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Female flowering in Scots pine (Pinus sylvestris L.) crowns in relation to the trunk and cardinal directions*)

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Summary

The distribution of conclets was studied on Scots pine (Pinus sylvestris L.) shoots in various positions on the previous year's apex relative to the cardinal directions and tree trunk. It was found that more flowers are induced in buds located distally on an apex than in those located closer to the trunk regardless of crown zone. This is true on all sides of the crown suggesting that direct insolation is not the differentiating factor. The possible role of nutrient transport and gravimorphism in the attainement of this strobile distribution most advantageous for cross pollination is discussed.

Key words: flowering, light intensity, gravimorphism, nutrition, growth rate, Pinus sylvestris.

Zusammenfassung

Bei Pinus sylvestris L. wurde die Verteilung der an den vorjährigen Triebspitzen vorhandenen Zapfenanlagen in verschiedenen Kronenbereichen in Bezug auf die vier Haupthimmelsrichtungen untersucht. Es wurde gefunden, daß auf der Außenseite der Triebe mehr blühinduzierte Knospen platziert sind als im Inneren der Baumkrone, wobei die absolute Höhe innerhalb der Krone ohne Bedeutung ist. Das gilt zugleich für die verschiedenen Himmelsrichtungen, woraus geschlossen wird, daß die direkte Sonneneinstrahlung kein differenzierender Faktor ist. Die Bedeutung des Nährstofftransports und des Gravimorphismus für die günstige Blütenknospenverteilung wird diskutiert.

Introduction

In a recent study it was demonstrated that shading of individual Scots pine buds from the south reduces floral induction relative to shading from the north (Giertych and **Królikowski** 1978). This study did not consider the position of the treated buds within the crown. It was often observed that there develop more female strobiles an the side of the crown which is more exposed to direct sunshine, this being the eastern, southern or western exposition depending on the time of day when skies are most commonly clear during the time of floral induction (Smith and Stanley 1969, Jackson and Sweet 1972 and others). Together with the observations that there are more cones on tree tops and on edge trees the rather obvious conclusion is usually reached that direct insolation is instrumental in the induction process.

We know of no report on the distribution of female strobiles on pine shoots in relation to the axis of the previous year's shoot and to the trunk. If insolation is the dominant external factor determining floral induction the shading effected by individual buds upon each other within a stem apex should be reflected in the distribution of flowers on shoots derived from those buds. It was the purpose of this study to consider this distribution.

Materials and Methods

The observations were conducted in August and September 1978 on bundles of shoots all derived from buds on a single 1977 shoot apex. Except for the terminal shoot of the bundle the others will be referred to here as whorls. Several dozons of these were selected in various parts of crowns of three Scots pine (Pinus sylvestris L.) grafts growing in the Kornik seed orchard. These three grafts (K-01-22, K-01-22' and K-01-16 2 clones) were treated as replicates. The crowns of these three trees were divided into four sectors corresponding to the cardinal directions N, S, E and W. The same split up was made of the shoots on each of the studied whorls, and these sectors similarily corresponded to cardinal directions however they were also designated as being in a distal (D), proximal (P), left (L) or right (R) position relative to the tree trunk (*fig.* 1). Since most of the shoots no longer had a vertical stance but were in various stages of bending away from the trunk towards a horizontal or even drooping position, it was not their present orientation that was considered but their presumed position in buds on the previous year's shoot when the latter was still in the vertical position in June 1977.

Note was taken which sectors of the whorls had female strobiles in 1978. Only flowering whorls were considered, and when there were more than one shoot per whorl-sector only a single score was made of the presence or absence of flowers in that sector. A note was made of the position of the abserved whorls relative to height in the crown and in which of the crown-sectors it grew. In all 332 whorls were investigated, 86, 111, and 135 from the three trees respectively. The data from each tree each crown-sector and each whorl-sector was pooled together and the result presented as the percentage of whorl-sectors with flowers per number of whorl-sectors with shoots. The height in the crown was not a factor considered in the statistical analyses due to insufficient numbers from the upper zones of the crown. The percentage values were treated by the arcsine trans-

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Table 1. — Variance analysis for the flowering percentages following angular transformation.

