Monoterpene composition patterns could be useful for identifying the seed origin of plantations and also for verifying origin of certified seed from seed orchards (SQUILLACE 1977; SQUILLACE *et al.*, 1980 a). Most portions of the species range are unique for monoterpene composition, but some areas, especially in the eastern portion of the range, are not readily distinguishable. Use of supplementary traits would be desirable. For such use, patterns for two seed traits, assuming that they are genetically controlled to an appreciable degree, are shown in *Figures 6* and *7* (adapted from THORBJORNSEN 1961).

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A complementary gene inheritance of a needle morphology of outward hooking in sugi, Crypto meria japonica D. Don

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Summary

It is concluded that outward hooking needles of a sugi variant found in a plantation is produced by an interaction of two dominant complementary genes. To elucidate the mode of this inheritance, crossing experiments were made. For crossing materials, F_1-normal individuals from outcrossed progenies (normal × variant) which segregated the variant and the normal in a ratio of 1:3, were used. Segregation ratios in F_2 families were examined after selfing, backcrossing and full-sib crossing.

From the effect of complementary genes that are heterozygous in the variant parent, no segregation of the variant was seen after the selfing of F_1-normal individuals. For back-crosses between F_1-normal individuals and variant parent, segregation of the variant was observed in all cross combinations. Segregation ratios of the variant and the normal were 1:3 and 3:5. After full-sib cross combinations of F_1-normal individuals that produced the variant in backcrossing, it was concluded that the genotype of one partner was Aabb and the other was aaBb. In the second of the full-sib crosses in 1978, individuals identified by their genotypes were used and the experimental results showed a good fit with expected segregation ratios. In this way, it was possible to determine the genotypes of the females (F_1-normal individuals) used as partners.

From these cross experiments, it was proved that two dominant genes, A and B, located on two different pairs of chromosomes, interact to produce the needle morphology with outward hooking and each of them alone result in normal needles.

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Key words: *Cryptomeria japonica*, sugi seedlings, Mendelian inheritance, complementary gene, needle morphology, outward hooked needles.

Zusammenfassung

Die nach außen gekrümmten Nadeln einer in einer Pflanzung gefundenen Variante von *Cryptomeria japonica* D. DON gehen auf 2 dominante Komplementärgene zurück. Um den Vererbungsmodus zu klären, wurden Kreuzungsversuche unternommen. Als Kreuzungsmaterial wurden normale F_1-Individuen benutzt, die aus Fremdungen (normal × Variante) hervorgegangen waren und im Verhältnis 1:3 Variante zu normalen Individuen aufspalteten. Die Aufspaltung in den F_2-Familien wurde nach Selbstung, Rückkreuzung und Vollgeschwisterkreuzung untersucht. Durch die komplementäre Wirkung der Gene, die in den Elternvarianten heterozygot waren, wurde keine Aufspaltung der Varianten nach dem Selbsten der normalen F_1-Individuen sichtbar. Bei den Rückkreuzungen zwischen normalen F_1-Individuen und den Elternvarianten spalteten die Varianten in allen Kreuzungskombinationen auf. Die Spaltungsverhältnisse von Varianten zu Normalen waren 1:3 und 3:5. Nach den Vollgeschwister-Kreuzungskombinationen normaler F_1-Individuen, die nach Rückkreuzung die Variante ergaben, wurde festgestellt, daß der Genotyp des einen Partners Aabb und der des anderen aaBb war. In der 2. Serie der Vollgeschwisterkreuzungen 1978 wurden durch ihren Genotyp identifizierte Individuen benutzt, und die Ergebnisse des Experimentes zeigten eine gute Übereinstimmung mit den erwarteten Spaltungsverhältnissen. Auf diese Weise war es möglich, die Genotypen der als Partner benutzten weiblichen Individuen (normale F_1-Individuen) zu bestimmen.

Aus diesen Kreuzungsexperimenten ging hervor, daß 2 dominante Gene A und B, die auf verschiedenen Chromo-

somenpaaren lokalisiert sind, eine Interaktion bewirken, die zu einer nach außen gekrümmten Nadelform führt, während jedes allein für sich normale Nadeln zur Folge hat.

