SOME OBSERVATIONS ON THE TRANSITION FROM FEMALE BEARING TO MALE BEARING IN BALSAM FIR[1]

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INTRODUCTION

The fact that megasporangiate (female) strobili tend to be produced on upper branches of the crown, and microsporangiate (male) strobili on branches somewhat lower in the crown is well known (e.g. Prat, 1936; 1945; Morris, 1951; Duff and Nolan, 1958; Wareing, 1958; Sarvas, 1962; Moorby and Wareing, 1963; Hard, 1964; Debazac, 1965). In most genera there is considerable overlapping of the female and male zones, but in balsam fir (Abies balsamea (L.) Mill.) the zones are fairly distinct (Balch, 1946; Morris, 1951; Powell, 1970b).

It is obvious from the positional differences between female and male strobili that branches, at least on trees which have been regular strobilus bearers, have the capacity first to bear female strobili and later to bear male strobili (cf. Prat, 1936; 1945; Moorby and Wareing, 1963). The position or time of the change from a capacity to bear female strobili to a capacity to bear male strobili has not been documented, probably because the change is indistinct in the genera in common use in tree improvement work. In balsam fir, the position of the change is clearly apparent because the female and male buds occur in distinctly different numbers, occupy different positions on the shoots, and are easily distinguishable morphologically (Morris, 1951; Powell, 1970a; 1970b). In this paper, the position of the female-male transition will be described for mature balsam fir trees, and related to branch aging and apical dominance.

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MATERIALS AND METHODS

Studies in the upper crowns of 13 mature, regularly flowering balsam fir trees growing in the University of New Brunswick Forest, Fredericton, New Brunswick, have been facilitated, since 1964, by steel-scaffold towers (Powell, 1970a; 1970b). The trees ranged in height, in 1964, from 10.3 m (34 feet) to 14.1 m (46 feet). Seven are of dominant crown class, five are codominant, and one is intermediate. Good flowering years occurred in 1964, 1966, and 1968 when the study trees bore totals of 2144, 3866, and 1110 female strobili. In 1968 one tree failed to produce female strobili, and the productive capacities of two other trees (see below) were seriously reduced. The positions of all female strobili produced in each flowering year were recorded on a shoot-by-shoot basis. The occurrences of male strobili on the upper branches of the male zones were also recorded.

Trees 5 and 9, both dominant trees, had their leading shoots accidentally removed in August of 1964. On each tree, four new whorl branches were present immediately below the point of reverence. The subsequent development, and pattern of strobilus bearing, of these two trees have provided information which adds significantly to that from the undamaged trees.

RESULTS

As is well known, the crown of balsam fir is composed of two kinds of branches, nodal or whorl branches, and internodal branches. During the period of study, internode-branch numbers produced per year ranged from zero to 38 on the trees under study, while whorl branches ranged in numbers from zero to six. Although some internode branches are lost, as a consequence of lack of vigor, as the tree increases in age, they clearly form a very important part of the uppermost portion of the crown, and rate greater attention than is implied by the "occasional internodal branching" of Bakuzis and Hansen (1965).

The whorl branches produced in any one year, being physically higher than the internode branches produced in the same year, are characteristically longer and more vigorous (Fig. 1) (cf. Debazac, 1965). Among internode branches of the same age, those which occur at a higher level are more vigorous, and hence grow to greater lengths, than those produced lower in the internode (Fig. 1). The yearly extensions of the main axes of the whorl branches tend to be shorter with increasing distance from the tree's apex, and hence, with increasing age of the branches. This is true also of internode branches of different ages. The decrease in vigor of branches situated in low internode positions is frequently such as to result in nondevelopment of many side shoots and, in some instances, of the main axes of the branches (Fig. 1). Reduction of branching occurs to a lesser extent on more vigorous internode and whorl branches (Powell, 1970b).

