EXPERIMENTAL STUDIES ON NATURAL SELECTION FOR TIME OF HEADING AND ITS INNER FACTORS IN SOME BARLEY HYBRID POPULATIONS*

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I. INTRODUCTION

Early maturity constitutes one of the chief objectives in breeding of cultivated plants. A tendency toward more intensive farming in Japan has especially strengthened the requirement of earlier varieties of barley and wheat, suited as the before-crops of early-planting rice. In cope with this situation, Japanese cereals breeders are now concentrating their efforts to breed such kind of varieties.

It is self-evident that maturity is a physiological character most sensitive to climatic conditions, and the inner factors responsible for maturity in turn affect adaptability of the variety to the ecological niche. Since climate in Japan varies considerably with regions, it is of necessity to know how far we can make time of maturity earlier in respective regions and what kinds of genotypes are most adaptive to the regions.

Takahashi and Yasuda (1957, 1958, 1960), in a series of studies on the physiology and genetics of heading time in barley, have confirmed that spring and winter habit of growth and responses of vernalized plants to short-day (photoperiodic response) and to long-day (earliness in a narrow sense), among others, are the most important inner factors that are responsible for time of heading of a barley plant. However, these three factors not always affect time of heading similarly. According to them, time of heading of barley sown outdoors in fall at Kurashiki with mild winters was chiefly determined by an inner factor to respond to short photoperiod, but almost indifferent of spring and winter habit or of the earliness factor in a narrow sense. Nevertheless, it is conceivable that the earliness factor in a narrow sense may play an important role in determining heading time of barley which are grown in northern regions wherein longer day-length predominates during heading time. As far as the previous experiments are concerned, spring and winter habit was found to matter little to earliness of fall-sown barley, but it certainly affects seriously the earliness of spring sown barley. Moreover, geographical regularities in distribution of spring-genes and of varieties differing in grade of spring habit, which have been confirmed by Takahashi (1943, 1955), naturally lead to a thought that this is one of the important factors controlling adaptability of barley plant to their habitats.

The present study aimed to contribute further to the fundamental knowledge about time of heading and especially adaptability of barley varieties to habitats

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from breeder's point of view. Accordingly, efforts have been centered upon the investigation of the effects of natural selection on heading time of barley hybrid populations which had successively grown nuder different climatic conditions. Furthermore, analytical studies were made as to how the constitutions of these hybrid populations had been changed regarding three important factors, namely spring and winter habit, responses to short and long photoperiod.

As already shown by Akemine and Kikuchi (1958) in rice hybrids, it was recongnized also in this experiment that the effects of natural selection were so marked that these hybrid populations originated from different locations have responded to their respective climatic conditions, and have been changed differently in heading time and also in their constitution regarding three inner factors within only 5 segregating generations. The results obtained in this experiment will be stated below.

II. MATERIALS AND METHODS

Four barley crosses were used in this series of experiments. Names of the parental varieties, origin and characteristics are shown in Table 1. It may be

Table 1
Characteristics of parental varieties of four crosses

Cross No.	Parent	Origin	Earliness (Fall-sown)	Grade of spring habit	Growth habit genes involved*	Plant type
1	Iwate Ōmugi No. 1	Iwate	very late	VI	$ShSh$ sh_2sh_2 sh_3sh_3	normal
	Indian Barley	Formosa	very early	I	$ShSh$ Sh_2Sh_2 sh_3sh_3	normal
2	Tammi	Finland	very early	I	$shsh$ Sh_2Sh_2 Sh_3Sh_3	normal
	Shimabara	Kumamoto	late	V	$ShSh$ sh_2sh_2 sh_3sh_3	uzu
3	Kuromugi No. 148	Shizuoka	early	II	$ShSh$ $Sh_2^{II}Sh_2^{II}$ sh_3sh_3	uzu
	Mensury C	Iwate	very late	I	$shsh$ sh_2sh_2 sh_3sh_3	normal
4	Kochi Wasehadaka	Kochi	very early	IV	$ShSh$ sh_2sh_2 sh_3sh_3	normal
	Mensury C	Iwate	very late	I	$shsh$ sh_2sh_2 sh_3sh_3	normal

* sh, Sh_2 and Sh_3 are the genes for spring habit.

pointed out in this table that parental combinations of these crosses are determined so as to be markedly different *inter se* in their genetic constitution for growth habit and also earliness in the open field. These hybrid populations were grown in bulk from F_2 to F_6 generation in successive years since the autumn of 1954 at the four locations; namely, Morioka, Konosu, Kurashiki and Kanoya which are located in northern, central, southern and southernmost Japan, respectively. Cross No. 4 was not grown at Konosu and Kanoya, however. Each hybrid population consisted of about 2400 plants. They were cultivated after the conventional method of the respective places. The sowing time was early October at Morioka, late October at Konosu, middle November at Kurashiki and late November at Kanoya. Day-length and temperature of four locations during the growth period of barley are shown in Figs. 1 and 2.

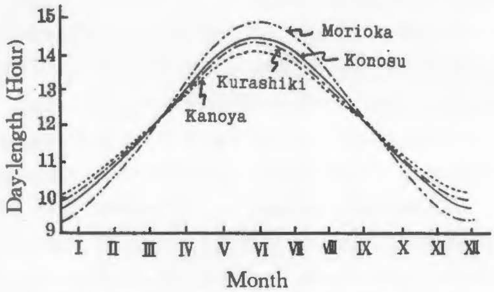

Fig. 1. Yearly changes in day-length in four locations.

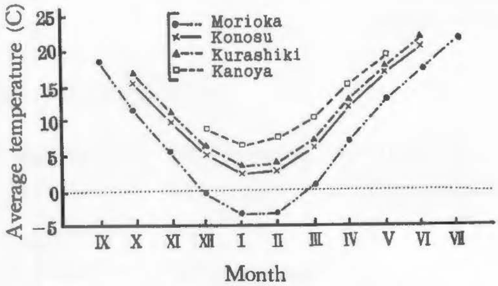

Fig. 2. Monthly average temperatures during growing periods of barley in 4 locations (average of 5 years)

In order to know the generational changes in genetic constitutions of the hybrid popnlations regarding chief ecological characteristics, analytical studies were made at Kurashiki. The materials for each of the following tests consisted of 300 or more seeds randomly taken from each of the hybrid populations and 20 or more seeds of their parental varieties. Sometimes, F_1 and F_2 hybrids, if available, were planted for comparison. The characters and methods of analysis are as below:

(1) Relative frequencies of spring and winter type plants among hybrid population: A seed sample of each hybrid population, together with the seeds of their parental varieties, were sown in two or more wooden flats of 38×62×12 cm in size, which permitted normal growth of 170 plants. The plants were reared throughout under 24 hour day in a greenhouse. The natural day-light were supplemented by 100 watt incandescent lamps suspended about 1 m above the plants from before sunset to sometime after sunrise. Records were taken on a single plant basis for the time of emergence of flag-leaf and the number of leaves on the main stem. As was previously reported by Takahashi and Yamamoto (1951), the discrimination between spring and winter types was easily feasible because of marked difference in time of heading between two types under 24 hour illumination.