Introduction

Sugi, *Cryptomeria japonica* D. DON is one of the domestic evergreen conifers in Japan and is the only species in the genus. The natural distribution of sugi lies between Mt. Yagura, Azigasawa, Nisitugaru-gun, Aomori-ken (40° 42' N) and Yaku island, Yaku-mati, Kumage-gun, Kagoshima-ken (30° 15' N) (HAYASHI, 1951). Some small plantations occur at Sapporo, Hokkaido (40° 03' N), beyond the natural range of distribution (IWATA, 1954 and UEHARA, 1975). Sugi is one of the most important forest tree species in Japan. It is a high tree with a straight bole, excellent growth, desired wood characteristics and easy processing. Its wood has various uses such as in house construction, furniture and instruments.

Sugi has been planted for several centuries over a wide range, and is now the most commonly planted species in Japan. Significant progress has been made in genetic improvement of the species, but continued work is needed.

The large variation in the characteristics of sugi has resulted in attempts to classify the species into various strains and horticultural cultivars by many scientists such as ISHIZAKI (1966), IWATA *et al.* (1954), MIKAMI *et al.* (1969), TODA *et al.* (1969) and UEHARA (1975). Morphological traits have been the most important criteria for discriminating among varieties which are mostly propagated by cuttings as reported by ISHIZAKI (1966) and MIKAMI *et al.* (1969).

Identification of major genes responsible for varietal differences has been made by various authors. Many genes responsible for the traits of albino, xantha, morphology and winter coloration of sugi needles have been detected by CHIBA (1953), OHBA *et al.* (1973, 1974) and KIKUTI (1977, 1978).

To clarify the inheritance of traits in sugi, we made selfing and out-crossing various phenotypic variants. From a series of these crosses, a morphological variant that shows abnormal needles, called outward hooking, was found. KIKUTI (1977) reported a dominant mode of inheritance of the trait. Results from previous work with the variant, Cr-54, involving reciprocal crosses with normal parents and selfing show that in all F_1 families, the variant was segregated as a discontinuous trait from the normal needle character. In most F_1 families outcrossed with normal sugi, the ratio was var. (1): nor. (3), in a few families the ratios were var. (1): nor. (1) or var. (3) : nor. (5). After selfing the variant, the segregation ratio was nearly var. (9) : nor. (7). With these results, it is postulated that two different dominant genes are working complementarily. The variant parent (Cr-54) was supposed to have a doubly heterozygous genotype for the genes. Most of the normal parents used for these crosses were suspected to be recessive homozygotes for the genes.

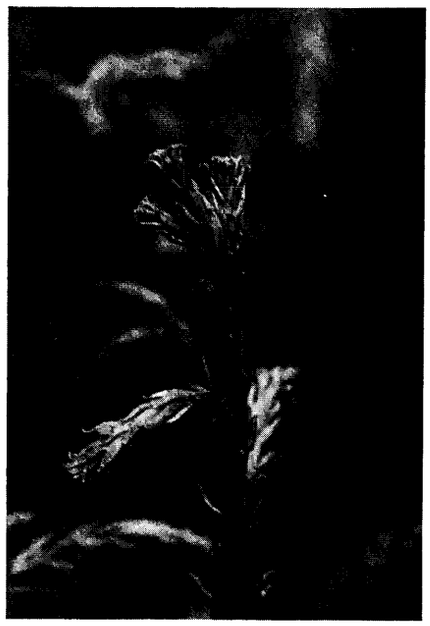

Fig. 1. — Needle characters and shape of shoot terminals of a sugi variant named outward hooked-needle sugi.

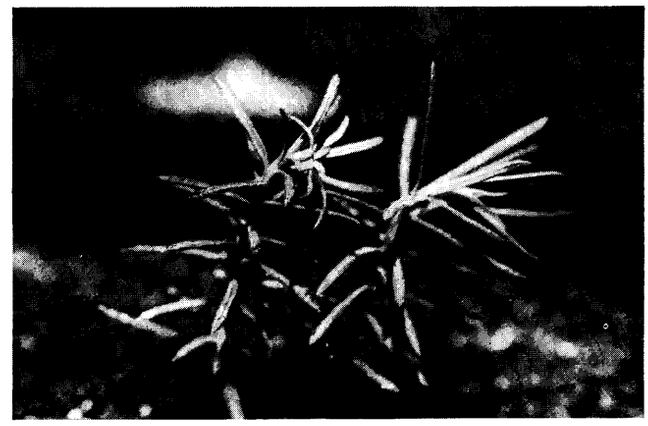

Fig. 2. — A variant (left) and a normal (right) seedling derived from a full-sib cross in which they were expected to have genotypes of Aabb and aaBb, respectively.