The differences in branch character are important in consideration of strobilus occurrences. Typically, as shown in figure 1, the lowest occurrences of female strobili are on whorl branches, and the highest occurrences of male strobili are on internode branches. Where overlapping of the two kinds of strobili occur, it is generally found that this is on different kinds of branches and thus related to shoot vigor. In the few instances where male and female strobili occur on the same branches (cf. Morris, 1951), the female

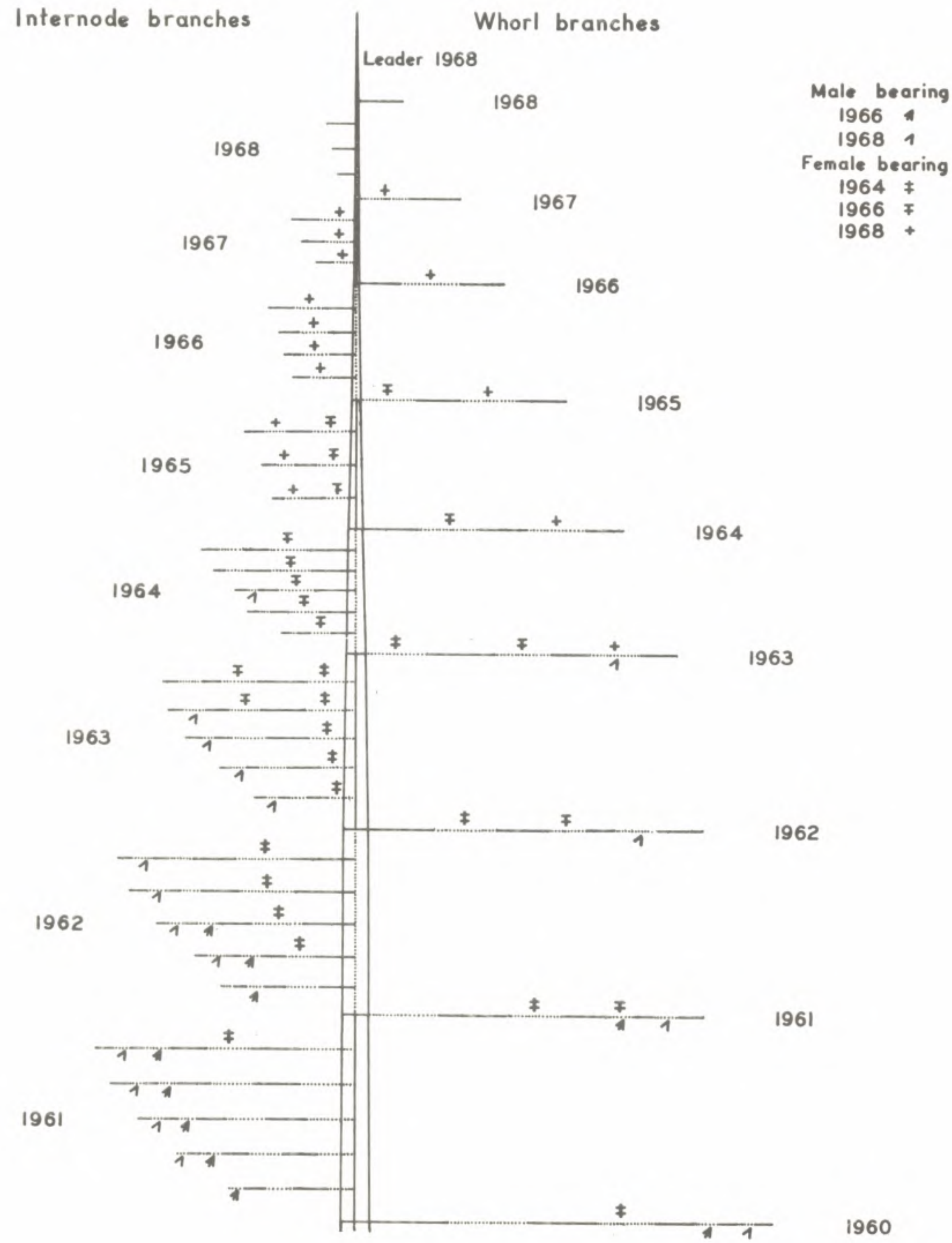

Figure 1.--Diagrammatic representation of the upper crown of a vigorously growing, dominant balsam fir tree indicating the distribution of female strobili and the highest occurrences of male strobili in each of three flowering years.

Table 1.--Mean numbers of whorls and internodes in the female zones and of male-free whorls and internodes on thirteen trees in each of three flowering years.

