슬래쉬소나무의 花芽原基 形成의 生理學的 研究

(I) 當年枝의 形態와 雌花의 着花와의 關係*[1]

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Physiology of Strobilus Initiation in Slash Pine I. Ovulate Strobilus Production in Relation to Shoot Morphology.*[1]

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採種園에서 18年生 接木苗인 슬래쉬 소나무를 對象으로 하여, 毬果形成과 가지의 形態學的인 相關關係를 조사했다. 春期에 조사한 枝當 雌花數와 상관관계가 가장 큰 것은 前年度 新梢枝의 枝當 葉重量이었다. (R^2=+0.41). 雄花數는 新梢枝의 葉重量과 負의 相關을 보여주었다. (R^2=−0.21). 雄花에서 雌花로의 性轉換은 그 가지의 生長力(vigor)이 증가함에 따라서 促進되었다.

雌花가 거의 着花되지 않는 個体木의 上部樹冠에서 採取한 頂芽와, 雌花나 雄花가 大量으로 着花한 個体의 頂芽로, 유관속 조직의 生長을 比較한 결과, 前者가 後者보다 훨씬 빨랐으며, 이는 雌花를 生産하지 않는 頂芽는 强한 營養生長의 傾向을 나타냄을 뒷받침하는 것이다.

Strobilus initiation in grafted, 18-year-old slash pine (*Pinus elliottii* var. *elliottii*) in a seed orchard was examined in relation to morphological and anatomical characteristics of shoots.

Needle weight (total fresh weight of needles per shoot produced during the current growing season) was the most closely related single variable to the number of female flowers produced the following year ($R^2 = 0.41$). The number of female and male strobili (per shoot) produced the following year was positively and negatively correlated, respectively, with the total weight of current-year needles per shoot. A transition from male to female flowering was associated with increasing vigor (number of needles) of the shoot.

Vegetative buds in the upper parts of the crown of poor-flowering trees showed more advanced growth of vascular tissues compared with female- or male-producing buds, indicating a strong favor for vegetative growth.

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INTRODUCTION

Shoot morphology in pines appears to be related to the male and female cone production on the same shoot. In *Pinus sylvestris*, reduction in the vigor of the shoot (measured by extension growth) is associated with a reduction in the formation of female cones and appearance of male cones(Wareing, 1958). Varnell (1970) reported that in *Pinus elliottii* average diameter and length of branches which produced female strobili were larger than those of branches which did not bear female strobili. Branch volume (Thorbjornsen, 1960; Hard, 1964) and branch weight (Rim and Shidei, 1974) were also reported to be significantly correlated with female cone production.

Implications of shoot vigor and morphology in physiology of flower initiation are not understood. The significance of shoot vigor in strobilus initiation indicates that the number of needles on the shoot, size of metabolite-transporting tissue, and the magnitude of the metabolic sink in the terminal buds might form an integrated system which regulates the carbohydrate availability to the terminal buds. It is assumed that size of the terminal buds might reflect nutritional status and carbohydrate availability of the shoot.

Objectives of this study were to identify a relationship between morphological and anatomical characteristics of shoots and strobilus initiation in *Pinus elliottii*.

MATERIALS AND METHODS

A slash pine (*Pinus elliottii* var. *elliottii* Engelm.) seed orchard was established in 1956 in School of Forestry at the University of Florida (Gainesville, Florida, U.S.A.), using vegetatively propagated, grafted clones. A flowering history of this orchard was reported by Goddard (1964). Clones with a history of abundant female cone production produced consistently more cones than those with a history of poor flowering. Five clones of abundant female cone production and five clones of poor female cone production were selected from the orchard and used in this experiment. Each clone consisted of two ramets, whose flowering behavior showed consistency of abundant or poor-flowering, indicating the strong genetic influence on flowering potential. Therefore, a total of 20 trees were involved in this study.

In the abundant-and poor-flowering groups, two types each of terminal buds within a tree were selected as described in Table 1. Thus, four types of terminal buds were recognized in this study.

1. Morphological Characteristics of Shoots :

Ten branches for each of the four types of terminal buds from the two flowering groups were selected, and the following characteristics were recorded : past female cone production(the number of first-year and second-year cones) and branch order. Terminal bud diameter increments were measured with a microcaliper on July 26, August 23, October 25, and on February 20 the following year. On February 20, number of female or male strobili produced, shoot length of the previous growing season, and number of flushes were recorded. Total needle fresh weight per shoot was measured after harvesting the entire shoots. Relations between female or male flowering and various shoot characteristics were analyzed with simple and multiple linear regression models.