(2) Response to short-day: All the seeds were fully vernalized prior to planting by exposing to low-temperature of 1~3°C for 60 days. They were sown in the wooden flats at a density of 150 per flat, and grown in a greenhouse under 8 hour day for 40 days and thereafter subjected to 24 hour-day. Records were taken for the time of flag-leaf emergence and number of leaves on the main stem.

(3) Earliness in a narrow sense (response to long-day): After vernalization, seeds were sown in some wooden flats at a density of 170 per flat and reared throughout under 24 hour day in a greenhouse. Days to flag-leaf emergence and number of leaves on the main stem were recorded.

(4) Time of heading in open field: The seeds were space-planted in the field with two replications in November 15 at Kurashiki. Manuring and other cultivating practice were made according to conventional methods. Daily records were

taken for the heading date of each of the plants.

All the four characters above stated were investigated for the three crosses, Nos. 1~3, but for the Cross No. 4 only two characters, spring and winter habit of growth and time of heading in open field were investigated.

III. EXPERIMENTAL RESULTS

1. *Relative Frequencies of Spring and Winter Type Plants in Hybrid Population*

Frequencies of spring and winter type plants were investigated in the F_3 and F_4 populations of Cross No. 1 (Iwate Ōmugi No. 1 × Indian Barley) grown at the four different locations. The results, expressed as percentages, are shown in Fig. 3. As it was known that one dominant gene Sh_2 for spring habit of growth was involved in this cross, the theoretical frequency of each generation was calculated on this basis and shown in the figure.

It is obvious in Fig. 3 that natural selection have remarkably affected survival

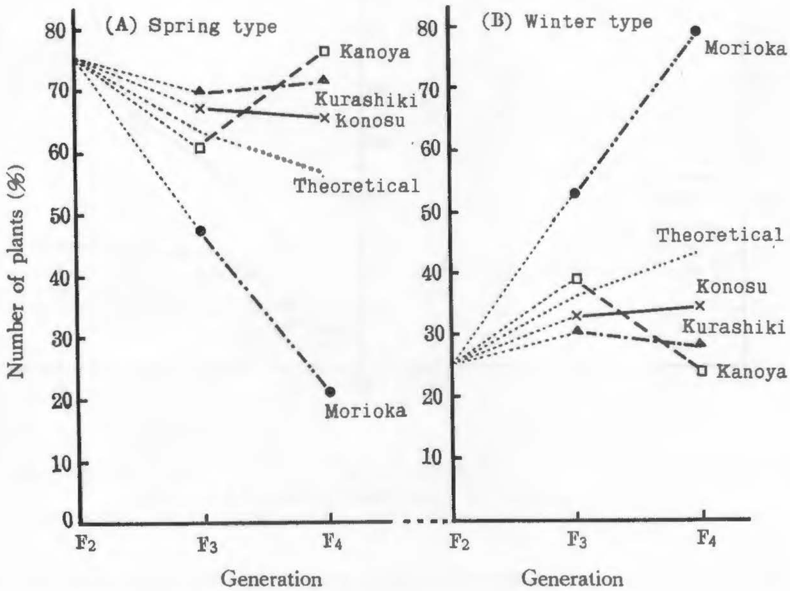

Fig. 3. Relative frequencies of spring type plants (A) and winter type ones (B) in the populations of Cross No. 1 grown at four locations.

rate of spring and winter type plants: When grown at Morioka, spring type plants have rapidly been eliminated from the population, and their frequency in F_4 generation have become about one third of the theoretical frequency. On the contrary, predominance of spring type plants was evident at three other locations, and this tendency was more pronounced as went down to south from Konosu to Kurashiki and finally to Kanoya, with an exception of F_3 population from Kanoya. Since no appreciable differences in climatic conditions could be found between the years when F_3 and F_4 populations had been grown, remarkable low frequency of spring type plants in F_3 may be attributed to sampling error.

As to Cross No. 2 (Tammi × Shimabara), frequencies of spring and winter type plants in the F_3 to F_6 populations from four locations were investigated. This cross is expected to give segregation of spring and winter type plants in a 61 : 3 ratio in F_2 generation, since it is known that one recessive (*sh*) and two dominant (Sh_2, Sh_3) spring genes have been involved in this cross.

As seen in Fig. 4, spring type plants were about 10 % less frequent than the

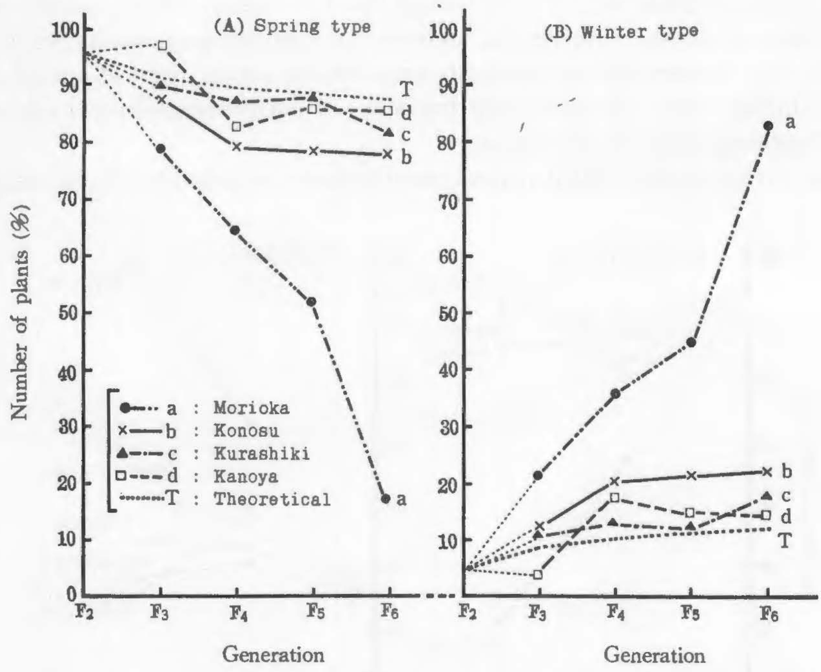

Fig. 4. Relative frequencies of spring type plants (A) and winter type ones (B) in the populations of Cross No. 2 grown at 4 locations.

theoretical at Morioka in F_3 generation and became less and less with the progress of generation. Their frequency in F_6 generation was only about one fifth of the theoretical. In contrast, spring type plants were not so much decreased at three other locations, although they were 2∼10% lower in frequency in Konosu population than in Kurashiki and Kanoya populations.

The parents of Cross No. 3 are both of spring habit, but, as seen in Table 1, they have different spring genes, namely, *sh* in Mensury and Sh_2 in Kuromugi No. 148. Therefore, 13 spring type and 3 winter type plants are expected in F_2 of this cross. Furthermore, the spring type segregants of this cross can be subdivided into two groups based on the difference in genetic constitutions with the reasons as follows: According to Takahashi *et al.* (1951, 1953, 1956), *Shsh* is linked with *Hshs* for sheath hair with 6.4 % of recombination, and a plant with gene *shsh* (grade I for spring habit) is definitely earlier in heading under 24 hour illumination at high temperature than a plant with gene $Sh_2^{II}Sh_2^{II}$ (grade II). By virtue of the visual differences in hairy condition on leaf sheath and earliness, plants with genotype of $shshSh_2^{II}Sh_2^{II}$ or $shshsh_2sh_2$ (these two types can not be discriminated because of the epistasis of *shsh* over $Sh_2^{II}Sh_2^{II}$) can be distinguished from plants with $ShShSh_2^{II}Sh_2^{II}$. Changes in frequencies of these different types of spring and winter plants were studied using F_3, F_4 and F_6 hybrid populations of Cross No. 3 originated from different locations.