The purpose of this study is to further elucidate the segregation ratios of outward hooking in sugi.

Materials and methods

Each needle of the sugi variant, Cr-54 has a peculiar outward crooking against the needle axis *(Figure 1).* The anomaly affects the primary leaves and is retained in mature needles. Outward hooked primary leaves in a seedling derived from a full-sib cross of F_1-normal individuals are shown in *Figure 2.*

In this report, the ortet and ramets of the plant with outward hooked needles is designated as Cr-54 and individuals with this anomaly in following generations are designated F_1-variant or F_2-variant. Plants with wild type needles are called normal. Symbols of gene marks, A and B for dominant, and, a and b for recessive are used for convenience.

In this experiment, four F_1 families were mainly used in which a segregation ratio of F_1-var. (1): F_1-nor. (3) was observed after crosses between Cr-54 and four normal parents. For crossing, young saplings of 3 to 5 years of age were treated with gibberellic acid to induce flowers. Owing to poor flowering of F_1-variants from these four F_1 families, F_1-normal individuals were mostly used for back-crossing to Cr-54 and the four normal parents. Each of the F_1-normal individuals is expected to have one of the three genotypes of Aabb, aaBb and aabb. F_1-normal individuals having genotypes Aabb (72-55-1) or aaBb (72-55-2), where A or B is arbitrarily adopted, are presented *(Figure 3).*

Cross combinations of the parents, number of F_1-normal individuals involved in the crosses and number of crosses are shown for each F_1 family *(Table 1).* Four types of cros-

Fig. 3. — Needles of F_1-normal individuals, 72-55-1 (left) and 72-55-2 (right). At present, genotypes of both plants were determined as follow: Aabb for 72-55-1 and aaBb for 72-55-2.

ses were made: (1) self, (2) back-cross with normal parents (test cross), (3) back-cross with the variant, Cr-54 and (4) full-sib cross among F_1-normal individuals in each family. In each cross with normal parents, the progeny seem to have a genotype of doubly recessive homozygotes as aabb, and the variant, Cr-54 has a genotype of AaBb as postulated with the previous experiments.

The crosses were made at the Hazama nursery in the Asakawa Experimental Forest, the Forestry and Forest Products Research Institute in both 1976 and 1978. All sugi plants expected to be used for the crossing were sprayed with gibberellic acid solution to induce flower differentiation in the previous summer. For the full-sib cross in 1976, pollen was collected from all F_1-normal individuals having male flowers, for pollination of all individuals having female flowers. In 1978, sib-crosses were mostly made with selected F_1-normal individuals as the males because these individuals contributed to variants produced in full-sib crosses in 1976. However, some of the F_1-normal individuals were used as males at random. Pollination of isolated strobili was conducted several times during the receptive stage of the female strobili by a pollen gun. For selfing, male- and female strobili were bagged together, and the bags were vigorously shaken to cause pollen dispersal. Seeds obtained from cone collection in October were cleaned and separated from unsound seeds.

The seeds were sown in spring, 1979 in boxes made of wooden plates or plastic. The ensuing seedlings were kept in the boxes within a plastic greenhouse for one growing season. Measurements were made periodically in the plastic greenhause, and at time of bud burst following transplanting in spring 1980.

Results

1. Determination of genotypes of F_1-normal individuals

It was postulated in a report by Kikuti (1977) that two dominant genes cooperating complementarily were responsible for the outward hooked needles. Our results add credence to the complementary gene system. If Cr-54 has a genotype of AaBb, five genotypes are postulated for the F_1-normal individuals as AAbb, aaBB, Aabb, aaBb and aabb.

In our experiment, only F_1 families which showed a segregation ratio of F_1-var. (1): F_1-nor. (3) were used, so the genotype of the normal parents, Cr-43, Cr-59, Cr-99

Table 1. — Numbers of F_1-normal individuals used for crossing and their crossing combinations.

