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Genetic Analysis of Tillering and Other Agronomic Characters in Foxtail Millet (*Setaria italica* (L.) P. Beauv.) Using the Progeny from the Cross between the Two Diverse Strains, Gai 53 and Kuromochi

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Introduction

Foxtail millet (*Setaria italica* (L.) P. Beauv.) is a highly self-pollinated diploid grass of Eurasia that shows a remarkable diversity in agronomic characters such as heading time, plant height, tiller number and caryopsis shape^{5, 10, 11, 12, 13, 14, 16, 17, 18, 19, 20}. Among these, tiller number is of main interest to us because of its evolutionary significance. The domestication of crop plants has often involved an increase in apical dominance (the concentration of resources in the main stem of the plant and a corresponding suppression of axillary branches)⁴. For example, most foxtail millet cultivars produce no tillers, but its wild ancestor green foxtail millet (*S. viridis* (L.) P. Beauv.) produces many tillers. A similar situation is seen in maize (*Zea mays* spp. *mays*) and its probable ancestor teosinte (*Z. mays* spp. *parviglumis*). Teosinte plants typically bear elongated lateral branches at most nodes on their main stems. In contrast, maize plants typically produce a lateral branch at only two or three of the nodes on their main stems⁴. These differences in plant architecture are governed by a small number of quantitative trait loci (QTL)². One QTL with a strong effect corresponds to *teosinte branched* locus (*tb1*), of which the mutant recessive gene *tb1* confers many branches in maize³. The *tb1* gene was cloned, and its function at molecular and biochemical levels was inferred⁴. Since most cereals, including foxtail millet and maize, have been shown to have similar genomes in terms of gene content and gene order, irrespective of chromosome number and genome size^{1, 6}, it is probable that the homolog of the *tb1* gene is involved in tiller number in foxtail millet. Another agronomic character of interest to us is caryopsis shape. It has been shown to be related to geographic distribution⁵. However, there has been very little information about the genetic mechanism controlling agronomic characters including tiller number and caryopsis shape. In the present study, genetic analyses of these agronomic characters were performed using the progeny from the cross between two strains differing in these characters.

Materials and Methods

Kuromochi (KM) and Gai 53 (G53) were selected from our collection¹⁶. KM is a native cultivar of Kagoshima Prefecture, Japan, and was collected in 1950. G53 is a strain collected in Leningrad, Russia, in 1965. Agronomic traits investigated in the present study of the two strains are

shown in Tables 1 and 2.

Table 1. Mean values and ranges of agronomic characters of G53 and KM under natural daylength condition

Characters ¹⁾	Unit	G53		KM	
		Mean	Range	Mean	Range
DH ²⁾	day	33.1	32-35	89.9	86-95
TN	number	10.7	6-16	1.0	1
CL	cm	91.12	64.2-107.3	160.94	146.1-170.7
PL	cm	13.91	10.4-16.2	11.21	10.2-11.9
LN	number	13.3	12-14	22.4	20-24
CRL	mm	2.499	2.32-2.61	2.035	1.99-2.14
CW	mm	1.584	1.46-1.67	1.540	1.44-1.63
WHC	g	0.286	0.27-0.30	0.224	0.20-0.25
SS	%	52.74	44.1-60.9	25.70	18.8-37.0
YM	g	2.640	1.86-3.20	1.813	1.20-2.39

1) Abbreviations: TN, number of tillers including main culm; CL, culm length; PL, panicle length of the main culm; LN, total leaf number of main culm; CRL, caryopsis length; CW, caryopsis width; WHC, weight of 100 caryopses; SS, seed set; YM, yield from the main culm.

2) The data for DH was obtained from Ichitani et al.⁷⁾

Table 2. Mean values and ranges of agronomic characters of G53 and KM under 10h daylength condition

Characters ¹⁾	Unit	G53		KM	
		Mean	Range	Mean	Range
DH ²⁾	day	26.9	25-29	35.3	33-38
TN	number	29.5	18-39	1.1	1-2
CL	cm	51.08	40.2-64.4	104.27	91.8-110.8
PL	cm	6.18	4.9-7.9	12.41	11.2-13.8
LN	number	9.5	9-11	12.9	12-14
CRL	mm	2.64	2.57-2.72	2.04	1.92-2.13
CW	mm	1.577	1.51-1.63	1.592	1.49-1.64
HC	g	0.289	0.28-0.30	0.244	0.23-0.26
SS	%	34.63	26.6-44.4	46.38	35.4-53.0
YM	g	0.758	0.32-1.14	2.845	1.57-3.47

1) The meanings of the abbreviations are shown in footnote¹⁾ of Table 1.

