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FRUITING HABITS OF LODGEPOLE PINE

by
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Project K. 68

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INTRODUCTION

Lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.) is receiving more and more recognition in recent years as a tree of commercial importance. It has a very wide geographic range and therefore its silvical habits should be of interest to many foresters who are suddenly being charged with its management. Of prime importance is a knowledge of its fruiting habits, for upon these there appears to be a variety of conflicting opinions.

Clements (1910) was one of the earliest investigators to report in detail on the life history of lodgepole pine, and he took care to upset the old belief that its cones opened in the forest only as a result of fire. He concluded that most cones normally opened by drying out during several years immediately following maturity, while the remainder opened during a second period which falls between the tenth and thirteenth years, and that cone opening resulted when the drying scales overcame the effect of the rosin which holds the scales together.

Slightly different observations were made by Mason (1915) who reported that "the cones often fail to open and discharge their seed as soon as mature". Such a conclusion does not attempt to establish the customary habit, other than inferring that opening upon reaching maturity is to be expected. Sudworth's conclusions (1917), that the cones on many trees open in late autumn, while the cones of others may remain closed for many years, also begs the question.

Bates completed a vast amount of detailed study on the fruiting and seeding habits of lodgepole pine and reported (1930) that the cones did not open immediately upon ripening. While he does not say so, it can be interpreted from such a statement that all cones were serotinous.

Clements (1910) was one of the first to note that the rosin bond which sealed the serotinous cones of lodgepole pine could be melted at temperatures above 45°C. Cameron (1953) investigated the same thing and reported comparable results, but neither of these investigators attempted to tie this information to the variable behaviour in cone opening experienced under natural conditions.

Observations in lodgepole pine stands in Alberta indicated that many cones do not open at the time of maturity, while others remain closed for many years, but the pattern of opening was confusing. Consequently a study was initiated to investigate cone behaviour in both young and old stands under conditions of open growth. In the initial stages of the study individual trees were selected and their cone crops studied in detail, and later the investigation turned to a study of the cone-bearing pattern of stands.

METHOD

Field observations indicated that, regardless of age, some lodgepole pine trees bore all their cones open, others bore them all closed, and still others varied between these two extremes. It was considered important to establish such fundamental principles by first studying the cone-bearing habits of trees free from competition, and this will be referred to as the first phase of the study. The second phase involved the comparison of cone-bearing habits of open-grown trees to those of trees growing under stand conditions, and the third phase attempted to relate cone-bearing patterns to crown and diameter classes in stands of varying ages, growing on different aspects and at different altitudes.

Keeping in mind the three major classes of cone-bearing trees—those bearing the majority of their mature cones closed, those bearing the majority open, and those intermediate between these two extremes—both open-grown and stand-grown trees were selected, felled and lowered with ropes to avoid breaking off the cones. Each cone was dated as to year of maturity by counting branch and stem growth-whorls. The details of the cone crop borne by each of the 11 selected trees are presented in Figures 1 to 11. It will be noted that in addition to the amount and nature of the mature and persistent cone crop borne by each tree, the figures present the immature cone crop borne at the time of felling. The trees that were felled in the spring of the year (Nos. 3, 4, 8, 9, 10, and 11) are represented by only one crop of immature cones since the flower buds had not yet been fertilized. The immature cones presented, and referred to as two years of age, are those that will ripen that autumn. Strictly speaking they are only one year old when tallied in the spring and $1\frac{1}{2}$ years old if tallied in the autumn.

In order to illustrate the nature of the cone crops borne by individuals, diagrams were prepared of three of the trees that were studied in detail (Appendices I, II and III). The first diagram is of Tree No. 11 which bore the majority of its cones closed and is classed as a "closed-cone" tree. The second is of Tree No. 10, which is classed as an "open-cone" tree, and the last is of Tree No. 3 which bore both open and closed cones and is therefore classed as an "intermediate tree".

Phase 1

The first phase of the study was confined to trees growing in the open where the cone-bearing habit and ability could be expressed free from the influence of surrounding trees. Five trees were felled and details of cone-bearing habit are presented in Figures 1 to 5.

It will be apparent from Figures 1 to 5 that there is a wide variation in cone crops borne by individual open-grown trees, particularly with respect to the proportion of serotinous and non-serotinous cones. This is summarized in the following table:

TABLE 1.—NATURE OF MATURE CONE CROP ON FIVE OPEN-GROWN TREES.

—	Tree No. 1 (49 years)	Tree No. 2 (49 years)	Tree No. 3 (56 years)	Tree No. 4 (78 years)	Tree No. 5 (71 years)
Open	511 (98%)	834 (97%)	909 (45%)	8 (1%)	4 (2 %)
Closed	12 (2%)	27 (3%)	1,102 (55%)	534 (99%)	183 (98%)
Total	523	861	2,011	542	187

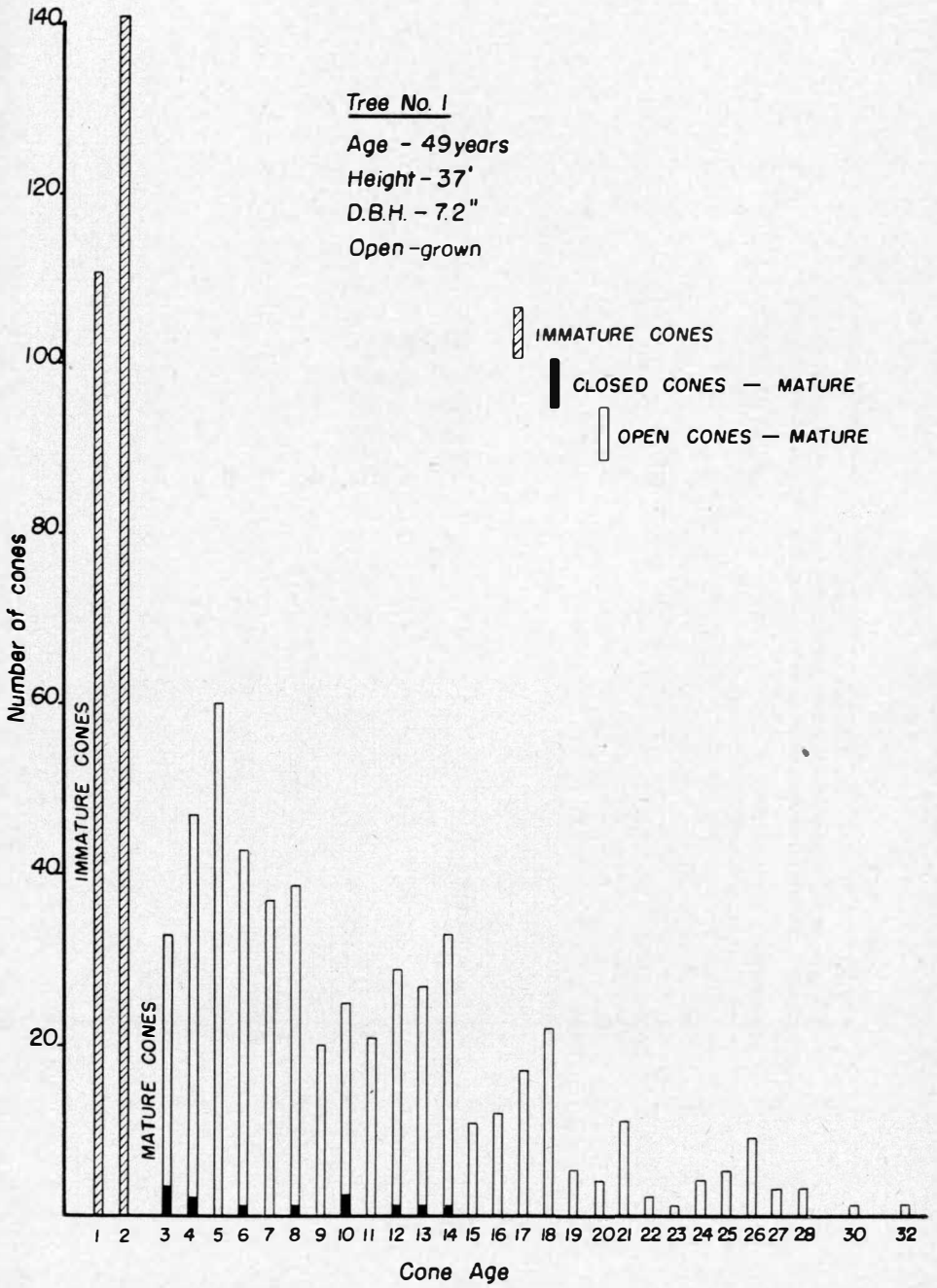

FIGURE 1.—Amount and nature of cone crop borne by open-grown lodgepole pine.

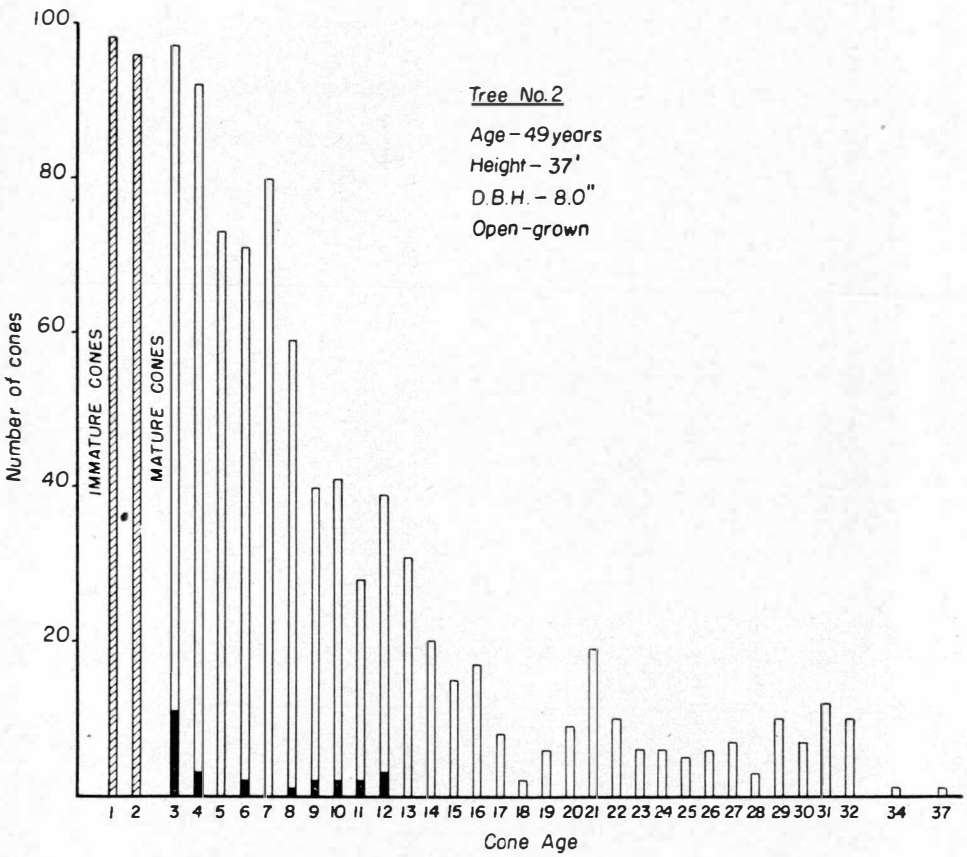

FIGURE 2.—Amount and nature of cone crop borne by open-grown lodgepole pine.