		Selfing		Backcross with normal parent		Backcross with variant parent		Sib-cross	
No. of F_1 family	Cross-combination of parents	Number of individuals	Number of crosses	Number of individuals	Number of crosses	Number of individuals	Number of crosses	Number of individuals	Number of crosses
72-22	Cr-43 x Cr-54	23	24	12	12	14	15	12	25
72-27	Cr-59 x Cr-54	6	6	2	2	6	6	5	11
72-34	Cr-99 x Cr-54	6	6	4	5	6	6	1	1
72-55	Cr-323 x Cr-54	11	11			3	4	10	23
Total		46	47	18	19	29	31	28	60

and Cr-323 should be doubly recessive homozygotes as aabb. In the crosses between Cr-54 and the normal parents, the following genotypic combination is expected: aabb × AaBb *(Table 1)*. From this cross, F_1-individuals should have four kinds of genotypes as AaBb, Aabb, aaBb and aabb with the same frequency. The phenotypic ratio is expected to be F_1-var. (1): F_1-nor. (3) *(Figure 4)*. Thus, F_1-normal individuals have three genotypes as Aabb, aaBb and aabb. By the analyses of the F_2-variant segregation from selfing, back-crosses and full-sib crosses using these F_1-normal individuals, the genetic behaviour of the outward hooked needles will be elucidated.

2. Selfing

Selfing of F_1-normal individuals involve three types of genotypic combinations: Aabb × Aabb, aaBb × aaBb and aabb × aabb. Each has an equal chance of occurring after random selection of the individuals and none will produce a genotype of the variant AaBb. As expected, only F_2-normal individuals were produced as shown in *Table 2*. From 46 F_1-normal individuals (one individual was selfed two times in different years, from 47 F_2 families) derived from 4 F_1 families, 1806 F_2 seedlings were produced, all of which were normal.

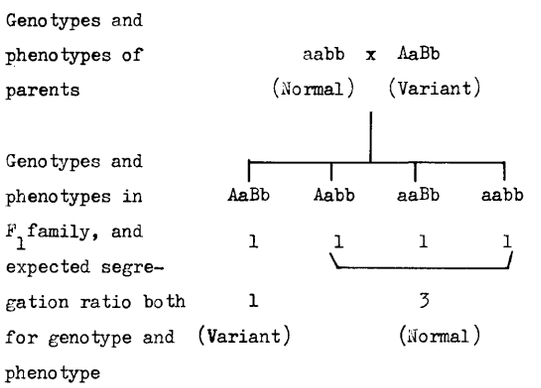

Fig. 4. — Schematic mode of inheritance involving two complementary genes where segregation of variant (1) : normal (3) was produced in F_1 family.

Table 2. — Results of F_2 segregation from selfing of F_1 normal individuals derived from normal parents × Cr-54, a variant with outward hooked needles.

Cross combination Selfing	Year of cross	Segregation Total	Variant	Normal
72-22-6, 1 family	1976	38	0	38
72-22- ,23 families	1978	607	0	607
72-28- , 6 families	1978	508	0	508
72-34-10, 1 family	1976	28	0	28
72-34- , 5 families	1978	400	0	400
72-55- ,11 families	1978	225	0	225
Total 47 families		1,806	0	1,806

Table 3. — Results of F_2 segregation from back-crosses of F_1-normal individuals × normal parents as male.

Cross combination	Year of cross	Segregation Total	Variant	Normal
72-22- , x Cr-43, 2 families	1976	65	0	65
72-22- , x Cr-43,10 families	1978	290	0	290
72-28- , x Cr-59, 2 families	1978	169	0	160
72-30-6 , x Cr-99, 1 family	1976	10	0	10
72-34- , x Cr-99, 4 families	1978	246	0	246
Total 19 families		771	0	771

3. Back-cross with the normal parents (aabb)

In this back-cross, three genotypic combinations are possible as Aabb × aabb, aaBb × aabb and aabb × aabb, and none will produce a genotype of the variant, AaBb. The results from 19 F_2 families derived from 4 F_1 families and totaling 771 normal seedlings from crosses of two different years are shown in *Table 3*. All seedlings were normal.

4. Back-cross with the variant parent, Cr-54 (AaBb)

In this back-cross, three genotypic combinations are possible as Aabb × AaBb, aaBb × AaBb, and aabb × AaBb, and all combinations will produce the variant genotype. A-B-. respectively. Moreover, two kinds of segregation ratios of F_2-var.: F_2-nor., as 3:5 and 1:3 are expected according to the genotypic combinations. If the F_1-normal individuals were selected at random, two thirds of the back-cross combination will show a 3:5 segregation ratio and one third of these will show 1:3. The experimental results are shown in *Table 4*. From all back-cross combinations of 29 F_1-normal individuals belong to 4 F_1 families, F_2-variant was segregated. Two kind of segregation ratios were noted as expected with 3:5 or 1:3. Although, F_2 individuals are fewer than expected in some families, the frequency of the segregation ratio of F_2-var. (3): F_2-nor- (5) seems to be more than that of 1:3.