2. Anatomical Characteristics of Terminal Buds :

Six buds (three large and three small buds) from each flowering group were harvested on July 26, August 17, and September 7 The buds were prepared for microscopic examination. The buds were fixed, dehydrated, paraffin infiltrated and embedded as described by Jensen(1962). A series of cross sections as well as median longitudinal sections of 10 to 20μ thick were made with a rotary microtome, and stained with a safranin-fast green combination. Within cross sections(sectioned at the most distal lateral appendages), cambial development was classified into one of five developmental stages :

1) discrete fascicular cambium stage ;
2) interfascicular cambium forming ;
3) vascular cambium completed ;
4) deposition of secondary xylem and phloem initiated and number of cells in secondary xylem in a radial direction was less than 25 ,
5) deposition of secondary xylem advanced and number of cells was greater than 25.

Diameter of phloem cells in cross section was measured with a micrometer. Also the number of cells in secondary phloem and undifferentiated phloem initials in a radial direction was counted and compared between the two flowering groups.

3. Relationships between Size, Weight, and Volume of Terminal Buds :

Ten terminal buds (five large and five small buds) from each flowering group were collected on September 7 and cut at the most distal lateral appendages. Their fresh weight, oven-dried weight, diameter, and length were measured. The ratios of dry to fresh weight and of weight to volume were calculated. To determine the volume of each bud, the bud was assumed to be conical in shape.

RESULTS

The classification of the clones into the two flowering groups was based on the flowering from 1960 to 1965 as mentioned previously. When female flowering was counted again in 1976, the abundant-flowering group(AFG) produced about five times more female strobili than the poor-flowering group (PFG), thus confirming the classification based on the earlier data.

1. Morphological Characteristics of Shoots:

A relationship between bud diameter growth and subsequent female or male flower production in the two flowering groups is shown in Table 2. Diameters of both large and small buds in AFG were larger in July than those of corresponding buds in PFG. However, subsequent diameter growth in August, October, and February showed no significant difference in size between the two types of large buds. A strong genetic influence on sexuality of the shoots (becoming male or female) was observed in this Table 2. Large buds in AFG produced exclusively female flowers (1.5 female strobili/bud), whereas those in PFG stayed in a vegetative state or produced male flowers (14.6 male strobili/ bud). Two times more strobili were produced in the small buds of PFG than in the small buds of AFG. None of the small buds in either flowering group produced female strobili.

A relationship between various characteristics of shoot morphology and female or male flowering is shown in Table 3. Needle weight (total fresh weight of needles per shoot produced during the current growing season) was the most closely related single variable to the number of female flowers produced the following year, with R^2 being 0.41 and statistically significant at 1% level. Shoot length was the second most closely related variable (R^2= 0.37), and bud diameter measured in August was the third one (R = 0.36). Thus, needle weight was better related to the number of female flowers than any other shoot characteristics. When two or more variables were used for a multiple linear regression, the regression was improved further. When all the nine variables in Table 3 were included in a model, R^2 of 0.695 was observed.

The number of male flowers produced per shoot showed a negative correlation with needle weight (Fig. 1). The number of male flowers showed a tendency to decrease with increasing needle weight, whereas the number of female flowers increased with increasing needle weight.

2. Anatomical Characteristics of Terminal Buds :

Table 4 shows characteristics of vascular tissues of four types of terminal buds in transverse section. In cambial development no significant difference between small buds of AFG and those of PFG was observed. When large and small buds within each flowering group were compared, cambial growth was more progressed in large buds than in small buds. The size of individual cells (diameter in transverse section) in the phloem

Table 1. Summary of the morphological characteristics and flowering behavior of four types of terminal buds in abundant-flowering and poor-flowering groups of slash pine.

	flowering group			
	abundant-flowering group		poor-flowering group	
terminal bud size	large buds	small buds	large buds	small buds
flowering in previous years	female	male	vegetative	male
expected flowering in following year	female	male	vegetative	male
position in the crown	upper	lower	upper	lower

Table 2. Bud diameter and subsequent female and male flowering in four types of terminal buds from abundant-flowering and poor-flowering groups of *Pinus elliottii*.

		diameter[1]				total needle weight per shoot	average number[2] of flowers/bud	
flowering group	bud size	July	August	October	February	February	female	male
		cm				g[3]		
abundant	large	0.795A	0.817A	0.853A	0.873A	123A	1.5	0.0
poor	large	0.757B	0.789A	0.840A	0.877A	158B	0.3	14.6
abundant	small	0.633C	0.664B	0.739B	0.751B	63C	0.0	13.7
poor	small	0.607D	0.645B	0.722B	0.739B	83D	0.0	27.0

1 : Bud diameter was measured with a microcaliper in July, August, October of 1976, and February of 1977. Each number is an average of ten observations.

2 : The number of flowers produced was counted in February of 1977.

