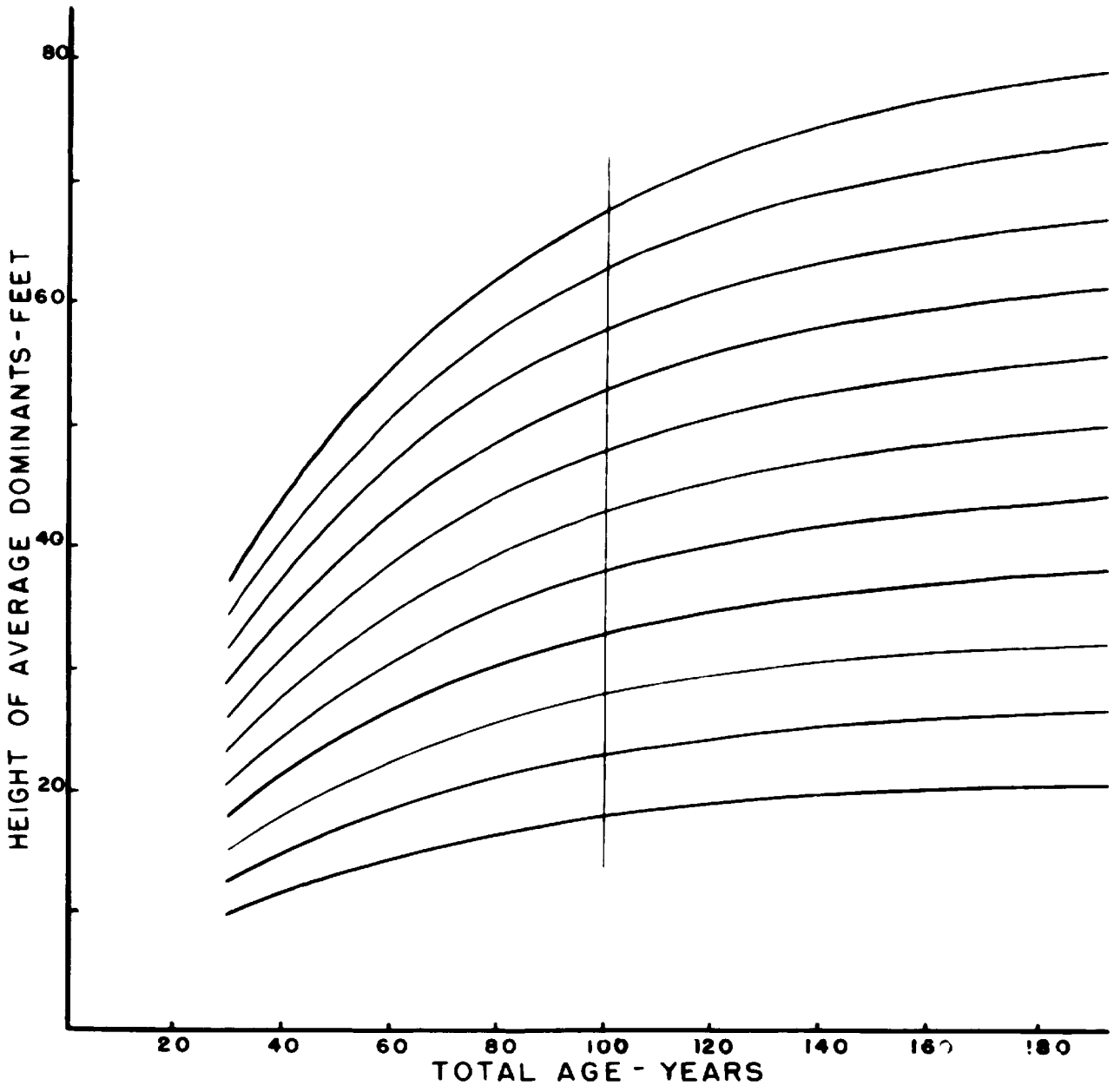


Fig. 5. -- Site index chart for Front Range ponderosa pine in Northern Colorado.

pine region as a measure of the productivity of the site. When an effort was made to fit Meyer's site index curves to ponderosa pine growing in the study area the curves did not fit. Much of the area was occupied by pine that fell below the lowest of Meyer's site class. Consequently it was necessary to construct a set of site index curves to fit the range of site qualities where the study was made. These curves are shown in Figure 5. Procedure for developing the site index curves is explained on page 96 of the Appendix. The results are summarized in Table 14.

Under endemic conditions the infested trees were, on the average, somewhat shorter than those uninfested, whereas under epidemic conditions the reverse appeared to hold true. But again, when the differences were analyzed statistically they proved to have no significance. Therefore it must be concluded that site index cannot be used alone as a measure of susceptibility to beetle attack.

Table 14

Influence of Site Index upon Susceptibility
(Based on height of average dominant trees in feet at age 100 years)

Ave. of inf. trees	Ave. of uninf. trees	Diff.	Stand. dev. of diff.	Stand. error mean diff.	Deg. of free-dom	Value 5% -t-	Value com-puted -t-	Level of sig.
EPIDEMIC PAIRED PLOTS								
38.5	36.0	2.5	10.38	2.21	21	2.08	1.13	70%
ENDEMIC PAIRED PLOTS								
40.8	41.3	0.5	7.32	1.64	19	2.09	0.30	50%

In order to further evaluate the effects of site conditions, particularly differences in moisture, the vegetative cover of infested and uninfested plots was contrasted. The amount of vegetative cover present on the plots was first compared. Wherever moisture is a limiting factor, the extent to which the ground is occupied by vegetation is a good indication of the available moisture in the upper soil. The "percentage of area covered by vegetation" represents the total proportion of the ground covered by vegetation including tree overstory, shrub understory and herbaceous ground cover. The parts of the plot not covered by vegetation included rock outcrops, open gravelly areas, and areas covered by forest litter. In the field the percentage of area covered by vegetation was estimated and recorded to the nearest ten per cent on each one-twentieth acre plot. The results are summarized in Table 15.

