

more intensive investigation in the Central States is probably valid for Lower Michigan as well. But in the more severe climate of Upper Michigan, northern Wisconsin, and Minnesota one should confine the search for superior seed sources to areas where the mean January temperature is less than 20 degrees F. This would reduce the chance of testing sources that are ill-adapted to the colder winters without reducing the amount of potential improvement.

#### Abstract

Seventeen seed sources of eastern white pine from throughout the species' natural range were studied in nurseries in Upper Michigan and Wisconsin and at 5 years of age in field plantings in Minnesota, northern Wisconsin, and Upper and Lower Michigan. No seed source or group of sources was consistently best either in the nursery or in all field plantings. The ranking (by height) of the seed sources growing in Lower Michigan very strongly re-

sembled the ranking of the same sources growing in southern Illinois, Indiana, Ohio, and North Carolina. There is little resemblance to the ranking of the same sources being grown in Wisconsin and Minnesota. The data suggest that the mean January temperature of the seed source will be a very useful guide in selecting sources for further testing in Minnesota and Wisconsin.

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## Cone Distribution in Crowns of Slash Pine (*Pinus elliottii* Engelm.) in Relation to Stem, Crown and Wood Increment<sup>1)</sup>

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Nitrogen fertilizers applied to slash pine *Pinus elliottii* ENGELM.) seed orchards in North Florida, increased the production of female cones (GODDARD and STRICKLAND, 1965). Similar observations have been reported in other pines and plant species. In pine, total cone counts are made to determine fertilizer effects. Pine buds and tissues are often removed for chemical analysis in physiological studies of cone induction or in studies of fertilizer effects on nutrient deficiencies. They are generally selected at random from the top or lower parts of the tree. Chemical assay of microscopically determined anatomical components of these samples (KUPILA-AHVANNIEMI et al., 1966) probably reflect microsite environmental differences.

The present study tested the hypothesis that female strobili are randomly distributed in *Pinus elliottii*. Such an assumption is generally made in recording reproductive responses and in removing tissues for chemical assay. Our results show that a non-random cone distribution often occurs in pine. Branch, crown, and wood growth patterns were measured as potential indicators of differential cone production. Possible reasons for a skewed pattern of female strobili formation, and implications for selecting tissue for physiological studies are discussed.

#### Related Literature

Sources of stimulation and environmentally induced differences in cone formation in pine have been reported. Flowering generally occurs in forest trees after a certain size or number of annual growth cycles (WAREING, 1959). This averages four to five years for pine (RIGHTER, 1939) but exceptions occur. *P. mugo* may produce staminate cones its first year (MERGEN and CUTTER, 1957); *P. densiflora* and

*P. sinensis* produce ovulate cones at two years (RIGHTER, 1939). *P. nigra* and *P. sylvestris* produce staminate cones earlier than ovulate cones. Absolute size has been proposed to control male flowering while some other factor induces female flowering (MATTHEWS, 1963). Slash pine usually produces cones of both sexes at about five years, and nitrogen fertilizer treatment appears to hasten the onset of larger crops.

Early flowering has been induced with gibberellic acid in *Cryptomeria* (SHIDEI et al., 1960) and with NAA and 2, 4-D in horticultural crops (PRIOL, 1962). In general, growth substances have been unsuccessful in hastening flowering in pine (MIROV and STANLEY, 1959) and have been most useful in horticultural crops through their effect on abscission.

Hormones and nutritional levels appear to be involved in pine sporangia induction. Treatments which probably alter the inherent levels of growth substances and nutrients usually stimulate formation. Some of these treatments are: (a) orientation of branches (LONGMAN and WAREING, 1959), (b) meristem removal by branch-pruning (MELCHIOR and HEITMÜLLER, 1961) or root pruning (HOEKSTRA and MERGEN, 1957), and (c) girdling or strangulation (MATTHEWS, 1963).