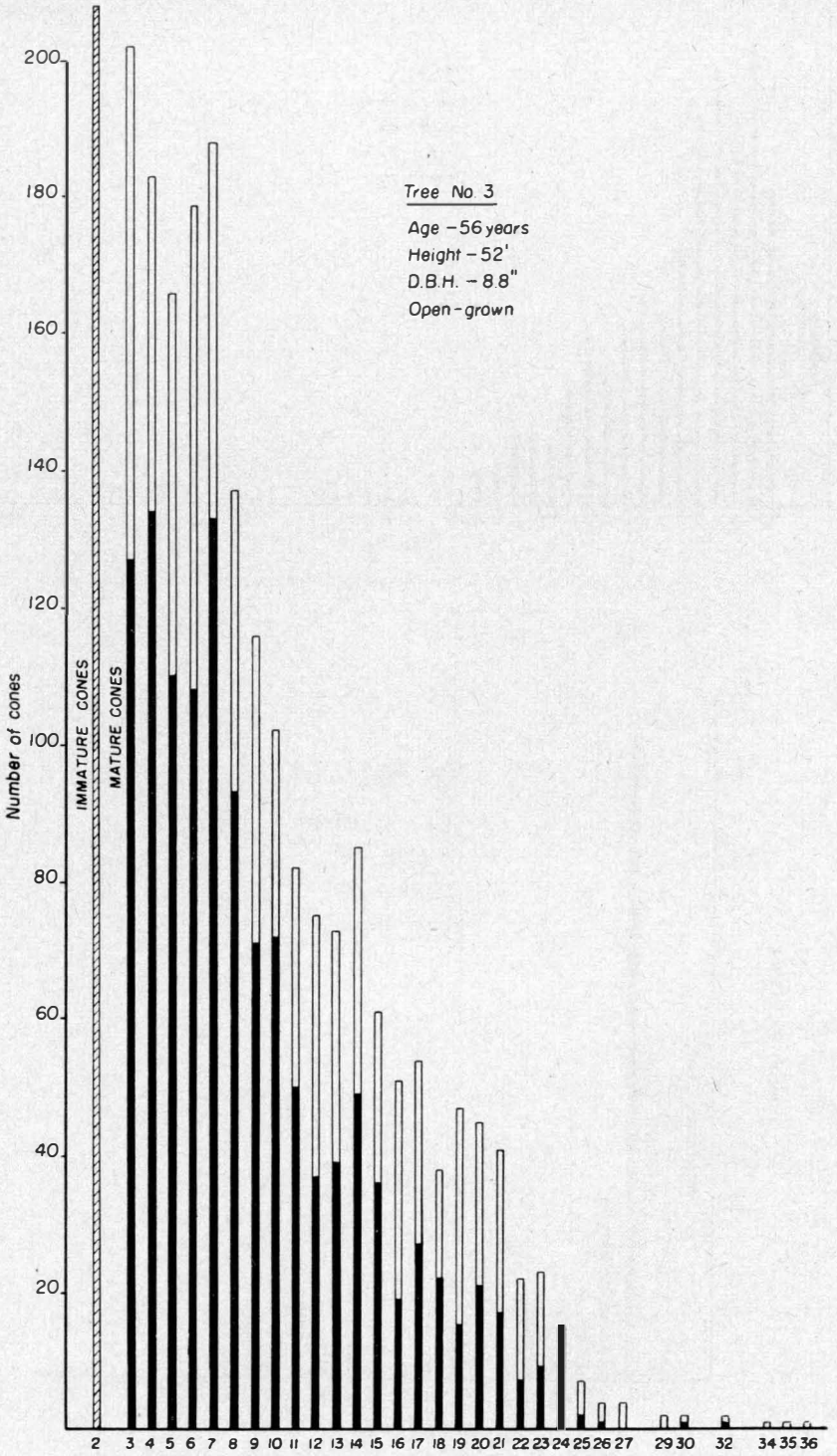

FIGURE 3.—Amount and nature of cone crop borne by open-grown lodgepole pine.

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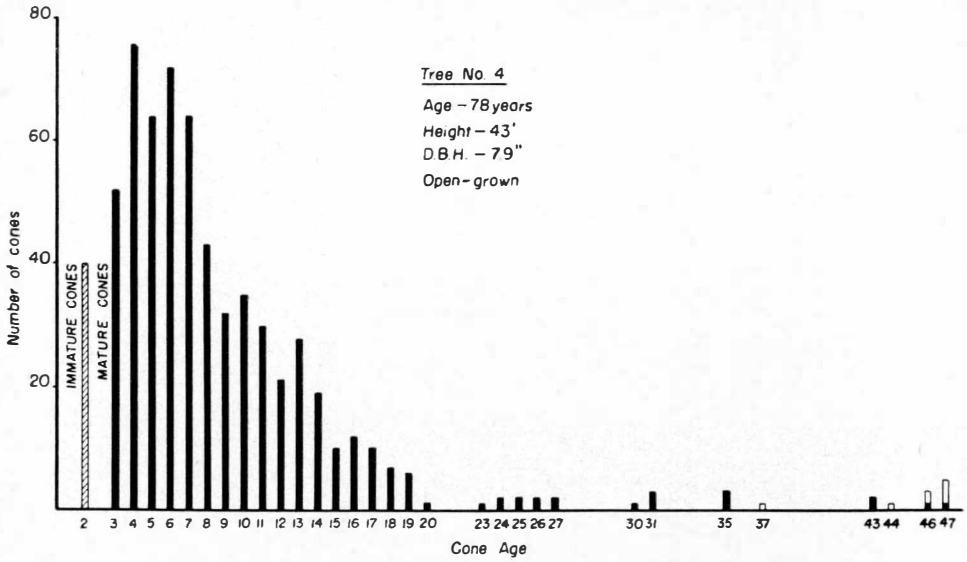

FIGURE 4.—Amount and nature of cone crop borne by open-grown lodgepole pine.

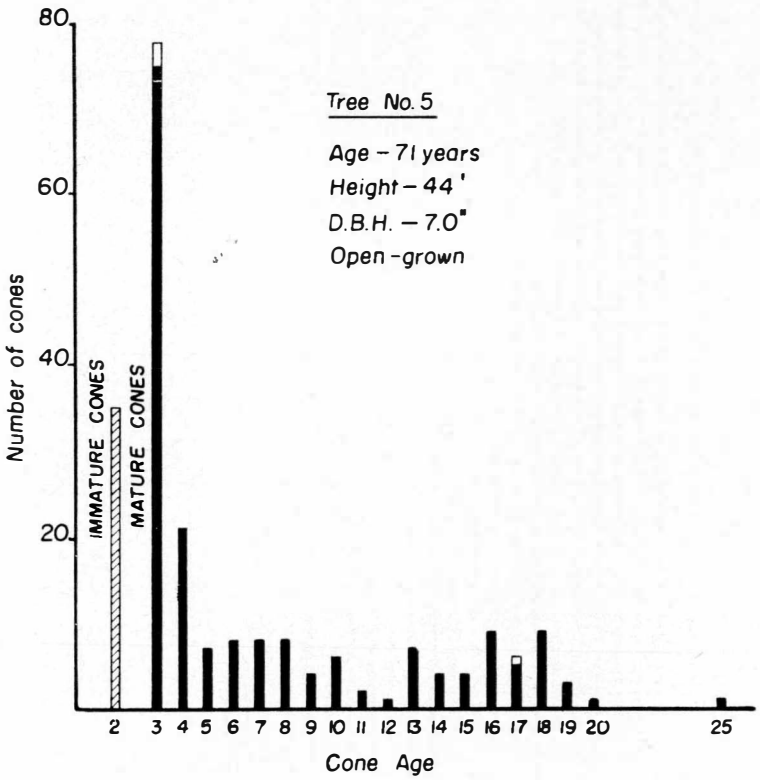

FIGURE 5.—Amount and nature of cone crop borne by open-grown lodgepole pine.

Thus we have trees that, for all practical purposes, bear all their mature cones open (Nos. 1 and 2); others that bear them all closed (Nos. 4 and 5); and another that exhibited intermediate characteristics (No. 3). Probably the most interesting and important fact arising from these data is that open-cone trees (Nos. 1 and 2) bore practically all of their cones open in the first year of maturity (cone age 3 years in Figures 1 to 5). That is, there was little or no evidence of gradual opening through the years succeeding maturity. Similarly, closed-cone trees (Nos. 4 and 5) showed no evidence of changing this habit with cone age. Such information suggests that the cones on trees that have been classed as "closed-cone" are truly serotinous, while trees classed as "open-cone" produce cones that are non-serotinous in nature, i.e. they either have no rosin bond to seal them closed, or the rosin bond exhibits a melting point considerably below the 45°C reported by Clements (1910) and by Cameron (1953). While no rosin bond extractions have been undertaken on such cones in order to determine melting points, other tests have been made that provide interesting information. In one test, 2-year-old closed cones were collected from trees in the autumn of the year just as they were ripening. Such samples were taken from "open-cone" trees, from "closed-cone" trees, and from intermediate trees bearing both open and closed cones. Each sample was placed in a paper bag and left in a heated building at room temperature which never exceeded a maximum of 72°F. Several weeks later the samples were examined and all the cones from open-cone trees were open, all those from closed-cone trees were tightly closed, while the samples from the intermediate trees exhibited both open and closed cones. A similar test was run the following autumn with similar results. Such results indicate that lodgepole pine trees bear their cones in various ways—either serotinously, non-serotinously, or in combination. That the habit is not irregular from year to year, at least during a decade or two, is apparent from an examination of Figures 1 to 5. Evidence will be presented later to show that such habits do change over long periods.

