REPRODUCTIVE BIOLOGY OF *CHAMAECYPARIS*

III. Development of Flowering Branches and Seed Production[1]

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Abstract: The relationship between the growth of branches and the subtending cones also between the number of female buds and growth vigor in *Chamaecyparis formosensis* and *C. taiwanensis* have been studied. The results indicate that the growth of the lateral branches was slightly reduced by the subtending cones, but the effect was not significant statistically. On the other hand, the number of female buds was negatively regressed on the length of the new shoots of the lateral branches. Seed production for the coming year cannot be forecasted on the basis of the cone crop of the previous year.

INTRODUCTION

It is obvious that the natural regeneration of forest depends upon seed production as was emphasized by Allen (1941), and it is also true that artificial forestation depends upon the seed supply. This problem is especially important for our two noble trees, the Taiwan cypresses, *Chamaecyparis formosensis* Matsum. and *C. taiwanensis* Masam. & Susuki, because very few seed trees remain and because of the poor germination of their seeds (Chen, 1966a & b; Li, 1972). The seed production of these two species varies from year to year and can hardly be forecasted before the female buds develop. Both foresters and seedsmen need reliable infornation concerning seed yield in order to make their plans for reforestration and seed procurement at an early date.

Most of the published reports concerning seed production of conifers have been devoted to the study of *Pseudotsuga mensiezii* (Allen, 1941; Ching and Ching, 1962; Eis *et al*., 1965; Krueger, 1967; Lowry, 1966; Owen, 1969; Silen, 1967). A few papers have appeared about *Pinus* (Koslowsky, 1964), *Sequoiadendron* (Buchholz, 1938), *Cunninghamia* (Hashizume, 1963b), *Thuja* (Pharis *et al*., 1969) and *Cupressus* (Owens & Pharis, 1967). There is only limited literature dealing with *Chamaecyparis* (Courtot et Bailland, 1955; Hashizume, 1963a; Li, 1972 & 1975). And these investigations dealt with theoretical studies on physiology and morphology except for those on *Pseudotsuga* by Allen and Silen.

Allen (1941) suggested a method for counting the ovulate buds at an early date in the crop-year. Silen (1967) developed another method for counting the number of staminate buds before the female buds began to initiate. However, very little applicable information can be gained from their papers because the flowering habit of *Chamaecyparis* is markedly different from *Pseudotsuga.* Many authors have indicated that the cone crop in a previous year may affect the shoot growth in the following year and in turn the number of reproductive buds and seed yield. Lowry (1966) stated that a good cone crop year in Douglas-fir is followed by a year considered to be a failure or very light. Owens (1969) also reported the same tendency namely that, the presence of an abundance of maturing cones on shoots formed in the previous year greatly reduces the number of bud-primordia and reduces the possibility of these buds becoming reproductive ones. Others reported that in *Pseudotsuga* and other trees the seed cone production reduces vegetative growth of new shoots and thus affects the seed

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productivity in the subsequent year (Ching & Ching, 1962: Eis *et al.*, 1965: Krueger, 1967: Mathews, 1963; Morris, 1951).

The purpose of the present study is to analyze the relationship between the number of female buds and the growth of the buds, cones, and branches in the previous year and to make the possible prediction of the seed crop for the following year.

MATERIALS AND METHODS

The branches used was collected from 50–60 year old trees of *Chamaecyparis formosensis* and *C. taiwanensis* growing at the elevation of about 2,300 meters in the Alishan region. The branching system of these two species was carefully investigated. The following items were measured and counted according to the branching order:

1. Number of matured cones on the lateral branches,
2. New growth of leaders on the lateral branches,
    a) Branches with matured cones,
    b) Branches without matured cones,
3. Number of femals strobili (or buds) on the lateral branches,
4. Length of internodes on the new growth of the lateral branches,
5. Number of mutured cones on the second branches,
6. Number of female strobili (or buds) on the second branches,
7. Length of the second branches.

Based on the data thus collected correlation and/or regression coefficients were calculated. The results were analysed and discussed and an effort was made to estimate the seed production of the following year.

RESULTS AND DISCUSSION

1. Observation on the branching system and fruiting habit

A. Branching system

(1) The trunk

As with most other gymnosperms, these two species have central axis which results in a main trunk. The meristem of the trunk maintains the terminal dominance for a very long time making the tree to have a pyramidal form (Fig. 1,*A*).

(2) The lateral branches

Branches grown from the trunk are called "Lateral branches" (Fig. 1). The growth rate of the lateral branches in the upper part of the crown are vigorous but the leaders of those branches on the lower part grow more slowly. The terminal bud of the trunk and the main bud of each lateral branch is always vegetative and the main cause for the elongation of the branches.

(3) The secondary branches

From the lateral branches many secondary branches are formed alternately in the same plan. From the view point of reporduction, each secondary branch is a separate unit. Only the vigorous secondary branches of two year old in the upper part of the crown can initiate ovulate buds (Fig. 1, *C-b*). The terminal buds of the secondary branches grow more slowly than the lateral branches.