Another indication that a bud-derived substance is active in formation of female strobili is that ovulate cones occur in the middle or upper crown on low-order branches where growth is most rapid and growth substances presumably highest (ANIKEYEVA and MININA, 1959; HARD, 1964; WINJUN and JOHNSON, 1964). The effect of bud removal on female flowering decreased from top to bottom leaders, and from branch tip to the insertion point of the branch on the stem (MELCHIOR and HEITMÜLLER, 1961). This effect is reversed for male flowers and conforms to the general observation that male flowers occur in the lower crown on higher-order branches (ANIKEYEVA and MININA, 1959).

Increasing flower numbers and seed production after the tree attains the physiological age or condition to flower

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is a concern of foresters interested in seed production. Increased seed production by mature trees in response to thinning is well documented (MATTHEWS, 1963). GODDARD (1964) reported that in a young slash pine seed orchard, the highest yields occurred in the most dense stands. The latter report, however reflects a larger number of flowering individuals rather than any influence of spacing since individual trees had fewer cones. In general, thinning stimulates growth which is usually accompanied by an increase in flower production. It is difficult to discern whether the flowering response is primarily light or growth related.

Variation in flowering and seed yields in pine have been related to several environmental factors, including light, temperature, moisture and nutrients. Formation of female cones was reported to be most profuse in pines grown in full sunlight, and the formation of male cones most profuse under shade; but SARVAS (1962) found more male flowers on the south side where illumination was greatest. Illumination differences, were suggested by GAL'PERN (1956) as the possible reason for flowerless branches occurring near branches with many flowers. MIGHTA (1960) imposed several degrees of shade on *Cryptomeria* trees; no flowers formed below 15 percent of full sunlight, and flower numbers increased up to full sunlight. Day length was reported to have a similar effect. However, MIROV, (1956) reported flowering response of pine to be insensitive to photoperiod. MATTHEWS (1955) examined 30 years of cone production data and meteorological variables and concluded that yield correlated with summer temperature and sunlight. HOLMSGAARD and OLSEN (1960) found on *Fagus* that only seed yield and temperature correlated. They suggested that light was involved only to the extent that it is related temperature.

Air temperatures above the long term mean have been related to increased tree seed production. In *Picea* (ANDERSON, 1965) and *Pinus* (KRECETOVA, 1960) chromosome aberrations occurred at low temperatures and decreased pollen fertilization. Thus, the temperature effect on seed or cone yield may be more an effect on pollen viability and fertilization than on flower initiation.

Female bud development was related to air moisture deficit by GIRGIDO (1960) and to spring rains by POZZERA (1959). However, HIROV's data (1964) disagreed with GIRGIDO's hypothesis and HIROV reached the usual conclusion that flower initiation was not related to moisture supply.

PRIOL (1962) concluded, in a review on reproductive ontogeny of apple, that light is the most significant ecological variable promoting bud differentiation. Female pine strobili, like apples, occur on the periphery of the upper crown. Many believe light affects carbohydrate synthesis and develops high C/N ratios which induces the formation of reproductive structures. Carbohydrates accumulation may actually follow induction instead of being the causal agent (Stanley, 1958). A more subtle role for light in a phytochrome-like system may be involved.

EIS *et al.* (1964) reported that during good seed years the bole diameter increments were reduced in *Picea*. They concluded that carbohydrates were essential primarily for cone development and not related to flower bud differentiation.

WENT (1952) considers all plant responses at temperature dependent. Light and temperature effects, particularly with photoperiod insensitive large plants like pine, are difficult to separate. Both factors probably mediate induction of strobili. Aerial temperatures would certainly differentially control levels of internal organic metabolites available for growth.

The effect of nutrient elements on stimulating flowering in forest trees were classified by MATTHEWS (1963). Nitrogen or complete fertilizers most often increased seed production. Reports of stimulation by phosphorus have since appeared (HALL, 1964 and HIROV, 1964). SWEET and WILL (1965) and LYR and HOFFMANN (1964), in sharp contrast, conclude that fertilizers reduced female flowers. In their studies nutrient deficiencies, especially nitrogen, increased reproductive organ formation in trees.

Differential response in reproductive organ formation in pines can occur from added nutrients and changes in levels of light and temperature. Cone production on the whole tree is generally considered to be affected by such treatments. Internal differences induced by local shading, different light levels, micro-temperature or directional root absorption could conceivably induce non-random differences in reproductive bud formation in trees. This would occur if the product of the inducing factor were not randomized during transmission to tissues associated with bud initiation.