	Year of strobilus bearing		
	1964	1966	1968
Whorls in female zone[1]	3.46 ± 0.91[2]** *	4.85 ± 0.48[2]** *	3.54 ± 0.48
Male-free whorls	4.92 ± 0.74	4.08 ± 0.52	4.54 ± 0.31
Internodes in female zone[1]	2.92 ± 0.79	3.38 ± 0.50	3.00 ± 0.89
Male-free internodes	3.69 ± 0.67	3.23 ± 0.50	3.77 ± 0.75

[1] Number of whorls or of internodes above the lowest female occurrence: the upper crowns of trees 5 and 9 were assumed to be complete in 1966 and 1968.

[2] 95 percent confidence limits.

* = Differences between adjacent means at the 5% level
** = Differences between adjacent means at the 1% level

Table 2.--Uppermost male-strobilus occurrences and numbers of female-bearing whorls and internodes in three flowering years on two trees from which leaders were removed in 1964.

	Tree	Year of strobilus bearing		
		1964	1966	1968
Highest male strobilus	5	1961 internode	1963 internode	1964 internode
	9	1959 internode	1962 internode	1964 internode
No. female-bearing whorls	5	5	5	1
	9	4	4	1
No. female-bearing internodes	5	5	4	1
	9	3	2	1

strobili are located on relatively vigorous main-branch axes or main side-branch axes, and the male strobili are borne on much weaker shoots of low morphological category (cf. Wareing, 1958). Shoots which extend the main axes of the branches tend to remain free from male strobili for a few years after the remainder of the shoots on the branches have become male bearing.

Since the position of the transition from female bearing to male bearing is clearly related to shoot vigor, evaluation of the changeover must take kind of branch into account, as well as level in the tree's crown. In table 1, data are presented on the position of the female-male transition in both whorls and internodes. From the data, it is clear that the number of both whorls and internodes in the female zone increased in the heaviest flowering year (1966). In an opposite fashion, the number of both male-free whorls and male-free internodes decreased in 1966, when the mean numbers were less than for female-bearing whorls and internodes. This means that, in 1966, male and female occurrences in both whorls and internodes overlapped, the male zone extending upwards and the female zone downwards.

In the poorer seed years (1964 and 1968) a gap existed between the lowest female occurrence and the highest male occurrence in both whorls and internodes (Table 1). This gap represents a buffer zone into which the actual bearing zones on either side can extend in heavy flowering years. Although, in each year, lateral buds in typically female positions are initiated on some of the more vigorous shoots, and lateral buds in typically male positions are initiated on some of the less vigorous shoots, on branches in this buffer zone, there are many shoots which initiate no lateral buds (Powell, 1970b). In some cases these shoots are of apparently equal vigor to others which do initiate buds. In a few cases, buds in both typically male and typically female positions are initiated on the same more-vigorous shoot. Whether or not initiated buds undergo further development depends on several factors (Powell, 1970b), discussion of which is outside the scope of this paper. Clearly, prior to an excellent flowering year, such as 1966, many do develop; in other years few develop.

From the foregoing, it is clear that as the tree ages, it maintains a potentially female zone near the apex of the crown. This potentially female zone undergoes no change in size, in terms of numbers of whorls and internodes, over a relatively short period of time. This means that the potentially female zone rises as the tree increases in height, and with it, the uppermost part of the potentially male zone also rises. The two trees from which leading shoots were accidentally lost in 1964 provide an interesting contrast of subsequent development of the upper crown, and hence of the strobilus-bearing zones.

The data in table 2 indicate how, for each tree, there was a normal rise in the uppermost level of the male zones. As this occurred, there was a consequent reduction in the sizes of the female zones, such that, in 1968, female strobili were borne only on branches of the 1964 whorl and internode, in the latter, only on the uppermost branches.