5. Full-sib cross between F_1-normal individuals in the same family

It is expected that there will be three genotypes in F_1-normal individuals as Aabb, aaBb and aabb. If they are mated at random, the following 6 genotypic combinations are possible with two different frequencies.

Genotypic combination	Frequency	Phenotypic segregation
Aabb × Aabb	2	Variant and normal
aaBb × aaBb	2	Normal only
aabb × aabb	2	Normal only
Aabb × aaBb	1	Normal only
aaBb × aabb	1	Normal only
Aabb × aabb	1	Normal only

Thus, only one combination, Aabb × aaBb will segregate the variant and the combination frequency will be 2/9 after random mating among the normal individuals. The F_2 segregation ratio will be var. (1): nor. (3). Results of the full-sib crosses of 1976 involving 7 of 19 F_2 families derived from 4 F_1 families showed the variant segregating with the ratio of F_2-var. (1): F_2-nor. (3) as expected *(Table 5)*.

The 1978 crosses were mostly made with pollen from F_1-normal individuals which contributed to produce the variant in the crosses of 1976. In some instances, pollen taken randomly from F_1-normal individuals was also used. In the F_1-normal individuals which produced the variant in a cross combination, one genotype presumed to be Aabb would cause the other genotype to be aaBb *(Figure 3)*. If pollen from F_1-normal individuals is used with a genotype of Aabb, the frequency of the F_2 family which segregates the variant will be 1/3. This is because the genotypes of the partners should be either Aabb, aaBb and aabb, and only the combination of Aabb × aaBb will produce the variant. The situation is the same for pollen from F_1-normal individuals with an aaBb genotype. From use of an Aabb geno-

Table 4. — Results of segregation from backcross of F_1-normal individuals × variant parent, Cr-54.

Backcross combination		Year of cross	Segregation			Two expected segregation ratios and their degree of fit			
						1 : 3		3 : 5	
Female	Male		Total	Variant	Normal	Chi-square	P	Chi-square	P
72-22- 4 x	Cr-54	1978	7	1	6	0.41	NS	1.61	NS
72-22- 5 x	"	"	3	1	2	1.00	NS	0.02	NS
72-22- 9 x	"	"	33	13	20	3.65	NS	0.05	NS
72-22-10 x	"	1976	19	5	14	0.02	NS	1.01	NS
72-22-13 x	"	"	38	17	21	7.89	**	0.85	NS
72-22-20 x	"	1978	10	3	7	0.13	NS	0.24	NS
72-22-23 x	"	"	30	11	19	2.18	NS	0.01	NS
72-22-24 x	"	1976	6	1	5	0.22	NS	1.11	NS
" x	"	1978	103	36	67	5.44	*	0.29	NS
72-22-26 x	"	"	5	2	3	0.60	NS	0.01	NS
72-22-27 x	"	"	7	4	3	3.86	*	1.15	NS
72-22-28 x	"	"	16	9	7	8.33	**	2.40	NS
72-22-34 x	"	"	33	10	23	0.49	NS	0.73	NS
72-22-36 x	"	"	25	5	20	0.33	NS	3.27	NS
72-22-37 x	"	"	35	6	27	0.82	NS	2.49	NS
			(368)	(124)	(244)				
72-28- 1 x	Cr-54	1978	187	45	142	0.09	NS	14.40	**
72-28- 2 x	"	"	35	3	32	5.04	*	12.50	**
72-28- 3 x	"	"	82	15	67	1.97	NS	12.91	**
72-28- 4 x	"	"	19	6	13	0.44	NS	0.28	NS
72-28- 5 x	"	1976	11	4	7	0.76	NS	0.01	NS
72-28- 8 x	"	"	8	3	5	0.67	NS	0.00	NS
			(342)	(76)	(226)				
72-34- 1 x	Cr-54	1978	53	14	39	0.57	NS	2.78	NS
72-34- 2 x	"	"	34	10	24	0.35	NS	0.95	NS
72-34- 3 x	"	"	102	35	67	4.72	*	0.44	NS
72-34- 5 x	"	"	16	5	11	0.33	NS	0.27	NS
72-34- 6 x	"	"	18	8	10	3.63	NS	0.37	NS
72-34-10 x	"	1976	19	8	11	2.96	NS	0.17	NS
			(242)	(80)	(162)				
72-55- 1 x	Cr-54	1976	8	3	5	0.67	NS	0.00	NS
" x	"	1978	78	26	52	2.89	NS	0.58	NS
72-55- 2 x	"	"	8	3	5	0.67	NS	0.00	NS
72-55- 6 x	"	"	82	19	63	0.15	NS	4.72	*
			(176)	(51)	(125)				