2) The data for DH was obtained from Ichitani et al.⁷⁾

Genetic analysis

The F₂ population derived from the cross between G53 and KM was subjected to genetic analyses of the following characters: number of tillers including main culm (TN), culm length (CL), panicle length of the main culm (PL), total leaf number of the main culm (LN), caryopsis length (CRL), caryopsis width (CW), weight of 100 caryopses (WHC), seed set (SS) and yield from the main culm (YM). The F₂ population was grown under two daylength conditions, namely, natural daylength condition and short daylength condition (10h) along with parental strains (10 plants under each condition) (Tables 1 and 2) in a greenhouse on the Experimental Farm of the Faculty of Agriculture, Kagoshima University, Kagoshima, Japan (31° 31'N). The sowing date was June 20,

2000. This population has already been analyzed for heading time, and the details of cultivation methods have already been described⁷⁾. LN was marked with paint on every fourth leaf, counting from the lowest. CL was expressed as the length from the base to the highest node of the main culm. PL was expressed as the length from the top of the panicle to the highest node of the main culm. CRL and CW were expressed as the mean of ten fully fertile caryopses. They were measured by projecting their magnified images on a display with a CCD camera. When caryopses were less than 100 in number, WHC was not measured. SS was expressed as the percentage of fertile caryopses out of about 500 caryopses.

Results and Discussion

Figs. 1-9 show the frequency distributions of agronomic characters of the F₂ population derived from the cross between G53 and KM under the two daylength conditions. Correlation coefficients among characters are shown in Tables 3 and 4.

Table 3. Correlation coefficients among agronomic characters examined in the F₂ population derived from the cross between G53 and KM under the natural daylength condition

Character ¹⁾	DH	TN	CL	PL	LN	CRL	CW	WHC	SS	YM
DH ²⁾		-0.484	0.374	-0.003	0.711	0.136	-0.226	-0.276	0.082	-0.027
TN			-0.394	-0.043	-0.463	-0.154	0.030	0.169	-0.430	-0.413
CL				0.360	0.641	0.122	0.022	-0.110	0.174	0.187
PL					0.236	0.023	0.133	0.113	-0.019	0.122
LN						-0.115	-0.144	-0.311	0.145	0.099
CRL							0.171	0.317	0.001	-0.007
CW								0.648	0.054	0.269
WHC									-0.148	0.068
SS										0.863
YM										

1) The meanings of the abbreviations are shown in footnote¹⁾ of Table 1.

2) The data for DH was obtained from Ichitani et al.⁷⁾

Table 4. Correlation coefficients among agronomic characters examined in the F₂ population derived from the cross between G53 and KM under 10h-daylength condition

Character ¹⁾	DH	TN	CL	PL	LN	CRL	CW	WHC	SS	YM
DH ²⁾		-0.289	0.214	0.254	0.599	-0.041	-0.050	-0.172	-0.019	0.140
TN			-0.181	-0.209	-0.249	0.096	0.092	0.076	-0.563	-0.514
CL				0.754	0.588	-0.056	0.228	0.134	0.271	0.485
PL					0.660	0.126	0.214	0.132	0.116	0.464
LN						0.132	0.081	0.129	0.149	0.348
CRL							0.144	0.404	-0.001	-0.019
CW								0.650	0.035	0.080
WHC									0.102	0.076
SS										0.824
YM										

1) The meanings of the abbreviations are shown in footnote¹⁾ of Table 1.

2) The data for DH was obtained from Ichitani et al.⁷⁾

The distribution of TN is shown in Fig. 1. KM usually produces only a main culm while G53 produces many tillers with much variance under both daylength conditions. The distribution was continuous and several transgressive segregants toward a large number of tillers appeared under both conditions. The number of F_2 plants producing only a main culm was about one third of the population under the natural daylength condition while it was only three out of 130 F_2 plants under the short daylength condition. As shown in Tables 3 and 4, TN was negatively correlated with SS and YM. These results suggest that TN was determined in some part by the balance between the total amount of starch synthesized in the leaves and the capacity of the main culm; when the panicle on the main culm could not store all the starch translocated from leaves, more panicles would be produced to store the rest of the starch. There seemed to be a strong relationship between TN and DH: (1) TN was highly negatively correlated with DH under the natural daylength condition. (2) Many plants headed early and produced many tillers under the short daylength condition. The negative correlation between TN and DH suggests that early heading plants continue active photosynthesis after heading, and that tillers are produced to store the starch not stored in the main culm. From these results, it appears that TN may be largely under the influence of other characters. However, KM under the short daylength conditions, similar to G53 under the natural daylength