(4) The tertiary branches

The tertiary branches are formed in the same growing season as the secondary branches. The terminal buds of the tertiary branches grow much slowly and do not have terminal do-

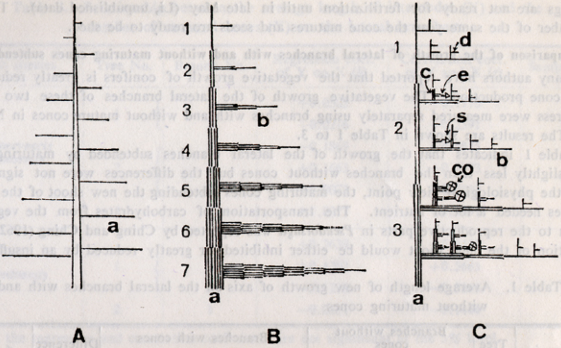

Fig. 1. Diagrams ov branching system and flowering habit in *Chamaecyparis* *A.* Tree form, *B.* a part of lateral branch, *C.* terminal part of lateral branch. (*a.* lateral branch, *b.* secondary branch, *c.* tertiary branch, *d.* quarternary branch, *e.* current growth of quarternary branch, *s.* female strobilus, *co.* matured cone, The numerals are the age of the branches).

minance. The buds on those tertiary branches are all vegetative. In fact, tne tertiary branches are the nourishing units of the tree (Fig. 1, *C–c*).

(5) The quarternary branches

If the growing season is long enough there are quarternary branches formed from the tertiary branches (Fig. 1, *C–d*). The quarternary twigs are usually arranged along the same side of the tertiary branch and make it a comb-like pattern. In the next spring the terminal buds of the quarternary twigs on the vigouous secondary branches can grow a short stem and initiate an ovulate bud on the tip (Fig. 1, *C–e*).

B. Fruiting habit

The female strobili are always borne on the new twigs of the quarternary branches in the upper part of the crown. On the other hand the staminate strobili are often found on the new tips of the quarternary branches in the middle and lower parts of the tree (Li, 1975).

The female and male buds are usually borne on separate branches. This particular type of sex expression is very different from the trees of Pinaceae (***Pinus*, *Pseudotsuga*, *Picea*, *Abies***, and ***Keteleeria***), where both the female and male buds are often borne on the same branch (Allen, 1941: Wareing, 1958: Silen, 1967: and Wang, 1948). In the genera of Cupressacae (***Cupressus*, *Chamaecyparis***, and ***Thuja***) and Taxodiaceae (***Cunninghamia*, *Cryptomeria*, *Sequeia***, and ***Taiwania***) the female and male strobili are borne on separate branches (Buchholz, 1938; Hashizume, 1963 a & b; Li, unpublished data; Owens & Pharis, 1967; and Pharis *et al.*, 1967).

The female buds of the two species in the present study are formed in August or even earlier on the tip of the current growth of the quarternary branches in the upper part of the tree. After which there is an arrested period of about six months for development and differentiation. The ovulate buds open in the following February and March before the embryosac has develop. Although pollination is completed in the blooming season the archegonia and eggs are not ready for fertilization until in late May (Li, unpublisned data). Then by November of the same year the cone matures and seeds are ready to be shed.

2. Comparison of the growth of lateral branches with and without maturing cones subtended

Many authors have reported that the vegetative growth of conifers is greatly reduced by heavy cone production. The vegetative growth of the lateral branches of these two species of cypress were measured separately using branches with and without mature cones in November. The results are shown in Table 1 to 3.

Table 1 indicates that the growth of the lateral branches subtended by maturing cones were slightly less than the branches without cones but the differences were not significant. From the physiological view point, the maturing cones subtending the new shoot of the lateral branches needed a lot of nutrient. The transportation of carbohydrates from the vegetative growth to the reproductive parts in *Pseudotsuga* was reported by Ching and Ching (1962). The elongation of the new shoot would be either inhibited or greatly reduced by an insufficiency

Table 1. Average length of new growth of axis on the lateral branches with and without maturing cones

Tree species	Tree No.	Branches without cones		Branches with cones			Difference (mm)	t'-test[a]
		No. of branches	Average length (mm)	No. of branches	No. of cones	Average length (mm)		
Chamaecyparis formosensis	1	10	117.44±13.95	20	4-48	75.89±15.61	+41.55	$t'=7.67$**
	2	7	98.08±13.17	24	1-39	88.26±17.87	+10.16	$t'=1.59$
	3	10	87.46±19.41	11	1-35	101.00±26.33	−13.54	″=1.45
	4	3	97.87± 9.29	15	1-42	101.92±16.05	− 4.05	$t'=0.60$
C. taiwanensis	1	3	128.13±19.22	7	3-16	114.78±27.93	+13.35	$t'=0.87$
	2	14	123.84±11.99	8	2-28	121.66±17.17	+ 2.18	$t'=0.24$

a. Cochran's t'test (Snedecor and Cochran, 1975),
** Significant at the 1% level.