Methods used in this study were designed to determine if non-random cone formation occurs, and if internal differences or environmental factors are related to patterns of cone production.

### Materials and Methods

Slash pine used in this study are located near the University of Florida, Gainesville, at latitude 29° N, and at a U. S. Forest Service research center 40 miles north at Olustee, Florida.<sup>3)</sup> The Gainesville seed orchards were established in 1956 and the Olustee orchards in 1957—59. Twenty four trees in Gainesville block 4, at 40' × 40' spacing and 24 trees in block 5, spaced 30' × 30' were assayed. Nitrogen treatments were applied annually to trees at Gainesville at 0, 8, and 32 oz./tree levels and the effects on cone production noted (GODDARD and STRICKLAND, 1965). Cones were counted on trees at all levels of nitrogen fertilization. In the Olustee orchard, cones on 48 trees spaced at 20' × 20' and fertilized with 150 lbs. of nitrogen/acre were counted.

For cone counting, tree crowns were divided visually into four quadrants relative to magnetic north. The counts were made from a step ladder placed on the east and west sides of the tree. For ease of visual detection cones were counted in spring before expansion of needles on the new shoots.

Female strobili data by quadrants on individual trees were collected in block 4 in 1965 and 1966; on block 5, and on the trees at Olustee in 1966. Cone counts were made by east-west distribution in block 4 and 5 in 1967.

Stem wood cores were removed from trees in blocks 4 and 5 at breast height. One core was removed from each quadrant in block 4 and tree diameter recorded at sampling height. Cores were taken from the east and west sides in block 5.

Crown radius measurements at the cardinal directions, and the branch counts east and west were made on the block 4 trees.

Cone counts for all years were subjected to analysis of variance. Relationships between numbers of female strobili, tree growth, and direction were defined by partitioning the total variance component among the degrees of freedom.

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## Results

Cone counts in 1965 showed significant differences among the quadrants. Cones predominated in the NE and SE portions of the upper crown (Table 1). Partitioning individual degrees of freedom showed most of the variation was east versus west. The 1966 counts again showed significantly more cones on the east than on the west side of the trees in block 4; namely ca. 2100 vs. 1600 (Table 1). The east > west skewed cone distribution persisted in 1967 (Table 1). Most of the variance was attributable to the east > west comparison. In 1966, the size of the south > north component increased, but was still not significant.

Table 1. — Numbers of female cone distributed by crown quadrants. University of Florida orchard, block 4.

Quadrant	1965	1966	1967			
NE	840	977				
SE	730	1137		E 1403		
SW	550	887				
NW	600	782		W 1118		
Comparison	Sum of Squares			F		
	1965	1966	1967	1965	1966	1967
Quadrants	$\Sigma$ 20.77	$\Sigma$ 15.41		3.38*		
East vs. West	19.0905	12.03	6.35	9.31**	12.03**	5.30*
South vs. North	0.9943	3.22		1 ns	2.77 ns	
NW + SE vs. NE + SW	0.6817	0.16		1 ns	1 ns	

\* = Significant at 5% level of probability  
 \*\* = Significant at 1% level of probability  
 ns = non-significant  
 n = 24 trees

To examine female cone distribution on a different site, counts were made at Olustee, Florida (Table 2). Significant differences in cone distribution among the crown quadrants of the Olustee trees also occurred. Only half of the variance was accounted for in the east > west comparison which showed highly significant differences (Table 2). Further comparisons were made until it was found that

essentially all variation among the quadrants was attributable to the northwest < all other quadrants. For example, 356 flowers were counted in the northwest quadrant of the tree crowns while about 500 flowers were counted in each of the other crown portions.

Counts made in block 5 of the Gainesville, Florida orchard in 1966 and 1967 failed to show any directional differences (Table 3); even though the northwest quadrant averaged much fewer cones than other quadrants in 1966.

Radial differences in the crown were analyzed (Table 4) to determine if more crown, either through length or number of branches, accounted for more cones on the east than the west side of the trees. Significant differences among the crown radii measured in the cardinal directions existed

Table 2. — Numbers of female cones distributed by crown quadrants. U.S. Forest Service orchard, Olustee, Florida, 1966 count.