Fig. 5A gives changes in frequency of spring type plants as a whole at each

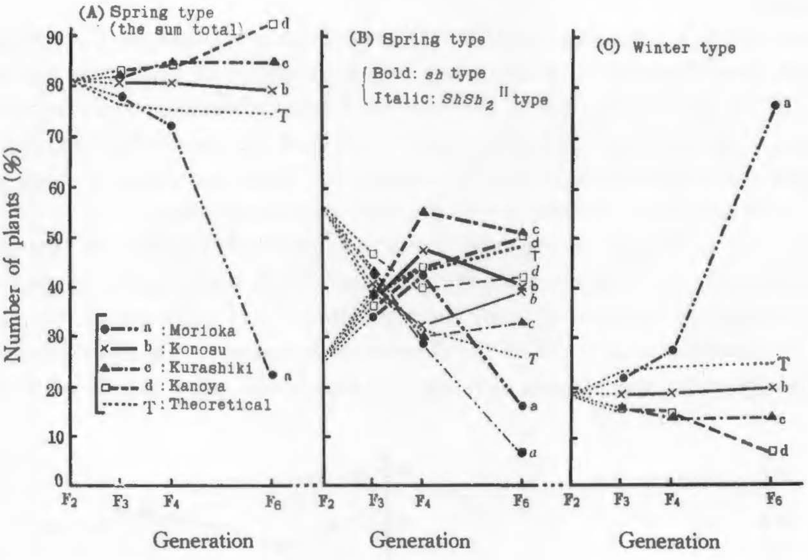

Fig. 5. Relative frepuencies of spring type plants (A) and winter type ones (C) in the populations of Cross No. 3 grown at 4 locations. (B) shows two groups of spring type plants which are divided by their genotypes.

location. It will be seen in this figure that in F_3 and F_4 generations only a little differences in frequencies are recongnized between locations, but in the succeeding generations location effects become apparent; namely, a striking fall in the frequency is evident in F_6 generation of Morioka population. On the other hand, natural selection seemed to favor to some extent the spring type plants at three other locations, especially at Kurashiki and Kanoya.

Let us compare the changes in frequency of spring types with Sh_2^{II}($ShSh_2^{II}$ type) and of those with *sh* (*sh* type) in Fig. 5B, in which are shown per cent frequencies of both types. It is perceived that, when grown at Morioka, actual frequencies of these two spring types in F_3 and F_4 populations are not so much apart from their theoretical ones, but abrupt drop of frequency is observed in F_6 generation. However, the rate of decrease of *sh* type is about twice than that of $ShSh_2^{II}$ type. In other words, selection pressure operating at Morioka at least in 1958 was by far stronger on *sh* type than on $ShSh_2^{II}$ type. In F_3 and F_4 populations grown at Konosu, the frequencies of both *sh*- and $ShSh_2^{II}$-types are similar to their theoretical ones. However, *sh* type in F_6 decreases about 10%, while $ShSh_2^{II}$ type increases more than 10% as compared with their respective theoretical frequencies. Consequently, it seems that the excess of the frequency of whole spring type plants in Konosu population may be contributed mainly by the increase of $ShSh_2^{II}$ type. An almost similar changes in frequency of spring type plants have been observed in both Kurashiki and Kanoya populations ; frequency of *sh* type is about the same as expected, and the frequency of $ShSh_2^{II}$ type is higher than what is expected theoretically.

Cross No. 4, a cross between Kochi-Wasehadaka and Mensury C, were grown at Morioka and Kurashiki. In this cross, the segregation of the spring and winter types in F_2 hybrid is expected to be in a 1 : 3 ratio, because only one recessive spring gene, *sh*, is included in this cross. In Fig. 6 are shown the frequencies of spring and winter types from F_3 to F_7 generations. However, owing to poor germination, no datum was available for F_3 population of Kurashiki.

As shown in Fig. 6, spring type plants in F_3 population grown at Morioka are about 7 % lower in frequency than the expected. With the progress of generation, they are gradually eliminated from the population, and in F_7 generation, its frequency becomes about one half of the theoretical frequency. On the contrary, the frequencies of spring type plants in Kurashiki population are always 3~5% higher

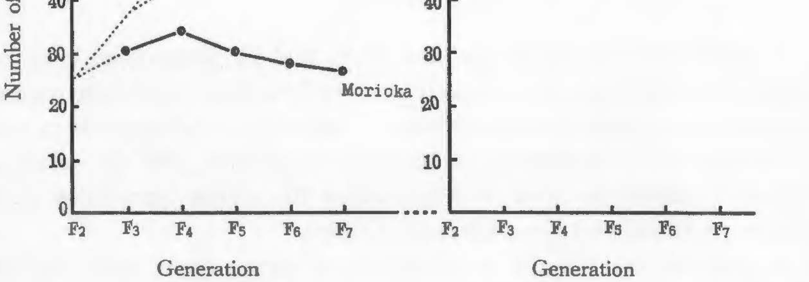

Fig. 6. Relative frequencies of spring type plants (A) and winter type ones (B) in the populations of Cross No. 4 grown respectively at Morioka and Kurashiki.

than the theoretical ones. It is possible to point out herewith that the changes in frequency of spring type plants (*sh* type) observed in this cross are almost similar to those of *sh*-type involved in Cross No. 3.

It was attempted further to estimate from the data of this cross the strength of selection pressure that has actually been operating on spring type plant with *sh* in homozygous condition. In this calculation it was necessary to determine the proportion of spring type plants which have been eliminated by selection on the spring plants during at least one growing season at a certain location. A test with a seed sample taken from the bulked seeds of a population of a certain segregating generation, say F_3, would only permit to know the proportion of spring type plant in the population, which are consisted of two kinds: one which survived the selection in F_3 generation and the other which have been segregated in F_4 from the winter type plants heterozygous for *Sh* (*Shsh*) in F_3. The latter could be estimated from proportion of the winter type plants in F_3 generation, if heterozygous (*Shsh*) and homozygous (*ShSh*) winter type plants had no differential selective advantage and occurred in the frequencies theoretically expected. The values estimated in this way were represented by selection coefficient, *s*. A selection coefficient of unity will be obtained when the selection for spring type plants is complete. An adaptive value (w) was calculated by $1-s$. Similar method was used in order to calculate the selection coefficient for winter type plant, but it was assumed in this case that both homozygote (*ShSh*) and heterozygote (*Shsh*) were all subjected to the same selection pressure.