Clements (1910) suggested that since cones were persistent on the tree, this fact could be used to obtain evidence on the period between maximum seed years, and concluded that, in spite of considerable variation from year to year, lodgepole pine, in the area in which his study was conducted, showed little evidence of a periodic alternation of seed years. From the writer's point of view the evidence available must be treated with caution because of the steady sloughing-off of cones through the years, but more particularly because of the irregular and unpredictable loss of closed cones to squirrels. Since these rodents gather the majority of cones just as they are ripening, it is not even possible to use the crops borne on open-cone trees to establish periodicity.

However, from the evidence at hand, it is possible to establish some important facts. First, it is apparent that nil cone crops are a rarity. Tree No. 2, for example, in spite of any loss, exhibits evidence of a crop of cones for each of 32 consecutive years. This is rather surprising and can perhaps be credited to the fact that flowering of this species occurs rather late in the season after the danger from spring frosts is over. Second, there can be marked variations in the size of the crop borne each year, as is evidenced by Trees 4 and 5. The immature cone crop is considerably lighter on both these trees than either of the mature cone crops still remaining on each tree. Third, it appears that some trees are consistently heavy cone producers and others light or intermediate. For example, Tree No. 3 appeared to have borne about 200 cones a year, at least for the past six years, while Tree No. 2 produced about half that number.

It seems likely that lodgepole pine trees that are consistently poor cone bearers are those that are exceptionally heavy producers of pollen. Such trees are steady producers of male conelets in such abundance that a distinctive appearance is imparted.

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PLATE 1.—Pattern of foliage that has resulted from abundant annual crops of pollen.

PLATE 2.—Distinctive appearance of a lodgepole pine that has been a consistently heavy producer of pollen.

It is possible to conclude from this preliminary part of the study that closed-cone trees always bear a good reserve of cones, and that there must be an annual release of seed as the crops borne by open-cone trees mature. Such annual release is attested to by a 3-year seed-trap study by this author (Crossley 1955) during which maximum lodgepole pine seedfall occurred around the first week in October.

Phase 2

The study of open-grown trees revealed some important fundamental cone-producing habits. Since the forest manager is interested in the stand rather than the tree, the second phase of the investigation involved the sampling of trees of varying crown classifications within stands. Dominant, codominant, and intermediate trees were selected, carefully felled as before, and cone ages were again established. The details of the cone crop borne by each of the six trees studied are presented in Figures 6 to 11. As in previous figures the solid bar indicates closed cones; the open bar, open cones; and the cross hatching denotes immature cones.

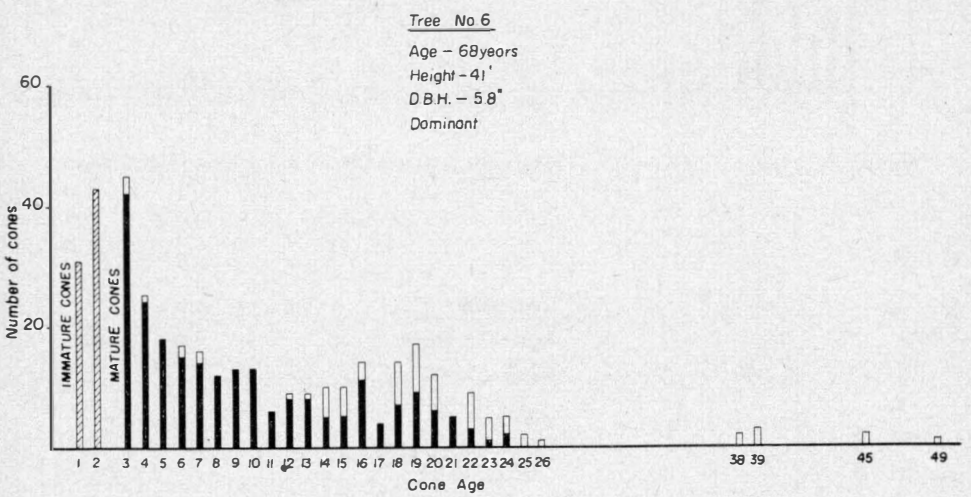

FIGURE 6.—Amount and nature of cone crop borne by a stand-grown dominant lodgepole pine.

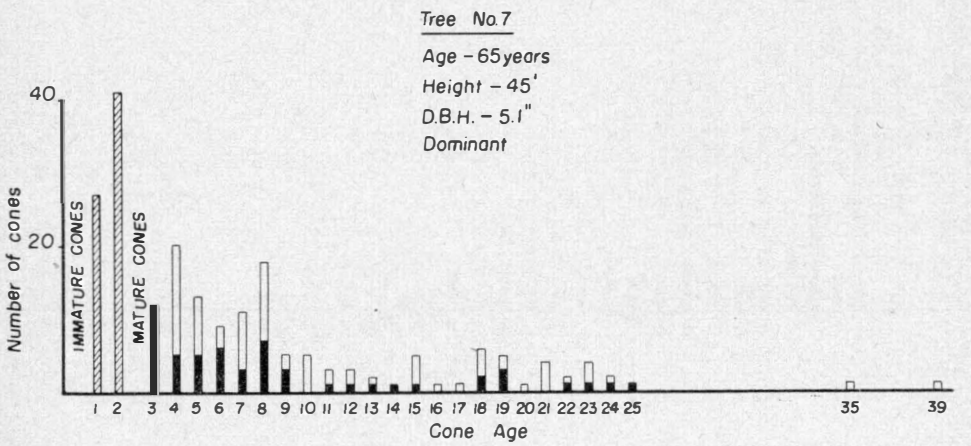

FIGURE 7.—Amount and nature of cone crop borne by a stand-grown dominant lodgepole pine.

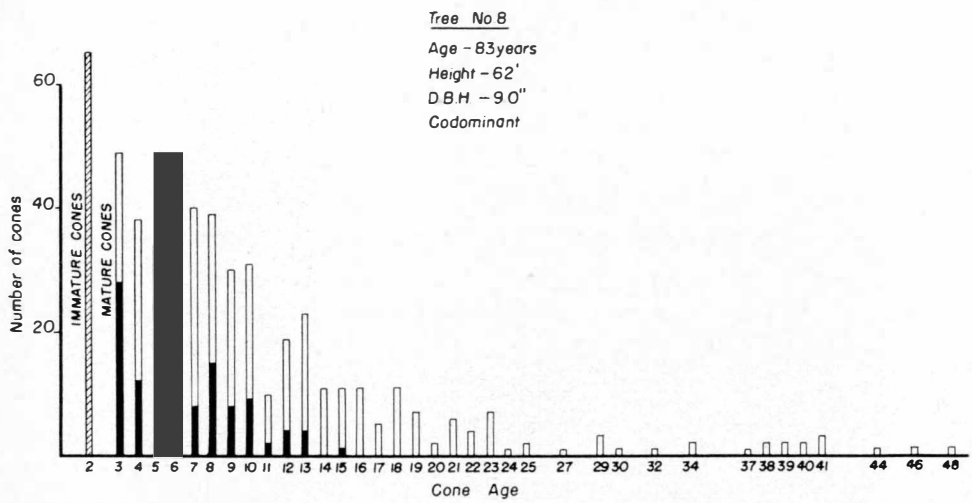

FIGURE 8.—Amount and nature of cone crop borne by a stand-grown codominant lodgepole pine.

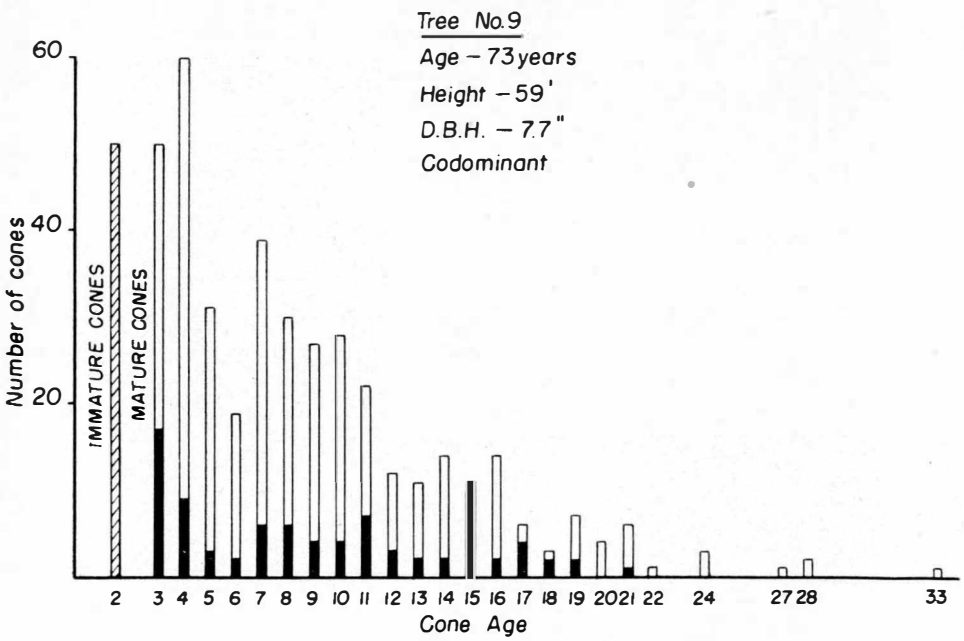

FIGURE 9.—Amount and nature of cone crop borne by a stand-grown codominant lodgepole pine.

