chromosome arms were found to be significant, and structural change by gradual accumulation of small duplications has been suggested as an evolutionary process in Pinus, despite the extremely strong selection against change of length which seems to have prevailed for many millions of years.

Chromosome structure therefore appears to offer a further useful criterion for determining species relationships.

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Multinodality, Branching, and Forking in Lodgepole Pine (Pinus contorta var. murrayana Engelm.)[1]

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(Received for publication April 16, 1969)

Introduction

Environmental sources of variation in multinodality, branching, and forking have long been recognized (cf. DOAK 1935; STONE and STONE 1943). Some earlier investigators postulated that inherent differences in these traits may exist among trees (cf. SHAW 1914; DOWNS 1949). Recent reports have shown this to be the case (FRANKLIN 1965).

Multinodality, branching, and forking were studied in 6 wind- and 9 control-pollinated 6-year-old families of lodgepole pine (Pinus contorta var. *murrayana* ENGELM.). The objectives were: (1) to observe the frequency and distribution of branch whorls in young trees; (2) to describe the branching and forking habits in young trees; and (3) to determine the relative importance of genetic, developmental, and environmental influences on multinodality, branching, and forking. Because of the relatively small number of families and the juvenility of the material, the results of the study can be applied only to the population actually measured.

Materials and Methods

Parent Trees

Six trees were selected to represent extreme and intermediate phenotypes in branching and forking characteristics. All grew in the Lake Tahoe Basin, at an elevation of 6,500 feet, near Meyers, California. There were two straight, unforked trees with light, flat-angled branches; one tree with three forks, and light, moderately flat-angled branches; two trees with four forlrs each, and moderately heavy flat-angled branches; and one tree with 10 forks, and extremely heavy, steep-angled branches. For more detailed information on the parent trees, see FRANKLIN (1965), Table 1, pp. 11.

Breeding *and Nursery* Procedures

Breeding procedures followed those described by CUMMING and RICHTER (1948). Of the 30 possible controlled crosses, all except selfs were attempted in 1957. Control- and wind-pollinated cones were collected in 1958. Sufficient numbers of seed for the study were obtained from nine of the 30 attempted controlled crosses.

Sowing was done in 1959 in the nursery at the U. S. Forest Service's Institute of Forest Genetics near Placerville,

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The authors acknowledge the help of Professor WILLIAM J. LIBBY, School of Forestry and Conservation, University of California, on statistical problems and of Mrs. RITA R. TAYLOR, formerly Geneticist, Pacific Southwest Forest and Range Experiment Station, on electronic data processing.

California. The nursery is about 45 miles west of the parent trees, at an elevation of 2,700 feet. Stratified seeds were sown at 6 by 6 inch spacing. Ten seeds from each cross were planted in rows in each of two blocks. Families were arranged systematically in the first block, but randomly in the second block.

Measurements

Seedlings were measured in their fifth growing season, in 1963 and again in 1964. Data included seedling height, numbers and angles of branches in each whorl, numbers of forks, apparent cause of forking, and positions of minor whorls in relation to the total distance between annual major whorls. A major whorl was defined as the first whorl of branches produced in a given year. Minor whorls were defined as all other whorls on the same annual shoot.

Branch angles were measured to the nearest 10 degrees with a protractor. Branches diverging 20 to 40 degrees from the main stem were arbitrarily designated as vertical branches. Those diverging 50 to 90 degrees were designated horizontal. And those which diverged less than 20 degrees from the main stem and were dominant or codominant to the main stem were designated as forks. Other branches diverging less than 20 degrees from the main stem were classified as ramicorn branches, but because only a few of these were found, the category was disregarded .

Two seedlings were left in each family row after the 1963 measurements; others were cut to facilitate measurement of all seedlings. In July 1964, data on the uncut trees were taken again. Branch numbers and angles, and numbers of forks were the only data taken in 1964 for the 1963 and 1964 whorls.

Analyses[3])

The basic analysis was a split-plot analysis of variance. Nursery blocks were treated as replications, families as whole-plots, and years as sub-plots (STEEL and TORRIE 1960). This was a completely fixed model with two replications, 15 whole-plot treatments, and a maximum of four sub-plot treatments.

