Intraspecific Competition in Forest Trees[1])

By Kan-Ichi Sakai[2]), Hiromasa Mukaide[3]) and Koji Tomita[4])

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Introduction

Not a few studies have been reported on intraspecific competition in annual or short-lived plants. The method of approach employed in those studies can be roughly classified into two: one is to grow different genotypes in purestands and mixtures and measure the increment or decrement due to mixing by the amount of growth or yield of a given genotype. The other way is to construct a population of various genotypes and to compare the propagation rate of the mixture with those of the respective purestands. To put such approaches into practice with forest trees is, however, though not impossible, rather difficult, inasmuch as trees generally require a very long time for attaining full growth and reproduction. Thus, the competition studies in forest trees have naturally to deal with the detection and assessment of competition in a standing forest not intentionally planted for the purpose.

Steneker and Jarvis (1963) and Stern (1966) have investigated the correlation between the growth of a given tree and the summed up growth of several trees growing in its proximity within a given area. They assume that the correlation may reveal the intertree competition in a forest.

The present paper deals with the results of an attempt to detect and to measure intraspecific-intergenotypilc competition by correlations between two adjacent trees in a standing forest whose trees are of the same age. This study was supported financially by the Forestry Agency of Japan, and also assisted technically by forestry officials of Hakodate, Akita, Miyagi, Shizuoka, Gifu and Hyogo prefectures, to all of whom our thanks are due.

Method of study

Suppose a number of trees of the same age of a single species forming a population are measured for their growth. If we arrange them in pairs of two, each tree selected at random from fhe population, the partners of the pairs will not be correlated in any way. If we measure, however, the correlation between two trees growing adjoiningly in the forest, they are expected to be positively correlated, because contiguous habitat patches are likely to be more similar in edaphic and/or other environmental conditions than those of distant trees. On the contrary, intertree competition, if it occurs, will make them dissimilar by favouring one and disfavouring the other, driving the correlation to the negative side. Thus, comparison between adjoining two or three trees may allow us to conjecture the occurrence, if any, of intertree competition in a forest.

Such a comparison can be made in various ways. Let the trees growing side by side in a row be designated by i, j, k, etc. We can measure the correlation between any two adjoining trees for a growth character, i. e., $r_{y_i y_j}$, or the correlation between two differences among three edjoining trees, $r_{(y_i - y_j)(y_j - y_k)}$. Information may also be obtained by measuring the variance of difference between two adjoining trees or variance of differences among three adjoining trees. These four criteria are summarized in ***Table*** 1.

Since $r_{y_i y_j}$, or for simplicity, r_{ij}, corresponds to V_d, and r_{ijk} to V_{dd}, either correlation coefficients or variances can be used for the purpose. In practice, correlation coefficients are more convenient than variances. In this study, therefore, the correlation coefficients were used.

Materials

Thirteen forests of *Cryptomeria japonica* D. Don, ten raised from seed and the remaining three isogenic clones afforested by cuttings, were selected from various parts of Japan. They were all planted artificially, and thus all trees within a single forest were of the same age. Number of trees in each forest was from 100 to a little more than 200. A brief description of the thirteen forests is given in ***Table*** 2. The trees were measured on their standing spots after they were marked and mapped on a section paper. Measured were the stem diameter or girth at breast height and tree height.

Results of the study

Correlation coefficients, r_{ij} and r_{ijk}, of stem diameter and tree height in thirteen forests are presented in ***Table 3.*** It is found from ***Table 3*** that in the three clone forests, the r_{ij} values of either stem diameter or tree height are highly positive while the r_{ijk}'s are more or less larger than —0.5. The test if those obtained values or r_{ij} in the three clone

Table 1. — Statistics for detecting intertree competition in a forest.

Statistics	Notation	Explanation	Intuitive judgement		
			Random samples	No competition	Under competition
Correlation coefficient	r_{ij}	r between two adjoining trees, i and j.	0	>0	$\leqq 0$
	r_{ijk}	r between two differences among 3 adjoining trees; (i—j) and (j—k)	—0.5	>—0.5	≧—0.5
Variance	V_d	Variance of (i—j)	$2\,V_{(1)}$*)	$< 2\,V_{(1)}$	$\geqq 2\,V_{(1)}$
	V_{dd}	Variance of (i—j) — (j—k)	$6\,V_{(1)}$	$< 6\,V_{(1)}$	$\geqq 6\,V_{(1)}$

*) $V_{(1)}$ stands for the variance measured on an individual tree basis.