3 : The numbers within a collection date are significantly different at 5% level if they are suffixed with a different letter.

Table 3. Linear regression between some morphological characteristics of shoots and number of female or male flowers produced in *Pinus elliottii*.

Model	R^2
F = NF	0.052
F = BDO	0.223
F = BO	0.246
F = BDJ	0.284
F = FYC	0.290
F = BDA	0.357
F = SL	0.371
F = NW	0.405
F = NW SL	0.409
F = NW BDJ FYC	0.510
F = SL BDA FYC	0.530
F = NW BDA FYC	0.532
F = NW SL BDA FYC	0.538
F = NW BDA FYC BO NF	0.617
F = NW BDA FYC BO NF SL SYC BDJ BDO	0.695
M = NW	0.214
M = FYC	0.251

Symbol identities :

F : number of female flowers per shoot produced in 1977
M : number of male flowers per shoot produced in 1977
NW : needle weight per shoot (fresh weight of needles produced in 1976 and measured in February of 1977)
SL : shoot length (shoot growth during 1976 and measured in February of 1977)
BDJ : bud diameter in July of 1976
BDA : bud diameter in August of 1976
BDO : bud diameter in October of 1976
FYC : number of female flowers produced in 1976 (number of one-year-old cones)
SYC : number of female flowers produced in 1975 (number of two-year-old cones)
BO : branch order
NF : number of flushes during the growing season of 1976

showed no significant difference between flowering groups or between large and small buds. However, large buds of PFG had a significantly greater number of secondary xylem and secondary phloem than large buds of AFG.

3. Relationships between Size, Weight, and Volume of Terminal Buds :

Fresh weight, dry weight, and volume of large buds within a tree in both flowering groups were about three times greater than those of small buds

(Table 5). Within a tree, the ratio of dry to fresh weight showed little difference between large and small buds. The ratio appeared to be a characteristics of individual trees as shown in column E of Table 5. The dry weight per unit volume of buds showed no significant difference between large and small buds of AFG, whereas large and small buds of PFG showed a significant difference (column F in Table 5), indicating a more compact structure in the small buds of PFG than in the large buds of the same group.

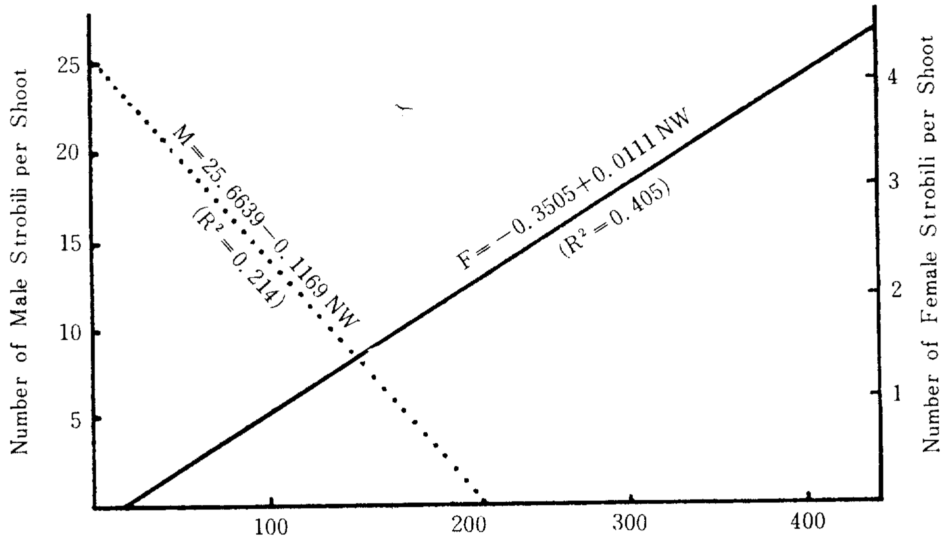

Figure 1. A relationship between needle weight (NW) and number of male (M) or female (F) flowers produced in *Pinus elliottii*. Needle weight refers to the total fresh weight of current-year needles per shoot produced during the growing season of 1976, and measured in February of 1977. The number of male or female strobili refers to the number of strobili per shoot produced in 1977. (n = 80, p = 0.01)

Table 4. Characteristics of vascular tissues (in transverse section) of four types of terminal buds collected from abundant-flowering and poor-flowering groups of *Pinus elliottii* during the period of floral bud initiation.

		stage of cambial development[1]			average diameter of phloem cells[2]			number of phloem cells[3]		
flowering group	bud size	Jul. 26	Aug. 17	Sep. 7	Jul. 26	Aug. 17	Sep. 7	Jul. 26	Aug. 17	Sep. 7
						μ				
abundant	large	2.8A[4]	3.8A	3.8A	12.2A	11.3A	11.2A	15.8A	15.0A	16.2A
poor	large	3.4B	4.2B	4.2B	10.9A	10.7A	11.2A	17.0B	19.4B	18.8B
abundant	small	2.3C	2.8C	3.2C	11.7A	11.2A	10.9A	15.0A	15.2A	15.4A
poor	small	2.0C	2.8C	3.0C	11.4A	10.9A	10.7A	14.3A	16.6A	15.2A

1 : Stage of cambial development in transverse section sectioned at the most distal lateral appendages (each number is an average of six discrete numbers from 1-5 as shown below).