The small number of families (15) precluded reliable estimation of either variance components or parent- offspring correlations.

Interrelationships of characteristics were studied using correlation analyses. The correlation coefficient (r) and the coefficient of determination (r^2) were calculated from plot means.

Results

Multinodality

Annual Trends in Number of Minor Whorls per Major Whorl

Annual differences in the production of minor whorls per major whorl were found statistically. In the first and second growing seasons, most seedlings were uninodal. In each of the following three growing seasons almost all seedlings produced at least one minor whorl. On the 1964 shoot, only 0.87 of a minor whorl was evident at midsummer just after winter buds had completely extended.

Genetic Effects

Analysis failed to show significant differences among families in number of minor whorls per major whorl.

[3]) For further details see FRANKLIN (1965).

Table 1. — Number of minor whorls arrayed by year of shoot elongation.

Year of shoot elongation	When counted	Mean
1959	1963	0.000
1960	1963	0.20
1961	1963	1.23
1962	1963	1.52
1963	1963	1.41
1963	1964	[1])1.16
1964	1964	0.87

[1]) The decrease from the preceding count reflects statistical sampling variation between data collected from all trees in 1963, but only from uncut trees in 1964.

Positions of Minor Whorls Along the Annual Shoot

Twenty percent of all annual shoots lacked minor whorls, 51 percent had one, 25 percent had two, 4 percent had three, and none had four or more. Distribution patterns of minor whorls along the annual shoot differed according to the number of minor whorls. If only one minor whorl was present, it was found most often along the upper third of the annual shoot *(Figure 1A)*. If there were two minor whorls, the lower was most often in the lower 40 percent of the annual shoot. The upper was usually between 70 and 80 percent of the distance to the next major whorl *(Figure 1B)*. If there were three minor whorls, one usually occurred along the lowest 20 percent of the annual shoot, and the other two were almost equally frequent between 40 and 90 percent *(Figure 1C)*. Minor whorls were never found in the upper 10 percent of the annual shoot.

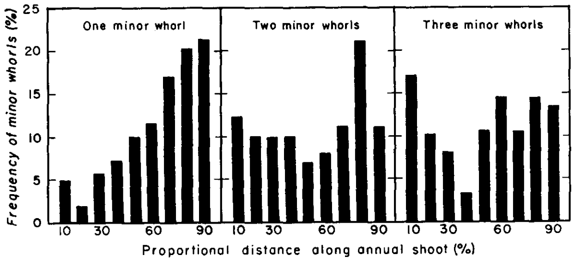

Figure 1. — How often minor whorls were found for each major whorl at various positions along the annual shoot varied according to number of such whorls. The number of observations were: one minor whorl = 458; two = 401; and three = 87.

Branching

Numbers and Angles of Branches at Major and Minor Whorls

Major whorls averaged 6.6 branches: 6.1 horizontal and 0.5 vertical. Minor whorls averaged 4.2 branches: 4 horizontal and 0.2 vertical. Numbers of horizontal and vertical branches at major whorls were significantly correlated with numbers at minor whorls (r = 0.52 and r = 0.61, respectively; $\alpha = .05$).

Angles of horizontal branches at major whorls averaged 71.4 degrees. Angles of horizontal branches at minor whorls averaged 78.5 degrees. Average horizontal branch angles at major and minor whorls were correlated (r = .61). Average vertical branch angles at major and minor whorls were equal but uncorrelated (r = .01).

Genetic Control of Branch Numbers and Angles

Family differences in total number of branches at major whorls and at minor whorls were statistically significant. Average angle of horizontal branches at major whorls also varied significantly by families.

Relationship between Height and Number of Branches

Seedling height at 5 years was significantly correlated with total numbers of branches per year ($r = 0.67$). Average angle of horizontal branches was significantly correlated with height at 5 years ($r = 0.52$).

Annual Trends in Numbers and Angles of Branches at Major and Minor Whorls

Total numbers of branches at major whorls successively decreased during the second, third, and forth growing seasons, but numbers on the first annual shoot were about equal to the numbers on the fourth *(Figure 2)*. Numbers of horizontal branches at minor whorls decreased each year, but numbers of vertical branches at minor whorls showed very little variation and no consistent trend *(Figure 2)*. Differences among years in numbers of vertical and horizontal branches at major whorls, and numbers of horizontal branches at minor whorls were statistically significant.