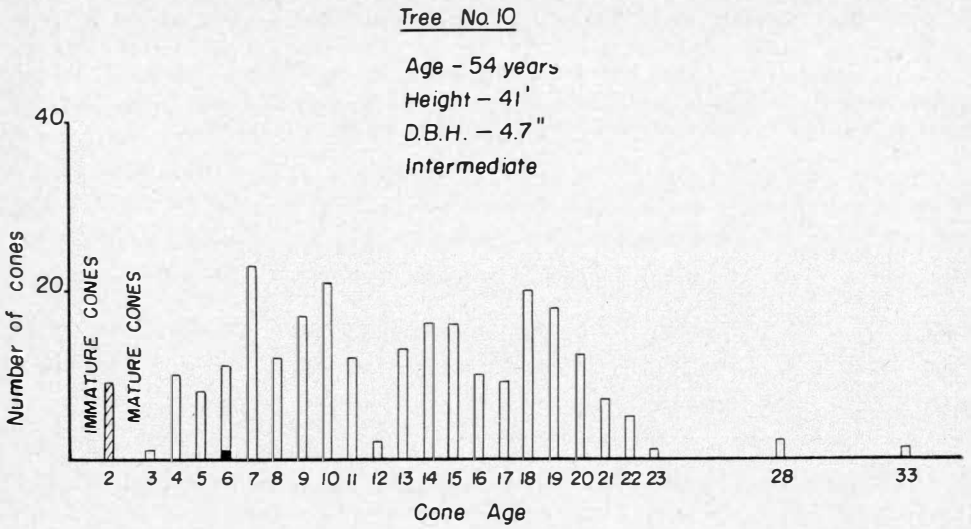

FIGURE 10.—Amount and nature of cone crop borne by a stand-grown intermediate lodgepole pine.

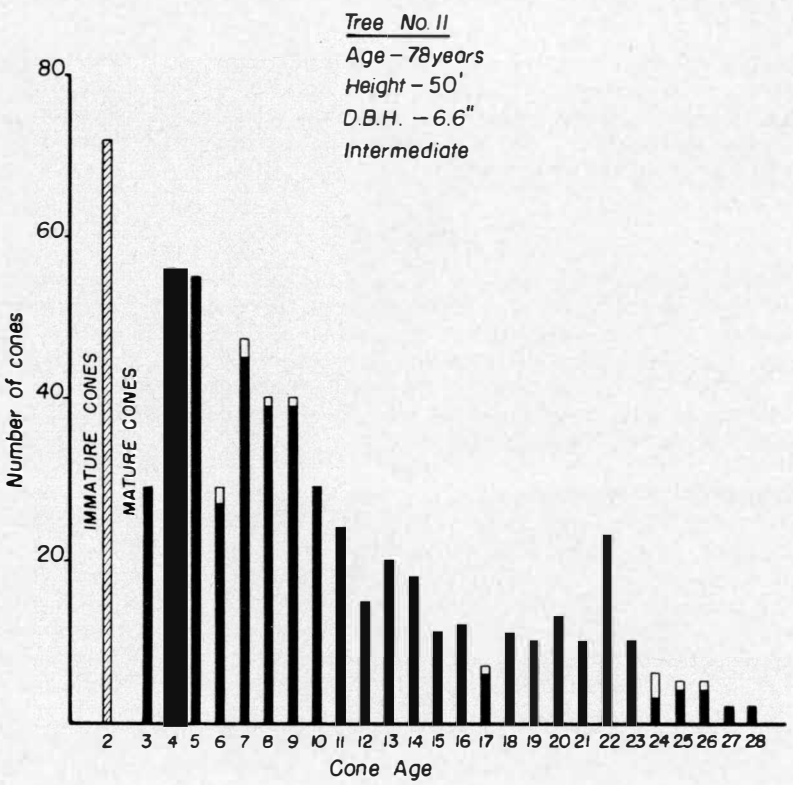

FIGURE 11.—Amount and nature of cone crop borne by a stand-grown intermediate lodgepole pine.

It is immediately evident that there are similar habits in the stands and in the open; namely, there are closed-cone trees, open-cone trees, and trees exhibiting intermediate fruiting habits. If the trees studied are a fair sample, then it is apparent from the Figures presented and from a comparison of Tables 1 and 2 that stand trees bear smaller quantities of cones than do open-grown trees. Clements (1910) came to a similar conclusion.

TABLE 2.—NATURE OF MATURE CONE CROP ON SIX STAND-GROWN TREES.

	Tree No. 6 (Dom.)	Tree No. 7 (Dom.)	Tree No. 8 (Codom.)	Tree No. 9 (Codom.)	Tree No. 10 (Inter.)	Tree No. 11 (Inter.)
Open	69 (24%)	76 (62%)	343 (75%)	322 (80%)	247 (100%)	27 (6%)
Closed	221 (76%)	47 (38%)	116 (25%)	80 (20%)	1	376 (94%)
Total	290	123	459	402	248	403

Perhaps a more convincing demonstration of this is the fact that the five open-grown trees bore an average of 104 second-year maturing cones at the time of felling, while the six stand trees bore an average of only 47.

From the evidence provided by the three crown classes of stand-grown trees it appears that there is no relationship between size of cone crop on individual trees and crown position in the stand. The variation in cone crop between individual trees is greater than the variation in crop between crown classes.

The stand-grown trees regularly bore annual crops of cones, but there is evidence of the possibility of marked variations in size of cone crops borne from year to year by individual trees, and that some trees regularly produce heavier crops than others. Such conclusions are similar to those arrived at from the study of open-grown trees.

Phase 3

Having established the variety of cone-bearing habits of lodgepole pine, the study entered its third and final phase of investigating the proportions of closed-cone and open-cone trees in stands of various ages and growing conditions. Cruises were conducted in three different ages of lodgepole pine stands. The first was a juvenile 17-year-old stand, the second an immature stand 55 years of age, and the third was an overmature stand and the trees varied from 140 to 250 years of age.

Sapling Stands (17 years)

These stands were the result of a severe burn in 1936. Horton (1953), working in the same area, has shown that the regeneration is not strictly even-aged. The heaviest regeneration apparently took place two years after the fire and has been continuous but progressively less until almost ceasing 14 years later. While every density can be found on this area up to one-half million trees per acre, the cone study was undertaken under density conditions normal for this age, about 7,000 living stems per acre. Milacre line plots were used and every tree on each plot was tallied for height, presence or absence and number and nature of cones. Two hundred and seven milacres were sampled, covering all aspects; 1,516 trees in all were tallied. Height class distribution is presented in Figure 12.

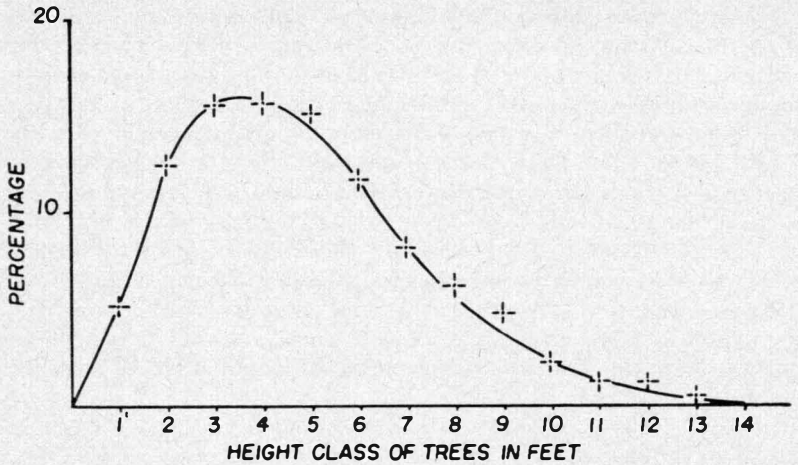

FIGURE 12.—Height class distribution of lodgepole pine 17 years after the stand originated from fire.

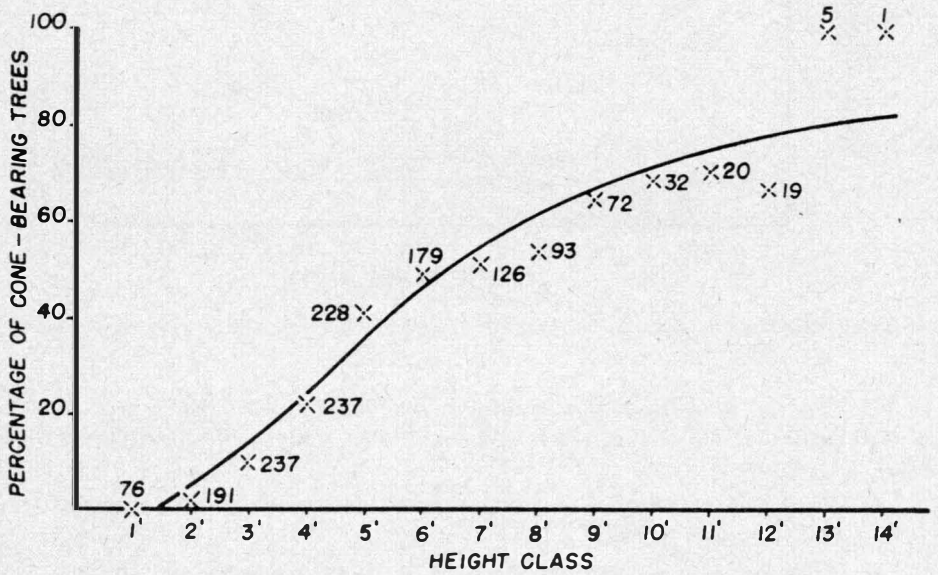

FIGURE 13.—Relationship between height class and cone-bearing ability in a 17-year-old lodgepole pine stand.

Figure 13 illustrates that trees had reached the 7-foot height class before cone-bearing became general, but that even the very small trees bore occasional cones. However, height per se may have little to do with the ability to produce a cone crop. Since the stand has seeded in over a number of years it is probable that height, and therefore cone-bearing ability, is related to age. Trees in the 7-foot class are probably about 12 years of age and cone-bearing became common at that age.