Quadrant	Number of Cones	Comparison	Sum of Squares	F
NE	500	Quadrants	$\Sigma$ 5.95	4.79**
SE	479	East vs. West	3.07	7.42**
NW	356	North vs. South	0.25	<1 ns
SW	486	NE + SW vs. NW + SE	2.62	6.33*
		NW vs. all others	5.62	12.12**

\* = Significant at 5% level of probability  
 \*\* = Significant at 1% level of probability  
 ns = non-significant  
 n = 48 trees

Table 3. — Numbers of female cones distributed by crown portion. University of Florida orchard, block 5.

Quadrant <sup>1)</sup>	1966	1967
NE	702	
SE	780	E 922
SW	779	
NW	653	W 910

<sup>1)</sup> There were no significant differences among any of the comparisons. n = 24 trees.

Table 4. — Crown and stem characteristics of trees in block 4, University of Florida orchard.

Measured	Direction	Mean Radius	Comparisons	Sum of Squares	F
Crown Radius		(meters)			
	East	3.12	Quadrants	$\Sigma$ 16.7500	4.17*
	South	3.14	S + E vs N + W	15.0416	11.23**
	North	2.83	E + N vs W + S	0.6666	<1 ns
	West	2.95	E + W vs W + S	1.0416	<1 ns
Number of branches	Direction	Mean Number			
	East	12	E vs W	12.000	5.23*
Stem diameter	Cone class	Mean dbh cm.	Among cone production classes	4.35	2.06 ns
	none	23.8			
	low	20.9			
	medium	23.2			
	high	22.7			

\* = Significant at 5% level of probability  
 \*\* = Significant at 1% level of probability  
 ns = non-significant  
 n = 24 trees

and further analysis showed that the branches were longer on the east and south sides of the crown. The radius north was considerably less than the other radii (2.83 vs. a mean of 3.01 m). GEIGER (1965) pointed out that during winter, edges with a northern exposure are completely deprived of sun and that light on the north side is always less than on the other crown exposures. This fact could partially account for the differential extension of the branches and the difference in cone numbers. *P. elliotii* growth flushes begin elongation in February or March at this locale.

The number of branches was actually slightly greater on the west, rather than the east side of the crown (Table 4). This occurrence could in part offset the increased crown on the east resulting from additional branch length.

Radial increment for each quadrant accrued at breast height since the trees began producing cones was found to be directly correlated with cone production (Figure 1). When variance among stem quadrants was partitioned by individual degrees of freedom, the component east > west was highly significant (Table 5). The south > north com-

parison was significant at the 10 percent level of probability. The stem radial increment was greatest in the same direction as the crown bearing the most flowers. In block 5 where no dominance of east over west in cone production was observed, the east-west radial increments were not significantly different. The results reported here seem to disagree with those reported by Eis *et al.* (1960).

Cone productivity of these trees, based on previous history of bearing female cones, does not appear to affect diameter increment. Stem diameters were measured for trees representing a gradient from previous production of zero to high cone yields. These means were not significantly different (Table 4). Gross stem diameters were not affected by production although the radial growth was skewed in favor of the east (Figure 1) and the side with greater cone production.

The distribution of annual growth increment was related to flower distribution (Figure 1). For the period (1963—1966), the radial growth from each quadrant was divided into early- and latewood (Figure 2). Differences among quadrants only occurred at the 10 percent level of probability (Table 6). Further analysis showed that at this same significance level, the north and west sides of the trees formed more latewood. When the latewood percentage for the northwest stem portion was compared to all the others (42.1% vs. 35—37%) the differences were highly significant. Latewood is presumably accrued during the