Source of variation	d.f.	M.S.	F
Total	47	119.20	
Variables	15	51.01	1.85*
Crown-sectors C	3	134.50	4.88**
Whorl-sectors relative to cardinal directions W_1	3	11.27	0.41
C x W_1	9	36.43	1.32
Whorl-sectors relative to tree trunk W_2	3	73.00	2.65*
C x W_2	9	15.70	0.57
Tress (replicates)	2	2005.48	72.82**
Residual	30	27.55	

*significant at 0.05 level, ** significant at 0.1 level.

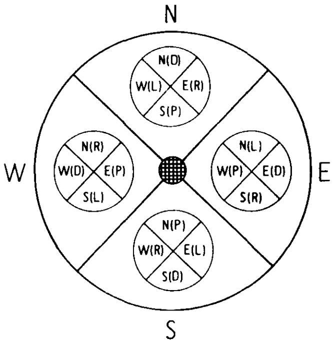

Fig. 1. — Split up of tree crown and of shoot whorls within it into sectors for the purpose of recording occurrence of cones. The cardinal directions are designated as N, S, E and W and the whorl sectors are also identified in relation to the tree trunk as distal (D), proximal (P), left (L) or right (R).

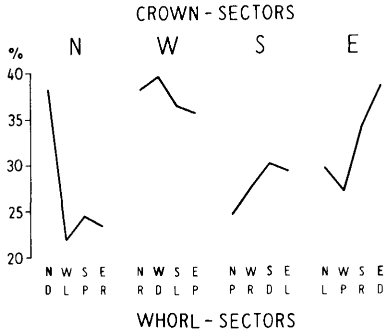

Fig. 2. — Percentage of whorl-sectors with flowers in different parts of the crown. N, S, E and W are cardinal directions and whorl-sectors are also defined as distal (D), proximal (P), left (L) and right (R) relative to the trunk.

formation prior to analyses and reconverted to percentages for the final presentation. The result of the variance analysis is given in *table 1*. There were 16 experimental variables, 4 crown-sectors and 4 whorl-sectors, however the latter were grouped in two different ways, by cardinal directions and in relation to the tree trunk (*fig. 1*), and the analysis of variance was performed twice for that source of variation.

Results

In the variance analysis the terminal shoots in a shoot bundle (central to the studied whorls) were not included since they do not belong to any of the whorl-sectors. These shoots had much more strobiles, but their intensity of flowering declined up the crown which was in contrast to the situation in the lateral or whorl-shoots where the reverse was true (*table 2*).

The variance analysis has shown that there were significant differences between crown-sectors and between whorl-sectors in relation to the trunk, but not in relation to cardinal directions. Of course trees also differ substancially. They were treated as blocks (replicates) in the variance analysis.

The main result of this study is presented in *figure 2*. The graphs shown there indicate the intensity of floral stimulation in various whorl-sectors and crown-sectors. As can be seen always the whorl-sector which agrees with the crown-sector has the highest flowering percentage. In relation to the trunk this is the distal (D) whorl-sector. Conversly lowest flowering percentages were usually observed in the sector opposite to the one agreeing with the crown-sector, or in the relation to the trunk in the proximal

Table 2. — Differences in flowering intensity on terminal and lateral shoots in various parts of Scots pine crowns. Averages from three trees.

Flowering % of shoots		Crown-sectors				
		N	W	S	E	$\bar{x}$
Above 5 m:	Terminals	73.3	61.5	83.3	69.2	71.8
	Laterals	46.6	55.6	27.3	67.4	49.2
At 4-5 m:	Terminals	91.3	89.7	87.9	96.9	91.5
	Laterals	23.8	40.2	26.0	31.5	30.4
Under 4 m:	Terminals	87.5	100.0	93.8	93.9	93.8
	Laterals	11.3	12.3	18.8	20.4	15.7
Whole crown:	Terminals	85.2	85.0	93.0	88.6	88.0
	Laterals	27.0	37.4	28.0	32.5	31.2

(P) one. However a Newman-Keuls Test has shown that only the distal (D) whorl sector differs from the other tree:

D	R	L	P
35.7	*29.7*	*27.7*	*26.9*

In the northern crown-sector the proximal whorl-sector had a somewhat higher flowering percentage than was the case in the left or right whorl-sectors (fig. 2).