[1]) Contributions from the National Institute of Genetics, Misima, Japan, No. 632.

[2]) National Institute of Genetics, Misima.

[3]) Governmental Forest Tsee Breeding Station in Hokkaido, Nopporo, Ebetsu-City, Hokkaido.

[4]) Department of Silviculture, Gifu University, Kagamihara-City, Gifu, Japan.

Table 2. — Description of the twelve forests of *Cryptomeria japonica* used in this study.

Name of strain	Provenance	Number of trees	Propagated by
Kumotoshi	Kyushu	144	cuttings
Funakoshi-3	Hyogo	169	cuttings
Funakoshi-5	Hyogo	146	cuttings
Kikonai	Hokkaido	128	seed
Otobe	Hokkaido	106	seed
Yakumo	Hokkaido	147	seed
Hayaguchi	Akita	140	seed
Moniwa	Miyagi	202	seed
Amagi	Shizuoka	170	seed
Gotemba	Shizuoka	167	seed
Yasutomi	Hyogo	198	seed
Hontani	Hyogo	208	seed
Hagiwara	Gifu	190	seed

forests can be regarded to be estimates of the common ϱ showed that the χ^2 value was 3.9666 for stem diameter and 3.2012 for tree height with 2 degrees of freedom. Thus, the r_{ij}'s of stem diameter as well as of tree height obtained from the three clone forests were concluded to be from the respective ϱ's since P lies between 0.20 and 0.10 or equals 0.20, with the mean values of 0.436 for stem diameter and 0.667 for tree height. The same test for the three r_{ijk}'s of stem diameter gave $P = 0.30 \approx 0.50$ with the χ^2 value of 1.7726 with 2 degrees of freedom, the mean value being -0.457. The r_{ijk}'s of tree height, however, were different. The χ^2 value of r_{ijk}'s of tree height was 6.3149, which corresponds to $P = 0.05 \approx 0.02$, or is statistically significant at the 5% level. The reason for this result is not clear at present, but it may suggest that r_{ijk} is more susceptible to sampling error than r_{ij}.

After determining the average r_{ij} or r_{ijk} values of clone forests, the corresponding values of seed-propagated forests were compared with them. As shown in *Table 3,* eight r_{ij}'s of stem diameter or nine r_{ij}'s of tree height were found to be significantly different from the respective r_{ij}'s of the clones, but a very few or none regarding both r_{ijk}'s. *Table 3* also presents in the last column tentative conclusions on the intensity of competition. They are based on the information from the r_{ij} of stem diameter; the reason for this is given below.

Another study being conducted in our laboratory is to partition the phenotypic variance of a forest into genotypic, environmental and competitional components. Details of this study are published in a separate paper (SAKAI and MUKAIDE 1967), but a part of the results is given in *Table 4.* The V_G, V_E and V_C in *Table 4* stand for genotypic, environmental and competitional variances, respectively. The c^2, or the index of competitive stress, given in the fifth and ninth columns is a parameter relating the intensity of competition in terms of the ratio of competitional variance against the phenotypic or total variance.

$$c^2 = \frac{V_C}{V_G + V_E + V_C}$$

Comparison between r_{ij} or r_{ijk} with c^2 in stem diameter is given in *Figure 1 A and 1 B,* and *Figure 2 A and 2 B,* that of tree height. It is found from *Figure 1 A* that the c^2 and r_{ij} values are definitely negatively correlated. This situation is not pronounced, however, for the other three cases illustrated by diagrams of *Figures 1 B, 2 A and 2 B.* The test of statistical significance of the regression coefficient, b, of c^2 values on r_{ij} or r_{ijk} gave the following results:

Stem diameter
$$\begin{cases} c^2 \text{ on } r_{ij}: b = -0.8326 \pm 0.1496 \ (P < 0.01) \\ c^2 \text{ on } r_{ijk}: b = -0.8285 \pm 0.3675 \ (0.05 < P < 0.10) \end{cases}$$

Tree height
$$\begin{cases} c^2 \text{ on } r_{ij}: b = -0.1797 \pm 0.1141 \ (0.10 < P < 0.25) \\ c^2 \text{ on } r_{ijk}: b = -0.1747 \pm 0.1908 \ (0.25 < P < 0.50) \end{cases}$$

As may be found from *Table 4,* the c^2 values of tree height are generally very low ranging between 0.1048 and 0.2257 in seed-propagated forests whereas those of stem diameter are considerably more variable ranging from 0 to 0.7111. This suggests that stem diameter is likely to be more susceptible to competition than tree height. This is again apparent from the comparison between c^2 and r_{ij} or r_{ijk} as above described, the regression coefficients of c^2 on r's being not at all significant for tree height.