Table 15

Influence of Percentage of Area Covered by Vegetation

Ave. cf inf. trees	Ave. of uninf. trees	Diff.	Stand. dev. of diff.	Stand. error mean diff.	Deg. of free-dom	Value 5% -t-	Value com-puted -t-	Level of sig.
EPIDEMIC PAIRED PLOTS								
43.2	46.8	3.6	26.8	5.7	21	2.08	0.64	50%
ENDEMIC PAIRED PLOTS								
46.0	41.5	4.5	17.3	3.9	19	2.09	1.16	70%

The percentage of area occupied by vegetation proved to be the same on infested and uninfested plots under both endemic and epidemic conditions, suggesting that moisture conditions as indicated by vegetative cover are the same.

Another possible means by which soil moisture may be determined involves the use of indicator plants. When the problem was first considered the plan had been to use herbaceous plants as indicators of site condition. However, it was found that current fluctuations in weather conditions and disturbance by cattle influenced the herbaceous plant composition. Therefore, only shrub species seemed to be suitable indicators of site, because their presence on a site is more permanent and they are less disturbed by cattle. The shrubs have been divided into three groups based on their moisture requirements, as follows:

Dry site species

Mountain Mahogany (Cercocarpus montanus)

Bitter brush (Purshia tridentata)

Medium site species

Squaw current (Ribes cereum)

Wild rose (Rosa spp.)

Wild plum (Prunus virginiana var. melanocarpa)

Bearberry (Arctostaphlos uva - ursi)

Low Juniper (Juniperus communis)

Nine bark (Physocarpus monogynus)

Wild red raspberry (Rubus strigosus)

Snow berry (Symphoricarpos albus)

Moist site species

Aspen (Populus tremuloides)

Willow (Salix spp.)

Honeysuckle (Lonicera involucrata)

Mountain mahogany and bitter brush occupy the dry gravelly slopes. Bitter brush and mountain mahogany appear to occupy a slightly different ecological nitch; the mountain mahogany being found more abundantly in the upper levels of the ponderosa pine type, and the bitter brush in the lower parts. In the middle elevations both are present, and are found growing together.

The indicators of medium site are those plants which disappear from the association under both the driest and most moist conditions. All are found throughout the ponderosa pine zone. Two species, barberry and low juniper, are associated with the pine overstory and are not usually found in the open. Other species in the medium site group can and do occur both in the open and under pine stands.

The indicators of moist conditions are aspen, willow, and honeysuckle. These occur only along streams or in moist bottoms of canyons or draws. They are present throughout the range of the pine.

The soil requirements of the shrubs closely parallel their moisture requirements, dry site species being associated with shallow rocky soil; whereas, the moist site plants require deeper, more mature soil.

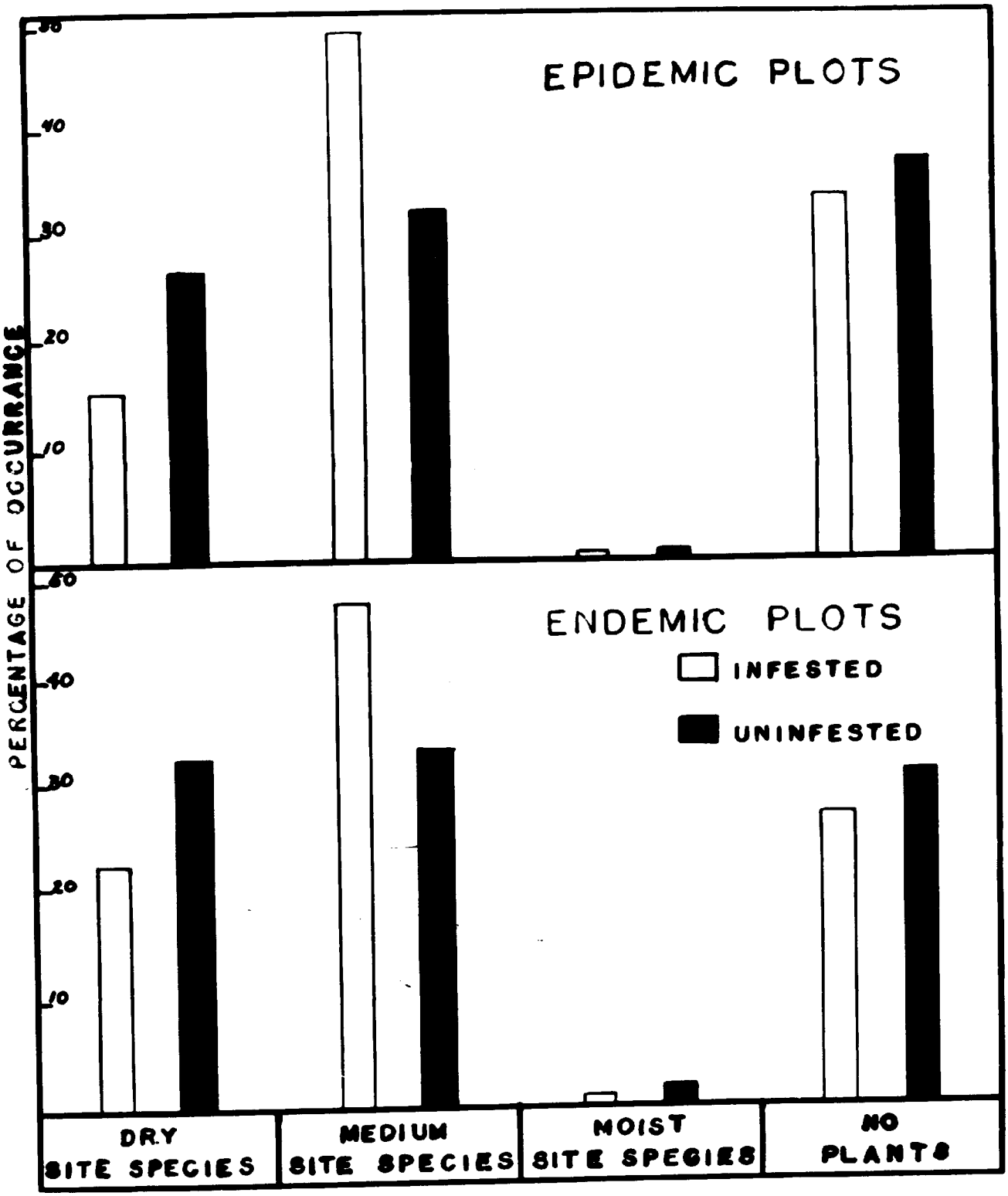


Fig. 6 -- Summary of site indicator species by classes.