Discussion

The most interesting result os this study is that female strobiles are most commonly induced in buds on the side of shoot apex which is furthest away from the trunk. Thus it is not on the side most exposed to direct sunshine. There is a tendency for female flowers to form as far as possible on the outside of the crown on all three trees.

The greatest differences between whorl-sectors were observed on the eastern and northern side of the crown (11% and 16% respectively) and the lowest on the western (about 4%) side (*fig. 2*). The western side of the crown was at the same time the most abundant in flowers on the whorl shoots (*table 2*). This was primarily so because of the low differences between whorl-sectors. The normally less flowering proximal sector as well as the right and left ones in this crown-sector were not much different from the distal sector.

An analysis of flowering in three altitudinal zones of the crown (*table 2*) has shown that on the terminal shoots there is a decline in flowering with altitude while on the whorl shoots the reverse is true. This is probably associated with the fact that terminal shoots play an increasingly important vegetative role up the crown. The common observation that there are more cones towards the tree top is therefore associated with the flowering of the lateral shoots. These have flowers less commonly than the terminals (*table 2*) but since they are much more numerous their pattern of vertical differentiation in flowering dominates.

The view that light and insolation are the prime external factors inducing the reproductive pathway in apex development, requires reconsideration. The common observations concerning distribution of cones in the crown, together with those reported here of there being more on terminal shoots than on laterals, more in the upper part of the crown, and less on the northern exposition (*table 2*), would tend to support that view. However the distribution of floral inductions between buds on a shoot apex does not easily fit in with this theory. Light as an inducing factor is a possibility here, particularly its low supply on the proximal side of the shoot could have been limiting. The terminal bud could have exerted a shading effect of its own. But direct insolation or the radiant heat it provides could not have been involved here since even on the northern side of the tree there were more floral inductions on the distal (northern) side of the shoot.

The other factors that could be involved here are differential nutritional supply and gravimorphism. During the intensive growth of shoots in early summer when flowers are being induced the movement of nutrients is primarily acropetal and centrifugal up and away from the trunk or stems with old needles on them. This is due to the better, more direct vascular connections of the distal parts of the crown which are also in a state of most intensive growth and represent the strongest *sink* together with their developing terminal and distal buds. It is possible that these buds would therefore have the greatest chances of producing stem primordia with female strobiles on them for nutritive reasons Wareing (1958). This is in agreement with what was observed in this study.

The possible gravimorphic effects are somewhat more complex. Their influence on flowering intensity selectively on vertical or horizontal branches has been demonstrated for many species of fruit trees and for Japanese larch (Longman and Wareing 1958, Longman *et al.* 1965, Jackson and Sweet 1972). These last authors when quoting Wareing (1958) suggest that in pine there is a greater female flowering on vertical shoots, it appears however that they were not justified in interpreting this reference in gravimorphic terms. Wareing wrote about the better flowering of terminal shoots relative to lateral ones without assigning any gravimorphic significance to this observation. At the time of floral induction in Scots pine all shoots start basically vertical, but not the buds sitting on shoot apices. It is possible that the growth of shoots taking place during floral induction, which is accompanied by an increase in their weight, results in the shoots bending away from the trunk towards a more horizontal orientation. As a result the distally located buds will attain a decidedly horizontal position while the proximal buds will first be brought to a more vertical position. The more intense flowering on the distal whorl-sectors observed in this study appears to be more akin to the flowering of horizontal branches in larch and apples (Longman *et al.* 1968) than of vertical ones in grapes or apricots (Jackson and Sweet 1972).

The spatial changes taking place in the orientation of a growing shoot may also influence the rate of growth of the bud axis and differences in this rate may perhaps be instrumental in the differentiation of flowering intensity. Rombberger and Gregory (1974) suggest that the change from a vegetative pathway of apex development to a reproductive one may be associated with differences in the rate of cell division and growth of the apical and subapical parts of the meristem. They assume that the female cone development is initiated by an increase in axis elongation leading to separation of lateral initials that allows for simultaneous initiation of fertile bracts between all the separated sterile ones. The gravitational bending of a shoot away from the trunk may result in the distal buds responding to negative geotropism by greater extension growth relative to the proximal buds, which would be also reflected in the greater extension of meristematic axes.