The b value is highly significant only in one of the two regressions of stem diameter. Looking again at the linear relation between c^2 and r_{ij} in *Figure 1 A,* the r_{ij} is considered to be an effective criterion for the detection of competition effect. The relation between r_{ij} and c^2 is given by the following formula:

$$c^2 = 0.3693 - 0.8326\, r_{ij}.$$

In order to substantiate the similarity of growth among neighbouring trees in a clone forest, differences in stem diameter between two adjoining trees from two forests are graphically shown in *Figures 3 and 4.* The solid line in

Table 3. — Intertree competition in forests of *Cryptomeria japonica.*

	Strain	Stem diameter		Tree height		Competition [1]
		r_{ij}	r_{ijk}	r_{ij}	r_{ijk}	
clone	Kumotoshi	0.57	—0.32	0.76	—0.11	Nil
	Funakoshi-3	0.31	—0.51	0.63	—0.47	Nil
	Funakoshi-1	0.43	—0.37	0.61	—0.39	Nil
	Average	0.436	—0.457	0.667	—0.340	Nil
Seed-propagated forest	Kikonai	0.08**	—0.75**	0.55	—0.21	+
	Otobe	—0.28**	—0.90**	—0.12**	—0.58	+++
	Yakumo	0.05**	—0.58	0.46*	—0.15	+
	Hayaguchi	—0.21**	—0.65*	—0.07**	—0.59	++
	Moniwa	0.06**	—0.25	0.42**	—0.34	+
	Amagi	—0.09**	—0.51	0.11**	—0.37	+
	Gotemba	—0.12**	—0.53	—0.001**	—0.53	++
	Yasutomi	0.33	—0.58	0.23**	—0.51	Nil
	Hontani	0.16**	—0.46	0.14**	—0.49	+
	Hagiwara	0.23	—0.41	0.39**	—0.39	±

[1]) Conclusion based mainly on the information from r_{ij} of stem diameter.
*, ** = Significant at the 5% and 1% levels, respectively.

Table 4. — Genotypic, environmental and competitional variances in a clone forest and six sexually propagated forests of *Cryptomeria japonica* D. Don.

Strain	Stem diameter				Tree height			
	V_G	V_E	V_C	c^2	V_G	V_E	V_C	c^2
Kumotoshi (clone)	1.06 ± 5.37	29.46 ± 0.94	1.29 ± 5.09	0.0406	0.30 ± 3.64	1.28 ± 0.70	—0.34 ± 3.34	0
Moniwa	1.19 ± 2.30	2.99 ± 0.59	1.89 ± 2.06	0.3114	—1.33 ± 0.85	2.17 ± 0.28	0.55 ± 0.66	0.2022
Otobe	3.48 ± 1.80	4.17 ± 0.30	18.83 ± 1.85	0.7111	—	—	—	—
Yakumo	4.72 ± 0.81	3.91 ± 0.11	4.62 ± 0.86	0.3487	0.76 ± 2.15	1.66 ± 0.37	0.57 ± 2.20	0.1906
Hayaguchi	10.73 ± 5.49	12.08 ± 1.51	25.79 ± 4.69	0.5307	4.40 ± 1.06	4.51 ± 0.30	2.61 ± 0.89	0.2257
Yasutomi	14.35 ± 3.62	1.80 ± 0.44	—2.12 ± 4.00	0	3.99 ± 1.46	0.71 ± 0.18	0.55 ± 0.66	0.1048
Hontani	15.12 ± 23.78	21.55 ± 17.90	2.55 ± 6.45	0.0650	1.56 ± 0.48	0.89 ± 0.17	0.33 ± 0.72	0.1187
Hagiwara	16.09 ± 8.89	1.24 ± 1.97	4.03 ± 8.06	0.1887	—	—	—	—

Figure 3 represents the distribution of differences in the Kumotoshi clone, while that in *Figure 4* shows the same of the seed-propagated Hayaguchi forest. The frequency polygons expressed by broken lines represent the distribution of differences between two randomly selected trees in the same forests, obtained by 10 replicated trials. It is found from *Figure 3* that in the clone the difference between two adjoining trees is definitely smaller than that of the random samples, the mean values of the actual differences being 2.99 cms. in contrast to 5.98 cms. of the random samples. In the seed-propagated forest, however, the situation is of other nature as can be seen from *Figure 4*. The mean difference between its two adjoining trees was 8.55 cms. as against 7.86 cms. of the random samples from the same population. This different behaviour of a clone and a seed-propagated forest is without doubt due to the pressure of intergenotypic competition which takes place in the latter.