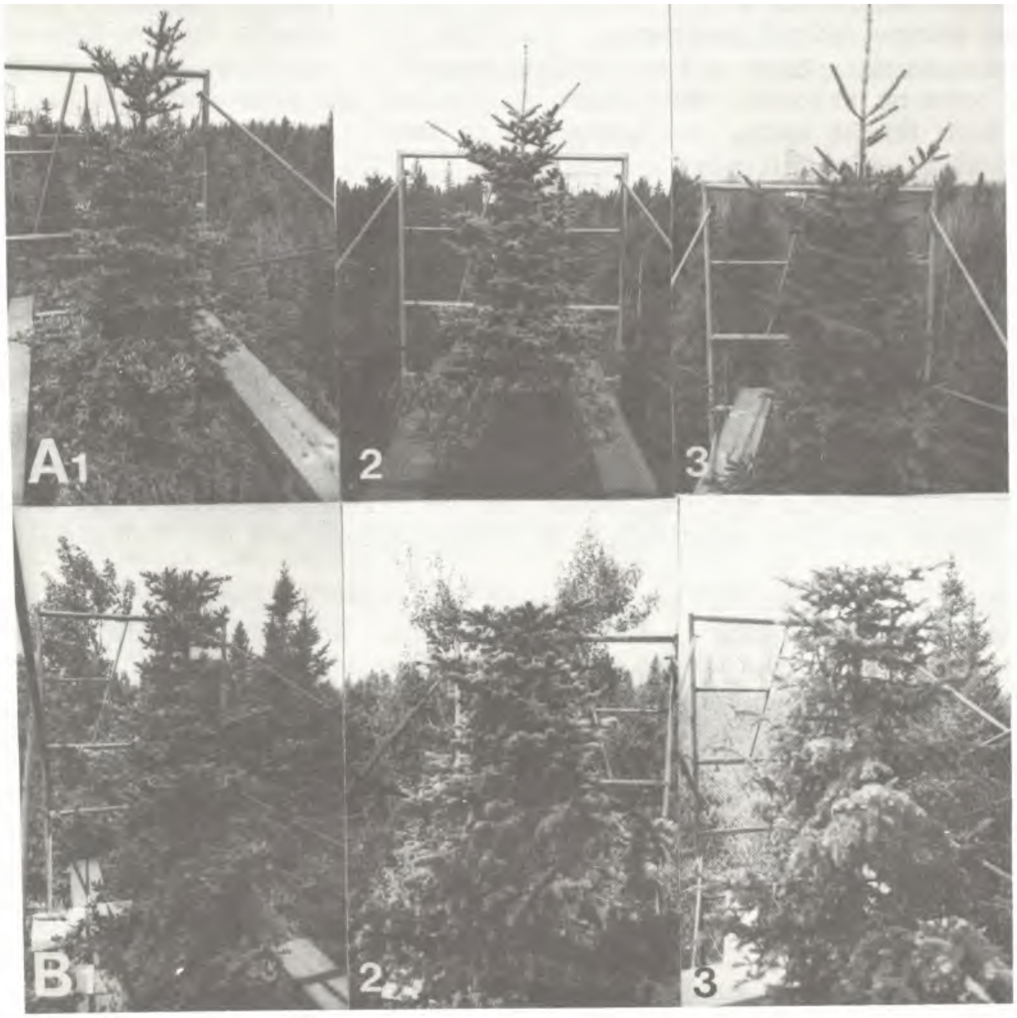

Figure 2.--Development of the upper crown of two balsam fir trees following loss of their leading shoots in August 1964: (A) tree 5, (B) tree 9; (1) 13 June 1967, (2) 5 August 1967, (3) 26 April 1969.

By 1967, however, the upper crowns of the two trees were strikingly different (Fig. 2). In 1965, three of the four 196)4-whorl branches on tree 5 had developed terminal shoots which turned upwards, and, by 1967, one of these had become dominant and had thus become the new leading shoot on the tree. Definite whorl branches were formed on this leading shoot in 1969, and 139 female buds were developed on the tree, all well above the normal level of the 1964 whorl. The 1964-whorl branch which had remained horizontal bore male buds only, as did lower shoots on the upturned branches. Thus, although female-strobilus bearing was much reduced in 1968, the capacity for increased bearing in subsequent years became great.

On tree 9, the 1965-terminal shoots on the 1965-whorl branches did not turn upwards, and almost horizontal growth has occurred in each subsequent year. The result was that tree 9 became flat-topped, with no tendency for any branch to assume apical dominance. In 1969, most shoots on the 1964-whorl branches developed male buds and the apical region of the tree became entirely male. There were no vigorous vegetative shoots and the tree had lost its capacity to form female buds, and hence had no female zone.