In Table 2 are shown two kinds of values, selection coefficient and adaptive value. The number of generations shown in the table are those in which the popu-

Table 2

Adaptive values and selection coefficients for spring and winter type plants involed in the populations of Cross No. 4

(A) Spring type (*shsh*)

Item	Location	F_2	F_3	F_4	F_5	F_6	Average
Selection coefficient	Morioka	0.272	0.105	0.214	0.145	0.081	(0.163)
	Kurashiki	—	—	−0.034*	0.046	0.027	(0.013)
Adaptive value	Morioka	0.728	0.895	0.786	0.855	0.919	(0.837)
	Kurashiki	—	—	1.034	0.954	0.973	(0.987)

(B) Winter type (*ShSh* and *Shsh*)

Item	Location	F_2	F_3	F_4	F_5	F_6	Average
Selection coefficient	Morioka	−0.109*	−0.052	−0.119	−0.066	−0.032	(−0.076)
	Kurashiki	—	—	0.037	−0.057	−0.030	(−0.017)
Adaptive value	Morioka	1.109	1.052	1.119	1.066	1.032	(1.076)
	Kurashiki	—	—	0.963	1.057	1.030	(1.017)

* Negative values indicate the selection coefficients when the spring type plants are adaptive to the environment.

lation have been grown at each location, but not the generation in which the test was made. It may be noted that the selection coefficients have, for convenience' sake, been shown in negative values, when the spring type plants were adaptive to the environment.

As expected from the results of Fig. 6, the selection coefficient for the spring type plants is higher in Morioka (the average 0.163) than in Kurashiki (the average 0.013) (Table 2); in Morioka, the selection pressure on the spring types per generation is estimated as 0.1~0.3, while in Kurashiki, it is as low as 0.05~0.03 depending upon the generations. Adaptive values (w) for spring type plants are naturally higher in Kurashiki population than in Morioka population which showed the values of less than 0.8 in both F_2 and F_4 generations. Therefore, selection for winter type plants are not recongnized in Morioka population, where the increase of frequency of such plants were rather greater than what expected theoretically. The adaptive values for winter type plants were more than 1. In Kurashiki population, it is recongnized that the winter type plants increase in both F_5 and F_6 generations, though their adaptive values are less than those of Morioka population. But winter type plants in F_4 generation tend to be slightly eliminated from the population.

2. *Response to Short-day After Vernalization*

Short-day response of a population may be represented by mean days to flag-leaf emergence of the plants constituting the population and also by the variation of days to flag within the population. Small or large mean days to flag of the population implies that the population is chiefly consisted of those plants which are insensitive or sensitive to short-day. Magnitude of variation within population as to the date of flag-leaf emergence, on the other hand, may indicate how far the individuals in the population are variable regarding the sensitivity to short photoperiod. These will be expressed in term of selection in such a way that the mean shows direction and intensity of selection, and that the variance within population shows intensity of selection on different genotypes in the population.

Investigations on the response to short-day were made of F_3 to F_5 populations of Cross No. 1 and of F_3 to F_6 populations of Crosses No. 2 and 3.

The population mean and variance of each population of Cross No. 1 originated from different locations are shown by a scatter diagram in Fig. 7.

As seen in Fig. 7, means and variances are always much larger in Morioka population than in those from three other locations. Furthermore, it is apparent in the figure that both mean and variance increased gradually with the progress of generation. This implies that Morioka populations are chiefly consisted of late type plants, and at the same time that they still include extremely early plants in lesser proportion. On the contrary, Kanoya populations have the smallest means and variances, and these situations become more marked with the advance of generation. Namely, F_4 and F_5 populations of Kanoya are one week or more earlier in flag-leaf emergence than those of the Morioka populations, and they are chiefly

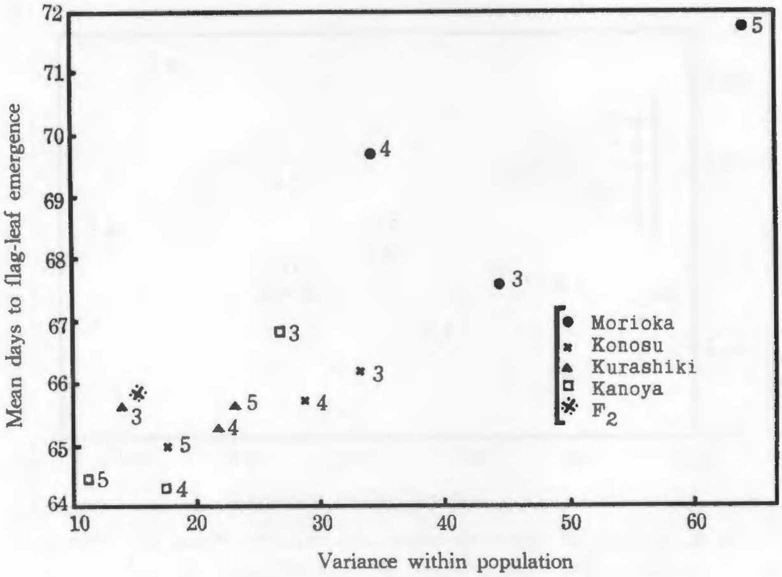

Fig. 7. Relation of population means and variances within population of days to flag under short-day after vernalization. F_3 to F_5 hybrid populations of Cross No. 1, which had been reared at 4 locations.

consisted of the early type plants. Konosu and Kurashiki populations are intermediate in general between Morioka and Kanoya populations regarding both mean and variance, although Konosu populations indicate a slight tendency to become earlier with the progress of generation, while Kurashiki populations are much the same as F_2 population.

In sharp contrast to two other crosses, the populations from the Cross No. 3 are characterized by very small differences in both mean and variance, namely, there can be recognized only 1.5 days difference in mean and 2.5 difference in variance between two extreme populations, though the differences are mostly significant because of the little error variances. Fig. 8 shows that the populations from Kurashiki and Kanoya are slightly earlier in flag-leaf emergence and somewhat smaller in variance than F_2 population and also those from both Morioka and Konosu.

The results obtained in Cross No. 2 are shown in Fig. 9, which clearly indicate a general tendency that rise in population means are always accompanied by the decrease in population variances. This is quite different from the tendency recongnized in Crosses No. 1 and 3. Morioka population is characterized by retardation of time of flag-leaf emergence and also by small variability as compared with those from three other locations, and this becomes more pronounced with the progress of generation. These imply that natural selection has wholly eliminated from the population those plants which are insensitive to short-photoperiod. On the other hand, Kurashiki and Kanoya populations are early on an average in time of flag-leaf

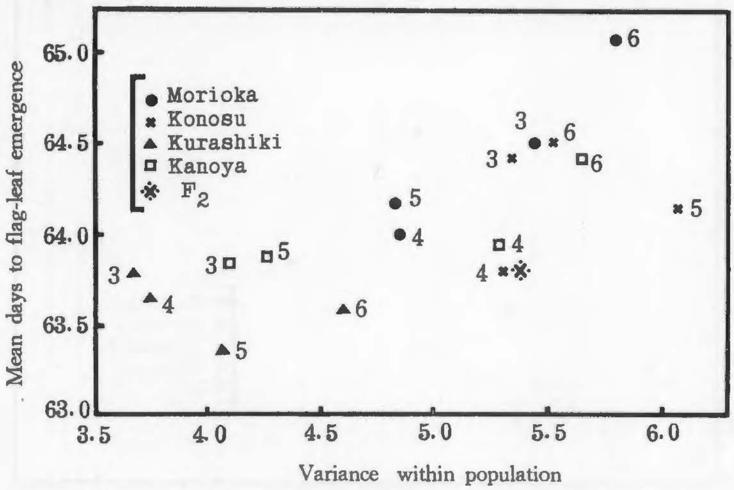

Fig. 8. Relation of population means and variances within population of days to flag under short-day after vernalization. F_3 to F_6 hybrid populations of Cross No. 3, which had been reared at 4 locations.