1. discrete fascicular cambium stage;
2. interfascicular cambium forming;
3. vascular cambium completed;
4. deposition of secondary xylem and phloem under way (number of cells in secondary xylem in a radial direction less than 25);
5. deposition of seconeary xylem advanced (number of cells greater than 25);

2 : Average diameter (in micron) of phloem cells in transverse section.

3 : Number of cells in secondary phloem and undifferentiated phloem initials in a radial direction.

4 : The numbers within a collection date are significantly different (at 5% level) if they are suffixed with a different letter.

Table 5. Relationships between dry weight, fresh weight, and volume of terminal buds of abundant-flowering and poor-flowering groups of slash pine collected on September 7.

			A	B	C	D	E	F
flowering group	clone no.	bud size	diameter (cm)	volume (cm^3)	fresh wt. (g)	dry wt. (g)	dry wt./ fresh wt.	dry wt./ volume
abundant	243-55	large	0.717[1]	0.349[2]	0.952	0.419	0.440A	1.20A
abundant		small	0.480	0.103	0.288	0.127	0.440A	1.24A
abundant	116-56	large	0.684	0.298	0.774	0.330	0.429A	1.14A
abundant		small	0.514	0.098	0.263	0.111	0.421A	1.15A
poor	123-56	large	0.718	0.567	1.627	0.625	0.382A	1.22A
poor		small	0.456	0.123	0.482	0.179	0.372A	1.48B
poor	248-55	large	0.694	0.338	0.771	0.340	0.441A	1.00A
poor		small	0.508	0.121	0.332	0.146	0.439A	1.21B

1 : Each number is an average of 5 observations.

2 : To calculate the volume, each bud was assumed to have a conical shape.
In columns E and F, two numbers within a clone are significantly different at 5% level if they are suffixed with a different letter.

DISCUSSION

Among various characteristics of shoot morphology observed in this study, the needle weight (current-year needles) per shoot was related best to the number of female flowers (per shoot) produced the following year. This relationship indicates that female flowers might be predicted on a shoot, based on the number of current year needles on that shoot or, in general, the vigor of the shoot.

However, this relationship may not be applied to poor-flowering trees because of low genetic capacity to produce female flowers.

The vigor of the shoot is generally expressed by the length of the shoot, diameter of the terminal buds, or in many cases by the number of needles on it. Whenever, male strobili are produced on a shoot, the number of current-year needles decreases due to conversion of potential needle primordia into male strobili primordia, and consequently the vigor of the shoot decreases as pointed by Wareing (1958). Once the vigor of the shoot is reduced, it is likely that carbohydrate relation of the shoot may not be favorable enough to produce female strobili in coming years.

The length of current-year shoots was the second best indicator for future cone production. This finding agrees with the report of Varnell (1970) who found that in *Pinus elliottii* secondary branches bearing female cones had longer and thicker shoots and terminal buds than branches bearing no female cones. He also showed that diameter of the shoot rather than shoot length was more closely related to production of female strobili, probably due to a more direct reflection of current environmental conditions on radial growth than on extension growth.

The significance of needle weight suggested that needles on a given shoot might contribute, in some way, to the initiation of floral bud primordia. The influence of current-year needles appeared to the qualitatively as well as quantitatively associated with flowering as judged by the tendency for transition from male to female flowering (a qualitative change) to be associated with increasing vigor of the shoot, and judged by the significant correlation of the number of female flowers (a quantitative measurement) with needle weight. Possibly the current-year needles either produce chemical stimuli that are transported to the terminal bud or simply improve carbohydrate nutrition of the terminal bud.

The relationships between size, weight, and volume of the terminal buds indicated that the large buds of PFG, which most likely had stayed in a vegetative state, maintained a less compact structure than the small buds of the same group. The less compact structure seemed to result from the active vegetative growth in the large buds of PFG. The active vegetative growth in this case is reflected in the greater number of secondary xylem and phloem cells in the large buds of PFG than in other three types of buds as shown in Table 4. It is likely that the secondary vascular tissues in an advanced stage might enhance transport of nutrients and carbohydrates into the large buds of PFG, which in turn could favor further vegetative growth.

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