type as a pollen parent, genotypes of the females are analysed by the variant segregation, *i.e.*, if the variant is produced, the genotype of the female is aaBb and if there is no segregation, the genotype is Aabb or aabb. If pollen of an aaBb genotype is fixed, similar analytical procedures are possible. When an individual is crossed with pollen of both genotypes, Aabb and aaBb, and no variant is produced, the genotype of the individual is aabb. With these analytical cross experiments, the genotypes of F_1-normal individuals used as females are estimated and presented in *Tables 6*, 7 and *8*. In these instances, complementation tests between different families were not done, so the dominant genes of A and B in each family were arbitrarily adopted separately for convenience. As shown in *Table 6*, the estimated frequency of females, F_1-normal individuals, are 3 for Aabb, 4 for aaBb and 2 for aabb in the 72-22 family. For the family of 72-28 in *Table* 7, the genotypic frequency was 1 for Aabb, 2 for aaBb and 2 for aabb. In the 72-55 family as seen in *Table 8*, it was 4 for Aabb and 4 for aaBb. Although there was no individual with the aabb genotype, it might be expected if the number of females was increased.

Table 5. — Results of F_2 segregation from random full-sib mating between F_1-normal individuals in 1976 derived from crosses of normal parents × variant, Cr-54.

CROSS COMBINATION	SEGREGATION		
	TOTAL	VARIANT	NORMAL
72-22-(11) x 72-22-(25)	11	3	8
" x 72-22-(36)	8	2	6
72-22-(13) x 72-22-(6)	32	8	24
" x 72-22-(12)	13	2	11
72-22-(16) x 72-22-(36)	3	1	2
72-55-(1) x 72-55-(2)	10	2	8
72-55-(5) x 72-55-(17)	3	1	2
(7 COMBINATIONS)	(80)	(19)	(61)
72-22-(13) x 72-22-10	5	0	5
72-22-19 x 72-22-(6)	9	0	9
" x 72-22-(25)	9	0	9
72-28-1 x 72-28-2	40	0	40
" x 72-28-3	17	0	17
" x 72-28-9	71	0	71
72-34-2 x 72-34-11	6	0	6
72-55-(1) x 72-55-6	16	0	16
" x 72-55-14	7	0	7
72-55-(5) x 72-55-13	3	0	3
72-55-6 x 72-55-(1)	24	0	24
" x 72-55-(17)	13	0	13
(12 COMBINATIONS)	(220)	(0)	(220)

(Circled figures are supposed that the F_1-normal individuals have only one complementary gene out of A or B.)

Discussion

Results from crosses between the variant parent, Cr-54, and the normal parents in 1972 showed discontinuous segregation of the variant and the normal. Most of the segregation ratios gave a good fit to var. (1): nor. (3), but, some F_1 families had ratios approximating 3:5 or 1:1. These results caused Kikuti (1977) to conclude that there might be more than one gene involved for inheritance of this needle character. There are many cases in which two alleles in different loci have several kinds of interactions such as

Table 6. — Results of segregation from crosses between F_1-normal individuals having genotypes of Aabb, aaBb or aabb. For each individuals, gene A or B is arbitrarily fixed for convenience.