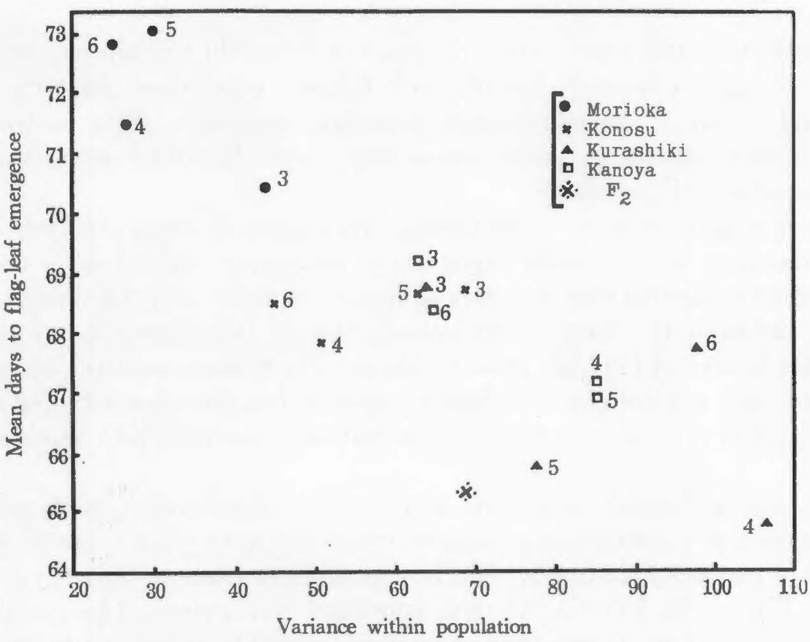

Fig. 9. Relation of population means and variances within population of days to flag under short-day after vernalization. F_3 to F_6 hybrid populations of Cross No. 2, which had been reared at 4 locations.

emergence, but still include a wide range of plants differing in sensitivity to short-day. Konosu population is almost intermediate between these two extremes.

Differences in the composition of different populations may be disclosed more distinctly by another measure of expression, tentatively named "earliness or lateness index" than by mean and variance (Table 3). These indexes are the numerals to show how many and to what extent early or late plant are involved in the population, and their calculation was made in the following way: As the critical date of earliness for the population the date of flag-leaf emergence of the last plant of the "early" parent is fixed and those plants which emerged their flag-leaves on the same day is given a coefficient of unity. Starting from the critical day, 1, 2, 3... days earlier plants are given a coefficients of 2, 3, 4, ..., respectively. Total sum of the products of these indexes and number of plants as expressed in per cent of the whole plants in the population is the "earliness index" for the population to be determined. Similarly, "lateness index" was calculated in the same principle. However, in this case critical date was fixed to be the date of the earlist plant of the late parent.

Table 3
Earliness- and lateness-indexes with regard to days to flag under short day after vernalization in the population grown at different locations. (See text)

Cross	Generation	Earliness index				Lateness index			
		Morioka	Konosu	Kurashiki	Kanoya	Morioka	Konosu	Kurashiki	Kanoya
Cross No. 1	F_2			(56.0)				(17.2)	
	F_3	52.6	69.3	74.6	56.6	55.6	36.5	18.0	33.2
	F_4	20.6	72.8	88.6	111.0	73.4	27.2	19.2	15.5
	F_5	13.5	78.5	74.2	96.6	147.1	11.9	16.9	7.3
Cross No. 2	F_2			(144.7)				(36.2)	
	F_3	37.9	97.7	76.1	79.6	94.4	97.1	87.3	94.7
	F_4	11.3	83.2	205.0	131.5	102.3	50.0	52.6	72.9
	F_5	14.4	81.3	141.2	137.0	150.5	74.5	30.9	56.4
	F_6	0	58.1	135.9	91.6	137.6	47.9	86.5	67.7
Cross No. 3	F_2			(47.5)				(46.9)	
	F_3	27.6	26.5	35.8	33.6	69.7	63.5	33.8	36.9
	F_4	41.6	41.8	45.9	39.1	46.7	46.7	29.3	51.0
	F_5	33.2	45.1	58.1	39.1	51.8	61.1	26.0	39.6
	F_6	12.4	23.0	53.8	31.7	93.4	68.2	37.5	69.0

In Cross No. 1, there is little difference in "earliness index" among four locations in F_3 generation. But, the "earliness indexes" in Morioka populations decrease gradually, while those in the others increase generation by generation. Consequently, the difference between the two became larger with the advance of generation. In the populations from three locations other than Morioka, their "earliness indexes" tend to become higher as go down to south with exception of some cases. These tendencies mentioned above are more pronounced in Cross No. 2 ; the "earliness indexes" of Morioka population, even in F_3 generation, are less than one half of those in the others, and hybrid plants as early as the "early" parent, Tammi, has completely been eliminated from the F_6 population. The populations from Konosu also indicate a slight tendency to become smaller in "earliness indexes" with the progress of generation. Moreover, it is noted that the "earliness indexes" in Kurashiki populations on and after F_4 are larger than those in Kanoya populations. The changes in "earliness index" among generations of Cross No. 3 are almost similar in tendency to those of Crosses No. 1 and 2, though the extent of differences between Morioka population and the others are far smaller in this cross than in Crosses No. 1 and 2.

"Earliness indexes" of the populations grown at Kurashiki and Kanoya decreased at F_6 in spite of gradual increase up to F_5 generation. This may be due to the fact that the F_6 populations were all exposed to the extra ordinarily low temperature in the early spring in 1958, and consequently, early plants, which had just attained to a stage of meiosis or anthesis in the southern locations, have suffered most severely from cold injury, whereas they were still at their vegetative stage at the northern locations, and escaped from cold injury.

As shown in Table 3, the changes in "lateness index" among generations are almost reverse of those in "earliness index"; with the progress of generation, the "lateness index" in Morioka populations increase gradually, and decrease in Kurashiki and Kanoya populations. In Konosu population, however, such changes as mentioned above are slight, except for Cross No. 1 which indicated similar tendencies to Kurashiki and Kanoya populations.

Increase of "lateness index" in both Kurashiki and Kanoya populations at their F_6 generation may be in part attributed to mark the elimination of early plants by the meteological cause mentioned above.