As the trees were tallied the number of cones borne by each was noted. The results at an average elevation of 5,300 feet are presented in Figure 14. The average of 0·9 cones per tree is lower than one might expect from a species that is a recognized early bearer. Since the cruise traversed a stand averaging 7,314 pine stems per acre, this means that it bore 6,583 cones per acre. However, only 17 per cent of these were closed cones, and therefore the reserve seed crop is borne in 1,119 cones per acre. Bates (1930) reported the average number of seeds per cone as 40. Using this figure we arrive at a reserve supply of 44,760 seeds per acre, or about $\frac{1}{3}$ of a pound. In the event of fire it is suggested that this reserve of seed would be insufficient to reproduce the stand. It is of interest to note (Figure 14) that by the time trees reached a height of seven feet they generally bore an average of 1·5 cones. As will be shown later it is quite possible that the seed-producing potential would increase with decreasing elevation and vice versa.

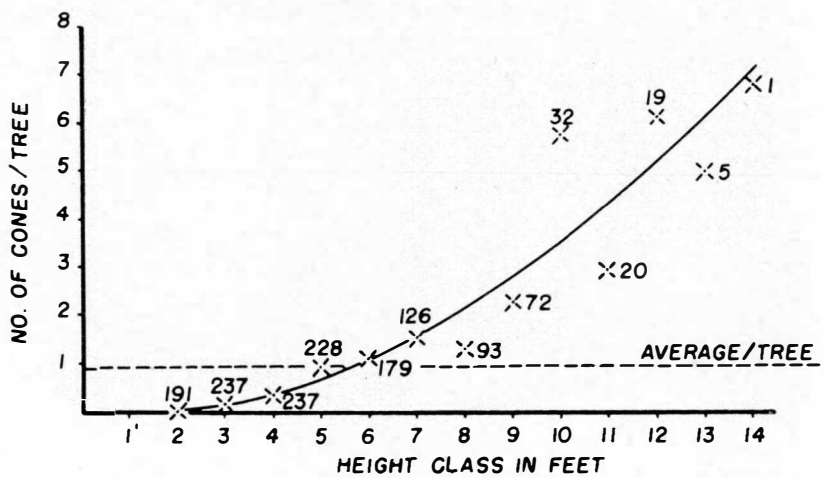

FIGURE 14.—Relationship between number of cones per tree and height class in a 17-year-old lodgepole pine stand.

During the collection of the data in the field, information was gathered on the nature of the cones borne by each tree. Three categories were recognized, as follows:

1. Trees bearing 90 per cent or more of their cones closed, referred to as "closed-cone" trees.
2. Trees bearing 90 per cent or more of their cones open, referred to as "open-cone" trees.
3. All cone-bearing trees not falling into either of the above categories, referred to as "intermediate" trees.

In Figures 15 and 16 the open-cone and closed-cone trees have been expressed as percentages of the number of cone-bearing trees.

In young sapling stands it appears that the majority of the trees are open-coned, and the relationship of those trees bearing their cones open and closed to height class is illustrated in Figures 15 and 16.

Data collected in these young stands showed that only 17 per cent of the cone-bearing trees bore their cones closed, while 66 per cent bore them open. The remaining 17 per cent fell into the intermediate category.

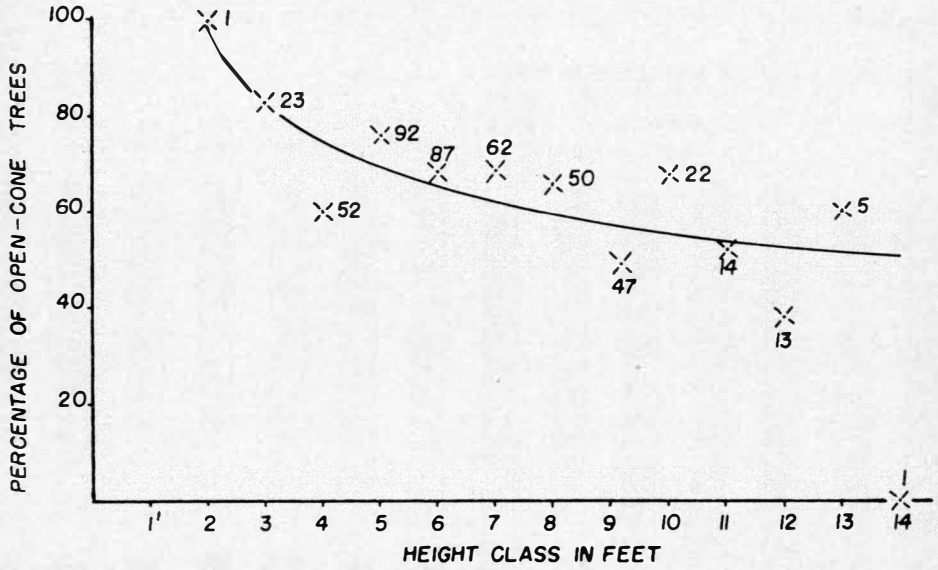

FIGURE 15.—Relationship between open-cone trees and height class in a 17-year-old lodgepole pine stand.

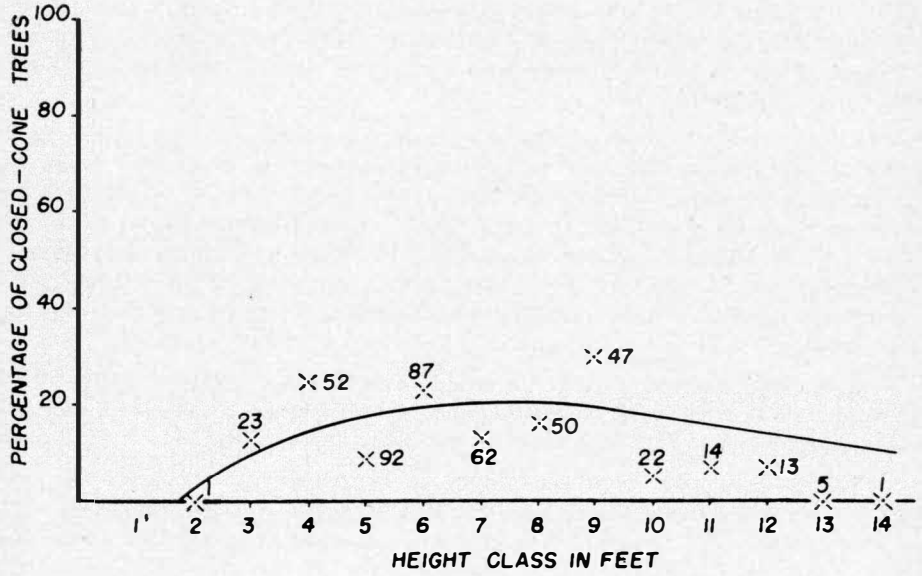

FIGURE 16.—Relationship between closed-cone trees and height class in a 17-year-old lodgepole pine stand.

Figure 17 graphically summarizes the cone-bearing relationship of *all* the trees in the sapling stands studied.* As the trees get older there is a rapid increase in the proportion of the stand able to fruit. The percentage of trees bearing their cones closed is very small and remains practically constant throughout the range of height experienced in any one stand.

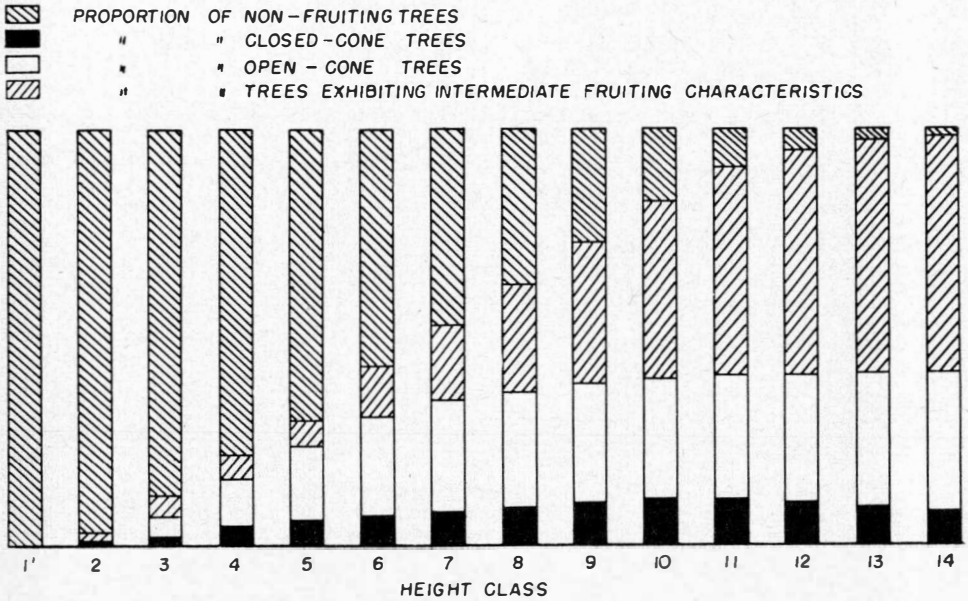

FIGURE 17.—Relationship between fruiting habit and height class in a 17-year-old lodgepole pine stand.

During this third phase of the investigation a record was kept of the aspect of stands whose cone-bearing habits were under study. The valley in the mountains in which this information was collected exhibits pronounced slopes, and the southwest winds are warm and dry in comparison to those from other directions.

In spite of the fact that the south aspect is oriented to the sun's rays to obtain the maximum heat, and to take advantage of the warm, dry, southwest winds, the percentage of open-cone trees is no greater than on the north aspect where such effects would be at a minimum. Such evidence supports the previously made suggestion that lodgepole pine cones are either serotinous or non-serotinous. If they are serotinous then a minimum temperature of 45°C. is required to rupture the rosin bond which seals them shut, and such temperatures are never reached under natural conditions in the tree crowns.

Since elevation was readily obtained from available contour maps of this mountain valley, the data were compiled in an attempt to establish any relationships between it and cone-bearing habits.

Figure 19 suggests that the ability to bear cones at this age (17 years) decreases with increasing elevation. The percentage of closed-cone trees remains fairly constant with elevation, but the percentage of open-cone trees increases rapidly with increasing elevation. In the light of the fact that the climate

* Previous comparisons in this age class were confined to cone-bearing trees.

becomes both cooler and more moist with increasing elevation, the relationships illustrated attest to the hypothesis that climate per se has nothing to do with rosin-bond rupturing of cones borne in the crowns of standing trees. No explanation is offered for the suggested relationships between elevation and cone-bearing habits.