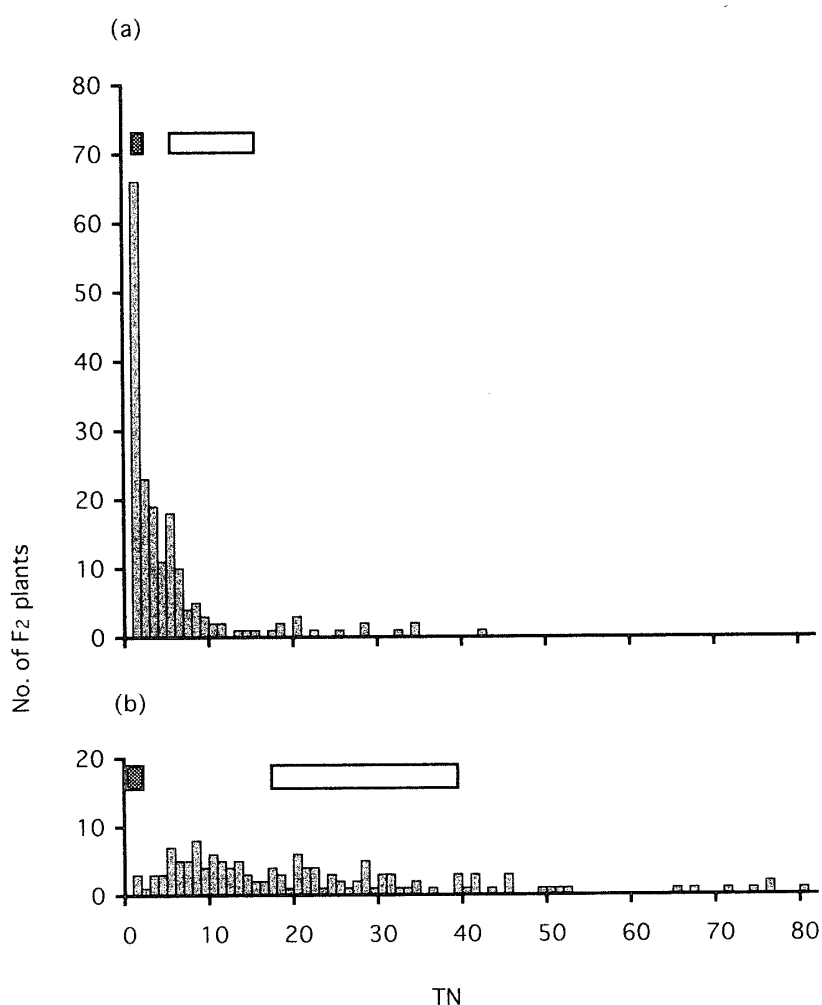


Fig. 1. Frequency distributions of tiller number (TN) for the F_2 population derived from the cross between G53 and KM. (a): natural daylength condition, (b): 10h-daylength condition. The open box and the shaded box indicate the ranges of G53 and KM, respectively.

condition in terms of DH, SS and YM, did not produce tillers except in the case of one plant. This result suggests that TN is in some part controlled by genes, though their effects are not as strong as *tb1* in maize. Ochiai¹⁴) classified foxtail millet strains into four types, Type I, Type II, Type III and Type IV. Type I strains have the largest number of tillers on the main culm, and further secondary and tertiary tillers. Type II strains produce only one or two primary tillers and no secondary tillers. Type III strains are non-tillering and produce only one panicle on the main culm. Type IV has characteristics intermediate between Type I and Type II. Only a late heading strain collected from Kochi Prefecture, Japan, was Type IV. Our results suggested that G53 and KM can be classified as Type I and Type III, respectively. No genetic relationship among the four types has been clarified. The existence of a late heading strain producing tillers suggests that the genetic system producing tillers of Type IV is different from that of Type I.

The distribution of CL is shown in Fig. 2. F_2 plants within the range of G53 under the natural daylength condition and those within the range of KM under the short daylength condition were very few. This result suggests that many genes were segregating in this population. CLs of parental strains were shorter under the short daylength condition, probably due to the short DH under this condition. There were many transgressive tall segregants under the natural daylength condition, but there were few such cases under the short daylength condition (Fig. 2). This result suggests that G53, though being short in stature, carries gene(s) conferring long CL that KM does not carry, and that its effect is inhibited under the short daylength condition.

The distribution of PL ranged between the values for parental strains with few transgressive

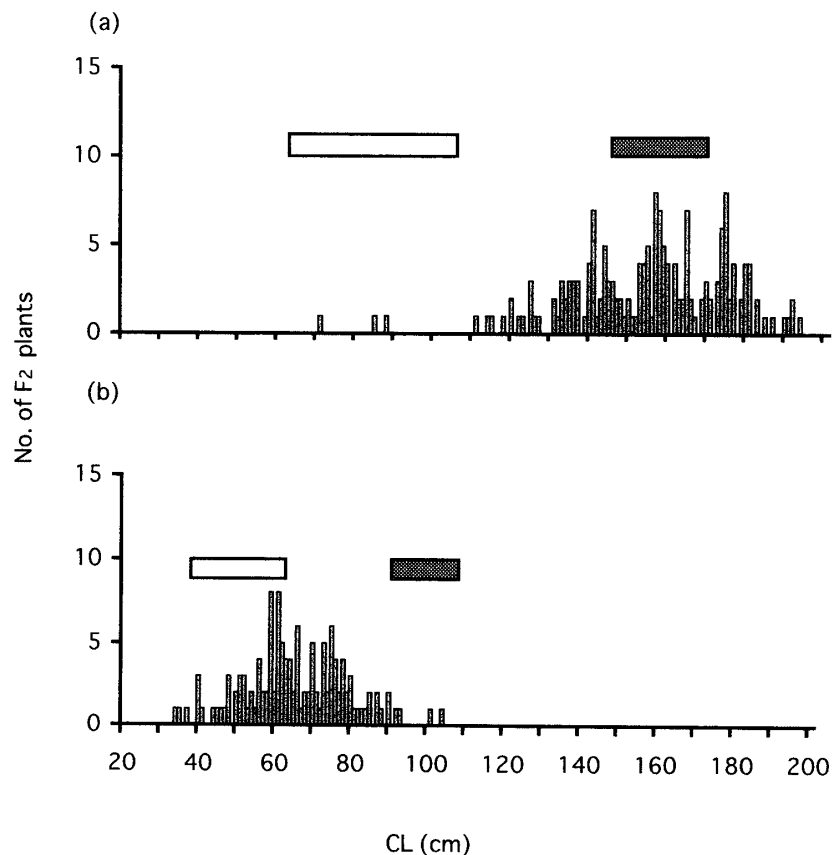


Fig. 2. Frequency distributions of culm length (CL) for the F_2 population derived from the cross between G53 and KM. (a): natural daylength condition, (b): 10h-daylength condition. The open box and the shaded box indicate the ranges of G53 and KM, respectively.