3. *Response to Long-day After Vernalization* (*Earliness in a Narrow Sense*)

The analyses of "earliness in a narrow sense" were made for F_3 to F_5 populations of both Crosses No. 1 and 3, and for F_3 to F_6 populations of Cross No. 2. Since a parent of either of Crosses No. 2 and 3 is of semi-brachytic or uzu type, it is expected to segregate the uzu type plants in these hybrid populations. According to Takahashi and Yasuda (1958), these uzu type plants are one or more days later than those of normal ones when grown simultaneously under the condition of 24 hour day at high temperature after vernalization. So, correction was made on this basis for the mean days to flag of uzu type plants appeared in these crosses. In Fig. 10 are shown means and variances of the populations of Cross No. 1.

As seen in Fig. 10, both the means and variances of Morioka populations are larger than those of the other locations, and are inclined to become larger with the progress of generation. On the other hand, the populations grown at Kanoya

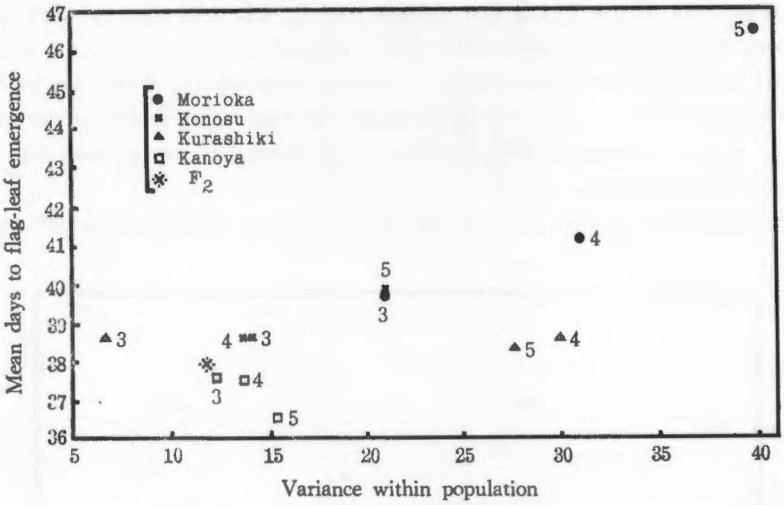

Fig. 10. Relation of population means and variances within population of days to flag under long-day after vernalization (earliness in narrow sense). F_3 to F_5 hybrid populations of Cross No. 1, which had been reared at 4 locations.

are the early in general and small in variability, and also indicate a slight tendency to become earlier with the advance of generation. Both Konosu and Kurashiki populations are almost intermediate between Morioka and Kanoya populations about their means and variances. Moreover, mean days to flag in both Konosu and Kurashiki populations are similar to that of F_2 population.

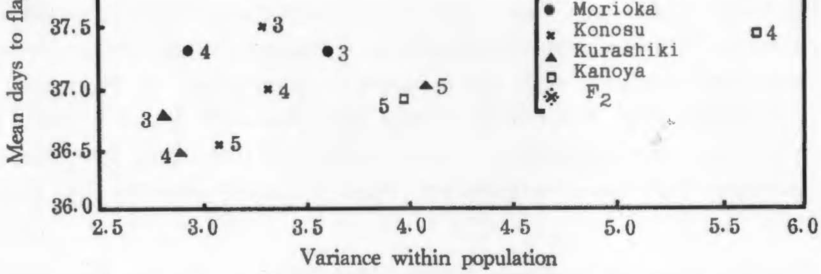

Fig. 11. Relation of population means and variances within population of days to flag under long-day after vernalization (earliness in narrow sense). F_3 to F_5 hybrid populations of Cross No. 3, which had been reared at 4 locations.

The results of Cross No. 3 are shown in Fig. 11. As seen in this figure, differences in means and variances between locations or generations are so small as compared with those of Cross No. 1. It seems hard to find a definite tendency in their changes. One thing to be pointed out in the result is that most of the populations, with a exception of F_5 population of Morioka, are earlier and more variable than F_2 population.

Fig. 12 shows the results of Cross No. 2. As seen in Fig. 12, Morioka popula-

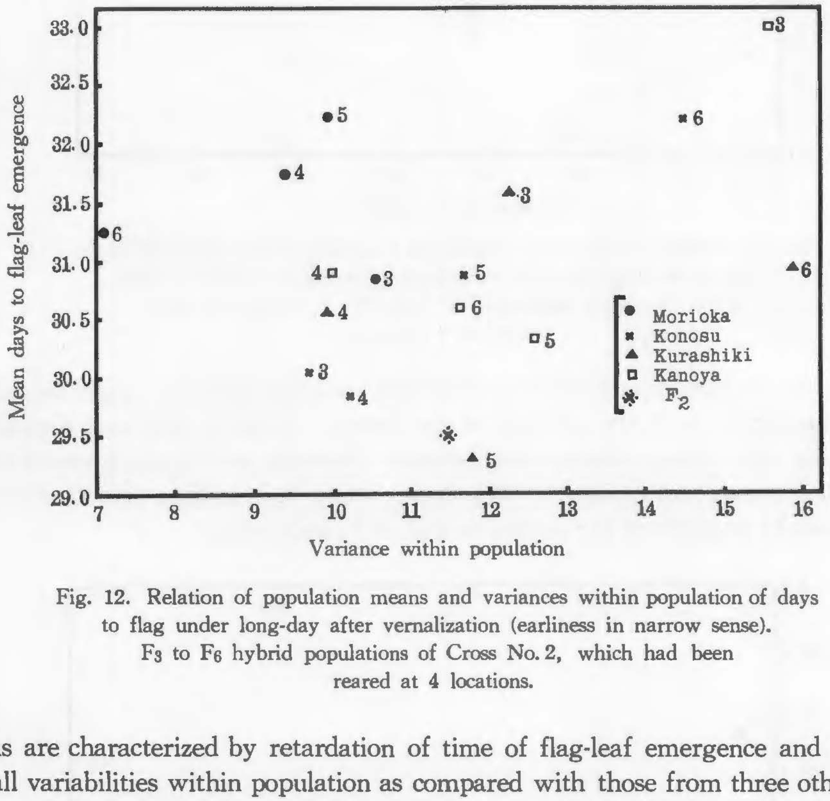

Fig. 12. Relation of population means and variances within population of days to flag under long-day after vernalization (earliness in narrow sense). F_3 to F_6 hybrid populations of Cross No. 2, which had been reared at 4 locations.

tions are characterized by retardation of time of flag-leaf emergence and also by small variabilities within population as compared with those from three other locations. This tendency becomes more pronounced with the advance of generation. On the contrary, Konosu populations indicate a tendency of becoming larger in both the mean and variance with the progress of generation. In Kurashiki and Kanoya populations, little differences among generations are found in mean and variance with only a few exceptions. It is noted also in this figure that almost all of the populations from four locations are larger in mean days to flag than F_2 population.

4. *Time of Heading in Open Field When Sown in Fall at Kurashiki*

Time of heading in open field were investigated of the F_4 or F_5 populations of each of Crosses No. 1, 2 and 3. The results obtained in these three crosses are shown in Table 4.