To test whether these plants occurred in different proportions on the infested and uninfested plots an analysis of their occurrence was made. During the field work the "per cent of occurrence" of each species on five milacre sub-plots was recorded. The percentage is based on total occurrence of all shrub species on each of the plots. For example, if only one species occurred on a plot it would constitute a one-hundred per cent occurrence, even though it might occupy only fifty per cent of the area of the plot. Some plots contained no shrub species and were tallied as "no occurrence." A complete summary of "per cent of occurrence" of all species on infested and uninfested plots under both endemic and epidemic conditions is included on page 98 of the Appendix. A summary by classes of dry, medium, and moist site indicator species, is found in Figure 6. This figure shows a composite or average occurrence of the shrub species on infested and uninfested plots under both endemic and epidemic conditions. The data represents the distribution on an average plot under the various situations. The similarity of occurrence of the various plants in endemic and epidemic areas is immediately evident. From this it is concluded that the moisture relations as measured by the site indicator plants, on the plots, are approximately the same under both endemic and epidemic conditions.

The second point brought out by the graph is that under both endemic and epidemic conditions the infested plots

have a higher percentage of medium site shrubs, and a smaller percentage of dry site species. From this it would appear that uninfested plots occur more frequently on somewhat drier sites. However, since the data do not lend themselves to statistical analysis it is uncertain whether this is a true difference.

Still another stand characteristic, that of crown closure, or coverage was tested. In order to do this the amount of shade, a function of crown coverage, was measured on infested and uninfested plots. These measurements also served another purpose -- they indicated whether differential shade condition influenced the distribution of site indicator plants. Surface soil moisture is greater under closed forest canopy than in the open, and thus, by altering or influencing the habitat might affect the shrub species present. Table 16 presents a summary of the results.

Table 16

Average Shade Conditions
(Per cent of crown cover or shade)

	Infested Plots	Uninfested Plots
Endemic	13.2	14.8
Epidemic	14.0	14.7

These values indicate the average percentage of shade that occurred on the plots. Since shade was recorded only to the nearest ten per cent, the differences were undoubtedly sampling differences. It is concluded, therefore,

that no difference exists between the shade on infested and uninfested plots under either level of infestation, and that the different shade conditions had little influence on the occurrence of site indicator shrub species.

Aspect or exposure of the land was considered for its possible influence on infestation. Although exact information was not available concerning the distribution of ponderosa pine on the different exposures, nevertheless based on the pattern of topography and the sites usually occupied by ponderosa pine an estimate can be made of its expected distribution. If the distribution of infested plots coincides with the expected distribution of pine it may be concluded that aspect does not influence infestation.

Pine is most abundant on the north and east exposures in the study area. The south and west slopes are usually too dry for germination and successful establishment of young pine. Therefore, although pines may become established on these slopes, they are never in the proportions found on north and east exposures. The ridges generally run east and west, resulting in proportionally greater area exposed to the north and south. Combining these two factors it is expected that the most extensive stands of pine would occur on the north slopes with east and south slopes following in that order. The distribution of infested plots followed this same pattern. Over three-fourths of the plots, 77.4 per cent, occurred on north, east and northeast exposures. About eleven per cent of the infested plots occurred on

south exposures. The remaining twelve per cent were found on other exposures. The occurrence of infested plots coincides with the distribution of pine, and it is concluded that aspect has no influence on incidence of infestation. If there were differential preference by the beetle for sites of a particular aspect, it undoubtedly would have been evident, because of the procedure employed in selecting plots. The infested plot was placed in a previously infested group of trees, and therefore any preference for a specific exposure had full opportunity to function.

In addition to slope direction there seemed to be a possibility that steepness might exercise an influence on susceptibility. Therefore records were made of per cent of slope of each plot. The slopes of the infested plots ranged from 2 per cent to 40 per cent, and averaged 16.5 per cent; the uninfested plots ranged from 0 per cent to 40 per cent and averaged 15.4 per cent. This difference is so small in view of the variation that no significance can be attached to it.

Similarly, elevation seemed to have little, if any, bearing on beetle infestation, since infestation was observed throughout the altitudinal range of the pine. However, no epidemic beetle populations were noted at either the upper or lower altitudinal limits. This was undoubtedly due to the scattered nature of the stand as it approached the distributional limits. Occasionally, of course, at both extremes some individual trees were

attacked, but always singly.

In summary it can be said that the measurable elements of site conditions did not appear to influence pine's susceptibility to Black Hills beetle attack on the Front Range. The soil of the study area all originated from the same parent material, and with the exception of small areas in valley bottoms all can be classed as Lithosol. The soil moisture conditions, as determined by an analysis of vegetation, appeared to be the same for both infested and uninfested areas. The aspect, slope, and elevation afford no measurable difference, and the site index, a measure of the tree's response to the total site complex, appeared to be the same in both infested and uninfested areas. In this connection, however, comment is in order on the ponderosa pine site conditions existing on the study area. The average site index for the whole area is about 40 feet at 100 years, the range being from 20 to 65 feet. To gain an appreciation of how very poor this land is for growing ponderosa pine it may be compared with Meyer's (1934) site index values for west coast ponderosa pine. He recognizes six index classes, using 100 years as the base age. His site index numbers and height of dominant trees at base age are as follows:

Site Number	Height in feet at 100 years
I	127
II	112
III	96
IV	80
V	65
VI	51

Obviously pine site index values for the study area were at best barely equal to his site VI, whereas many sites fell far below his minimum. These comparisons lead to a better appreciation of the extremely adverse growing conditions on the Front Range in Colorado. This adversity of site for ponderosa pine should be kept in mind when considering the results of this study, and in applying them to other areas caution must be used.

Stand Density

When soil moisture is a limiting factor for tree growth, as is true in the ponderosa pine type in Colorado, density of stocking is known to have an important influence on the tree growth. It was speculated that perhaps ponderosa pine stands with greater number of stems per acre might be more susceptible to beetle attack than stands with fewer stems. The results of this comparison are summarized in Table 17.