Horizontal branch angles at major and minor whorls were greater in each successive growing season over the 4-year period. Horizontal angles at major whorls were 13 degrees steeper than at minor whorls in 1960, but by 1963, horizontal angles at major and minor whorls were about equal *(Figure 3)*. Differences among years in average horizontal branch angles at major and minor whorls were highly significant. Vertical branch angles at major whorls showed little annual variation. A slight increasing trend in vertical branch angles at minor whorls was evident *(Figure 3)*.

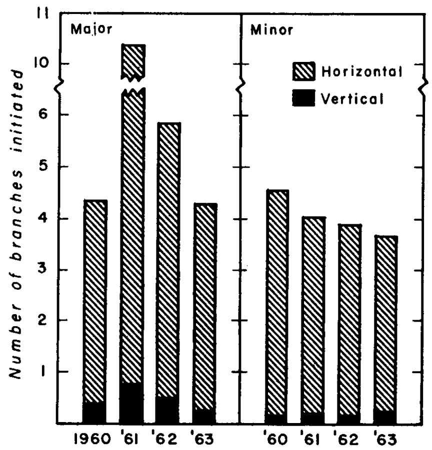

Figure 2. — The number of horizontal and vertical branches initiated at major and minor whorls, by year of annual shoot, fluctuated.

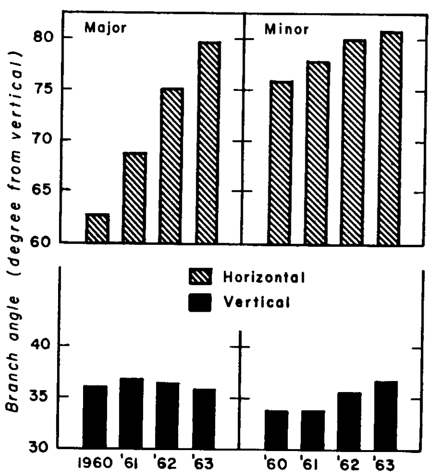

Figure 3. — Angles of horizontal and vertical branches at major and minor whorls by year of annual shoot.

Table 2. — Numbers and angles of branches on the 1963 annual shoot, measured in 1963 and again in 1964.

A. Angles of Horizontal Branches			B. Angels of Vertical Branches		
Year measured	Major whorls	Minor whorls	Year measured	Major whorls	Minor whorls
1963	71.0°	64.1°	1963	35.6°	32.9°
1964	79.7°	81.0°	1964	35.7°	36.7°
Net increase	8.7°	16.9°	Net increase	0.1°	3.8°

C. Numbers of Vertical Branches			D. Numbers of Horizontal Branches		
Year measured	Major whorls	Minor whorls	Year measured	Major whorls	Minor whorls
1963	1.1	1.0	1963	4.8	2.8
1964	0.2	0.2	1964	4.2	3.7

Branches on the 1963 annual shoot were measured in 1963 and again in 1964. Branch angles in the second year were consistently flatter than in the first year. Horizontal and vertical branches at minor whorls showed the greatest changes in branch angles *(Tables 2A and 2B)*. Consistent with the increase in branch angle, numbers of branches classified as vertical decreased markedly from 1963 to 1964 *(Table 2C)*. Numbers of horizontal branches at minor whorls showed a substantial increase. But the numbers of horizontal branches at major whorls did not show a concomitant increase. Perhaps the smaller sample size in 1964 introduced enough random sampling variation to obscure the expected increase *(Table 2D)*.

Forking

Forking at Major and Minor Whorls

Major whorls contained 80 percent of all forks. The difference in number of forks at major and minor whorls was statistically significant ($\alpha = 0.005$), based on a nonparametric analysis.[4])

Genetic Control of Forking

Family differences in number of forks per tree were significant with 90 percent confidence. Number of forks per forked whorl was used as a measure of propensity to form multiple forks. Family differences in this trait were significant at the 95 percent level.

Influence of Forking on Height

Correlation analysis failed to show a relationship between seedling height and number of forks per tree.