It is likely that these differences are maintained also later during the development of these buds into shoots since female flowers form on the better growing, longer shoots (Wareing 1958, Damian *et al.* 1965). The terminal shoot is in this context quite naturally the more readily flowering one being faster growing and of course initially longer as a bud.

It is obvious that from the evolutionary point of view it is more advantageous to have female flowers located on the outside of the crown to reduce the possibility of self pollination, and to expose the flowers to incident foreign pollen. However the physiological mechanism of the development of this distribution of flowers in a crown may depend on both internal factors such as the centrifugal acropetal transport of nutrients and on external ones such as gravity and light.

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Improved Estimators for Provenance Breeding Values

By F. H. KUNG[1])

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Summary

The provenance mean of a trait is a sample estimate for the breeding value of that provenance. However, if there are more than three provenances unter test, a shrinking factor should be applied to each sample mean to obtain the breeding value. The best shrinking factor to be used with the prediction depends on the F-statistics and the number of provenances in the plantation. Advantages of such adjustment by a shrinking factor are illustrated by a computer simulated example.

Key words: Provenance test, selection differential, genetic gain, STEIN's estimator.

Zusammenfassung

Der Mittelwert eines gegebenen Pflanzenmerkmals für ein bestimmtes Ursprungsgebiet ist ein Proben-Schätzwert für den Zuchtwert dieses Gebietes. Werden mehr als drei Gebiete getestet, so sollte ein Schrumpffaktor auf jeden Proben-Mittelwert angewandt werden, um den Zuchtwert zu erhalten. Der beste Schrumpffaktor für eine Voraussage hängt von der F-Statistik und der Anzahl der Ursprungsgebiete ab, welche bei der Anpflanzung in einer Plantage herangezogen werden. Die Vorteile einer derartigen Anpassung durch einen Schrumpffaktor werden anhand eines computer-simulierten Beispiels erläutert.

Introduction

Provenance testing is useful in screening the naturally available genetic variation and in providing the best available types for reforestation or future breeding work. It is particularly necessary to do provenance testing prior to more intensive breeding work when dealing with an exotic (WRIGHT, 1975). Besides providing basic genetic information, selection of superior geographical sources can be done and the test plantation may be converted to a seedling seed orchard (NANSON, 1972).

When selection is made based on provenance test data, should we use the provenance mean as the breeding value for that provenance? In comparing provenance performances, should we consider the superiority as genetic gain or merely as selection differential? For example, if provenance A averaged 50 m and the plantation mean was 40 m, can we expect that the seed collected from provenance A will be 50 m, or 10 m better than the population mean? Some people think so. The argument is based on the fact that the genetic difference, not the environmental difference, among provenances, can be transmitted from the native range to the test site. Thus, the provenance mean is a sample estimate of the breeding value of that provenance. The superiority is the genetic gain.

Statistically speaking, the sample mean is the best predictor for a population mean under random sampling. It has minimum variance among all unbiased estimators and likewise mong all translation invariant estimators. Moreover, it is minimax (minimizes the maximum expected squared error), admissable (no competing estimation rule has smaller squared error for all values of the true mean), and it is the maximum likelihood estimator (choosing the population mean equal to sample mean maximizes, among all values of true mean, the probability of obtaining the value of sample mean actually observed). However, statisticians lately have begun to realize that biased estimation rules have definite advantages over the usual unbiased estimators (EFRON, 1975). If there are more than three population means to be predicted, sample means are not the best predictors (STEIN, 1955). The best one involved a shrinking factor for each mean (JAMES and STEIN, 1961).

Provenance testing is not without experimental error. The experimental error pushes the sample mean above or below its true breeding value. If we have many provenances being tested, there are more provenances near the plantation average than near the extreme. In other words, the distribution of provenance breeding value will most likely follow a normal distribution rather than a uniform distribution. So, there are more central genotypes being pushed outward from the center. The outcome is a flatter distribution of phenotypic means. In order to reconstruct the breeding value from phenotypic provenance means, the provenance means need to be pushed (shrunken) back toward the center to resemble the original distribution of provenance breeding values.

The Shrinking Factor

The breeding value of a provenance Z can be expressed as:

$$Z = \bar{Y} + C(Y - \bar{Y}) \qquad (1)$$

where $\bar{Y}$ = Plantation mean, or the average of all provenance means.
Y = Provenance mean observed in the plantation.
C = Shrinking factor.

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