segregants under both conditions (Fig. 3). There was no distinct gap in the distribution. Ranges of parental strains overlapped under the natural daylength condition while the PL of KM was obviously longer than that of G53 under the short daylength condition. This suggests that PL is influenced by daylength. There was a slight positive correlation of PL with CL under the natural daylength condition (Table 3), and PL was highly positively correlated with CL under the short daylength condition (Table 4). This result suggests that PL is influenced by CL. These results indicate that no major gene(s) controlling PL was segregating in the F_2 population.

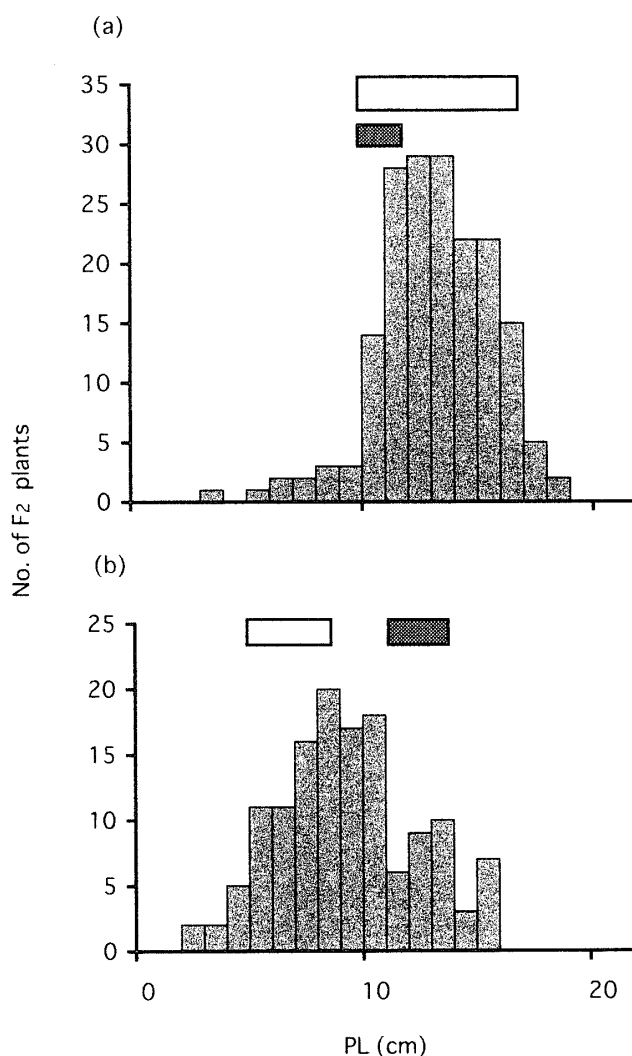


Fig. 3. Frequency distributions of main-panicle length (PL) for the F_2 population derived from the cross between G53 and KM. (a): natural daylength condition, (b): 10h-daylength condition. The open box and the shaded box indicate the ranges of G53 and KM, respectively.

The distribution of LN on the main culm ranged between the values for parental strains continuously with few transgressive segregants under both conditions (Fig. 4). There was no distinct gap in the distribution. LN was much smaller under the short daylength condition than under the natural daylength condition. The correlation coefficient between DH and LN was large under both conditions (Tables 3 and 4). That between CL and LN was also high. These results suggest that LN largely depends on DH and CL.

The distributions of CRL and CW are shown in Fig. 5 and Fig. 6, respectively. The distribution