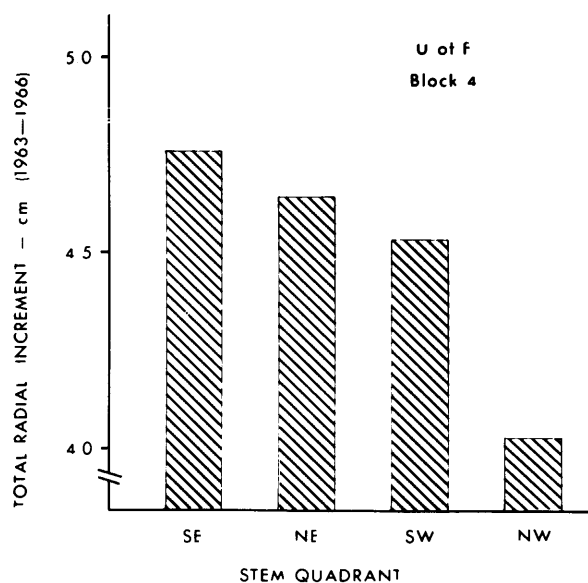


Figure 1. — Radial increments formed in the stem quadrants of *Pinus elliotii*.

Table 5. — Radial increment (1963—1966) by quadrant or direction in blocks 4 and 5 of the University of Florida orchard.

Block 4	Total increment	Comparison	Sum of squares	F
Quadrant	cm			
NE	111.3	Quadrants	$\Sigma$ 5.21	4.14*
SE	114.2	East vs West	3.19	7.61**
NW	99.3	South vs North	1.58	3.76 <sup>1)</sup>
SW	108.7	NE + SW vs NW + SE	0.44	<1 ns
Block 5	Total increment	Comparison	Sum of Squares	F
Direction	cm			
East	83.7	East vs West	3.65	<1 ns
West	79.9			

\* = Significant at 5% level of probability  
 \*\* = Significant at 1% level of probability  
<sup>1)</sup> = Significant at 10% level of probability  
 ns = non-significant  
 n = 24 trees

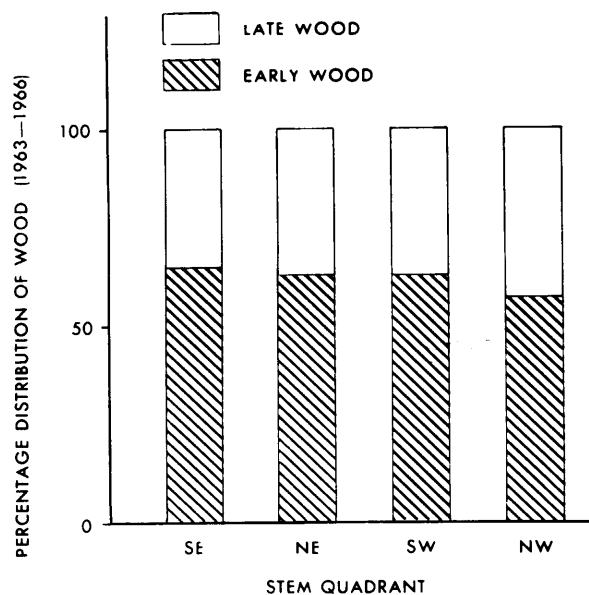


Figure 2. — Distribution of the radial increments between early- and latewood in the stem quadrants of *Pinus elliotii*.

Table 6. — Latewood percentage formation by stem quadrants. University of Florida orchard, block 4. Means of 24 trees.

Quadrants	Latewood percent	Comparisons	Sum of Squares	F
NE	36.9	Quadrants	$\Sigma$ 656.8	2.5 <sup>1)</sup>
SE	35.1	W vs E	318.3	3.62 <sup>1)</sup>
NW	42.1	N vs S	281.5	3.2 <sup>1)</sup>
SW	37.2	NE + SW vs NW + SE	57.0	<1 ns
		NW vs all others	592.0	6.76**

<sup>1)</sup> = Significant at 10% level of probability  
 \*\* = Significant at 1% level of probability  
 ns = non-significant

time of female strobili bud formation by slash pine. The northwest crown part consistently formed the fewest cones. Thus it appears from this distribution of latewood that materials not used in flower formation are possibly diverted to stemwood formation.