DISCUSSION

It appears reasonable to state that, for the trees under study, the average maximum size of the female zone is 4.8 whorls and 3.4 internodes (the 1966 values, table 1); of these, 4.1 whorls and 3.2 internodes are free from male strobili. Morris (1951) stated that the female zone of balsam fir had a length of between four and five feet (1.2 and 1.5 m). However, dimensions mean little without reference to tree size and tree vigor since zone length will depend on the lengths of the internodes over a four-year or five-year period. Numbers of whorls and internodes can be related to branch age and position and hence are more meaningful in morphological and physiological terms.

The time-span involved in the study was too short to indicate whether or not there are long-term trends in female-zone size. However, female strobili frequently occur on only one or two whorls and internodes on trees bearing for the first time (Powell, 1970b), thus there must be a build-up in zone size as a tree matures. For the trees used in this study, zone size in terms of number of whorls actually carrying cones was significantly and positively correlated with tree height and with live-crown length in 1964 and 1968, but not in 1966 (Powell, 1970b). In 1966 larger trees did not increase their female-zone size to the same degree as smaller trees, presumably because of the proximity of the upper part of the male zone. If the female-zone is expressed in terms of potential-zone size, the relationships with tree height and crown length disappear, thus indicating a relatively constant zone size for the range of tree sizes involved in the study.

It seems that once branches produce lateral buds in male-bud positions they lose their capacity to produce buds in female-bud positions. This effectively limits the possible size of the female zone. Balsam fir trees growing elsewhere have been observed, on occasion, to carry cones on up to eight whorls. It is thus possible that the change to maleness may be delayed as a tree matures, up to a certain age or state, or that different trees have different inherent capacities in terms of female-zone size. However, it is clear from the results of this study that maleness is associated with lessening vigor. Thus, the capacity to produce female cones decreases with declining vigor in the upper crown, which can be associated with age. As this occurs, the female zone is slowly replaced by the rising male zone. A decreasing capacity to produce cones with advancing age (Baldwin, 1942; Fowells and Schubert, 1956; Matthews, 1963) could thus be explained.

For the trees studied, it is apparent that most whorl branches retain the capacity to produce female buds for about five years. However, when seed years are biennial, as was the case at Fredericton over the period of study, this means that some whorl branches produce three sets of female strobili, others only two (Fig. 1), before producing male strobili. Internode branches produce female strobili only once or twice before producing male strobili in their fourth or fifth year. The change to male-strobilus production is thus a function of branch aging, as Wareing (1958; 1959) found to be the case in Pinus sylvestris L. However, in balsam fir, the kind of branch is of great importance; branches which are inherently and positionally weaker, age more rapidly than the stronger whorl branches.

Further support for attributing the change from female to male to aging is provided by the continued rise of the male zones in the decapitated trees: their branches became male in a normal time sequence. Flat-topped balsam fir trees are of relatively common occurrence. Several examined by the author have proved to bear only male strobili. Others, like tree 5, where one or more branches have turned upwards and become more vigorous, have carried some female strobili on branches produced on the upward-turned new leaders. It seems, therefore, that a continued capacity to carry female strobili is contingent upon the maintenance of apical dominance, or re-establishment of apical dominance if this has been lost. This can be likened to the manner in which a shoot from the male zone of a tree, when grafted onto seedling stock and allowed to develop as the apically dominant portion of the ramet, may grow vigorously and eventually produce female strobili (Moorby and Wareing, 1963). Similarly, Yunovidov (1950) indicated that weaker, entirely male branches of Pinus sylvestris could develop female-bearing shoots if the conditions of growth became much better.

Crown development, in terms of vigor relationships and strobilus distribution, is basically similar in other coniferous genera to that in Abies (Prat, 1936; 1945; Wareing, 1958; Moorby and Wareing, 1963; Debazac, 1965). Although precise influences of aging And of apical dominance on male and female flowering vary between genera and species, knowledge of the principles involved, may prove to be of value in seed orchard and propagation work, and in interpreting topophytic responses.

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