Table 17

Influence of Stocking upon Susceptibility
(Trees on 1/20 acre two inches
diameter breast high and above)

Ave. stems per inf. plot	Ave. stems per uninf. plot	Diff.	Stand. dev. of diff.	Stand error mean diff.	Deg. of free-dom	Value 5% -t-	Value com-puted -t-	Level of sig.
EPIDEMIC PAIRED PLOTS								
13.8	11.4	2.4	10.3	2.2	21	2.08	1.07	70%
ENDEMIC PAIRED PLOTS								
12.6	12.0	0.6	3.8	0.8	19	2.09	0.71	50%

Although the infested plots under both levels of infestation had a slightly greater number of stems two inches and over, the differences lacked statistical significance, and it appears that number of stems per acre does not influence ponderosa pine's susceptibility to beetle attack.

In some respects basal area provides a better measure of stocking than does the number of trees per acre; therefore, to further evaluate the possible influence of stocking, basal area for all trees four inches in diameter and over was computed, and differences between infested and uninfested plots compared. The results are presented in Table 18. No significant difference appeared as a result of this comparison on the endemic plots. However, on infested plots occurring in areas of epidemic beetle

populations the basal area was greater than that of the uninfested plots. This difference is highly significant. It would appear from this that basal area per unit of area is a more sensitive measure of the influence of site upon susceptibility than is the number of stems. Site utilization, therefore, influences susceptibility under epidemic conditions. The greater utilization of the productive capacity of the site by a dense stand influences adversely the vigor of the trees, and thus increases their susceptibility to beetle attack. When the insect population is low the influence of stocking is relatively less important than under epidemic conditions because the degree of vigor necessary to maintain low susceptibility is relatively lower. However, as the intensity of beetle attack is increased with increasing population the trees must have a relatively higher vigor in order to remain

Table 18

Influence of Basal Area on Susceptibility
(Basal area in square feet for all trees 4 inches in diameter and over on 1/20 acre plot)

Ave. of inf. trees	Ave. of uninf. trees	Diff.	Stand. dev. of diff.	Stand error mean diff.	Deg. of free-dom	Value 5% -t-	Value com-puted -t-	Level of sig.
EPIDEMIC PAIRED PLOTS								
4.980	3.997	0.983	1.363	0.295	21	2.08	3.33	99%
ENDEMIC PAIRED PLOTS								
4.428	4.887	0.459	1.530	0.342	19	2.09	1.34	80%

unattractive to the beetles. Thus, under epidemic conditions the reduction of tree vigor associated with complete utilization of the site causes more trees under these conditions to become susceptible to attack, whereas, under endemic conditions the influence of stocking does not reduce vigor to a point where trees generally become susceptible.

Previously it has been demonstrated that a tree in order to be less susceptible under epidemic conditions must be of higher relative vigor than under endemic conditions. This evidence referred to above sheds further light on this relationship. Under epidemic conditions the more densely stocked groups are attacked, because of their reduced vigor, whereas under endemic conditions the reduction of tree vigor due to greater density of stocking exerts relatively less influence.

Movement of the Beetle

Bark beetles have been known to travel great distances, crossing canyons or lakes to attack new groups of trees. On the other hand, groups of beetle killed pines have been found that contained trees killed over a three year period -- the group of killed trees becoming larger each year. In order to determine how far and in what direction the Black Hills beetles usually move, measurements were made from infested trees to the nearest possible source of infestation. A special attempt was made to study the attack pattern characteristic of the Black Hills beetle

by locating the position of trees infested during the previous season in reference to current attacks. The distance was measured from currently infested trees to the nearest infestation of the season before. This was done by locating the nearest tree or trees that had contained beetle broods during the spring prior to attack of the currently infested trees. For example, trees were located that had contained broods of beetles in the spring of 1952 which could have attacked ponderosa pine in the summer of the same year. Measurements were made to the nearest chain. The results of these measurements are presented in Table 19.

Table 19

Distance in Chains to Possible Sources of Infestation

	Endemic		Epidemic	
	No. Plots	%	No. Plots	%
Brood trees on plot	5	25.0	11	50.0
Brood trees 1 chain from plot	4	20.0	3	13.7
Brood trees 2 chains from plot	1	5.0	2	9.1
Brood trees 3 chains from plot	1	5.0	1	4.5
Brood trees 4 chains from plot	0	0.0	1	4.5
Brood trees 5 chains from plot	3	15.0	2	9.1
Brood trees more than 5 chains from plots	6	30.0	2	9.1

More than two thirds of the trees attacked in endemic areas were within five chains of a source of beetles, whereas under epidemic conditions 91 per cent were within



Fig. 7. -- Group of ponderosa pine killed by beetles over a three year period.

five chains of an infestation source. It would appear from this that the chance of attack by the Black Hills beetle is greatly increased by the proximity of brood trees, the probability of attack being almost inversely proportional to the distance from a beetle source.

The direction from the source of infestation also seemed to influence the pattern of beetle distribution. The direction to old infestations which could have been a beetle source was determined for 81 per cent of the plots, whereas on 19 per cent the source of infestation could not be determined. In 96.9 per cent of these plots the nearest possible source of beetles was toward the south, west or southwest. In 3.1 per cent, the advance appeared to be from the southeast. The directional relationship seems to be strongly correlated with the direction of the prevailing summer winds, which are from the southwest and west. Although the local air currents flow perpendicular to the slope, upward during the day and downward at night, these currents are usually masked by the stronger prevailing wind, and except for local spots would not influence flight direction of the beetle. It may be concluded, therefore, that the flight of the beetles, which occurs during midsummer, is undoubtedly influenced in its direction by the prevailing summer winds. These conclusions from examination of infestations are substantiated by direct observations made of the actual flights of the Black Hills beetle during the summers of 1952 and 1953. Beetles were

first observed on July 25, 1952. At that time they were in a group of trees, and their flight seemed to be erratic, moving from one tree to another seemingly without purpose. However, later that same day a group of beetles was observed flying along the edge of a stand of pine and they were moving with the wind which was from the southwest. Groups of beetles were seen in flight five different times during the next two weeks and on each occasion they were moving with the prevailing wind. During the summer of 1953 beetles were observed in flight on only two occasions, and at these times the beetles were also moving with the wind.

INFLUENCES OF ENVIRONMENTAL FACTORS AFFECTING RESISTANCE TO ATTACK

From the discussion of susceptibility of ponderosa pine on the Front Range to attack by the Black Hills beetle we see that vigor plays an important role. Let us now consider the factors that influence the ability of a tree to throw off an actual attack, thus giving positive evidence of their resistance.