		MALE							
FEMALE		72-22-13 Aabb		72-22-6 aaBb		72-22-12 aaBb		72-22-34 aaBb	
		VAR.	NOR.	VAR.	NOR.	VAR.	NOR.	VAR.	NOR.
	EXP.	RATIO, N(1)		EXPECTED RATIO, V(1) : N(3)					
72-22-11	Aabb	–	–	–	–	2	5	–	–
72-22-13	Aabb	0	15	8	24	7	30	–	–
72-22-26	Aabb	–	–	3	9	3	15	1	7
		(0)	(15)	(11)	(33)	(12)	(50)	(1)	(7)
				[24] : [90]					
		V(1):N(3)		EXP. RATIO, N(1)					
72-22-6	aaBb	–	–	0	44	0	13	0	11
72-22-12	aaBb	3	13	–	–	0	16	0	46
72-22-36	aaBb	6	7	0	16	–	–	0	22
		(9)	(20)	(0)	(50)	(0)	(29)	(0)	(79)
				[0] : [158]					
			N(1)	EXP. RATIO, N(1)					
72-22-23	aabb	0	10	–	–	0	112	0	34
72-22-35	aabb	0	5	0	12	–	–	0	17
		(0)	(15)	(0)	(12)	(0)	(112)	(0)	(51)
				[0] : [175]					

Table 7. — Results of segregation from crosses between F_1-normal individuals having one of the genotypes of Aabb, aaBb or aabb. For each individuals, gene A or B is arbitrarily fixed for convenience. The same procedures as in *Table 6* are used here.

		MALE			
FEMALE		72-28-2 Aabb		72-28-4 aaBb	
		VAR.	NOR.	VAR.	NOR.
72-28-2	Aabb	0	69	4	26
72-28-4	aaBb	6	34	0	84
72-28-6	aaBb	17	81	0	22
		(23)	(115)	(0)	(106)
72-28-1	aabb	0	70	0	117
72-28-3	aabb	0	188	0	124
		(0)	(258)	(0)	(241)

complementation and inhibition. To interpret the experimental results, two situations were postulated. One is complementary genes and the other is inhibitor genes. Fitness of these postulations to the experimental results will be determined by the segregation ratios which are tested by selfing, back-crossing and full-sib crossing of the F_1-normal individuals taken from F_1 families that segregated F_1-var. (1): F_1-nor. (3).

If we postulate an inhibitor gene for the inheritance of this trait and a segregation ratio of var. (1): nor. (3) in the F_1 families, the genotypic combination in the first crosses may be Aaii (Cr-54) × aaIi (normal). In F_1-normal individuals, four types of genotypes will be produced as AAii (variant) and three normals with AaIi, aaIi and aaii *(Figure 5)*. In the F_1-normal individuals with a genotype of AaIi, the activity of A gene is suppressed by I inhibitor and the result is a normal phenotype. The variant will be expressed only in the genotype of Aaii. From selfing of randomly selected F_1-normal individuals, the plants with an AaIi genotype will segregate the variant. Moreover, back-crosses (test crosses) such as AaIi × aaIi and AaIi × aaii should produce the variant. When using the variant as a back-cross partner, all cross combinations will produce the variant with different ratios according to the genotypes of the F_1-normal individuals being randomly selected. The F_2 families segregated the variant with a probability of 5/9, and the segregation ratios vary with the genotypes of the partners.

The experimental results refute the inhibitor model, because variants are not produced from selfing of F_1-normal individuals.

For the complementary gene system, theoretical segregation ratios are summarized in *Table 9*. If the variant is expected to b an A-B- genotype, no variant will be produced after selfing of F_1-normal individuals. In some back-cross combinations of F_1-normal individuals which have an A or B gene from the variant parent, the variant will be segregated in F_2 progenies. The segregation ratio will be var. (3): nor. (5), and the genotypic combination is Aabb × AaBb or aaBb × AaBb. The result is var. (1): nor. (3) which is similar to results of the cross of aabb × AaBb.

In full-sib crosses, only one combination of genotypes as Aabb × aaBb out of six different genotypic combinations produce the variant and no other combination will segregate the variant.

As shown in *Tables 2* and *3*, no variant was segregated from selfing of F_1-normal individuals and from back-crosses of F_1-normal individuals with the normal parents as male. However, back-crosses of F_1-normal individuals with

Table 8. — Results of the segregation from crosses between F_1-normal individuals having one of the genotypes of Aabb, aaBb or aabb. For each individual, gene A or B is arbitrarily fixed for convenience. The same procedures as in *Table 6* are used here.