Discussion

The word competition has been used in various ways and detailed discussions have been given by some zoologists (Birch 1957; Milne 1961). In plants, Harper (1961) recommended the use of the term interference in place of competition in discussions among agronomists, ecologists, geneticists and evolutionists, because of "their very different preconceived notions of what the subject is about". Donald (1963) has mentioned from the agronomist's standpoint that "competition occurs when each of two or more organisms seeks the measure it wants of any particular factor or thing and when the immediate supply of the factor or thing is below the combined demand of the organism".

Let competition simply mean an interaction between individuals of a population which brings profits to some and inflicts a loss upon others. The response of plants to density-induced shortages or the scramble among organisms for the common resources which is probably very likely to be accepted by most biologists as the definition of competition seems to be not correct, because the shortage should not necessarily cause the scramble, or the scramble, if it occurs, would not always result in favouring one organism and disfavouring another. Competition does not designate the condition where it might occur, but the process or result of the process which brings profits to one organism at the expense of another.

In this paper, intertree competion in forests of *Cryptomeria* has been studied by using r_{ij}, i. e. correlation between two adjoining trees, or by r_{ijk}, correlation between differences among three adjoining trees.

Let us first consider the r values in clonal forests. The results of the study have shown that the r_{ij}'s of the three clone forests were all positive and high, having average values of +0.436 for stem diameter and +0.667 for tree height. The r_{ijk} values for stem diameter and tree height in clone forests were −0.457 and −0.340, respectively. As was described in *Table 1*, r_{ij} and r_{ijk} values for random samples should be zero and −0.5, respectively. The values of r_{ij} above mentioned are far larger than zero, and r_{ijk} values are also more or less larger than −0.5. Those larger values of r in clone forests indicate a heterogeneous distribution of environmental conditions which brings about a similarity of environmental effects upon adjoining trees, but possibly little effect of competition.

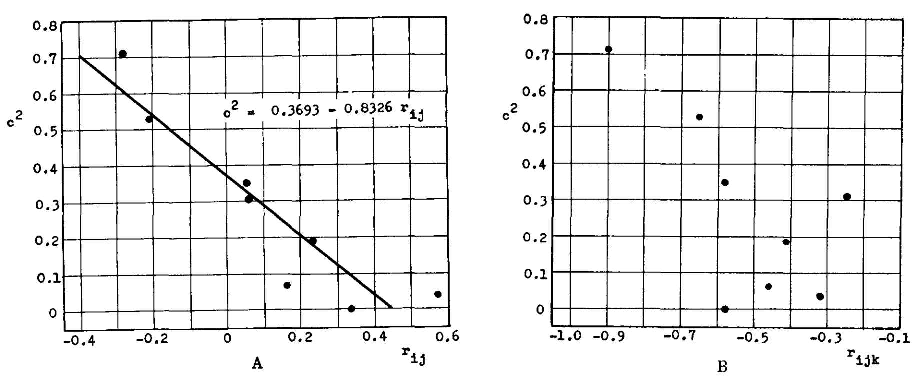

Figure 1, A and B. — Relation between the competitional parameter, c^2 and r_{ij} (A) or r_{ijk} (B) in *Cryptomeria japonica*. Stem diameter.

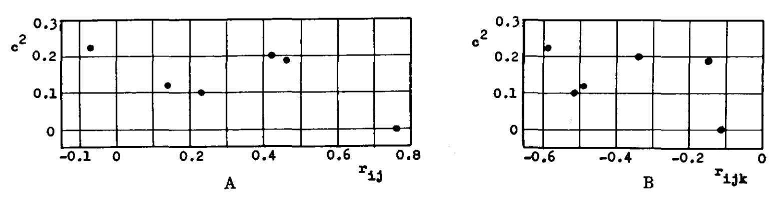

Figure 2, A and B. — Relation between the competitional parameter, c^2, and r_{ij} (A) or r_{ijk} (B) in *Cryptomeria japonica*. Tree height.