Throughout the pine forests, trees are encountered that have been attacked by the beetles and have survived. Upon examination it is discovered that the intensity of attack varies greatly; some trees sustain only a few attacks, others a great many. Superficially, it would appear that all these trees were able to resist the beetle successfully. It is possible, however, that some of the lightly attacked individuals would have been killed if subjected to heavier injury. Therefore, the procedure of selecting resistant trees in the field, and establishing the validity of their resistance was the first problem. Obviously, the only concrete evidence of a tree's resistance is the actual "pitching out" of an attack. Therefore, only trees that had undergone severe beetle attack and had successfully overcome it were selected as being resistant individuals. As a result the selected resistant trees were those that possessed this quality to a high degree. Although there are many trees in the pine forest that sustain light beetle attacks and live, and thus exhibit



Fig. 8. -- A resistant ponderosa pine that has been severely attacked by Black Hills beetle.

some degree of resistance, it was uncertain whether or not these lightly injured trees had survived because of their inherent resistance or because they had not experienced a full scale attack. Therefore, they were not included on the grounds that their resistance was not fully established. The observational design was based on paired trees, the resistant individual being selected and its mate, which had been killed, chosen randomly as previously described (p. 15). An attempt was made to select pairs which had sustained attacks of comparable severity. One-hundred pairs of trees were included in this phase of the study.

To determine quantitatively whether the trees were comparable, two evaluations were made. The number of pitch tubes and entrance holes on the lower ten feet of the bole of the tree was counted. Also, the number of beetle attacks per square foot was determined, from counts of entrance holes on the inside surface of two one-half foot square sections of bark that had been removed from the tree at breast height. Results of the two tests appear in Table 20, and show that, on the average, the resistant trees were selected more conservatively than necessary.

The average number of attacks per square foot of bark surface was more than fifty per cent heavier on the resistant trees. Similarly a far greater number of attacks had occurred on the lower ten feet of the bole of the resistant trees than on their non-resistant mates. It must therefore be accepted that the uninfested trees included in this phase of the study were those which were not only truly

resistant to Black Hills beetle attack, but resistant to a very high degree.

Table 20

Comparison of Attack Severity on Resistant and Non-Resistant Pairs

Ave. non-resist. trees	Ave. resist. trees	Diff.	Stand. dev. of diff.	Stand. error mean diff.	Deg. of free-dom	Value 5% -t-	Value com-puted -t-	Level of sig.
NUMBER OF BEETLE ATTACKS ON LOWER 10 FEET OF BOLE								
71.2	97.8	26.6	31.7	3.2	99	1.98	8.40	99%
NUMBER OF BEETLE ATTACKS PER SQUARE FOOT OF BARK								
3.76	7.27	3.51	3.58	0.41	75	1.99	8.56	99%

To evaluate the differences existing between resistant and non-resistant trees, thirteen comparisons of tree characteristics were made. Ten showed significant differences, whereas three did not.

Those comparisons which produced significant differences between resistant and non-resistant trees lead to the conclusion that the resistant trees were far above the average vigor of the stands in which they occurred. They were a full crown vigor class higher than the non-resistant trees when evaluated according to Keen's tree classification. They were on the average older, larger in diameter, and taller; they had more pointed crowns, had longer average needle length and occupied a more favorable position in the forest canopy. Furthermore, they exhibited greater current

diameter growth and had a greater number of resin ducts in their outer ten growth rings than the non-resistant trees. Injury by lightning and porcupine did not appear to influence pine's resistance, nor did a current slow-down in diameter growth.

Keen's Classes

The relation of Keen's tree classes to resistance was analyzed first. When resistant and non-resistant trees were compared it was found that the difference between them was significant and that the resistant trees fell into Keen's high vigor classes. The same method used previously to convert Keen's classes to numerical weights that could be statistically evaluated was used. The results of the evaluation are summarized in Table 21.

Table 21

Comparison of Keen's Tree Classes As Related to Resistance

(Values expressed in Inches of Decadal Diameter Growth)

Briegleb class weights			Stand. dev. of diff.	Stand. error mean diff.	Deg. of free-dom	Value 5% -t-	Value com-puted -t-	Level of sig.
Ave. inf. trees	Ave. uninf. trees	Diff.						
0.78	0.96	0.18	0.19	0.02	99	1.98	9.91	99%

The justification for this conversion, as previously shown, is that the average of both resistant and non-resistant trees fell into the same age group, namely, Keen's group two, and therefore the test becomes essentially

a measure of tree vigor, permitting the use of Briegleb's growth indices. When growth indices are reconverted to tree classes, the non-resistant trees fall slightly above the 2C class, while the resistant trees are just below, 2B. This difference in class value between resistant and non-resistant trees is larger than that of the susceptible and less susceptible trees in the earlier analysis. This indicates that resistant ponderosa pine must be of relatively higher vigor than is the case with trees that show a low susceptibility to beetle attack. It would then be logical to expect that individual measures of tree vigor would indicate that resistant trees are more vigorous.

Current Periodic Diameter Growth

As mentioned above, this hypothesis proved to be correct in a great majority of instances. For example, when current five year growth in diameter for resistant and non-resistant trees was compared, growth of the resistant trees proved to be greater, as shown in Table 22.

Table 22

Influence of Current Periodic Diameter Growth upon Resistance
(Diameter growth in inches breast high during five years prior to attack)

Ave. non-resist. trees	Ave. resist. trees	Diff.	Stand. dev. of diff.	Stand. error mean diff.	Deg. of free-dom	Value 5% -t-	Value com-puted -t-	Level of sig.
0.26	0.32	0.06	0.16	0.02	99	1.98	3.00	99%

The difference in growth between resistant and non-resistant trees although relatively slight in terms of actual increment is nevertheless highly significant, statistically, and clearly shows that the relative current diameter increment is an indicator of resistance.

Leader-Lateral Ratio

Also, crown condition proved to be a reliable outward manifestation of tree health and vigor. Prominent among the factors that make up the crown complex is its general shape, resulting from the ratio of leader to lateral growth. When the leader-lateral ratios were contrasted it was found that the average ratio of the resistant trees was significantly greater than that of their non-resistant mates, as is indicated in Table 23.