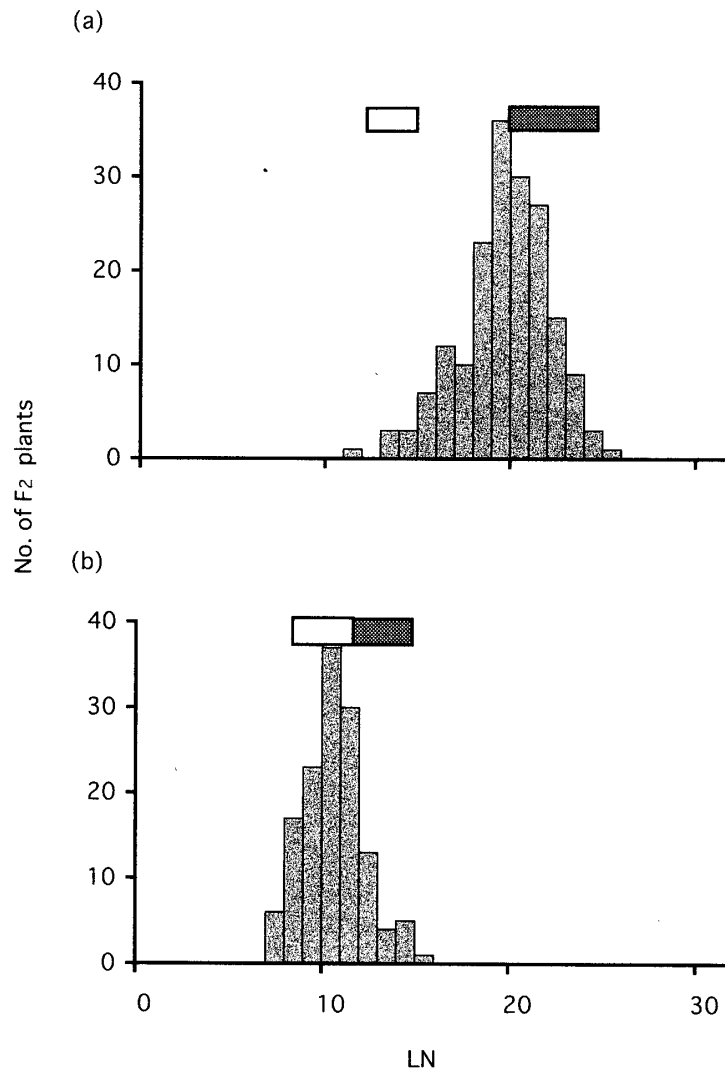


Fig. 4. Frequency distributions of leaf number on the main culm (LN) for the F_2 population derived from the cross between G53 and KM. (a): natural daylength condition, (b): 10h-daylength condition. The open box and the shaded box indicate the ranges of G53 and KM, respectively.

of CRL ranged between the values for parental strains. The number of F_2 plants within the range of G53 in CRL was obviously small, indicating that genes conferring small caryopsis were dominant over those conferring large caryopsis. This result also indicates that many genes controlling CRL were segregating in this F_2 population. The parental ranges of CW almost completely overlapped with each other. Transgressive segregants toward narrow caryopsis appeared under the natural daylength condition while those toward wide caryopsis appeared under the short daylength condition. The reason for this remains unknown. Fukunaga et al.⁵⁾ calculated CRL \times CW and CRL/CW for 272 foxtail millet strains and designated them as size factor and shape factor, respectively. A significant difference was detected in the caryopsis size between strains originally collected from an area extending from the Far East to Southeast Asia and those from other regions. The center of diversity in caryopsis size and shape was located in south Asia, particularly India and its northwestern vicinity. European strains have large size factors while Japanese strains have small size factors. The size factor and shape factor of G53 and KM were within the ranges of European strains and Japanese strains, respectively. Distributions of the F_2 population for the two factors were continuous between parental strains under both daylength conditions (data not shown). Our results suggest that