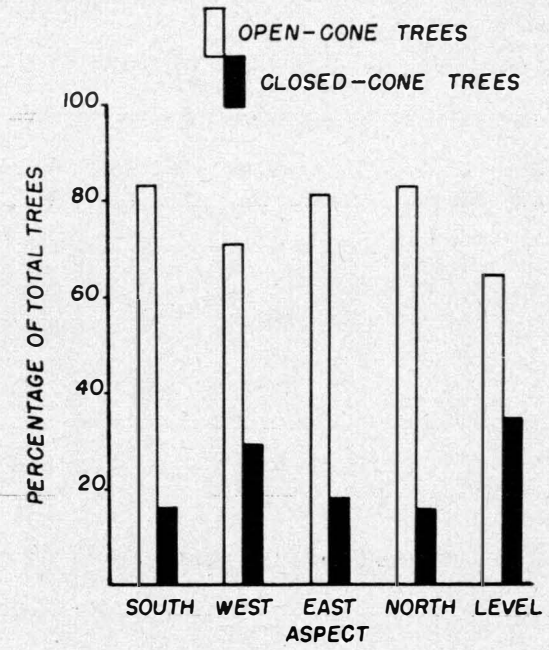

FIGURE 18.—The effect of aspect on cone-opening in 17-year-old lodgepole pine stands.

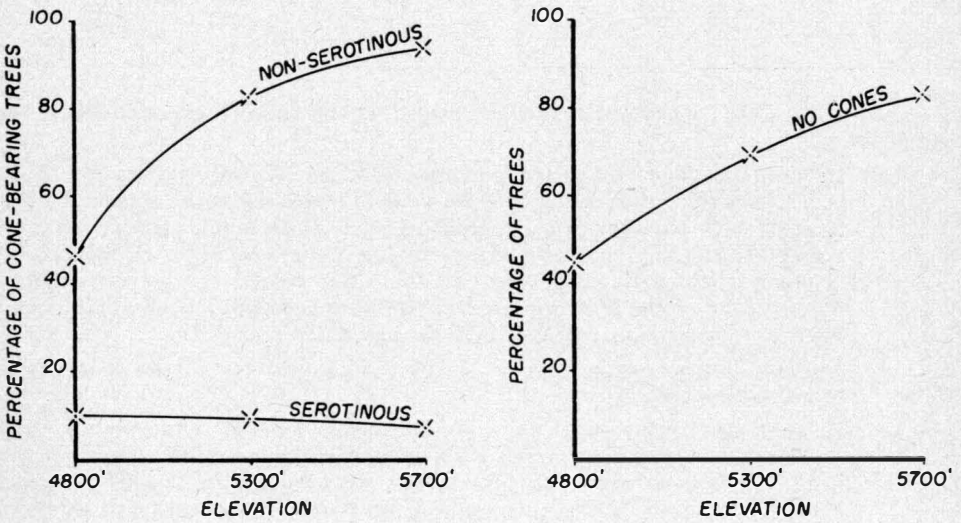

FIGURE 19.—Relationship between cone-bearing habits and elevation in a 17-year-old lodgepole pine stand.

Immature Stands (55 years)

Seven hundred and eighty-six trees were observed in immature stands by strip cruising with contiguous 1/20-acre line plots. The nature of the cones borne by each tree by diameter classes and by crown classes was observed. Twenty-three per cent of the trees in the stands bore no fruit at all, with only five per cent of these trees belonging in the dominant classification and 65 per cent in the suppressed.

TABLE 3.—FRUITING HABITS OF CONE-BEARING TREES BY CROWN CLASSES IN IMMATURE STANDS.

Crown Class	Closed-cone	Open-cone	Intermediate	Total
	%	%	%	%
Dominant	94	1	5	100
Codominant	81	6	13	100
Intermediate	83	8	9	100
Suppressed	75	16	9	100
Average	82	8	10	

TABLE 4.—PERCENTAGE OF TREES IN IMMATURE STANDS BY CROWN CLASSES IN RECOGNIZED FRUITING CATEGORIES.

——	Dom.	Codom.	Interm.	Supp.	Total
Closed	15	30	36	19	100
Open	2	20	36	42	100
Intermediate	7	41	33	19	100

From the data presented in Tables 3 and 4, the following conclusions are suggested:

(a) In comparison with the fruiting habits of the 17-year-old stands there is a complete reversal in the 55-year-old stands with regard to the relationship between the percentages of closed-cone trees. In the young stand, 17 per cent of the fruiting trees bore their cones closed, in comparison with 82 per cent in the older stand. At the same time, 66 per cent of the fruiting trees in the younger stand bore their cones open in comparison to 8 per cent in the older stand.

(b) Increased suppression appears to result in a decrease in the percentage of closed-cone trees.

(c) In spite of the fact that the dominant class exhibits the greatest percentage of closed-cone trees, this class actually produces the lowest number of such trees per acre in the stands studied simply because the percentage of dominants making up a stand is comparatively low. The intermediate and codominant portions of a stand apparently

include well over half of the closed-cone trees. For a similar reason an almost negligible number of open-cone trees are dominant. Forty-two per cent of the open-cone trees in the stand are found in the suppressed class, in spite of the fact that only 16 per cent of the suppressed trees were classified as non-serotinous. This simply means a high proportion of the stands were made up of suppressed trees.

In Figures 20 and 21 the numbers of open-cone and closed-cone trees are expressed as percentages of the number of cone-bearing trees.

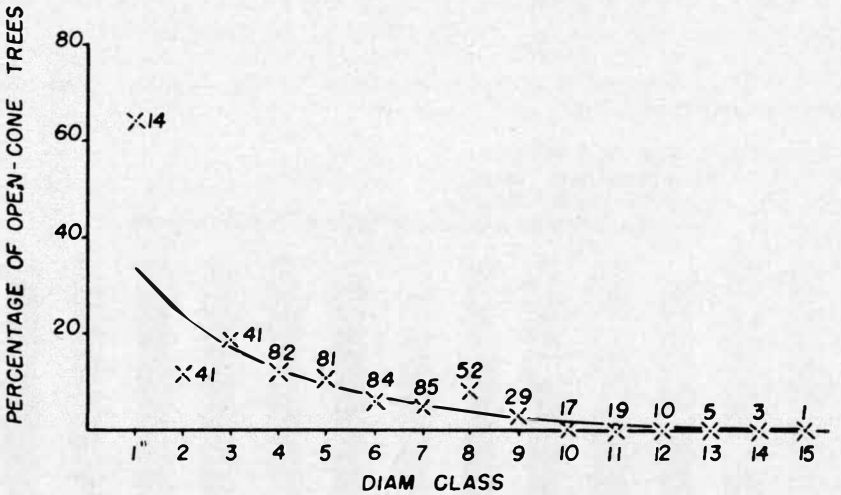

FIGURE 20.—Relationship between open-cone trees and diameter class in lodgepole pine stands in the 55-year age class.

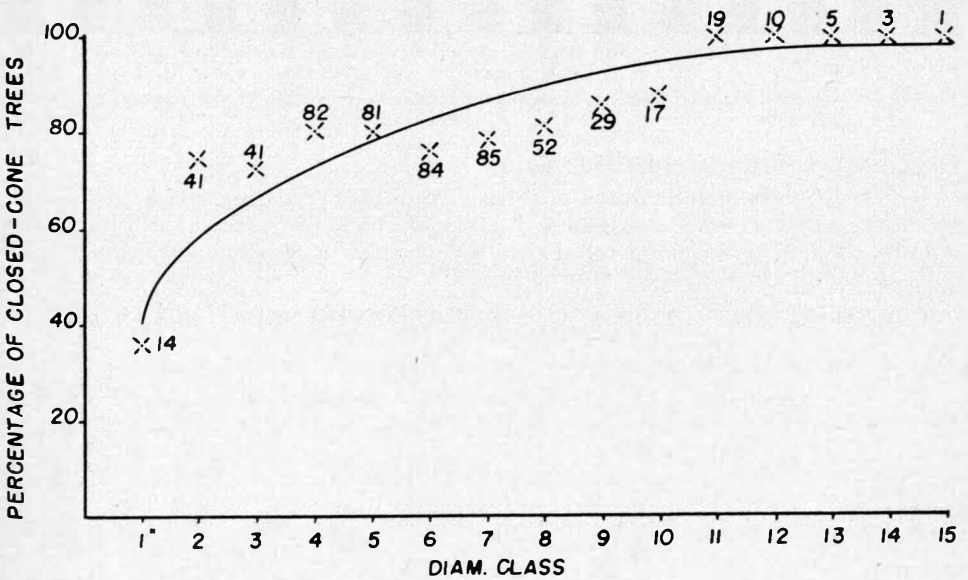

FIGURE 21.—Relationship between closed-cone trees and diameter class in odgepole pine stands in the 55-year age class.

A comparison of Figures 15 and 20 illustrates that, while the curves exhibit similar trends of a decreasing percentage of open-cone trees with increase in tree size, or position in the crown canopy, there is a pronounced decrease with age in the percentage of such cone-bearing trees in the stands studied.

A similar comparison between Figures 16 and 21 illustrates the striking difference between closed-cone bearing habits in the two age classes of pine.

Figure 22 graphically summarizes the cone-bearing relationships of *all* the trees in the 55-year age-class stands that were studied.* As the diameter classes increase there is a rapid increase in the number of closed-cone trees. This is very probably related to the decreased suppression and the position of the tree's crown in the main crown canopy. Comparing Figure 22 with Figure 17, the difference in cone-bearing habit of the sapling stand and the immature stand is striking.