		Male							
Female		72-55- 1 Aabb		72-55-17 Aabb		72-55- 2 aaBb		72-55- 5 aaBb	
		Var.	Nor.	Var.	Nor.	Var.	Nor.	Var.	Nor.
72-55- 1	Aabb	0	31	0	26	2	8	17	45
72-55- 3	Aabb	0	18	–	–	16	22	–	–
72-55- 6	Aabb	0	24	0	5	14	22	13	39
		(0)	(73)	(0)	(31)	(32)	(52)	(30)	(84)
72-55- 2	aaBb	6	10	5	25	0	5	–	–
72-55- 4	aaBb	3	21	–	–	0	15	–	–
72-55- 5	aaBb	22	67	3	23	0	88	0	47
72-55-11	aaBb	7	13	13	32	0	34	0	69
		(38)	(111)	(21)	(80)	(0)	(142)	(0)	(116)

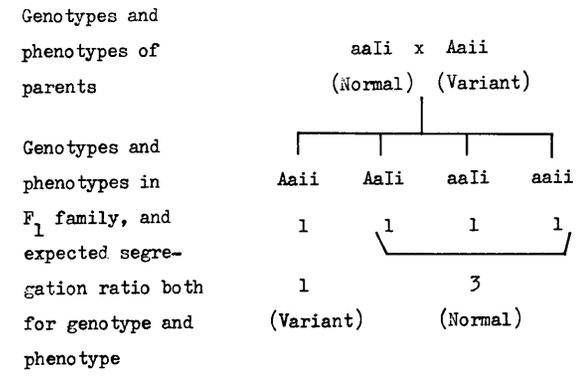

Fig. 5. — Schematic mode of inheritance involving one inhibitor gene where segregation of variant (1) : normal (3) was produced in F_1 family.

Table 9. — In the complementary two gene system, the expected phenotypic segregation ratios after several cross combinations such as selfing, backcrosses among F_1-normal individuals in the families showing the segregation ratio of the variant (1) : normal (3) in the normal parents × the variant parent, Cr-54 are shown.

Selfing

Genotypic combination	Expected phenotypic segregation Variant	:	Normal
Aabb x Aabb	0	:	1
aaBa x aaBb	0	:	1
aabb x aabb	0	:	1

Backcross with double-recessive homozygote

Genotypic combination	Expected phenotypic segregation Variant	:	Normal
Aabb x aabb	0	:	1
aaBb x aabb	0	:	1
aabb x aabb	0	:	1

Backcross with double-heterozygote, Cr-54

Genotypic combination	Expected phenotypic segregation Variant	:	Normal
Aabb x AaBb	3	:	5
aaBb x AaBb	3	:	5
aabb x AaBb	1	:	3

Full-sib-cross

Genotypic combination	Expected phenotypic segregation Variant	:	Normal
Aabb x Aabb	0	:	1
Aabb x aaBb	1	:	3
Aabb x aabb	0	:	1
aaBb x aaBb	0	:	1
aaBb x aabb	0	:	1
aabb x aabb	0	:	1

the variant parent, Cr-54 segregated the variant in all combinations (*Table 4*). Moreover, some cross combinations among full-sibs produced the variant as shown in *Table 5*. If it is assumed that an inhibitor gene is involved in this inheritance, F_1-normal individuals being selfed and backcrossed with normal parents should segregate the variant.

In full-sib crosses, some male parents with a supposed dominant gene which is effective for fixed production of the variant, the genotype of the F_1-normal individuals was estimated by the segregation of the variant. With all these analyses, the existence of an inhibitor was denied and they supported a complementary gene system. Moreover, KIKUTI (1981) found that by selfing the variant parent, Cr-54, the segregation ratio was good fit for var. (9): nor. (7) indicating the presence of complementary genes. This result was not surprising because there are many examples of inheritance in which complementary genes are involved such as in comb shapes of poultry, fur color of mice, ornamental pumpkins, flower color of sweet-peas and of morning glory and others (See, TANAKA, 1955).

In the inheritance of the needle character of the sugi variant, Cr-54, two dominant genes, A and B, are postulated on different pairs of chromosomes. By the co-existence of both dominant genes, it is expected that a variant having outward hooked needles will result and that any one of the dominant genes produce only normal phenotypes. Sugi has twenty two (2n) somatic chromosomes. It is clear that two pair of alleles are located on a different pair of chromosomes. It is observed that many variant individuals in different generations have much shorter needles than those of normal ones. This might be explained with a pleiotropic effect of the dominant genes and/or by linkage of dominant genes with other genes responsible for short needles (KIKUTI, 1977).

The next steps is to produce homozygous individuals for the dominant genes such as AABB, AAbb and aaBB. The geographical distribution of these dominant genes will be clarified utilizing these homozygotes as testers. The gene effects of A and B will also be studied in relation to other characters.

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