Table 2. Relationship between the growth of lateral branches (Y) and the number of matured cones (X) on the branches[a]

Tree species	Tree No.	Branch No.	Regression coefficient of Y on X (b)	Correlation coefficient of X and Y (r)	Sample size
Chamaecyparis formosensis	1	1	−0.0393	−0.1570	10
		2	+0.3108	+0.3168	10
	2	1	+0.2818	+0.1733	6
		2	−0.2521	−0.4204	5
		3	−0.0513	−0.0260	15
	3	1	+0.6282	+0.4277	15
C. taiwanensis	1	1	−0.6995	−0.2040	8
		2	−0.1924	−0.0790	9
		3	−3.5432	−0.4207	7
	2	1	+1.3495	+0.7006	5

a. All the regression and correlation coefficients are not significant at the 5% level.

Table 3. Relationship between the average length of internodes (Y) and the number of matured cones (X) on the lateral branches[a]

Tree species	Tree No.	Branch No.	Regression coef. of Y on X (*b*)	Correlation coef. of Y and X (*r*)	Sample size
Chamaecyparis formosensis	1	1	+0.0305	+0.1776	10
		2	+0.0216	+0.2591	10
	2	1	−0.1869	−0.4875	6
		2	+0.1663	+0.4773	7
		3	+0.0073	+0.0149	20
	3	1	+0.0327	+0.1891	18
C. taiwanensis	1	1	+0.2639	+0.3457	8
		2	+0.4202	+0.5663	10
		3	−0.5213	−0.3345	10
	2	1	−0.0651	−0.1444	7

a. All the regression and correlation coefficients are not significant at the 5% level.

of necessary food. But this effect is not evident in this investigation. The insignificant regression and correlation shown in Table 2 is another evidence to support the phenomenon above mentioned. Perhaps, the trees observed were too young to produce cones.

The growth rate of branches can be observed by measuring the length of internodes of the new shoot. The results obtained in these two species are shown in Table 3. The regession and correlation coefficients are not significant at the 5% level. The average length of the internodes in the new shoots of the lateral branches were not affected by the number of maturing cones borne on them.

3. Relationship between number of ovulate buds and the new shoot of the lateral branches

As mentioned in the previous sections the terminal dominance of the lateral leaders are so strong that the growth of secondary branches, on which the female buds are borne, are inhibited. If the secondary branches are checked by the vigorous growth of the lateral new shoots, the initiation of female buds would be reduced. The number of female buds on the secondary branches may be regressed negatively on the growth rate of the lateral leaders. The regression and correlation coefficients of these two characters in *C. formosensis* were calculated and shown in Table 4.

Table 4. Relationship between number of female buds and length of new shoot of lateral branch in *C. formosensis*

Character	Branch number							Mean
	1	2	3	4	5	6	7	
Length of new shoots (mm), X	119	111	108	98	97	92	78	$\overline{X}=100.43$
Number of female buds, Y	3	4	2	11	20	12	31	$\overline{Y}=11.86$

Regression coef. $b_{y.x}=-0.7041$**; Correlation coef. $r=-0.9040$*

The significant negative regression and correlation of Table 4 indicates that the number of female buds is closely correlated and regressed on the new growth of the lateral branches at least in the range of 78 to 119 mm of length. The rapid growth of lateral branches can waste much food. As indicated in Table 1 to 3, the maturing cones did not significantly reduce the growth of the lateral branches. So that the number of female buds which will bloom the next spring are not affected by the matured cones of last year. It is supposed that the growth of the lateral leaders whether with or without maturing cones may be caused by the vigor of the lateral branches. Form the results of Table 4 the moderately developed branches would initiate more female buds.

This tendency is also true for the growth of the secondary branches. Table 5 showed the relationship of female buds with the length of the secondary branches on which the buds were borne. The branches of middle length produced more buds than the short or long ones.

Table 5. Relationship between number of female buds and the length of secondary branches in *C. formosensis* (number of branches)

Number of female buds	Range class of branch length (mm)						Total no. of branches
	50-69	70-89	90-109	110-129	130-149	150-169	
1-3	6	3	8	12	2	1	33
4-6		4	3	1			7
7-9			1	1			2
10-12			1				1
13-15			1	1			2
16-18			1				1
Total no. of branches	6	7	15	15	2	1	46

The lengthening of branch has been usually explained by many authors as resulting from gibberellic acid (Hashizume, 1959; Hillman, 1962; Owens & Pharis, 1967; Pharis 1969). But the effect of GA was positive with the dosages used in a definite range (Pharis & Morf, 1968; Yu, 1967). Too much or to little GA would give a negative result. This concept of development is supported by the results of our recent study.

From our results it is evident that the number of female buds is influenced by the growth rate of branches and is not correlated with the number of cones matured last year. Therefore, the cone production of this year can not be predicted by the number of cones produced last year.

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