Table 23

Analysis of Leader-Lateral Ratio
(Ratios are the result of dividing length of current leader growth by average length of associated laterals)

Ave. non-resist. trees	Ave. resist. trees	Diff.	Stand. dev. of diff.	Stand. error mean diff.	Deg. of free-dom	Value 5% -t-	Value com-puted -t-	Level of sig.
1.4	1.7	0.3	0.84	0.08	99	1.98	2.86	99%

Thus greater ratio for resistant trees would impart to them a more pointed crown and would explain, to some degree, the placing of resistant trees in a higher position according to Keen's tree classification.

Relation of Needle Length to Resistance

Needle length, another indicator of tree vigor, also proved to be a significant indicator of resistance, as it was of susceptibility. The resistant individuals possessed on the average significantly longer needles than their non-resistant mates, as shown in Table 24.

Table 24

Influence of Needle Length upon Resistance
(Needle length in inches)

Ave. non-resist. trees	Ave. resist. trees	Diff.	Stand. dev. of diff.	Stand. error mean diff.	Deg. of free-dom	Value 5% -t-	Value com-puted -t-	Level of sig.
3.73	4.28	0.55	0.68	0.07	99	1.98	8.10	99%

From this it seems clear that greater needle length provides good evidence of high vigor, and therefore may be used as an indication of relative resistance.

Crown Class

Still another characteristic related to vigor is the position of the crown in the forest canopy as expressed in terms of crown dominance or suppression. This obviously influences the growing potential of ponderosa pine, those in a more favorable position in the canopy usually exhibiting better growth. If this is true, resistant trees, exhibiting as they do greater growth, could logically be expected to occupy the dominant positions in the canopy. When crown positions of resistant and non-resistant pine were contrasted using the index

units described previously (p. 38), the resistant trees proved to be in a superior position, as shown in Table 25.

Table 25

Influence of Crown Class upon Resistance
(Crown class expressed in index units)

Ave. for non-resist. trees	Ave. for resist. trees	Diff.	Stand. dev. of diff.	Stand. error mean diff.	Deg. of free-dom	Value 5% -t-	Value com-puted -t-	Level of sig.
11.9	13.6	1.7	3.58	0.36	99	1.98	4.66	99%

The superior position of the resistant pine accounts for at least a part of their growth advantage, which in turn is evidence of their vigor.

Tree Age, Diameter, Height and Bark Thickness

Ponderosa pine in the study area form continuous forests of more or less uniform age. This is accounted for by Crandall (1901) who points out that these forests developed following extensive fires about 1850. He estimated, also, that nearly 70 per cent of the Front Range in northern Colorado was burned over between 1850 and 1900. Even in forests that are considered to be even aged certain trees became established some years ahead of others. If the growing conditions are favorable, such trees gain an advantage over their associates. When tree age is considered as a measure of the resistance of ponderosa pine, it must be considered in this light and not as a direct contributor to resistance. Ages of resistant and non-resistant trees were compared, and the

results are summarized in Table 26.

Table 26

Analysis of Tree Age
(Age in years at breast height)

Ave. non-resist. trees	Ave. resist. trees	Diff.	Stand. dev. of diff.	Stand. error mean diff.	Deg. of free-dom	Value 5% -t-	Value com-puted -t-	Level of sig.
86.5	91.8	5.3	18.4	1.8	98	1.98	2.85	99%

The results of the analysis would strongly suggest that those trees that became established ahead of their neighbors gained an advantage and exhibit a relatively higher degree of resistance to beetle attack. Because of this the resistant trees should be taller and have greater diameter. When these conditions were analyzed the hypothesis proved to be correct, the taller and larger trees having the greater resistance, as is shown in Table 27.

Table 27

Influence of Relative Diameter and Height upon Resistance

Ave. non-resist. trees	Ave. resist. trees	Diff.	Stand. dev. of diff.	Stand error mean diff.	Deg. of free-dom	Value 5% -t-	Value com-puted -t-	Level of sig.
Diameter b.h. in inches								
9.5	10.9	1.4	1.76	0.18	99	1.98	8.12	99%
Total height in feet								
45.4	47.0	1.6	7.86	0.79	99	1.98	2.08	95%

The growth advantage of earlier establishment is thus demonstrated by greater diameter and height of the resistant trees, and accounts in part for their greater vigor, and consequently their resistance to the Black Hills beetle.

Still another characteristic which is correlated with the rate of diameter growth is bark thickness. Through the early and middle stages of a tree's life the more rapidly growing trees have thicker bark than other trees. Upon reaching maturity, however, this correlation becomes unimportant. Since the pines included in the study were comparatively young, the resistant trees should have thicker bark than their mates. This hypothesis also proved to be correct, as is indicated in Table 28.

Table 28

Influence of Relative Bark Thickness upon Resistance
(Bark thickness at b.h. in inches)

Ave. non-resist. trees	Ave. resist. trees	Diff.	Stand. dev. of diff.	Stand. error mean diff.	Deg. of free-dom	Value 5% -t-	Value com-puted -t-	Level of sig.
0.66	0.71	0.05	0.21	0.02	99	1.98	2.33	95%

The greater bark thickness of the resistant trees is considered to be a function of greater diameter, and does not act as a deterrent to the entry of the beetles into the phloem of the tree.

Resin Flow

Greater vigor of the resistant trees is directly

manifested by their ability to produce a copious resin flow which floods the entrance holes and overwhelms the attacking beetles. Thus it was postulated that the resin conducting tissue of the resistant pines might be such that they move resin to the point of beetle attack more quickly than could the non-resistant individuals. This ability should be related to the relative number of resin ducts in the xylem. When resistant and non-resistant trees were compared, it was found resistant trees possessed a significantly greater number of these ducts than did the susceptible individuals. A summary is included in Table 29.

Table 29

Relation of Resin Duct Number to Resistance
(Number of resin ducts in last ten growth rings in increment cores)

Ave. non-resist. trees	Ave. resist. trees	Diff.	Stand. dev. of diff.	Stand. error mean diff.	Deg. of free-dom	Value 5% -t-	Value com-puted -t-	Level of sig.
17.3	25.0	7.7	8.06	2.55	9	2.26	2.78	95%

Resin ducts were counted on the last ten growth rings of increment cores. The comparison indicates that resistant ponderosa pines have a greater number of resin ducts per unit of wood than non-resistant trees. As a result they possess more resin conducting tissues to aid them in their defense against the Black Hills beetle. This suggests that genetic studies might lead to the development of beetle resistant strains of ponderosa pine.