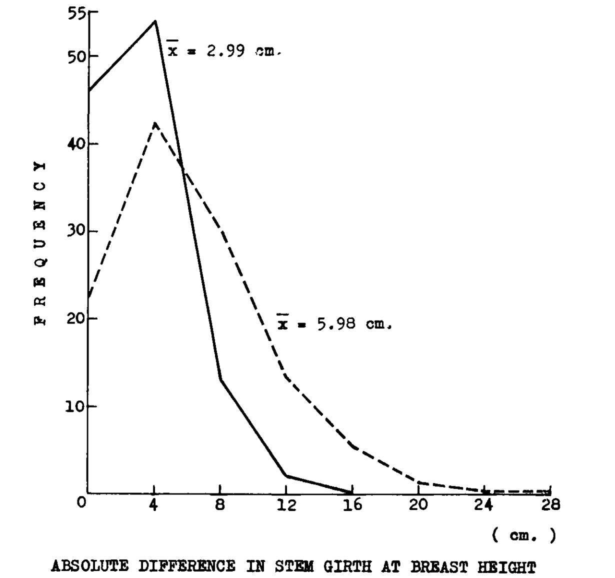

Figure 3. — Distribution of absolute differences of stem diameter between two adjoining trees in a clone of *Cryptomeria japonica.* — Broken line: Random combination of two's from the same forest.

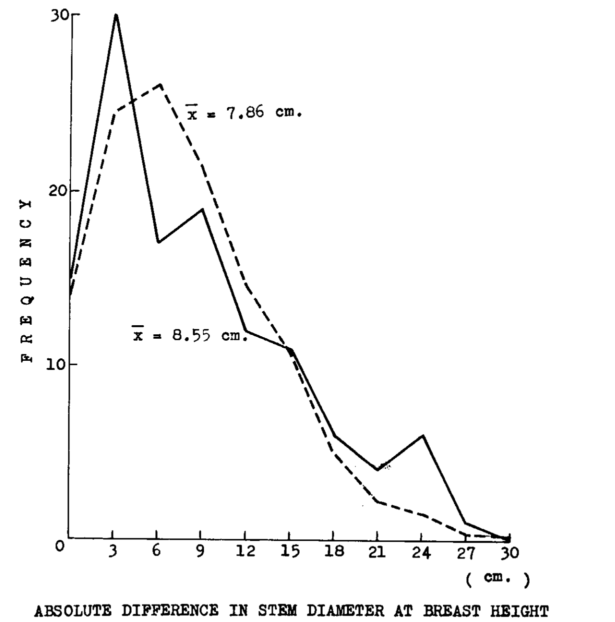

Figure 4. — Distribution of absolute differences of stem diameter between two adjoining trees in a seed-propagated forest of *Cryptomeria japonica* where inter-tree competition is apparently occurring. — Broken line: Random combination of two's from the same forest.

In seed-propagated forests, the r values were in general smaller than the figures given above indicating the pressure of competition. If we compare r_{ij} with r_{ijk}, then we find that r_{ij} is more useful than r_{ijk} for the detection of inter-tree competition, because the difference between clones and seed-propagated forests was very distinct in r_{ij} but not in r_{ijk}.

Studies on the estimation of genotypic, environmental and competitional variances in one clone- and seven seed-propagated forests as given in *Table 4* showed that the variance due to competition was approximately zero in the clone forest whereas seed-propagated forests often showed higher values. Comparison among b values or the regressions of c^2, i. e. the index of competitive stress, on r_{ij} or r_{ijk} shows that r_{ij} is more effective than r_{ijk} and the stem diameter is more sensitive than the tree height for assessing intensity of competition.

Two conclusions are drawn from these facts. One of them is that the r_{ij} of stem diameter is most critical in detecting intertree competition. Another conclusion is that the inter-tree competition in clone forests may be nil or very slight, if any, whereas in seed-propagated forests, it generally occurs intensively, moderately or slightly.

Of great interest in this connection are studies reported by KIRA and his associates. KIRA, OGAWA and SAKAZAKI (1953) found that the coefficient of variability within a single variety-population of soybean did not show any increase when the density increased. They also found that the weight of a plant in the soybean population showed positive correlations with the average weight of six plants surrounding it. The correlation coefficients were as high as 0.553 or 0.735. They concluded from this fact that "the result of intensified competition was quite uniformly shared among all plants, and plants equally suffer or prosper in the changing environment (density)". They noticed that "this fact is opposed to the common view that, once an individual surpassed its neighbors by chance, its dominance would be more and more accelerated by the process of competition". Two years later, however, some of this group of researchers (HOZUMI, KOYAMA and KIRA 1955) found that the correlation of fresh weight or length of shoot between adjoining plants in a population of yellow dent corn was negative, and concluded that "this type of interaction is truly competitive".