Annual Trends in Forking

Number of forks produced per seedling per year increased each year. Total number of forks per seedling approxi-

[4]) Done by CHARLES H. LITTLE, graduate student, University of California, Berkeley, 1964.

mately doubled in 2 consecutive years *(Table 3)*. Highly significant differences among years for number of forks per major whorl were found. Annual differences at minor whorls were not significant.

In 1963, 1 fork per seedling was recorded for the 1963 annual shoot. When re-examined in 1964 the number of forks for the 1963 annual shoot was only 0.7.

Only two statistically significant relationships between forking and branching were found. Average vertical branch angle was significantly negatively correlated with number of forks both at major and at minor whorls ($r = -.54$, and $r = -.52$ respectively).

Discussion and Conclusions

Multinodality

Multinodality was frequent and appeared to be the normal condition. Minor whorls were characteristically produced in one or more of three different ways: (1) by the winter bud; (2) by late season flushing; and (3) by growth of previously latent buds. Only a few minor whorls were formed by growth of previously latent buds. These findings corroborate SHAW's (1914) contention that *P. contorta* is characteristically multinodal.

The relatively small number of minor whorls on the 1964 annual shoot was not unexpected *(Table 1)*. When the count was made at midsummer, late season flushes were seen on some seedlings. Those late season flushes added minor whorls to the 1964 annual shoot. In addition, sprouting of latent buds in 1965 would add even more. This was true in 1964 when many minor whorls developed from latent buds on the upper portion of the 1963 annual shoot. Therefore, observations on multinodality should be delayed until the second growing season if any whorls produced by sprouting of latent buds are to be counted.

The distribution pattern of minor whorls along the annual shoot varied according to the number present. This phenomenon reflects the differences in origin of the minor whorls. Minor whorls formed in the winter bud were on the lower portion of the annual shoot. Minor whorls resulting from summer flushing were concentrated in the upper portion of the annual shoot. Sprouting of latent buds occurred with equal frequency along the annual shoot.

Results of this study concerning the genetic control of multinodality are inconclusive.

Branching

Branching traits differ markedly at major and minor whorls, emphasizing the over-all differences between the two whorl types. Major whorls had more branches than minor whorls. Branches at major whorls were more steeply inclined than those at minor whorls. Branching traits,

Table 3. — Mean annual and total number of forks per seedling.

Year	Forks per seedling per year	Total forks per seedling
	No.	
1960	0.00	0.00
1961	0.24	0.24
1962	0.33	0.57
1963	[1])0.70	1.27

[1]) Excluding insect-caused forks.

number and angles, showed moderately high correlations between major and minor whorls.

Branches were characteristically more steeply inclined in their first growing season than in later seasons. And branches in the lower whorls were more steeply inclined than those in the upper whorls, in spite of the tendency for branches to flatten out with age. Therefore, measurements of branch angle at a given whorl should be delayed at least until the second growing season, since most of the flattening occurs the first and second growing seasons.

The tendency of branches to flatten out in their first few growing seasons has been reported for *Picea abies* (L.) KARST. by PRIEHAUSSER (1958), for *P. sylvestris* L. by JANKIEWICZ (1967), and for several *Populus* varieties by SAUER (1959). SNYDER (1961) recognized and equilibrium zone for branch angle in the middle to upper third of crowns of longleaf pines, where branch angle had more or less stabilized; KELLISON (1967) found a similar zone in tulip poplar. Both authors found that to best characterize the branch angle of a tree with a few samples, measurements should be taken within this equilibrium zone. Seedlings measured in this study were too young to have developed an equilibrium zone.

Genetic control of branching characteristics, as indicated by significant F-tests for family effects, corroborates reports by BANNISTER (1959), GODDARD *et al.* (1960), and NIKLES (1962) for other species.

The moderately strong correlation between total number of branches and height at 5 years probably reflects overall vigor to some extent, i. e., the most vigorous trees grow tallest and produce the most branches, other factors being equal. Similarly, a branch which grows faster may flatten out more in response to greater weight pulling down on a longer lever arm. This reaction could explain the positive correlation between height and horizontal branch angle. These findings are similar to those reported by SAUER (1959).