### Discussion

Female cones are often non-randomly distributed on crowns of pine trees. The trees are seldom symmetrical. The skewed pattern for the distribution of female strobili and the skewed circumference of the tree crown in this study are depicted by Figure 3. Our limited comparisons

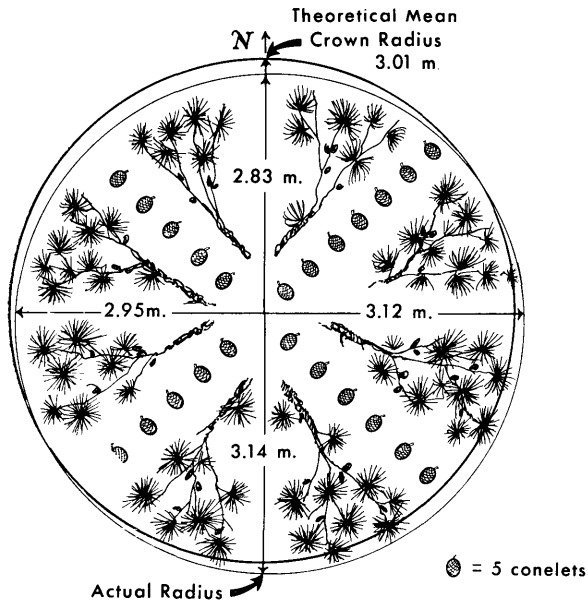


Figure 3. — Distribution of female cones on *Pinus elliottii* crowns compared to crown radial symmetry. Block 4, University of Florida orchard.

suggest that the absence of crown closure favored an east > west cone distribution pattern. At Gainesville in block 5 (Table 3), with closer spacing and greater crown closure, random cone distribution occurred. Although a significant east > west distribution occurred for the cone counts made at Olustee, the distribution was not as strong as that for block 4 in Gainesville. The Olustee orchard is younger but closer-spaced than the older, open-spaced trees in block 4 of the Gainesville orchard.

Light is probably the principle factor modifying pine reproductive growth pattern. Variations in light quality and quantity may be related to both spacing and geographical location.

Southern exposure in northern latitudes receive more solar energy than other sides. The northern side receives no direct solar radiation during the winter (GEIGER, 1965). A south > north dominance appears to occur only in the cone distribution at Olustee (Table 2). Primarily, the low cone production in the northwest accounted for the differences.

The reproductive response of pine is represented by several ontogenetic stages (Figure 4). Cone counts reported here reflect only initiation and emergence since counts were made after pollination in year two. The effect of the several environmental factors on all of these stages are usually measured by seed or cone yield data (MATTHEWS, 1963) which also reflect the success of pollination, fertiliza-

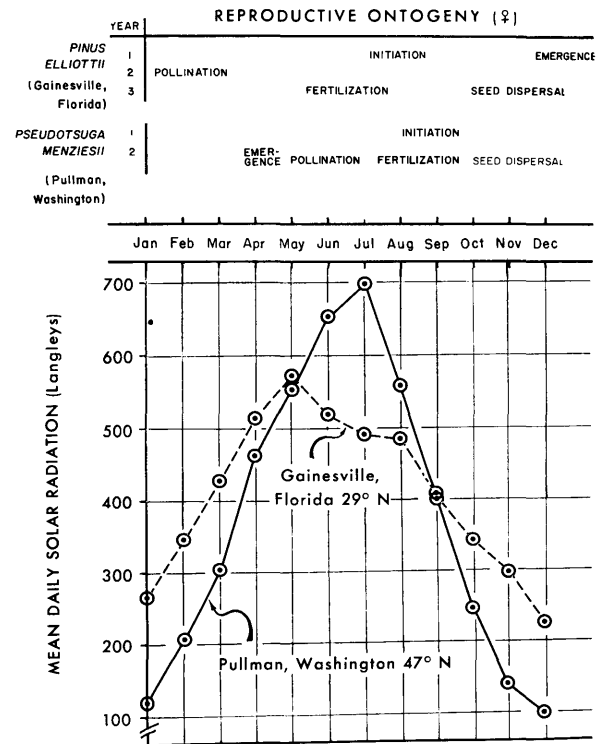


Figure 4. — The relationship of solar radiation to cone ontogeny of two conifers at different latitudes. (Radiation data from: U. S. Weather Bureau, Office of Meteorological Research and Office of Climatology, 1964 edition, Washington, D. C.).

tion and subsequent development. The data reported here suggest that variations in microclimate may also affect the number of flowers on different parts of the tree.