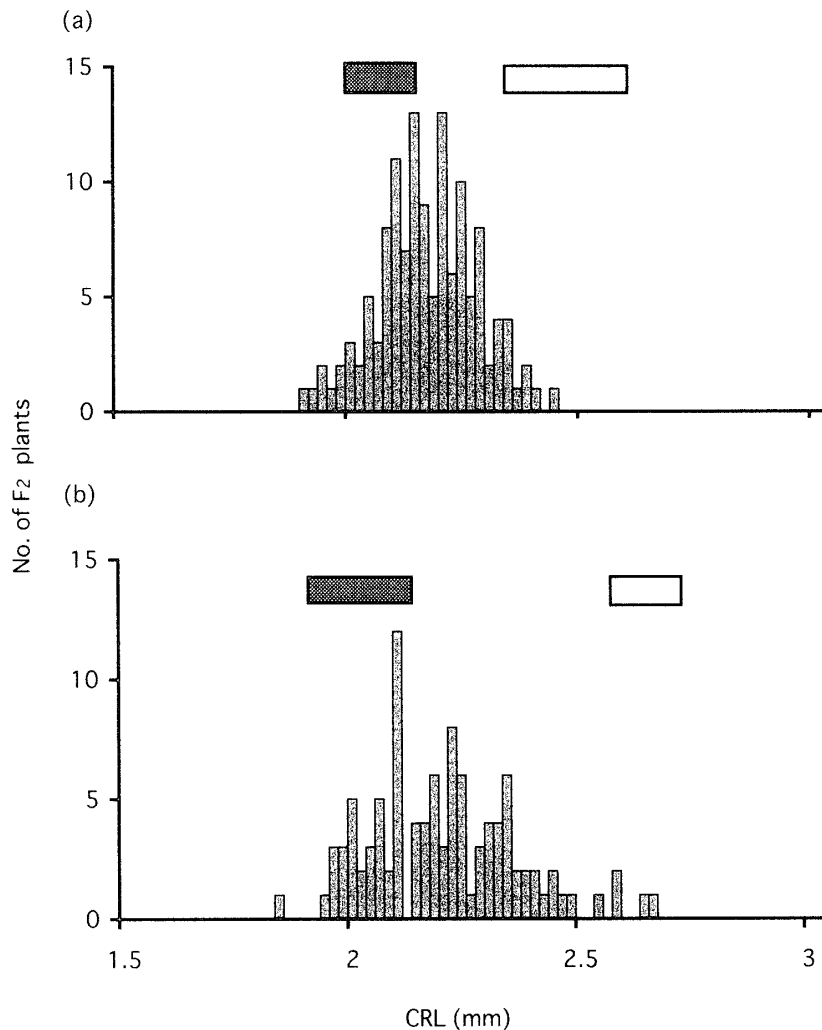


Fig.5. Frequency distributions of caryopsis length (CRL) for the F₂ population derived from the cross between G53 and KM. (a): natural daylength condition, (b): 10h-daylength condition. The open box and the shaded box indicate the ranges of G53 and KM, respectively.

caryopsis shape and size as designated by Fukunaga et al.⁵¹ are under polygenic control.

The distribution of WHC is shown in Fig. 7. The distribution was continuous and ranged between the values for parental strains. WHC was a complex character composed of caryopsis volume and density. Grain density was not analyzed in the present study, but there was a slight difference in caryopsis width and length between the parental strains. Under both daylength conditions, WHC was observed to be most strongly correlated with CW, while its second strongest correlation was with CRL. This result is plausible if the variance in caryopsis density was negligibly small.

The distribution of SS is shown in Fig. 8. Many transgressive segregants toward low SS appeared under both conditions. Our preliminary observation indicated that the F₁ plants showed low SS. Such low SS was often seen in F₁ between distantly related cultivars in rice^{9, 151}. Low SS was caused by dysfunction of pollen and/or egg. Many loci for egg and pollen dysfunction have been detected in rice. Kawase and Sakamoto⁵¹ showed that SS might be influenced to a greater extent than pollen fertility by some environmental conditions in foxtail millet. They classified foxtail millet cultivars into six groups by pollen fertility of the hybrid with three tester strains. We did not determine whether pollen or egg was dysfunctional in F₂ plants showing low SS because we did not examine

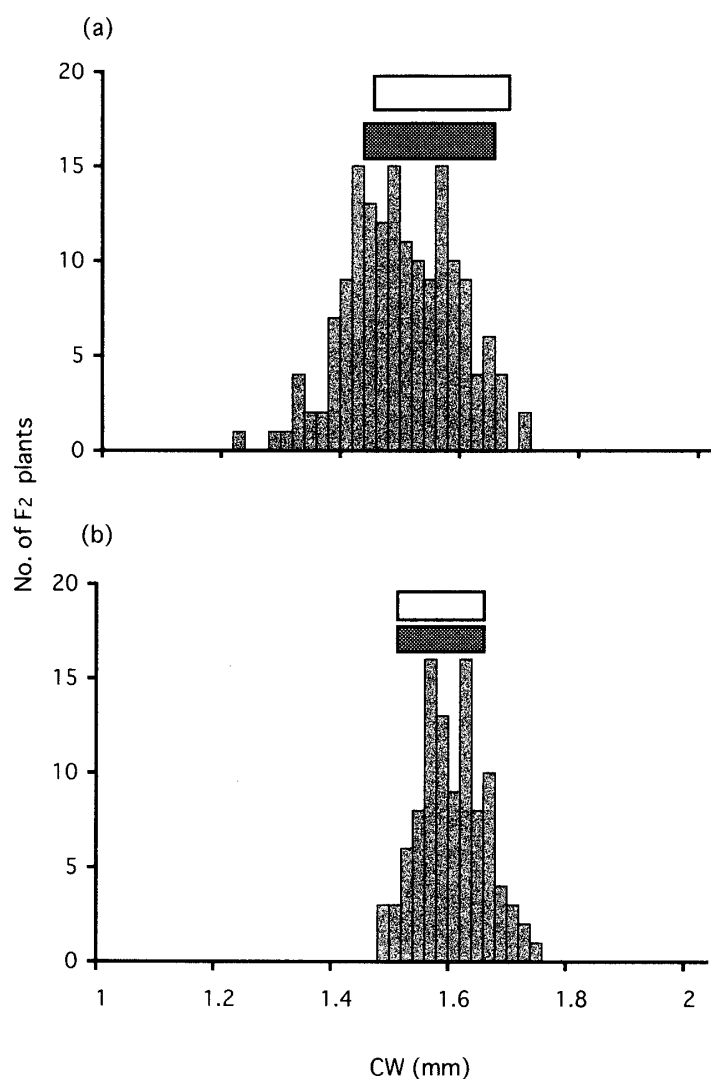


Fig. 6. Frequency distributions of caryopsis width (CW) for the F_2 population derived from the cross between G53 and KM. (a): natural daylength condition, (b): 10h-daylength condition. The open box and the shaded box indicate the ranges of G53 and KM, respectively.

pollen fertility. Anyway, the existence of many transgressive segregants toward low SS suggested that the parental strains were genetically distantly related to each other.

Fig. 9 shows the distribution of YM. Many transgressive segregants toward low YM appeared under both conditions. This could have been due to the great number of low SS plants (Fig. 8). The large variance observed in parental strains suggests that YM might be greatly influenced by some environmental conditions.