Table 4
Time of heading and earliness- and lateness-indexes in the different populations when sown outdoors in fall at Kurashiki

Cross	Location and item	Mean*	Variance	Earliness** index	Lateness** index
Cross No. 1 Iwate Ōmugi No. 1 × Indian Barley (F_5, 1958)	Morioka	28.62	71.7178	14.0	39.3
	Konosu	26.42	64.0003	54.5	10.0
	Kurashiki	22.75	77.2423	112.7	6.5
	Kanoya	23.03	45.8287	59 6	1.0
	F_2	22.01	61.1361	85.0	1.0
	Mid-parent	24.97			
Cross No. 2 Tammi × Shimabara (F_5, 1958)	Morioka	23.70	4.7823	3.0	40.5
	Konosu	22.54	26.3199	61.1	43.2
	Kurashiki	22.28	26.9745	72.6	64.3
	Kanoya	20.69	27.5563	103.7	24.9
	F_2	15.26	36.6158	306.8	3.0
	Mid-parent	22.08			
Cross No. 3 Kuromugi No. 148 × Mensury C (F_4, 1957)	Morioka	30.22	17.2034	43.2	125.2
	Konosu	29.37	16.3666	56.8	90.9
	Kurashiki	28.93	19.3462	92.9	89.9
	Kanoya	29.43	19.4067	70.1	104.7
	F_2	28.16	10.4929	53.5	44.0
	Mid-parent	29.99			

* Number of days from April 1st. ** See text.

As seen in Table 4, difference between locations regarding population means is most remarkable and statistically significant in Cross No. 1, but it is quite slight in Cross No. 3. As compared with mid-parent of each cross, Morioka populations are always considerably late, while mean date of heading of Konosu populations are mostly similar to mid-parental value. On the other hand, time of heading becomes more or less earlier in the southern locations such as Kurashiki and Kanoya. It may be of some interest to note in the same table that F_2 mean is always smaller to some extent than the mid-parental value of each cross, suggesting heterosis toward early heading. It is most evident in Cross No. 2, in particular.

As to the variance within population, no appreciable differences can be found among the populations of different locations in all crosses, with only two exceptions, namely, Kanoya population of Cross No. 1 and Morioka population of Cross No. 2. The latter is especially small as compared with the variances of populations of the same cross.

In order to show the differences between populations in earliness or lateness in open field, "earliness and lateness indexes" were calculated by the same way as was adopted to represent the results concerning the response to short-day. As seen in Table 4, the "earliness index" is very small in Morioka populations, and, as go down to south from Morioka, it tends to become larger. The relation for "lateness index" is recongnized to be almost the reverse with that for "earliness index".

The results obtained in Cross No. 4 are shown in Table 5 with the exception of that of F_3 generation in Kurashiki population because of poor germination.

Table 5
Comparison of time of heading and earliness- and lateness-indexes between Morioka and Kurashiki populations of Cross No. 4. when sown outdoors in fall at Kurashiki

Generation and item	Average heading time[1)]			Earliness index		Lateness index	
	Morioka	Kurashiki	Difference	Morioka	Kurashiki	Morioka	Kurashiki
F_2	(29.54)			(181.24)		(78.56)	
F_3	31.05	—	—	177.12	—	164.36	—
F_4	34.55	30.75	3.80**	99.63	212.11	303.75	160.64
F_5	32.90	29.95	2.95*	128.31	254.29	196.54	163.99
F_6	36.80	31.68	5.12**	62.59	161.81	432.71	148.21
F_7	35.78	33.00	2.78*	80.89	121.49	342.15	239.28
Mid-parent	(30.32)						

1) Number of days from April 1 st. * and ** significant at 5 % and 1 % levels, respectively.

Population means of time of heading in Morioka populations are three or more days larger than those of Kurashiki populations in every generations, and tends to become larger with the progress of generation. As is recongnized from the changes in "earliness and lateness indexes", this fact may be caused by the decrease of early type plants, and also by the increase of late type ones with the advance of generation. On the other hand, the "earliness indexes" of almost all of Kurashiki populations are two times or more larger than those of Morioka populations. However, there was found among Kurashiki populations a slight tendency that population mean became larger and "earliness index" smaller, with the progress of generation. In addition, the "lateness indexes" of Kurashiki populations were always much larger than those of F_2 population. Accordingly, it may be suggested that in Cross No. 4, adaptability of late type plant is somewhat higher than early type, if they are grown at southern locations with mild climate.

IV. DISCUSSION

It was investigated first in this experiment how to change in relative frequencies of spring and winter type plants when hybrid populations of barley grown successively during several generations at different climatic locations. The result indicated that in Morioka with severe cold winter, spring type plants have rapidly been eliminated from the population, and hence have become less frequent with the progress of generations. In Kurashiki and Kanoya with mild winter, on the other hand, both of the spring and winter type plants could survive winter safely, so that their relative frequencies remained almost similar to the expected, though spring type plants showed a slight tendency to become dominant in some cases.

It has already been well-established that a spring type plant can attain competence to form ear-primordia without exposure to cold and/or short-day and become highly sensitive to cold, while a winter type plant remains vegetative until winter is over, so that it is more tolerable to a severe climatic condition than the spring type plant. Consequently, winter type plants are regarded to have a selective advantage over the spring type plants in the habitat where winter climate is extremely severe. On the other hand, winter climate in southern Japan are not so severe as to kill the spring type plants, but nevertheless, are sufficiently cold to convert the winter type plants into the spring type during the winter months. This will enable both spring and winter type plants of barley thrive well in the regions with mild winters.

Takahashi (1943) has found that barley varieties of highly winter nature are distributed in the northern or mountainous regions with severely cold winters, while varieties of spring habit and those of moderately winter type are grown in the central and southern regions of Japan with mild climate. According to Wada and Akihama (1934), northern Honshu are chiefly occupied by wheat varieties with high winter habit, but, as go down to south, moderately winter type varieties bacome predominant and in the southern most parts are found chiefly varieties of extremely spring habit. The slight differences existing in the distribution of wheat and barley types in the southern Japan may probably due to the fact that, as compared with the winter wheat, winter barley more easily becomes competent than winter wheat by being exposed to low-temperature and short-day prevailing in southern Japan. In any way, these geographical regularity of distribution of spring and winter barley and wheat varieties may reasonably considered to have resulted from natural selection having operated for long period. It is pointed out without hesitation that the increase or decline in frequencies of hybrid populations which have been subjected to different climatic conditions is substantially the same in tendency as has been found by Takahashi. Naturally, the changes in relative frequencies of spring and winter type in these populations may also be attributed mainly to the natural selection though effects of competition between different genotypes can not entirely be ruled out. It is interesting to note, moreover, that the effects of natural selection on spring and winter nature in barley are so strong as to result in remarkable changes in frequency as stated above within only a few generations. However, it has been found that adaptability of spring type plant varies slightly with their genic constitutions regarding spring and winter habit of growth. This is an interesting problem remained in the future.

It is well-known that day-length and temperature are chief external factors determining adaptability of barley varieties (Doroshenko 1927, Forster *et al.* 1932, Forster and Vasey 1935). In the study of responses of barley varieties to photoperiod and temperature, Takahashi and Yasuda (1958, 1960) have found that when several spring barleys were grown under the most suitable photoperiodic condition for heading (24 hour day), these varieties were accelerated their heading uniformly with the rise of temperature, at least within the range of 8 to 21°C, but they did not show any marked differential response to temperature. They also have indicated that responses of varieties to short-day have an intimate bearing on the earliness of fall-sown barleys including varieties of winter as well as spring growth habit.