Reduction of Diameter Growth

Short-time reduction in diameter growth occurring prior to the year of attack did not show a measurable difference between resistant and non-resistant trees. This is shown in Table 30. Evidently annual fluctuations in growth of an individual tree have little if any influence upon the resistance exhibited by that tree. This would seem to indicate that resistance is not greatly influenced by seasonal conditions.

Table 30

Influence of Currently Reduced Growth Rate on Resistance
(Values indicate differences between current and mean five year diameter growth in inches)

Ave. non-resist. trees	Ave. resist. trees	Diff.	Stand. dev. of diff.	Stand. error mean diff.	Deg. of free-dom	Value 5% -t-	Value com-puted -t-	Level of sig.
0.24	0.24	0.00	0.18	0.02	99	1.98	0.00	50%

Barking and Lightning Damage

In the few instances when such observations could be made, records were kept concerning the effect of lightning injury and barking, especially by porcupines, upon trees resistant to beetle attack. When analyzed statistically no evidence was apparent that there was any relation between either type of injury and resistance of pine, as indicated in Table 31.

Table 31

Influence of Barking and Lightning Damage upon Resistance

Total non-resist. trees	Total resist. trees	Diff.	Value 5% chi square	Value computed chi square	Level of sig.
Total number of trees struck by lightning					
0	3	3	3.38	3.04	90%
Total number of trees barked					
16	11	5	3.38	1.07	70%

One might expect that injuries causing heavy exudation of resin from a tree through breaks in the bark might weaken the tree and reduce its resistance to attack. Since the data presented in Table 31 are based only on a small number of observations it must be admitted that there is still a possibility that injury by porcupine, lightning and other agencies that cause resin to exude may prove to be of some significance.

No general survey was made to determine the frequency of occurrence of resistant trees on the entire Front Range; nevertheless, observations made in the areas studied were widespread and probably representative. The estimates ran from two to eight per cent of the trees attacked by the beetle, the average being about five per cent of all trees attacked. However, even this small number may provide forest geneticists with materials for breeding

a resistant variety of ponderosa pine.

In conclusion it appears that only trees of very high vigor are able successfully to resist bark beetle attack. These trees will maintain their resistance only as long as their vigor remains high. If their vigor were reduced, they would become susceptible to beetle attack. A significant reduction in vigor, and associated resistance, is not likely to take place suddenly, however. The resistant trees are the largest, thriftiest trees in the stand, occupy the dominant positions in the forest canopy, and manifest the greatest current growth. The site on which the trees are growing has sustained them in their present state for almost one-hundred years, and it can be expected that it will be able to continue to support them in the same fashion in the future. The competition from associated trees in the stand undoubtedly will not materialize in the present generation. Therefore, it is felt that when the resistant trees are reduced in vigor it will be from advancing age, and not from change in stand or site conditions.

SUMMARY AND CONCLUSIONS

Two problems are explored in this study: The first, an examination of ponderosa pine's susceptibility to attack by the Black Hills beetle; the second, an evaluation of pine's resistance to the beetle subsequent to its attack.

The observational design employed both paired plots and paired trees. The standard error of the difference for paired data, and chi square statistical techniques were used to evaluate differences which resulted when infested and uninfested trees were compared.

SUSCEPTIBILITY

In the portion of the study concerned with the susceptibility of pine to beetle attack, the following comparisons were made with results as follows:

1. Under both endemic and epidemic conditions the infested trees were of lower vigor, as indicated by Keen's Tree Classification system, than were the uninfested trees.
2. Under epidemic conditions the infested trees showed a greater slowdown in current diameter growth when contrasted with the mean periodic diameter increment than did the uninfested trees. Under endemic conditions no significant difference was found.
3. Under epidemic conditions infested trees were

found growing in groups with greater basal area than were the uninfested trees. This difference was not established under endemic conditions.

4. Under endemic conditions infested trees demonstrated smaller current periodic diameter increment than did the uninfested trees. This diameter growth difference was not evident under epidemic conditions.

5. Under endemic conditions infested trees had produced shorter needles than did the uninfested trees. Under epidemic conditions this difference was not observed.

6. Under endemic conditions a strong relationship existed between presence of mechanical barking and incidence of beetle infestation. No such relation was established under epidemic conditions.

7. Under neither endemic nor epidemic conditions did comparisons of any of the following conditions or characteristics result in significant differences between infested and uninfested trees:

   a. Age, diameter, and height.
   b. Bark thickness
   c. Site index
   d. Plant indicators of soil moisture
   e. Leader-lateral ratio

f. Crown class

g. Twig growth

h. Number of stems per acre

i. Injury by lightning

j. Slope, aspect or elevation of the land

The conclusions reached concerning susceptibility of ponderosa pine to Black Hills beetle attack are:

1. A difference does exist in susceptibility among ponderosa pine to Black Hills beetle attack under both endemic and epidemic conditions.
2. Susceptibility of pine to beetle attack is a function of a tree's existing general vigor or health. The more vigorous a tree is the less susceptible it is to beetle attack.
3. Vigor requirements associated with ponderosa pine's susceptibility to beetle attack vary directly with the level of the beetle population; the greater the population, the more vigorous must a tree be in order to maintain low susceptibility.
4. Black Hills beetles, upon leaving the brood tree, do not fly great distances, but attack nearby susceptible pine. The direction of their travel is determined by the wind direction during the flight period.
5. A tree growing in an area of low beetle population that has sustained current barking damage

is more subject to beetle attack than an unbarked tree.

6. Paired trees is the preferred sampling unit in the design of the experiment. The variance of the mean differences of the plots was not appreciably less than the variance of the individual tree measurements and the number of degrees of freedom are greatly reduced which in turn lowers the sensitivity of the design itself. In addition, when individual tree characteristics are to be analyzed the use of plot averages masks the measurements so no significant difference develops unless the difference is very large. Also, primary interest in this study is focused on individual tree characteristics rather than on area relationships, and thus paired trees become the preferred sampling unit.