The results of the present study indicate that agronomic characters are controlled by many genes. Many quantitative trait loci (QTL) controlling agronomic characters analyzed in the present study have been detected in rice and other cereals with the help of DNA markers such as restriction fragment length polymorphism (RFLP) and simple sequence repeats (SSR). Since most cereals, including foxtail millet, have been shown to have similar genomes in terms of gene content and gene order^{1, 6)}, the number of QTL controlling agronomic characters in foxtail millet is expected to be comparable to that in other cereals.

Throughout the present study, DH largely influenced variance of other agronomic traits. TN

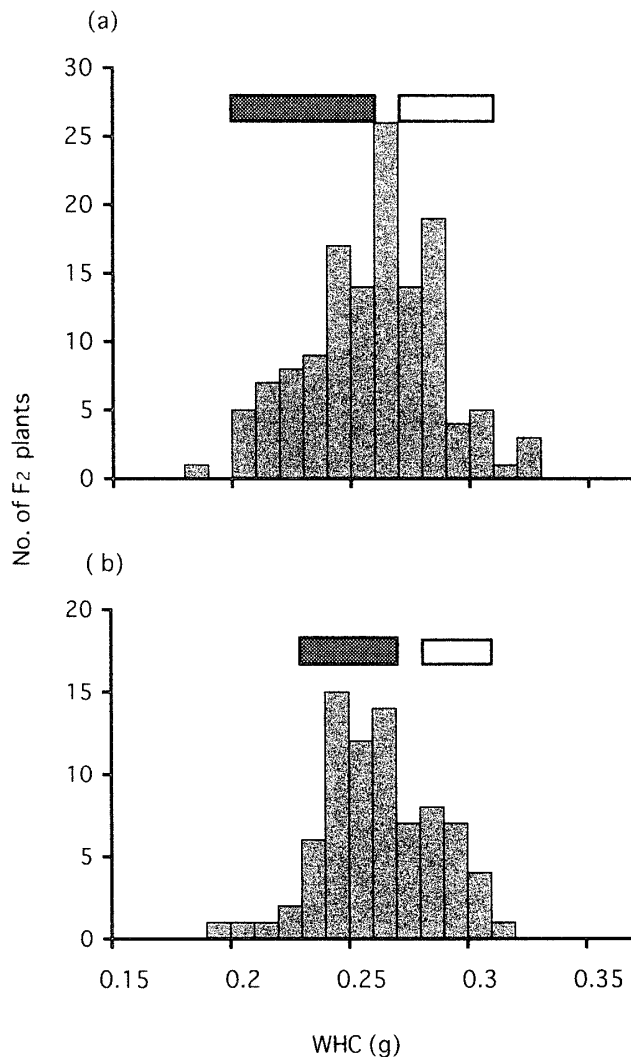


Fig. 7. Frequency distributions of weight of 100 caryopses (WHC) for the F₂ population derived from the cross between G53 and KM. (a): natural daylength condition, (b): 10h-daylength condition. The open box and the shaded box indicate the ranges of G53 and KM, respectively.

was largely influenced by other characters such as DH, SS and YM. Therefore, such noise should be removed for the genetic research of each agronomic trait. Genes are fixed by successive selfing. Therefore, genetic dissection of these agronomic traits can be performed by selecting populations whose genes are segregating only at the loci controlling the trait of interest in the process of successive selfing. DNA markers will be of much help in selecting such populations with high probability. The development of such populations is being undertaken.

Summary

Foxtail millet (*Setaria italica* (L.) P. Beauv.) is a highly self-pollinated diploid grass of Eurasia that shows a remarkable diversity in agronomic characters. However, there has been very little information about the genetic mechanism controlling agronomic characters. In the present study, genetic analyses of agronomic characters were performed using the F₂ population from the cross between two strains differing in their characters, Kuromochi (KM) and Gai 53 (G53), under two different daylength conditions. The agronomic characters examined were as follows: number of