What do the two contradictory observations obtained by KIRA and his associates mean? It is important to notice that the soybean it a typically autogamous plant, while corn is allogamous. It is accordingly very probable that the soybean population was approximately isogenic whereas the corn population could have been highly heterogeneous genetically. Thus, their findings are in good agreement with our observations in *Cryptomeria* forests that competition is not operative in an isogenic population but it is in seed-propagated or genetically heterogeneous populations.

SAKAI and IYAMA (1966) investigated plant response to population density of twelve cultivars of barley on the one hand and their competitive ability on the other. The correlation between density response and competitive ability was not high enough to be regarded as significant, or often apparently very low. They concluded that density response and competitive ability are rather different traits controlled by different genetic entities. In the same paper, they assumed nine factors affecting plant growth in a population. Among them were plant density and three kinds of competition, i. e. intragenotypic, intraspecific-intergenotypic and interspecific competition. The present study of *Cryptomeria* indicates that competition hardly occurs between trees of the same genotype at least in the plant species investigated.

KIRA, OGAWA and SAKAZAKI (1953) worked out a formula,

$$w\,d^a = K,$$

in which w is the average weight per plant in a population and d is the population density, while a and K are constants. They called the above relation "competition-density effect" and a "competition-density index". This formula, however, expresses only the effect of population density on the average plant growth and has nothing to do with competition. The terms of KIRA and his associates should therefore be corrected and replaced by "density effect" and "density index", respectively.

By a comparative study between r_{ij} and the "index of competitive stress" regarding the stem diameter of *Cryptomeria* forests, that index can be roughly estimated by the formula,

$$c^2 = 0.3693 - 0.8326\, r_{ij},$$

although the r_{ij} is a statistic which is affected not only by intensity of competition but also by heterogeneity of soil or environmental conditions, i. e. it will take various values depending upon the combination of the measure of such heterogeneity and intensity of competition.

We are not yet fully aware of the role of intertree competition in a forest. We can only say safely that competition lowers the heritability value of growth characters and makes the effective selection of the mother tree difficult.

Estimation of genetic parameters has often been made by comparing variances between a clone- and a seed-propagated forest (for example, see TODA 1963). The problem involved in the technique of this estimation is that the "genotypic variance" thus estimated in a seed-propagated population may involve competitional variance in addition to the genuine genotypic variance, because the variance estimated within a clone is purely environmental without any competitional effect. In other words, there is a great chance of over-estimation of heritability values. This is an important problem in the improvement scheme of a tree species where competition is likely to occur, but no detailed discussion can be given at present.

Conclusion

Conclusions on intraspecific competition in *Cryptomeria japonica* D. DON drawn from the present study are as follows:

(1) Detection and measurement of competition intensity in a standing forest were carried out by using r_{ij}, i. e. the correlation of stem diameter between two adjoining trees, so far as an artificial plantation of a forest consisted of trees of the same age.

(2) The r_{ij} in a clone takes a positive value, but in seed-propagated forests the values are smaller. From this and other facts, it is concluded that competition occurs between trees of different genotypes, but not within the same genotype.

(3) Stem diameter is more susceptible to competition than tree height .

(4) Response of plants to population density should be discriminated from competition, though most agronomists and also some ecologists seem to mix them.

(5) Intraforest competition makes the selection of mother trees difficult, lowering the heritability of economically important characters.

(6) Estimation of heritability in the broad sense by subtracting variance of a clone from that of a seed-propagated forest is not correct because of competitional variance involved in the estimated "genotypic" variance.

Summary

Intraspecific competition was studied in *Cryptomeria* forests by means of the correlation of stem diameter or tree height between adjoining trees. Correlation between two adjoining trees was superior to that between the differences among three adjoining trees in the detection and assessment of intertree competition. Main findings from the present study are: (1) Stem diameter is more susceptible to competition than tree height. (2) Correlation between two adjoining trees was definitely positive in the clones, but it turned to zero or minus in most seed-propagated forests. (3) Differences in stem diameter between two adjacent trees in a clone tended obviously to being small in comparison with those in the seed-propagated forest. (4) Thus, it is concluded that trees of the same genotype do not compete with each other. Competition occurs only between different genotypes. (5) Comparison between the correlations and the index of competitive stress or the proportion of competitional variance to the total variance suggests that the latter can roughly be estimated by the former.

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