Forking

A twofold annual increase in number of forks per tree was observed for the third and fourth growing seasons. Multinodality has relatively little influence on forking because only 20 percent of all forks were produced at minor whorls. Presumably this high rate of increase in number of forks per seedling would decline as crown competition became more severe.

Branches tended to flatten out during their second growing season *(Table 2)*. Many of the very small branches in the upper 1963 minor whorls were at angles of ten degrees or less from the stem, and were counted as forks in 1963. In 1964, many of those "forks" in the highest minor whorls had flattened out and were identified as branches. To distinguish positively between very small-angled branches and forks in their first growing season was impossible.

Insect-caused forks were identified in 1963 and 1964. In 1963, insects caused at least 10.5 percent of the forks. But, even when forking caused by insects was discounted, the number of forks increased in each succeeding year.

Frost damage can cause forking when late season flushing exposes succulent tissues of the main leader to early fall freezes. The results of frost damage were observed on some seedlings in the summer of 1963. The main leader was dead or dying and two or more buds in the uppermost whorl had assumed codominance, thus initiating one or more forks. Leader breakage or dieback caused by pathogenic agents presumably could cause similar results.

Many forks were observed where there was no indication of pathological or mechanical damage. It seems quite likely that many forks resulted from physiological control of apical dominance, in the absence of injury. On that basis, the relatively strong negative correlation between branch angle and number of forks at a whorl may indicate that the buds that potentially can produce the most steeply inclined branches, have the greatest tendency to become forks. The negative correlation between number of forks and number of branches per whorl lends support to this interpretation.

Genetic control of forking is necessarily related to causal the factors for forking. Insect resistance and frost hardiness are genetically influenced traits which were directly related to the incidence of forking. Genetic control in that case would be indirect. Physiological factors which affect the incidence of forking may be under more direct genetic control. Considering the diversity of causal factors and related genetic systems, genetic control of forking by a few major genes is not likely. It is more likely that genetic control of this trait is quantitative in nature.

Summary

Multinodality, branching, and forking were studied in six wind- and nine control-pollinated families of *Pinus contorta* var. *murrayana* ENEGLM. This species typically produces multinodal annual shoots by (1) formation of multinodal winter buds, (2) late-season flushing, and (3) sprouting of latent buds. The first, or major, annual whorl in a season has more branches, and steeper-angled branches than minor whorls produced later in the season. Major whorls contained 80 percent of all forks observed.

Branches had steeper angles in their first growing season than in subsequent seasons. This flattening phenomenon caused some very small branches in minor whorls to be classified as forks in the first season and reclassified as high-angled branches in the second season. Branches produced in each succeeding year had flatter angles than those produced in previous years.

Average number of forks per tree doubled annually from the second through the fifth year. Insects caused a significant but small proportion of the forks: about 10 percent in 1963. Frost injury was the apparent cause of a large proportion of forks, but the cause of many forks was not apparent. Lack of apical dominance due to physiological conditions was hypothesized as a probable cause of forking.

Genetic control of branching traits and forking was indicated by large amounts of variation associated with families. Nonparametric tests of data on families for presence or absence of forks also indicated genetic control of forking.

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The incidence of graft incompatibility with related stock in Pinus çaribaea Mor. var. hondurensis B. et G.

By M. U. SLEE[1] [2]) and T. SPIDY[1])

Introduction

Some grafted scions do not develop satisfactorily even though they appear to have become successfully established on the stock plants. This phenomenon is known as incompatibility or uncongeniality and has received considerable study from horticulturists (see MAHLSTEDE and HABER, 1957; HARTMANN and KESTER, 1959; MOSSE, 1962 and numerous others).

Failures due to incompatibility are a more serious problem in forestry than in horticulture. In horticultural practice grafts are made between scions of one clone and stock plants of another clone, and when particular combinations of clones prove incompatible other compatible combinations with the same attributes can be used instead. However, the forester usually propagates selected breeding trees by grafting these not onto clonal stocks, but onto stock plants raised from seed. In these circumstances the proportions of grafts that become incompatible vary from clone to clone. Severely affected clones may have to be omitted from the breeding programme, and such omissions are serious losses. In less severe cases the development of incompatibility also presents problems; incompatible grafts cannot be detected for some time after establishment, and their occurrence modifies irrevocably a planned graft lay-

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