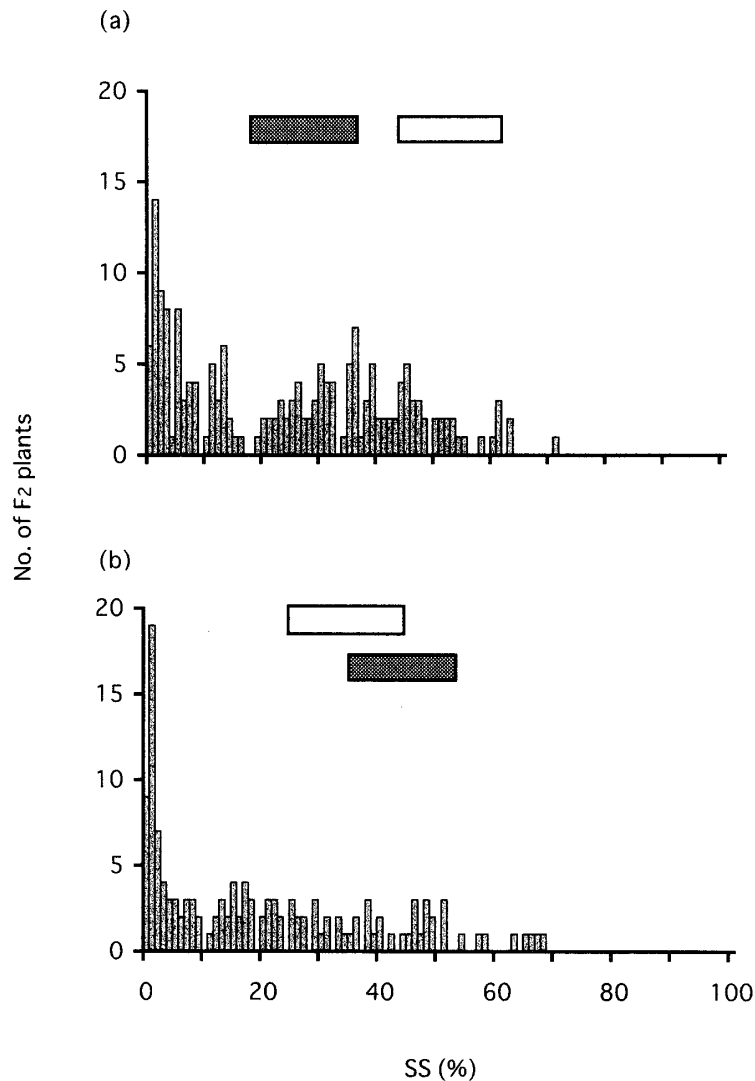


Fig. 8. Frequency distributions of seed set (SS) for the F_2 population derived from the cross between G53 and KM. (a): natural daylength condition, (b): 10h-daylength condition. The open box and the shaded box indicate the ranges of G53 and KM, respectively.

tillers including main culm (TN), culm length (CL), panicle length of the main culm (PL), total leaf number of the main culm (LN), caryopsis length (CRL), caryopsis width (CW), weight of 100 caryopses (WHC), seed set (SS) and yield from the main culm (YM). The frequency distributions of these characters were continuous, suggesting that many genes control these characters. Distribution patterns were different between the two daylength conditions, and many characters were negatively correlated with days to heading (DH). These results indicated that DH greatly influences the variance of other agronomic traits. The strategy for genetic dissection of agronomic traits was discussed.

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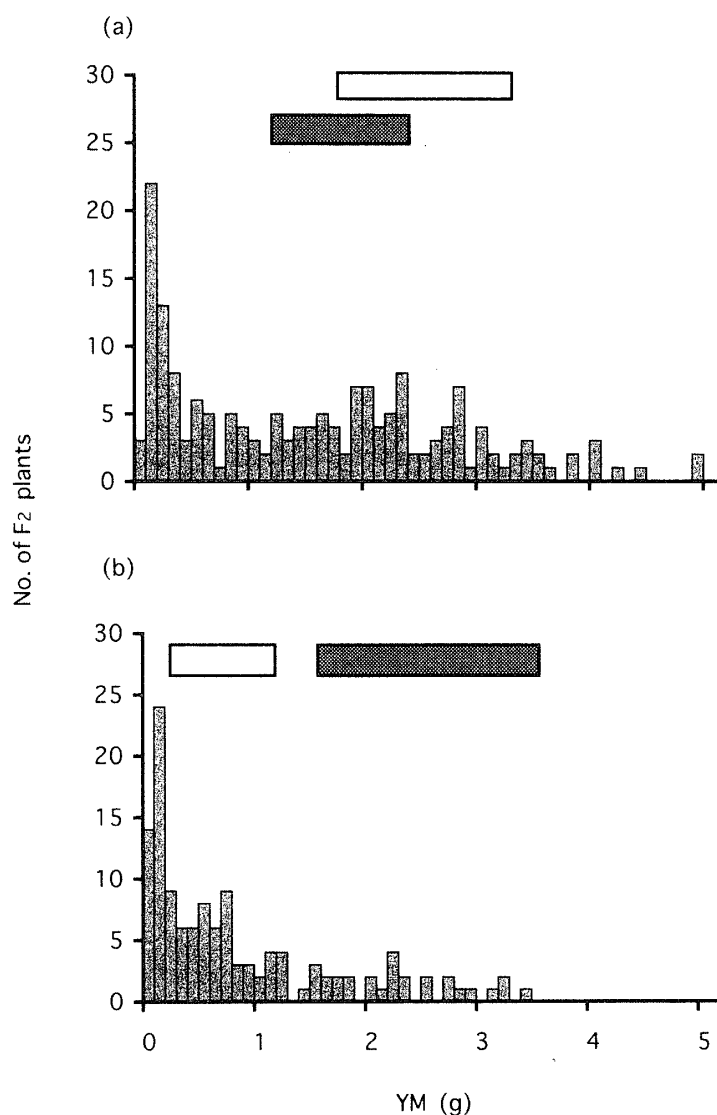


Fig. 9. Frequency distributions of yield from the main culm (YM) for the F₂ population derived from the cross between G53 and KM. (a): natural daylength condition, (b): 10h-daylength condition. The open box and the shaded box indicate the ranges of G53 and KM, respectively.

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