The differences existing between susceptible and less susceptible trees are of such magnitude that they are not readily discernible in the field, but become evident only through a careful sampling procedure. Consequently, a guide or rule for selecting susceptible trees in the field would be difficult to devise and would certainly be involved in its field application.

RESISTANCE

In the portion of the study concerned with the resistance of ponderosa pine to Black Hills beetle attack the

results of the comparisons are as follows:

1. Resistant trees had a higher vigor classification in Keen's tree classes for ponderosa pine.
2. Resistant trees were older, and had greater diameter and height than the non-resistant trees.
3. Bark of resistant trees was thicker than on non-resistant trees.
4. Current periodic diameter increment was greater in the resistant trees.
5. The resistant trees occupied a better crown position in the forest canopy than did the non-resistant trees.
6. Leader growth in relation to associated lateral's growth was greater for the resistant trees than for the non-resistant trees.
7. Resistant trees produced longer needles than did non-resistant trees.
8. The number of resin ducts in the last ten growth rings was greater in resistant trees than in non-resistant trees.
9. No true differences were found when the following tree characteristics for resistant and non-resistant pine were compared:
   a. Current slowdown in diameter increment.
   b. Injury by lightning or mechanical injury.

The conclusions reached concerning resistance of ponderosa pine to Black Hills beetle attack are:

1. There are ponderosa pine that are truly resistant to Black Hills beetle attack, and are able to "pitch out" the insect even when they attack in great numbers.
2. Resistance in ponderosa pine is a reflection of good vigor or health. A pine, in order to demonstrate resistance to beetle attack, must have a degree of vigor that exceeds the average of the stand in which it is growing.
3. Resistant trees appear to have a very low susceptibility to beetle attack, and are discovered almost exclusively in areas of high epidemic beetle populations where the beetles are forced to attack them for lack of other more susceptible trees.
4. The occurrence of resistance in ponderosa pine can be traced back to earlier establishment in a group. By gaining a time advantage on its associates, it achieves dominance early in its life, and if growing conditions are good is able to broaden the difference in size and vigor from its neighbors. Consequently, resistant trees are the largest, have the best crown development, and occupy the best positions in the forest canopy.

5. Resistant trees appear to have a greater number of resin ducts with which to move resin and "pitch out" the attacking beetles.
6. The number of resistant trees is relatively small. Only about five per cent of trees attacked by the beetle are able to successfully resist attack.

APPENDIX

Standard error of the difference method for paired data

1. Determine the algebraic difference for each pair.
2. Compute the standard deviation of the series of differences.
3. Calculate the standard error of the differences by dividing the standard deviation by the square root of the number of observations.
4. Compute the average difference to be tested by dividing the algebraic sum of the differences by the number of differences.
5. Compute the actual t value by dividing the average difference by the standard error of the mean difference.
6. Look up 5% t value in table and compare with computed t value.

Chi Square

1. Calculate expected occurrence of values. In this study it was assumed that one-half of values should occur in each class.
2. Establish difference between expected occurrence and actual occurrence for all groups.
3. Square differences and divide by the expected occurrence for all groups.
4. Add quotients for all groups which is the chi square value.
5. Look up 5% chi square for one degree of freedom.

CONSTRUCTION OF SITE INDEX GRAPH

1. For each plot in the study the average height and age of the dominant trees were determined.
2. Plot averages were classified by 10-year age classes.

Age Class in years	Average Age in years	Average Height in Dom. in feet	Number of plots
50	57	38	2
60	64	35	6
70	78	36	2
80	85	36	8
90	96	37	20
100	103	36	17
110	115	38	5
120	124	45	11
130	132	46	2
140	143	46	6
150	154	69	1
170	174	38	2
200	207	46	1
230	234	39	1

3. Average height was plotted over average age for each plot and a smooth curve drawn through the points and balanced. This served as a guide curve.
4. The guide curve is anamorphosed as follows:
   A straight line is drawn from the zero-zero intersection of the axis of graph through the guiding curve, intersecting it above age one-hundred years.

5. An anamorphosed age scale was constructed by adjusting the uniform scale so the same height value would be read from the anamorphosed curve as for the guide curve for a given age.
6. The next step was to draw a set of curves through the 100-year heights, each curve representing one 5-foot site index class showing the development in average height of dominant trees for that site class throughout the age range. This was accomplished by drawing straight line curves through the 5-foot site index classes marked out along the 100-year age line, then connecting these points with the zero-zero points on the axis of the graph.
7. To facilitate easier reading the anamorphosed curves and age scale were reconverted back to curved lines and a uniform age scale.

CURRENT VERSUS MEAN PERIODIC DIAMETER GROWTH CALCULATIONS

1. Diameter o.b. for each tree was measured.
2. Diameter o.b. was divided by two.
3. Single bark thickness was subtracted from radius o.b. to get radius i.b. for each tree.
4. Age of each tree at b.h. was determined from increment cores.
5. Age at b.h. was divided by five to find the number of five year periods in the life of the tree.
6. The average radius was divided by the number of five year periods to determine mean periodic growth in radius.

7. The radial growth during the current five year period was determined from increment cores.
8. The mean periodic radial growth was compared with current radial growth and the difference noted.
9. The differences of the infested and uninfested trees were contrasted and a statistical evaluation made to determine if they were from the same or different population of differences.

PER CENT OF OCCURRENCE OF SHRUB SPECIES ON AVERAGE PLOT

Species	Endemic		Epidemic	
	Inf.	Uninf.	Inf.	Uninf.
Mtn. Mahogany	1.00	0.30	0.91	6.69
Antelope Brush	22.30	32.80	15.51	21.25
Skunk Bush	0.00	0.00	0.00	0.00
Wild Currant	14.30	8.10	16.52	12.50
Wild Rose	5.40	4.20	6.37	1.54
Choke Cherry	0.00	0.00	0.00	0.00
Bearberry	16.30	11.60	2.73	5.37
Low Juniper	6.65	7.10	13.37	7.45
Nine Park	1.00	1.70	7.45	6.55
Wild Raspberry	1.40	0.00	0.82	0.00
Snow Berry	2.20	0.90	3.22	2.45
Aspen	0.01	1.60	0.09	0.64
Willow	0.00	0.00	0.00	0.00
Honeysuckle	1.25	0.00	0.00	0.00
Per cent of no occurrence	28.90	31.70	33.83	37.61
	100.00	100.00	100.00	100.00

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