According to the result of this experiment, natural selection has opperated differently on hybrid plants sensitive or insensitive to short-day at different locations. When grown at higher latitudinal locations, the hybrid plants insensitive to short photoperiod were gradually eliminated from the populations, and consequently, population means became larger with the progress of generation. Quite the reverse condition was observed for the populations grown at lower latitudinal locations. As was found by Takahashi and Yasuda, the plants insensitive to short-day can head out earlier than sensitive type plants when sown outdoors in fall. In fact, the results obtained in the experiment about the responses of different populations to short-day are almost the same in tendency as the results obtained when they were sown outdoors in fall at Kurashiki.

It is also very interesting to consider the reason why natural selection has disfavored the day-neutral plants and drastically eliminated them from the populations at the northernmost location, while in the southern locations hybrid plants sensitive to short-day have become more or less infrequent, on the other. As repeatedly stated before, a day-neutral plant starts to elongate ear-primordia, whenever temperature is sufficiently high for some time in early spring, but a plant more or less sensitive to short-day remains at the vegetative stage in the same season. It is noted that in Morioka, heading time of barley is late May when the day-length becomes 14∼15 hours, while in Kanoya, it is middle of March to early April when the day-length is 12∼13 hours. Therefore, when day-neutral plants are grown in the northern location like Morioka, they are prone to start developing ear-primordia and become highly sensitive to cold too early season in spring, and consequently they are severely damaged by cold which often follows some temporary warm days in that season. In southern regions, on the contrary, such a event seldom occurs, because temperature never drop too low to do damage on the young heads and plants in very early spring. However, extremely long-day type plants begin to develop their heads too late in spring when temperature becomes too high to grow normally.

Comparison of hybrid populations drived from different locations regarding the response to long photoperiod has revealed that the hybrid plants sensitive to long-day were eliminated from the populations grown at northern location, but slightly increased in southern location. However, it has a already been known that varietal difference in response of barleys to long-day was not so apparent as compared with short-day response, and that this inner factor was not affected directly the earliness of barleys sown outdoors in fall at southern location (Takahashi and Yasuda 1958, 1960). Nevertheless, it is conceivable from the result in this experiment that the earliness factor in a narrow sense may play a significant role in determining heading time in open field of barley plants which are grown at northern location as Morioka wherein longer day length predominates during heading time.

When the hybrid populations from different locations were sown outdoors in fall at Kurashiki, early type plants were eliminated from the populations drived from northern locations, and increased in the populations from southern locations. Consequently, the average heading time of the population became earlier with the growing locations went down to south. Adair and Jones (1946), Akemine and Kikuchi (1958) and Nagamatsu (1958), in their extensive studies with hybrid populations of rice which had been grown at different locations for three or more generations, unanimously confirmed that when grown at northern locations, the late plants were markedly eliminated from the population, and as went down to south, date of heading of the populations became later. These results are apparently the reverse with the case of barley confirmed in this experiment, but in any way, all of these results clearly indicated that natural selection has strongly operated on the time of heading of the populations and within rather short period resulted in a marked shift in genetic constitution of the populations.

All the evidence obtained in this experiment clearly indicate that in northern Honshu (represented by Morioka in this experiment) wherein severely cold weather lasts for more than three months in winter, very rigid natural selection operates especially on early heading type plants with spring nature, and consequently those plants insensitive to short-day and intrinsically early under long-day conditions can not survive the winter there, even if they are of winter habit. It seems necessary for the barley adaptive to this region to have at least a nature of relatively late heading combined with highly winter habit. However, down to the south and entering into Kanto district, winter climate becomes comparatively mild, so that pressure of natural selection is considerably relaxed, allowing survival of various types of barley. Nevertheless, extremely early heading type with high spring nature seems to be less adaptive to this region than in the more southern regions like Chugoku and Kyushu. In southern Japan, represented by Kurashiki and Kanoya in this experiment, on the other hand, winter climate seems to be favorable to the growth various types of barley, but high temperature at the ripening stage of late barley plant does harm to them. So, early to medium-early type plants of both spring and winter habit are more adaptive to these regions. In consequence, high sensitivity to short photoperiod and extremely high grade of winter habit, both of wihch cause the retardation of heading and maturity, are regard to make the barley plants non-adaptive to these regions.

V. SUMMARY

In order to know how far we can make the time of maturity earlier in the regions differing climatic condition and what kind of genotypes are most adaptive to the regions, an experiment was performed. The study was made under the

following scheme: Four crosses were grown in bulk from F_2 up to F_6 generations in successive years since autumn in 1954 at four locations; namely Morioka (North), Konosu (Central), Kurashiki (South) and Kanoya (Southernmost). These hybrid populations were used as the materials. The present paper especially deals with the results of a study of the effects of natural selection on time of heading and some inner factors that may affect time of heading and ecology in barley. The characters studied are as follows; time of heading sown outdoors in fall at Kurashiki, spring and winter habit of growth, photoperiodic response (response of vernalized plants to short-day) and "earliness in a narrow sense" (response of vernalized plant to long-day). The results obtained are summarized as follows:

(1) Natural selection has brought about marked changes in the relative frequencies of the spring and winter type plants in the populations. When grown in Morioka, spring type plants were rapidly eliminated from the population, and in some crosses, their frequencies became about one half of the theoretical ones during only one generation. At three other locations, spring type plants increased, though slightly, and this tendency seemed to become marked as the locations went down to south.

(2) Among the spring type plants survived in the populations grown at southern locations, the plants having dominant spring gene, Sh_2^{II}, were more adaptive for their environments than the spring type ones having only recessive spring gene pair, *shsh*.

(3) Responses of hybrid plants constituting each of the populations to short photoperiod were studied in order to know the generation changes and differences between locations in average sensitivities of these populations. The result indicated that hybrid plants day-neutral or insensitive to short-day were much reduced in Morioka, but increased gradually in the southern locations. Consequently, population mean became larger in Morioka and conversely it decreased markedly in Kanoya as the hybrid generation advanced. With respect to this inner factor populations were affected by natural selection, almost similarly at Konosu and Kurashiki, the extent of the effects being intermediate between the conditions at Morioka and Kanoya.

(4) Vernalized hybrid plants were grown under 24 hour day, and mean days to flag of different populations and their variances were compared. The result was that early plants became less frequent in the populations of northern locations, while in the populations of southern location, such plants tended to increase gradually, and population means became smaller with the advance of generation. However, effect of natural selection on this factor seemed not to be so strong as on the short photoperiodic response, and to be different according to crosses in its extent.

(5) When hybrid populations derived from different locations were sown outdoors in fall at Kurashiki, average heading time of population showed marked tendencies to become earlier with their growing locations went down to south. This was caused by the facts that natural selection operated mainly on the early

type plants in northern locations and on the late type ones in southern locations.

(6) The contribution to adaptability of barley to ecological niche of each of the inner factors and the mechanisms by which the natural selection affected time of heading in open field of hybrid populations were discussed on the basis of these results and from relations between heading time in open field and the inner factors.

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