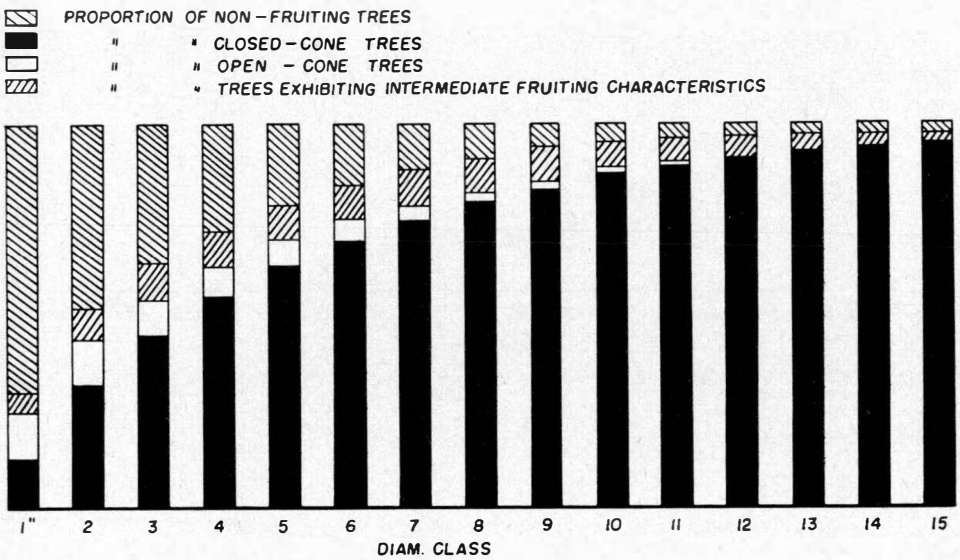

FIGURE 22.—Relationship between fruiting habit and diameter class in lodgepole pine stands in the 55-year age class.

Overmature Stands (140–250 years)

Three hundred and ninety-one trees were observed in overmature stands by strip cruising with contiguous 1/20-acre line plots. As in the immature stands, data were collected on the nature of the cones borne by each tree in each diameter class, and by crown classes.

TABLE 5.—FRUITING HABITS OF CONE-BEARING TREES BY CROWN CLASSES IN OVERMATURE STANDS.

Crown Class	Closed-cone	Open-cone	Intermediate	Total
	%	%	%	%
Dominant	76	0	24	100
Codominant	83	0	17	100
Intermediate	87	0	13	100
Suppressed	91	4	5	100
Average	83	0	17	

* Previous comparisons in this age class were confined to cone-bearing trees.

TABLE 6.—PERCENTAGE OF TREES IN OVERMATURE STANDS BY CROWN CLASSES IN RECOGNIZED FRUITING CATEGORIES.

—	Dom.	Codom.	Interm.	Supp.	Total
Closed	25	41	26	8	100
Open	0	0	0	100	100
Intermediate	36	43	18	3	100

The conclusions to be drawn from Tables 5 and 6 are:

(a) The percentage of open-cone trees has decreased at these ages to a negligible quantity, regardless of the crown classifications.

(b) The dominant crowns now include the lowest percentage of closed-cone trees, and the suppressed the highest. This reverses the situation existing in the immature stands studied.

Figure 23 illustrates the lack of any regression in the overmature stands between the closed-cone bearing habit and the size of the tree. It appears that 83 per cent of the cone-bearing trees in the stands studied bore their cones closed regardless of size.

Figure 24 is presented to summarize the cone-bearing relationship of *all* the trees in the overmature stands studied.* It will be evident when compared with the similar Figure 22 prepared for immature stands that the percentage of trees bearing cones increases with maturity. This might be explained by the fact that the smaller, non-fruiting diameter classes that were present in the immature stands have now dropped out of the picture. At the same time the percentage of closed-cone trees has decreased with maturity, and open-cone trees have disappeared entirely.

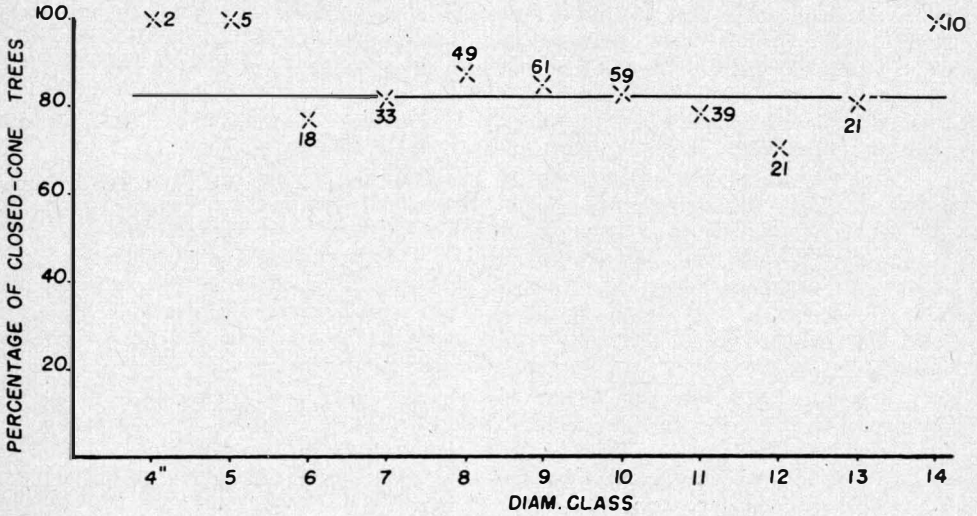

FIGURE 23.—Relationship between closed-cone trees and diameter class in overmature lodgepole pine stands.

*Previous comparisons in these age classes were confined to cone-bearing trees.

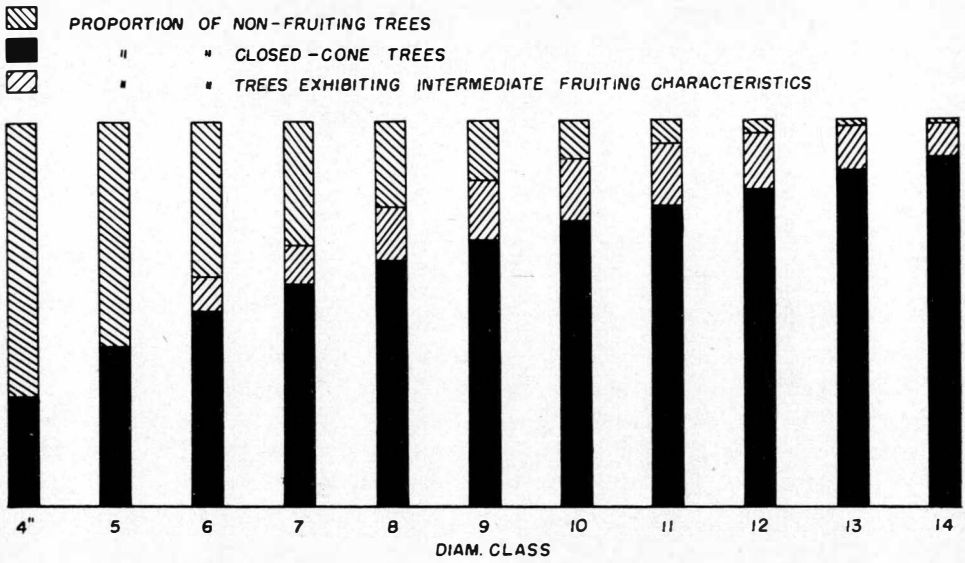

FIGURE 24.—Relationship between fruiting habit and diameter class in overmature lodgepole pine stands.

As was the case in immature stands, non-fruiting appears to be correlated with degree of suppression. The similarity of Figures 24 and 22 in this respect suggests that the proportion of non-fruiting trees is fairly consistent and that the non-fruiting characteristic is constant.

DISCUSSION

In his study of lodgepole pine cones under natural conditions, Clements (1910) credited their opening to temperature. He noted that individual cones behaved differently but found it impossible to formulate a general rule that would cover the effect of temperature. Tower (1909) credited such behaviour to varying amounts of lime in the soil; his observations led him to believe that on lime-rich soils the cones remain closed, and on soils deficient in lime the majority of the cones open at maturity. Finally, Mason (1915) suggested a general tendency of cones to open less promptly on dry soils.

The results of the present study indicate that none of these suggestions is acceptable. Maturing cones kept at similar temperatures have behaved differently, but each in a predictable manner that is in accordance with the habit of its parent tree, and stands subject to extremes of solar insolation have shown no differences in cone-opening pattern. The effect of the amount of lime in the soil as well as the dryness of the site is discredited due to the fact that individual trees in the same stand growing on uniform soil and moisture conditions show extreme but constant differences in the habit of cone-opening.

The constancy of cone behaviour on any one tree during periods of its life provides the clue, and suggests a difference in rosin bond melting temperatures between cones on different trees, or between individual cones on the same tree, or even the possibility that the rosin bond is absent on some cones. Whatever the explanation, the habit is not fixed throughout the life of the tree since a complete reversal takes place between youth and maturity. The fact that the percentage of cones borne in a closed condition increases with the age of the tree results in an increasing storehouse of seeds available to reproduce

the species in case of fire. However, and in spite of the fact that lodgepole pine commences cone production at a very early age, a very small percentage of the cones in a light crop are borne closed. Consequently, adequate reproduction following fire in juvenile stands would be very unlikely. Mason (1915) reports that in one area studied, five-sixths of the cones opened at maturity in stands less than 55 years of age, while in the stands over this age only one-fourth of the cones opened. The present study suggests that on the area studied the critical age is somewhat younger than this, and lies somewhere between the ages of 17 years and 55 years.

In the management of lodgepole pine stands the forester is vitally interested in the supply of seed at his disposal in the persistent cones. The fact that at some time prior to a stand age of 55 years the trees commence bearing their cones closed means that, no matter when he harvests his crop after this age, the forester is assured that the majority of the cone crop retains its seed and is available for his use. Since it is unlikely that he will ever wish to make a harvest cut before this age, his interest will centre around any difference in quantities of stored seed by crown classes in his maturing or mature stand. Unfortunately this study did not include observations in stands just reaching maturity but from the data obtained from immature stands of 55 years of age, and overmature stands varying from 140 to 250 years, it is apparent that the greatest number of closed-cone trees per acre are found in the codominant and intermediate crowns. The information gathered on the comparative number of cones borne by each crown class was rather meagre but there was no suggestion that there was any decrease in numbers of cones borne by individual trees in the first three classes (dominant, codominant and intermediate).

If the annual release of seed from cones opening at maturity on standing trees is to be relied upon for the new crop, then it must be recognized that the older the stand, the lighter the supply of seed. When stands become overmature they cease to contain open-cone trees, and the proportion of trees of intermediate cone-bearing characteristics is greatly reduced. Therefore, at such ages, residual stands cannot be expected to release much seed annually.