Female cone initiation for slash pine occurs during the late summer and like Douglas fir (*Pseudotsuga menziesii* [MIRB.] FRANCO) during the decline of solar radiation from its annual maximum (Figure 4). The incident heat and light are presumably the components of solar radiation involved in cone initiation.

In the southern hemisphere distribution of solar radiation is reversed and favors the northern tree crown face. FIEBING (1967), in Australia found more flowers were produced in the north side of young *Pinus radiata* crowns. He also found that flowers occurred on a greater number of branches and branchlets. He concluded that training of branches in the direction of the wind, as well as solar radiation, influences this distribution.

In Washington state, Douglas fir formed considerably more cones on the south than on any other side of the crown and more on the west than the east side (WINJUN and JOHNSON, 1964). Solar energies received are equal on the east and west sides on clear days although the south always receives more energy than the north. On the Pacific coast, the distribution of sunshine during the day is symmetrical about the noon high or slightly favors the afternoon (VISHER, 1954). If solar energy is involved then more cones should be induced on the south and west than the north and the east crown faces. In Washington, this distribution of cones is in fact the case.

In our region of Florida, clouds during summer rains reduce the incident solar energy even before the June solstice occurs (Figure 4). Most cloudiness occurs in the afternoon; the maximum sunshine occurs in the morning and begins to diminish after about 11:00 a.m. (VISHER, 1954). Incoming solar radiation is received during the day

faster than it is being lost until about midafternoon; therefore, the daily march of temperature increases until a daily maximum is reached about 2-4:00 p.m. This suggests that the east > west distribution of female strobili in Florida is probably related to the morning sunshine received by the east crown face. In the Pacific northwest where incoming radiation is not strongly mediated by clouds, an east-west gradient does not appear, but the south-north gradient is strong in the same radiant energy relationship.

When tree spacing causes mutual shading as in block 5 (Table 3) the east-west gradient disappears. Perhaps, the essential wavelengths of light are screened out by adjacent crowns similar to the effect of afternoon clouds on the west side of open-grown trees. Alternatively, the effect of light may not be primarily a quality factor but an expression of increased growth and of substances related to growth. For example, the branches are longer on the side where the most flowers occur (Figure 3) and the stem accrued a larger radial increment on the same side (Figure 1); but more branches occurred on the west face (Table 5). Number of axes alone does not appear to determine flower numbers since FIELDING (1967) found more branch axes on the side of maximum radiation and that the branch angles were more acute and directed into more direct radiation.

Level of available photosynthates are probably greater on the east and south sides where the direction of radial crown growth and stem is also greatest (Figure 1 and 3). GEIGER (1965) cites data showing maximum stem increment to be on the side protected from the wind. In Florida, the distribution of the winds (VISHER, 1954) does not suggest that wind is a major factor in determining diameter increment. However, the synthesis of wood during the flower initiation period (Figure 4) is greater on the side where fewer flowers are formed and this fact suggests that nutrient substrates are diverted to the formation of cones. According to this hypothesis, greater levels of substrate or growth factors essential for induction of female cones are available on the east than the other crown faces where mainly diffused radiation occurs. This postulate would explain the persistent east > west distribution.

### Summary

Female flower counts made in three stands of slash pine in the vicinity of Gainesville, Florida, show that in open grown trees there is a predominance of female cones produced on the east crown. This distribution appears to be affected by the morning sunshine during the summer cone initiation period.

This distribution was contrasted with the south > north distribution for Douglas fir in the Pacific northwest. In the latter location the morning-afternoon sunshine differential does not exist and neither is there an east-west cone gradient.

Slash pine crown radii are greater in the east and south directions and a larger radial increment accrues in the same stem direction parallel to the dominant pattern of cone formation. During cone initiation the northwest stem and the side of fewest cones, forms more wood while energy on the other side is presumably diverted into cones. The branch count is higher on the crown side with least cones. Distribution and concentration of metabolites essential to cone induction in pine, and possible other trees is presumably reflected by numbers of reproductive primordia initiated.

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