Harvest cuttings such as shelterwood or seed-tree will be most successful from the point of view of subsequent regeneration if the residual trees are selected with a view to their open-cone bearing characteristic and to the size of the cone crop borne. The open-cone heavily bearing dominant would best satisfy the requirements of an annual seed supply from thrifty windfirm trees.

SUMMARY

Lodgepole pine trees are reputed to store large amounts of viable seed in their persistent serotinous cones. Such storage can be of immense assistance in the management of a forest, and in order to obtain more detailed knowledge of the nature and amounts available, a detailed study was undertaken on the Kananaskis Forest Experiment Station in the subalpine region of Alberta. The persistent cone crop borne on individual open-grown and stand trees was tallied in detail, as well as the relationship of the crops borne to stands, and to size and crown classes within the stands. Three different age classes of stands were examined, namely juvenile (17 years), immature (55 years), and overmature (140 to 250 years). The results of the investigation are summarized as follows:

1. Although a single tree usually behaves consistently in the cone crop it produces, there is a wide variation between trees.
2. A few trees, at least under stand conditions, apparently are non-fruiting, the percentage increasing with increased suppression.

3. While pronounced variations can be expected in the size of the annual crop on any individual tree, no years of nil crop on any fruiting tree studied were experienced during at least the past 20 years.
4. Individual cones of lodgepole pine are either non-serotinous or serotinous. That is, they open immediately they mature, or they remain closed until they are subject to a considerable heat (45°C. or more). Such temperatures do not occur in the crowns of trees under natural conditions.
5. Individual trees can bear all, or practically all, their cones closed, or all their cones open, or they can bear a mixture. However, the pattern, once set, remains unchanged for many years.
6. The great majority of trees in juvenile stands (17 years) bore their cones open, while similar majorities in immature stands (55 years) and overmature stands (140–250 years) bore theirs closed. Thus the pattern reversed between the 17th and 55th years. None of the trees in the overmature stands could be classed as open-coned.
7. The habit of bearing open or closed cones does not appear to have any connection with the amount of lime in the soil, or the existing moisture conditions, as has been suggested. It appears more likely to be an inherited characteristic.
8. There is an annual release of seed, at the time of cone ripening, from non-serotinous cones. Previous seed-trap studies indicate that the quantities of seed from such a source in a stand of lodgepole pine are quite light, and the present study suggests that the amount decreases as the stand gets older.
9. Fruiting habits of stand trees vary in a similar fashion to those of open-grown trees, with the exception that individual stand trees bear smaller quantities of cones.
10. If "suppressed" trees are left out of account, the evidence obtained did not suggest any relationship between the size of cone crop and crown position in the stand. Since the sample was small, this conclusion should be treated with caution.
11. Under immature stand conditions the dominant trees exhibit the greatest percentage of closed-cone trees. The percentage of such trees decreases with increasing suppression (or with decreasing diameter class).
12. The ability to produce cones occurs at a very early age in lodgepole pine, although the percentage of cone-bearing trees decreases, at least in sapling stands, with major increases in altitude. At elevations between 4,800 and 5,700 feet, cone-bearing became general by the time trees reached a height of seven feet.
13. Since young stands are not prolific fruiters, and since very few of the cones are serotinous, it is suggested that adequate reproduction following fire would be unlikely.
14. Since the trees in mature stands fruit prolifically, and since most of the cones borne are serotinous, fire will usually leave an adequate, if not superabundant, supply of seed available for regeneration. While a similar supply of seed is available on overmature pine it must not be forgotten that such stands are breaking up and the percentage of pine in comparison to other species is rapidly diminishing. Under such conditions the available supply of pine seed will be considerably less.
15. In shelterwood or seed-tree cuts where trees are to be relied upon to seed annually, those classed as open-coned will be the most efficient and should be reserved.

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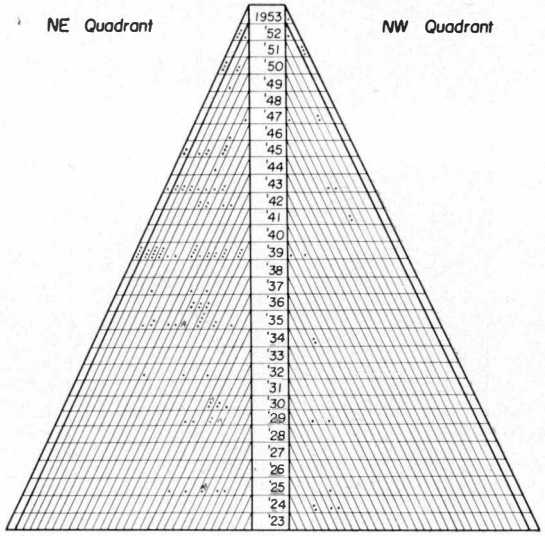
APPENDIX I

Tree # 11

Lodgepole Pine – K.F.E.S.
Age - 78 years
Ht. – 49.5'
D.B.H. – 6.6"
Intermediate

NE Quadrant

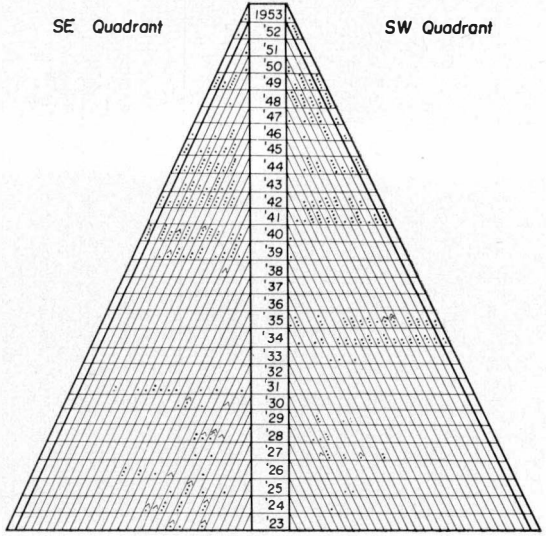


NW Quadrant

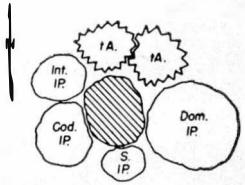
Annual Height Growth

1953	7.0"
'52	5.3
'51	6.8
'50	4.3
'49	4.4
'48	4.8
'47	4.1
'46	3.2
'45	5.5
'44	7.2
'43	6.4
'42	12.3
'41	7.7
'40	7.2
'39	6.6
'38	9.2
'37	4.5
'36	4.4
'35	4.2
'34	5.1
'33	6.1
'32	6.3
'31	6.1
'30	8.8
'29	6.0
'28	6.2
'27	7.9
'26	11.9
'25	8.9
'24	9.6
'23	6.9

SE Quadrant



SW Quadrant

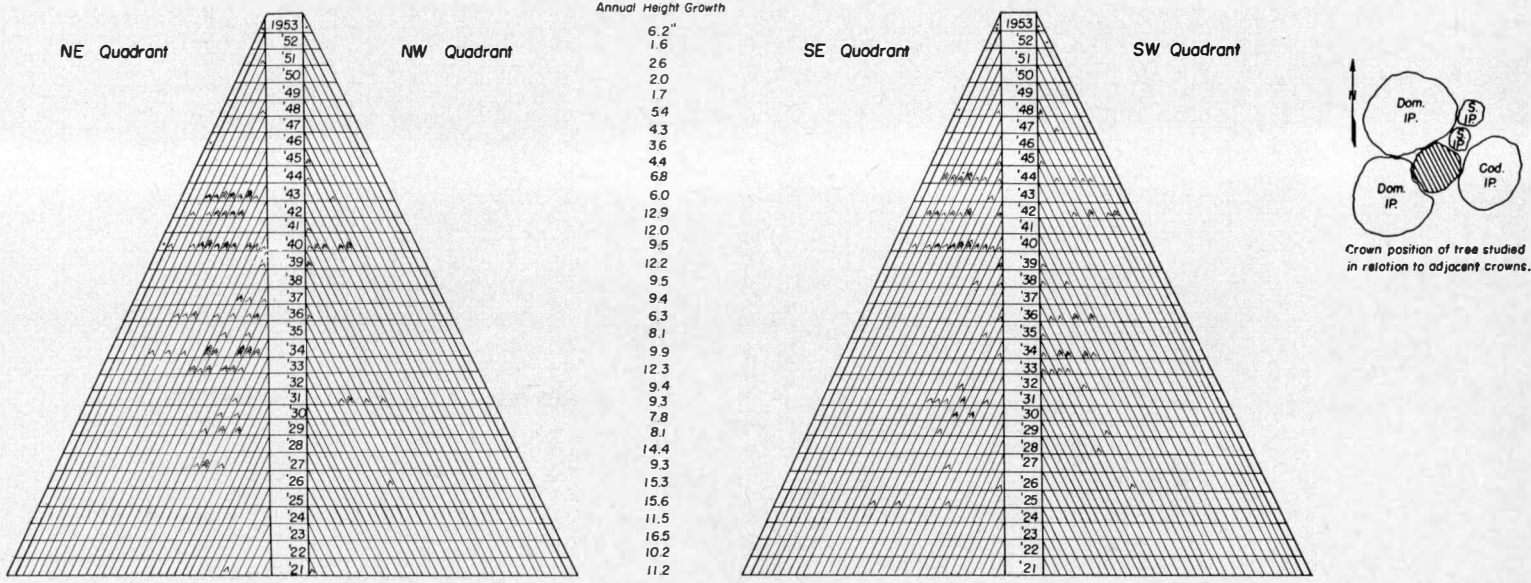


Crown position of tree studied in relation to adjacent crowns.

APPENDIX II

Tree # 10

Lodgepole Pine – K.F.E.S.
Age – 54 years
Ht. – 40.7'
D.B.H. – 4.7"
Intermediate



Crown position of tree studied in relation to adjacent crowns.

APPENDIX III

Tree # 3

Lodgepole Pine – K.F.E.S

Age – 56 years

Ht. – 52.4'

D.B.H. – 8.8"

Open – grown

Legend . closed cone
^ open cone